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Javier Lobon-Cervia
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Advances in the Ecology of Stream-Dwelling Salmonids

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Advances in the Ecology of Stream-Dwelling Salmonids

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Introduction

Many salmonids inhabit streams during their entire or a substantial part of their lifetime. Streams, defined for the purposes of this book, as networks of cold waters of variable current velocities running along narrow, shallow V-shaped channels in mountainous landscapes (often U-shaped in glacial landscapes), over rifles, pools and beds of gravel, pebble and stony substratum, are fed by rainfall and snowmelt and may be subject to unpredictable episodes of floods and droughts. Hence, these lotic systems are heterogeneous by nature and vary substantially seasonally and annually in temperature and discharge along their environmental gradients. In these complex habitats, salmonids encounter suitable reproductive and feeding habitats to complete their life cycles and exhibit a dizzy array of life-history traits and an overwhelming variability in size, growth, and density.

Stream salmonids shift their trophic status during their lifetime. Though essentially predators upon organisms drifting in the water column, from either instream or terrestrial sources, they often become apex piscivores at large sizes. Concomitantly, at the youngest life stages they may serve as prey for larger fishes and aquatic macro-invertebrates and as they grow, they may serve as prey for birds and mammals. Moreover, many populations play a major role in the re-cycling of biogeochemical elements critical for the trophic dynamics of their home streams. These particularities hold for both native populations in the northern hemisphere and for those introduced wherever naturalized populations occur worldwide (Keshner et al. 2019).

Empirical assessment of the ecological functioning of stream salmonids has been a tireless endeavor since the pioneer studies by Allen (1951), McFadden (1961), Chapman (1966), and Northcote (1969) further enhanced by the International Biological Program (IBP 1964-1974; Gerking 1966) and extended to experimental approaches during recent decades (Northcote and Lobón-Cerviá 2007; Lobon-Cervia and Sanz 2017). Nevertheless, increasing awareness that streams supporting salmonids are severely threatened or at risk, because of human abuse and misuse including overextraction, diversion, damming, and pollution all interacting with the existential threat of global climate change. In addition, salmonids themselves are directly threatened by genetic introgression, diseases, and parasites induced by uncontrolled introductions of individuals from aquaculture and over-exploitation by angling. Collectively, these threats have triggered important social and political concerns, to the extent to be considered a research priority by major agencies and institutions (Dauwalter et al. 2020). In this context, we attempt to add an overview to this endeavor by reviewing, updating, and summarizing the documented ecology of stream-living salmonids with particular reference to the factors and mechanisms underlying growth, density, and life history and their concordant interactions which ultimately determine the size and number of individuals encountered in any wild, naturally reproducing population. Therefore, we track the Rumsfeld's statements. Firstly, addressing "Known knowns," we update information associated with the overwhelming variability of salmonid dynamics observed within and among populations across scales of space and time. Secondly, by "Known unknowns," we identify major gaps of knowledge that warrant further research, and finally, by "Unknown unknowns," we emphasize the depth of the ocean of our ignorance and the challenges for subsequent human generations.

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Contents

Embryo Temperature Has Knock-on Effects on Later Traits in Salmonid Fishes

Bror Jonsson

Abstract Through a phenotypic plastic response, early temperatures have knock-on effects on later appearing traits of organisms such as stream-spawning salmonids. Moderately warmer water during embryonic development has carry-over effects to later developing life history characters such as body shape, metabolic rate, growth rate, egg and gonad sizes. Also, adult size and time of the spawning migration may be affected by temperatures experienced at the embryo stage. These responses to early temperature may be regulated by epigenetic mechanisms, such as DNA methylation. The plasticity may be favourable for invasive organisms and for those living in changing habitats and climates. It has been hypothesized that over time, this plasticity may lead to speciation. Research on these early knock-on effects of early temperature is still in its youth, but is rapidly growing, and at the end of the review, issues for future research are suggested.

Keywords Body shape · Embryogenesis · Environmental influence · Epigenetic mechanisms · Life history · Metabolic rate · Migration · Phenotypic plasticity · Temperature effects

1 Introduction

Temperature during embryogenesis has pervasive effects on many later appearing, fitness-related, and ecological characters for a variety of organisms (Fusco and Minelli 2010; Jonsson and Jonsson 2019). These thermal effects are for instance related to morphological, population ecological and behavioural traits (Schmid and Guillume 2017). In ectotherms, growth and metabolic rates increase with temperature, but still, many populations from cold environments exhibit similar or higher growth rates than conspecifics from warmer habitats (Conover and Present 1990).

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By use of common garden experiments, it has been demonstrated that such variation in genetic expressions can be a phenotypic knock-on effect of temperature experienced by the organisms during embryogenesis (Finstad and Jonsson 2012; Durtsche et al. 2021).

Through influences on the embryos prior to hatching, the incubation temperature may prepare organisms for thermal conditions that they may encounter later. A relatively high egg temperature may prepare organisms for life in a warm climate, and a lower egg temperature may prepare them for a colder environment. This mechanism may be particularly important for ectotherms having the same body temperature as their surroundings (Booth 2006, 2018; Taylor et al. 2021), and is known from a variety of animal and plant kingdoms (Nijhout et al. 2017; West-Eberhard 2003; Bateson et al. 2014).

As a phenomenon, phenotypic plasticity has been long known (Johannsen 1911), but the understanding that early environments may change reaction norms of organisms to function better under conditions that they may experience later, is more recent (e.g. Bateson et al. 2004; Lafuente and Beldade 2019). This mechanism does not influence the genetic population structure or composition, but may result from parental effects (Mousseau and Fox 1998), environmental quality provided by the parents (Booth 2018), or through epigenetic mechanisms (Singh et al. 2020), responds within generations, and may even have trans-generational effects (Salinas and Munch 2012; Jonsson and Jonsson 2016).

Epigenetic influences may result from DNA methylation, histone modifications that regulate gene expression at the level of chromatin structure and DNA, and micro RNAs (miRNAs), i.e. small non-coding RNAs that constitute a post-transcriptional mechanism regulating abundance and translation of mRNAs (Bollati and Baccarelli 2010). The understanding of these effects is rapidly growing although still in its infancy.

Here, I review how temperature during embryogenesis may influence later emerging ecological traits of river-spawning salmonids. Traits investigated are meristic characters of the skeleton, body shape, fin size, muscle development, growth and metabolic rates, egg size and age of the feeding migration to sea and timing of spawning migration. Although we report the various traits separately as they often are in the scientific literature, one should keep in mind that it is the entire phenotype that is influenced by the early temperature and that the various traits may be associated with each other. At the end, I briefly discuss mechanisms allowing the plasticity, its wider ecological significance and give topics for further research.

2 Characters Studied

2.1 Anatomy and Morphology

Egg incubation temperature influences anatomic and morphologic characters of stream-living salmonids. For instance, it affects the number of vertebrae and fin rays developed in many fish species, amongst which brown trout *Salmo trutta* was the first species studied (Jonsson and Jonsson 2011). Tåning (1952) reported that this fish developed fewest vertebrae at 6 °C stable embryo temperature and more vertebrae at lower and higher temperatures. The vertebral numbers were determined during gastrulation, shortly before the so-called eyed-egg stage. Thus, the relationship between vertebral numbers and egg temperature is V-shaped, but there is still open whether the effect of temperatures above and below the minimum number of vertebrae is similar. Experiments with a model species, Mexican tetra *Astyanax mexicanus*, exhibited that fish incubated at low temperatures developed more precaudal vertebrae whilst conspecifics developed at higher temperatures developed more caudal vertebrae (Corral and Aquirre 2019), and possibly, this may also hold for other species.

Tåning (1952) also reported that maximum number of rays in the dorsal and pectoral fins occurred at 8–10 °C, and in the anal fin at 5–6 °C. The generality of these early knock-on effects of early temperature on meristic characters has been demonstrated for some other fishes, such as galaxids (McDowall 2003, 2008), ladyfish (Elopidea) (McBride and Horodysky 2004), Atlantic silversides *Menidia menidia* (Billerbeck et al. 1997), and three-spined sticklebacks *Gasterosteus aculeatus* (Ahn 1999). Skeletal variations may affect body shape and fin sizes (Aquirre et al. 2019; Corral and Aquirre 2019), and this thermal effect may explain why Atlantic salmon parr incubated as eggs at 5.6 °C, had more streamlined body shape than conspecifics incubated as eggs at 2.6 °C as demonstrated by Greenberg et al. (2021) (Fig. 1). Atlantic salmon also had smaller pectoral fins relative to body size if incubated at 5.6 °C relative to 2.6 °C (Fig. 2). Early temperature conditions may thus affect the maximum critical water velocity for juvenile fish (Sfakianakis et al.

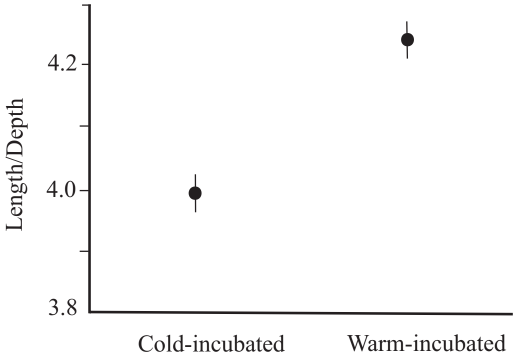

Fig. 1 Standard length on body depth of juvenile Atlantic salmon incubated from conception until first feeding fry in either cold (2.6 °C) or heated (5.6 °C) water, and then reared at natural water temperature until measured as 1-year-old juveniles. Error bars represent standard error (from Greenberg et al. 2021)

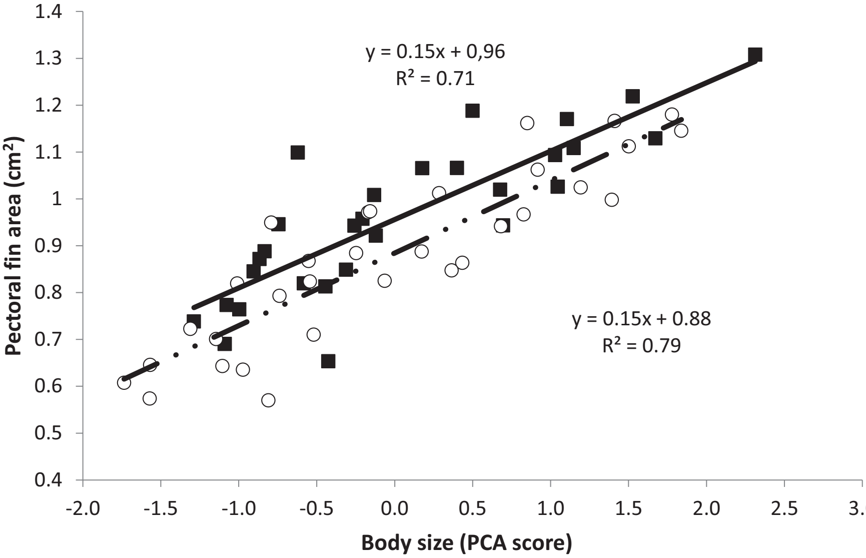

Fig. 2 Relationship between pectoral fin area and body size of 1-year old, juvenile Atlantic salmon incubated from conception until first feeding in either cold (ca. 2.6 °C, open circles, dashed-dot-dot line) or warm (ca. 5.6 °C, solid squares, solid line), and then reared until measured at the same natural water temperature (from Greenberg et al. 2021)

2011), with effects on feeding activity and predator defence (Nathanailides et al. 1995).

Body shape may be also influenced by muscular development, and early temperature may affect the rate of myogenesis, including composition of the functional structures within the cells, number, size and distribution of muscle fibres, fibre diameters and myofibril areas (Stickland et al. 1988; Johnston 2006; Scott and Johnston 2012). For instance, Stickland et al. (1988) reported that post-hatching embryos of Atlantic salmon develop larger but fewer muscle fibres at higher incubation temperatures. However, larvae developed from cold incubated eggs have higher muscle fibre hypertrophy so that the difference in muscle fibre size at hatching and later is small. Differences in hypertrophy between warm and cold incubated salmon may be due to a reduction in number of cell nuclei in the muscle fibres of warm incubated fish (Nathanailides et al. 1995). Also in other species, such as Senegal sole *Solea senegalensis*, incubation temperatures have both short- and long-term effects on muscle growth and cellularity (Carballo et al. 2018), suggesting a generality of the finding that embryo temperature influences muscle development of fish.

2.2 Growth, Size and Metabolic Rates

The effect of embryo temperature on later muscle growth is also reflected in how fast individuals grow in size later in life. For instance, juvenile Atlantic salmon produced from 3 °C warmer incubated eggs grew faster and became larger than those from eggs incubated in colder water when growth was tested 3 months after first feeding. The difference in growth rate was significant at the optimal temperature for growth, 18–20 °C (Fig. 3; Finstad and Jonsson 2012). The improved growth in fresh water results in increased size and reduced time until the juveniles are ready for seaward migration (Burgerhout et al. 2017). Moreover, the increased growth in fresh water increased size at maturity after 1 year at sea (Jonsson et al. 2014). However, a similar growth experiment with brown trout from the same Norwegian River Imsa, revealed no similar growth effect of temperature during the embryogenesis in this species (Jonsson and Jonsson 2021) suggesting that the effect of embryo temperature on later growth can vary even between very similar species.

Early temperature affects metabolic rates of trout. For instance, Cook et al. (2018) reported that incubation temperatures experienced by brook trout *Salvelinus fontinalis* embryos affected routine metabolic rates of free-swimming fry. Furthermore, Durtsche et al. (2021) reported that the standard metabolic rate (SMR), maximum metabolic rate (MMR), and aerobic scope (AS = MMR − SMR) of juvenile brown trout were higher for those incubated as embryos at 4 than 7 °C when tested for metabolic rates at 13 °C, i.e. at the optimal temperature for growth of this species (Elliott 1994; Forseth et al. 2009). All metabolic measures were lower in fish incubated as embryos in warm than colder water. The latter results are

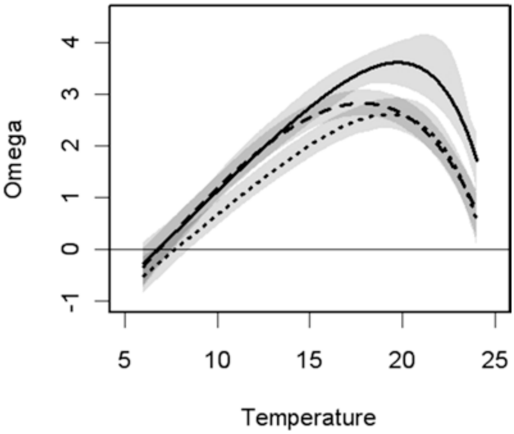

Fig. 3 Temperature scaling (°C) of growth standardized to 1 g body mass (Ω, %, Ostrovsky 1995) of juvenile Atlantic salmon incubated as embryos in natural water (dotted line), in natural water but kept in ca. 4 °C warmer water from hatching until first feeding (stippled line), or incubated in ca. 4 °C warmer water from conception until first feeding (solid line). Grey-shaded areas are 95% confidence intervals. Horizontal line indicates zero growth (From Finstad and Jonsson 2012)

consistent with the countergradient variation (CGV) hypothesis saying that CGV occurs when an environmental gradient counteracts the phenotypic variation of a trait as influenced by genetics (Levins 1969; Conover and Schultz 1995). In this case, variation in metabolic rates are inversely related to the thermal conditions during egg incubation. Whilst previous studies have suggested that CGV is caused by genetic differences between conspecific populations (Álvarez et al. 2006), this study exhibits that thermal differences encountered at the embryonic stage can have a phenotypic effect consistent with the CGV hypothesis. A similar negative correlation between egg temperature and metabolic rate has been demonstrated for the snapping turtle *Chelydra serpentine* (O'Steen and Janzen 1999; Steyermark and Spotila 2000) showing that this relationship holds for more than brown trout.

2.3 Reproductive Traits

Atlantic salmon typically feed and gain most of its size in the ocean, whereas the adults spawn in rivers where the young (parr) grow up. Experimentally, Jonsson and Jonsson (2018) showed that egg incubation temperature influenced the timing of their return migration from the sea. Atlantic salmon incubated as eggs in either natural river temperature, which in this case was 2–5 °C from conception to first feeding, returned 2 weeks earlier for spawning than those incubated in ca. 3 °C warmer water (Fig. 4). From first feeding onwards, the juveniles where reared at the same natural river temperature until released at smolting (the physiological transition stage when they become ready for sea life), 1 or 2 years later. The fish fed at sea for more than 400 days before they returned to the river of release. Similar results were demonstrated for three populations, 2 year classes and in 3 different years. Thus, the temperature experienced at the embryo stage influenced the timing of the spawning migration through a phenotypically plastic reaction norm.

The expressions of reproductive traits such as egg and gonad size in Atlantic salmon, are also influenced by the temperature the fish experienced during the embryogenesis (Fig. 5). This was experimentally demonstrated when Atlantic salmon eggs were incubated under 3 embryonic thermal regimes: cold, mixed and warm treatments (Jonsson et al. 2014). The cold group received ambient river water (mean ± SD: 2.6 ± 0.4 °C) and the warm group received water at 4.6 °C above ambient temperature, from fertilization until first feeding. The mixed group received ambient river water until hatching, whereupon the larvae received heated water until the start of external feeding. Thereafter, all groups were reared under identical, natural thermal conditions. In adulthood, fish that developed from warm incubated eggs were the largest and had the highest mass–length relationship. The females developed larger eggs and both sexes had higher gonad mass relative to their own body size. There was no similar effect of increased temperature during larval development.

There is also a trans-generational effect on the egg size of fish that were exposed to heated water during the egg maturation prior to spawning. Their offspring

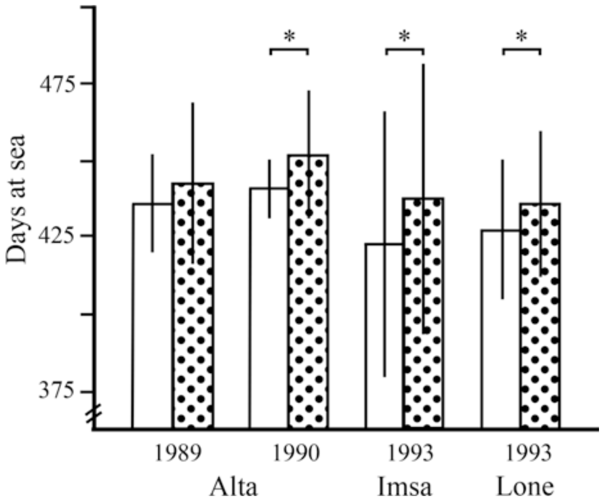

Fig. 4 Mean (SD) number of days at sea of one-sea-winter(1SW) adult Atlantic salmon of the strains from the Norwegian Rivers Alta, Imsa and Lone, released as smolts at the mouth of the River Imsa in 1989, 1990 and 1993 and recaptured on the Norwegian coast as maturing adults. Produced from eggs incubated in natural, cold River Imsa water or in ca. 3 °C warmer water from conception to first feeding. *Asterisk*, mean significantly different ($P < 0.05$) (From Jonsson and Jonsson 2018)

produced larger eggs than females that were kept in colder water during egg maturation (Jonsson and Jonsson 2018). Apparently, there was a maternal effect on the egg size of their offspring.

Thermal treatments during egg incubation had no effect on the age of maturity or fecundity of Atlantic salmon. However, Baum et al. (2005) reported that male Atlantic salmon parr exposed to heated water were larger than conspecifics living in colder water, and suggested that early temperature might increase the threshold size for maturation in male parr, i.e. maturation prior to smolting and seaward migration.

Thus, early thermal conditions affect expressions of adult life history traits of stream-spawning salmonids, a mechanism by which they may change the size of their propagules to the anticipated thermal offspring environment.

3 Discussion

Environments have pervasive roles in phenotypic plasticity. They determine the degree of variation and choose between possible phenotypes. This is not unique for ectothermic vertebrates, but can be found across the animal and plant kingdoms (Bateson et al. 2014). However, it may be particularly important for ectothermic organisms having the same temperatures as their surroundings. By being able to

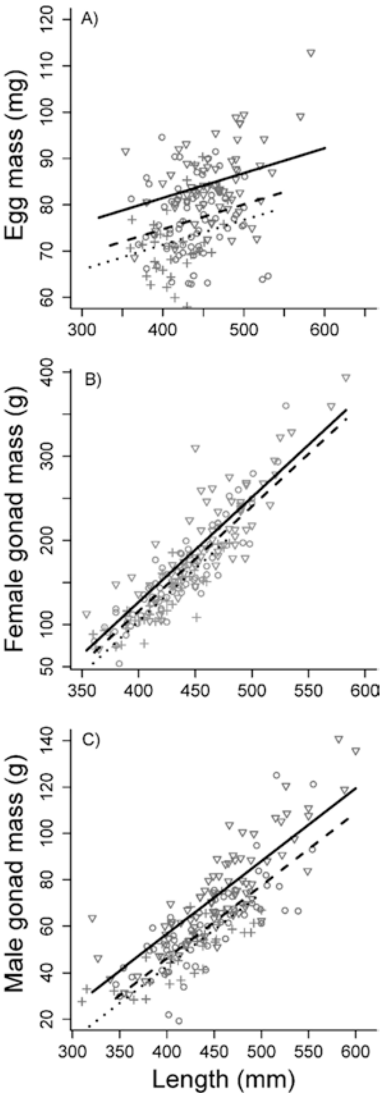

Fig. 5 Mean mass of (**a**) single eggs, (**b**) female gonads and (**c**) male gonads over total length (mm) for adult Atlantic salmon incubated in natural water during embryonic and larval development (+, dotted lines), natural water during embryogenesis and heated water during larval development (s, dashed lines), and heated water during embryonic and larval development (n, solid lines). Lines are predictions from the best-fit model with regression parameters given in Jonsson et al. (2014)

adjust their optimum performance temperature, plasticity may significantly increase their fitness (Salinas and Munch 2012).

Despite differences amongst species, the cited research suggests that embryonic temperature influences traits such as body shape, metabolic rates and aerobic scope, growth rate, smolt age, timing of spawning migration, size at maturation, gonadal and egg size of salmonid fish spawning in streams and rivers. Within temperatures naturally experienced by the fish, they may become more or less streamlined, grow faster or slower, return for spawning early or later in the season and produce larger or smaller gonads and eggs depending on the temperature during the embryogenesis. The changes parallel those observed along climatic gradients where growth rate decreases and smolt age and egg size increase with increasing latitude in Atlantic salmon and brown trout (L'Abée-Lund et al. 1989; Metcalfe and Thorpe 1990; Jonsson et al. 1996; Jonsson and Jonsson 1999).

This plasticity appears adaptive rather than caused by some form of developmental stress, and seems to prepare the young for conditions they may experience later in life. For instance, when developed as embryos in warmer water, they exhibit characters later in life that is favourable in warmer environments. A more streamlined body shape may improve the swimming performance and reduce cruising and foraging costs (Webb 1984; Swain 1992; Ackerly and Ward 2016). Furthermore, as shown for brown trout, the juveniles exhibit reduced aerobic scope in warmer water, and a more streamlined body may reduce energetic costs (Durtsche et al. 2021). Predation pressure may also increase in warmer water, and if so, a more streamlined body shape may improve their ability to escape predators more than deeper bodies do. However, if fish incubated in warmer water experience a colder climate, they may be less well adapted because of less surplus energy with negative effects on movement activity, feeding and defence behaviour (Durtsche et al. 2021).

Atlantic salmon incubated as embryos in relatively warm water, grew better as juveniles and transform for sea life younger, than those incubated in colder water do (Finstad and Jonsson 2012; Burgerhout et al. 2017). This finding is consistent with field-based observations that cohorts of juvenile Atlantic salmon that undergo embryogenesis in warm winters tend to grow faster and move to sea at a younger age than cohorts developed from eggs incubated during colder winters (Jonsson et al. 2005). This may reflect an expectation of better feeding opportunities and willingness to feed more if developed in warmer water, as there is a close relation between growth rate and the amount of energy consumed (Jonsson et al. 2001).

In general, aquatic production increases with water temperature, and fishes that are incubated in a relatively warm habitat, may expect to encounter relatively rich feeding opportunities and keen competition as juveniles in the river. On the other hand, in a cold environment, a high appetite may be less advantageous not only because of poorer growth opportunities, but also because faster growth has increased costs in the form of higher mortality (Mangel 2003; Metcalfe and Monaghan 2003; Sundt-Hansen et al. 2009). In addition, fish are heterothermic, meaning reduced swimming speed and poorer ability to avoid homothermic predators in cold water. Thus, it may be advantageous to feed less and thereby be less exposed if the water is cold.

Larger, more yolk-rich eggs in warmer water may be advantageous because the efficiency of yolk conversion to body tissue is reduced in a warmer environment (Fleming and Gross 1990). Furthermore, the oxygen content in water decreases with increasing temperature, and larger eggs survive better than smaller ones do under poor oxygen conditions (Einum et al. 2002). Also, lower metabolic rates, as found for warm incubated brown trout (Durtsche et al. 2021), may be advantageous in warmer water in agreement with the CGV hypothesis. Also, a later return of Atlantic salmon from the ocean appears adaptive in warmer rivers as the fish should spawn later for the offspring to emerge at the proper time for first feeding in spring because the duration of the egg incubation period is shorter in warmer water (Jonsson and Jonsson 2018).

Thus, temperature during embryogenesis is important for later emerging phenotypic expression. It may prepare offspring for environmental conditions that they may encounter later. This can contribute to adequate responses as it facilitates adaptive evolutionary reactions to directional change (Kingsolver and Buckley 2017). For instance, adaptive phenotypic plasticity may be important for how fish are able to cope with climate change (Merilä and Hendry 2014; Kingsolver and Buckley 2017). Climate warming does not only mean that the fish must cope with an increased mean temperature, but also respond adequately to increased thermal variability (IPCC 2013), and the experiments summarized above exhibit how salmonids change when the embryos develop under warmer conditions allowing them to produce larger eggs, grow faster, feed more, use less oxygen, swim faster and return later for spawning, adequate responses in both a warmer and a more variable climate.

Such a phenotypic plasticity may be also important for invasive species, such as trouts, facilitating colonization of thermally different habitats (Vogt 2017; Ardura et al. 2018). Offspring of strays to foreign rivers should adapt readily to the thermal conditions of their new home river. Invasive species typically exhibit higher phenotypic plasticity than non-invasive species, although the plasticity is not always associated with a fitness benefit, especially when resources are limited (Davidson et al. 2011; Wang and Althoff 2019).

There is still little known about the mechanisms that enable such a phenotypic programming. Possibly, epigenetic mechanisms, activating or silencing genes, are involved. In ecology, epigenetics is a new, but fast-moving field with several recent advances (Flores et al. 2013; Venney et al. 2019). It is known that DNA methylation is sensitive to environmental changes (Anastasiadi et al. 2017), thermal climate (Varriale and Bernardi 2006), water quality, nutrition and environmental structure (Morán et al. 2013; Le Luyer et al. 2017). Furthermore, DNA methylation with silencing of genes, is most prevalent in cold habitats (Verrale 2014). It is known that both maternal food deprivation and temperature during maturation influence gene expression of offspring up to maturity (Jonsson and Jonsson 2016; Fan et al. 2019). These effects may be promoted by DNA methylation (Venney et al. 2019), but other epigenetic mechanisms such as histone modifications and micro RNA may be also involved, and it is important to intensify studies of the significance of these for phenotypic expressions.

Effects of environments on phenotypes vary by genotype, i.e. epigenetics may cause variation in phenotypic plasticity depending on the genetic makeup of the specific individuals at relevant loci (Banta and Richards 2018). It is hypothesized that epigenetic mechanisms may have the potential to develop into genetic variation and ultimately trigger speciation, although evidence is still meagre (Venney et al. 2019). One such proposed mechanism is “Plasticity First” (e.g. Levis and Pfennig 2016), where phenotypic plasticity leads to a range of phenotypes, some of which are favoured by selection. Over time, mutations can fix the favoured phenotypes, and ultimately the phenotypes initially resulting from plasticity will have a genetic basis. Therefore, epigenetic variation might provide the first substrate for selection during evolutionary divergence.

4 Future Research

The understanding of how the thermal climate during embryogenesis influences later occurring ecological traits is limited. Only a few species and populations have been tested, and there is almost no knowledge about how the plasticity influences costs and benefits for organisms. Thus, the generality of the present findings should be tested across traits, populations and species. One should also work out the reaction norms for the various traits over a wide range of temperatures. Already now, however, it is evident that these knock-on effects are important for the ecology of many species.

The embryo temperature influences the body and fin shapes of Atlantic salmon, but no one has quantified what this means for their swimming performance. Furthermore, early temperature influences growth and metabolic rates of salmonids and thereby affects their aerobic scope (Álvarez et al. 2006; Finstad and Jonsson 2012; Durtsche et al. 2021). However, ecological consequences of these rates have not yet been investigated, but possibly, this will influence behavioural activities as it does for lizards (Siviter et al. 2019). In particular, this may influence the scope for activity at low temperatures when maximum power capacity is low (Pried 1985).

It is hypothesized that environmentally induced plasticity may facilitate and speed up the processes of adaptive evolution (Ghalambor et al. 2007; Levis and Pfennig 2016). There is, however, little evidence exhibiting the role of plasticity in facilitating the evolution of natural populations (Warner et al. 2010). Early temperature may play a critical role in the diversification of sympatric phenotypes in salmonid species as exhibited in experiments with European whitefish *Coregonus lavaretus* where co-occurring large and dwarf forms of the species developed at different water temperatures (Steinbacher et al. 2017). As much of the phenotypic difference disappeared when offspring of Arctic charr *Salvelinus alpinus* morphs were raised under similar thermal conditions (Hindar and Jonsson 1993), one may suspect that environmental differences play a role in the morph differentiation in this and possibly other salmonid species.

Much evidence show that cues experienced in early life can affect the development of phenotypes with consequences for life in environments encountered at a later stage. As yet, however, there are few examples that actually test if observed changes are adaptive and improve the fitness of organisms. Thus, such tests are needed. The capacity of salmonids to display adaptive plasticity in changing environments may determine their future success.

The understanding of how knock-on effects influence the development of phenotypes may in many cases involve epigenetic processes, although little is known about how these affect the development of ecological trait variation (Verhoeven et al. 2016). Investigations of how the environment influenced ecological traits through epigenetic changes without influencing the genetic structure of populations is an urgent research need and may include also other mechanisms than DNA methylation, although this mechanism may be particularly important because of its temperature dependence.

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Field Observations of Deformed Atlantic Salmon (*Salmo salar*) Embryos Incubated in the Hyporheic Zones of Seven Cold Region Rivers

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Abstract There is little research reporting deformities of naturally incubating salmonid embryos. The objective of this study was to report the prevalence of deformed Atlantic salmon (*Salmo salar*) embryos across a range of incubation habitats. We assessed 3234 embryos that had been incubated to approximately the "eyed" stage in simulated redds at 20 sites in seven rivers across two basins (the Tobique and the Miramichi River basins of northern New Brunswick, Canada) over three winters (2012–2015). A range of incubation habitats were represented: regulated rivers warmed by bottom-draw dams; unregulated, ice-covered rivers of different sizes; and a long-residence groundwater-fed brook that remained ice free. Deformities were unusually prevalent (1.4–95.7% deformed) in the Tobique River basin com-

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pared with the Miramichi River basin (0–7.7%) and hatchery controls (1.1%). Within the Tobique River basin, warmer sites near dams had the fewest deformities. Deformity data were collected opportunistically as part of other studies within our research group, therefore, we do not make any firm conclusions about what environmental or intrinsic factors may have contributed to the prevalences reported herein; instead, we discuss pertinent differences between basins and present possible hypotheses for future study.

Keywords Salmonid · Embryo · Deformity · Winter ecology · Atlantic salmon · Natural habitat

1 Introduction

Salmonid embryos incubate in the hyporheic zone of freshwater water bodies, where they are stationary and unable to escape potentially unsuitable conditions (e.g., Lavery and Cunjak 2019). As a result, they may suffer sublethal damage (e.g., Johnston et al. 2000) that can manifest as impaired survival or developmental deformities. For species like Atlantic salmon (*Salmo salar*) that are threatened or economically valuable, embryo deformities may be particularly important since they are linked to decreased survival (suggested by, e.g., Leatherland 1993, Einum et al. 2002, Eriksen et al. 2006). Thus, in natural incubation settings, embryo deformities contribute to early life stage population bottlenecks (e.g., Linnansaari and Cunjak 2010) and, in hatchery settings, reduce the number of individuals able to be successfully reintroduced to the wild as part of population recovery efforts or fishery supplementation programs.

From studies of salmonid embryos incubated in natural river habitats, there exist only a few reports documenting the proportions of survival to hatching (Lacroix 1985; Malcolm et al. 2005; Julien and Bergeron 2006; Lavery and Cunjak 2019), and none of embryonic deformities or their prevalence in Atlantic salmon. At the alevin (i.e., early post-hatch) life stage, only one study reports deformity prevalences within a population of naturally incubated coho salmon embryos (*Oncorhynchus kisutch*: Leatherland 1993). Hatchery operators anecdotally report that a consistently small proportion of incubating embryos and hatched alevins are deformed, but actual prevalences are not regularly reported and vary from year to year and between parental crosses (J. Whitelaw, former Biologist, Mactaquac Biodiversity Facility, pers. comm.). In laboratory studies, baseline alevin deformity prevalences (reported in control groups) ranged from 2.5% to 7% (Takle et al. 2005; Wargelius et al. 2005; Ytteborg et al. 2010; Sánchez et al. 2011). Such studies have investigated the causes of alevin deformities, some of which include: artificially induced stress (e.g., Eriksen et al. 2006), breeding techniques (e.g., Bonnet et al. 2007; Young et al. 2009), or exposure to environmental toxins (such as selenium: e.g., Kennedy et al. 2000, Holm et al. 2003, Covington et al. 2018; pesticides: Du

Gas et al. 2017, Marlatt et al. 2019; polyaromatic hydrocarbons: Carls and Thedinga 2010; nitrate: McGurk et al. 2006).

Studies of salmonid embryo deformities are exceedingly rare, which has several implications. First, we do not have an understanding of the baseline embryo deformity rate in nature, which limits our ability to assess the cause of departures from baseline (i.e., environmental or genetic factors). Second, because alevins are the earliest life stage at which deformity prevalences and causes are currently reported, we are limited in our understanding of when (as well as why and how) deformities in early life stages originate. These considerations are of clear importance for conservation, but also for environmental monitoring, since embryos may act as ecological sentinels when deformities reflect environmental conditions such as the presence of contaminants, especially at stages prior to the development of organ systems important for detoxification and excretion (i.e., liver, kidneys, and the circulatory system) (e.g., Mizell and Romig 2002, Holm et al. 2005, and for amphibians: LeBlanc and Bain 1997).

This study examined Atlantic salmon embryo deformity prevalence for the first time in the wild, and across a range of natural habitats, incubation temperatures (average over incubation period: ~0.3–7.0 °C), and genetic stocks with a considerable sample size. Our findings are based on an examination of 3234 embryos from river-appropriate genetic stocks that were incubated from fertilization to approximately the "eyed" stage of development (~90–170 days) in 20 incubation sites spread across seven rivers, and were alive at the time of sampling. However, the present study was not designed to specifically examine the causes of embryo deformities, and instead our collection of embryos was sampled as part of other studies (i.e., Smokorowski et al. 2011; Lavery and Cunjak 2019). Nor could we assess deformity prevalence among embryos that died before sampling, due to fungal colonization in the field that occurred prior to sampling. Thus, the objectives of this study were to: 1) report the prevalence of deformed, naturally incubated Atlantic salmon embryos that survived to the "eyed" stage of development, observed in samples from the Tobique and Miramichi River basins; and 2) based on known differences between sites and basins with varying deformity prevalences, recommend a suite of hypotheses for future testing.

2 Methods

2.1 Study Location

In this study, Atlantic salmon embryos were incubated in natural gravel habitats in rivers in two adjoining river basins in northern New Brunswick (Fig. 1): the Tobique River basin, a major mid-basin tributary of the St. John (traditionally: Wolastoq) River, and the Miramichi River basin. The two river basins drain the Miramichi Highlands and Highland Foothills landscape regions, characterized by high relief with thin glacial soils at higher elevations and thicker glacial deposits in valleys (Pronk and Allard 2003). These basins consist primarily of public and private forestry lands. The study rivers were chosen because they had observed or historical records of Atlantic salmon spawning activity (Francis 1980) and substrate suitable for salmonid spawning (Crisp and Carling 1989; Kondolf and Wolman 1993). The study rivers in the Tobique basin are separated from ocean habitats by three large dams that are significant barriers to upstream fish passage; whereas the unregulated Miramichi basin is home to a relatively intact spawning population of Atlantic salmon (DFO 2019).

Embryos were incubated in four rivers in the Tobique River basin over one winter (2012–2013, Fig. 1). The rivers were selected based on streamflow regulation regime and because they had comparable morphologies. Two rivers, the Gulquac River (N46°56′29.1″ W67°4′52.4″) and the Wapske River (N46°52″23.6″ W67°11′46.3″) had unregulated headwaters. The other two rivers, the River Dee (N47°4′33.7″ W67°1′20.7″) and the Serpentine River (N47°10′48.1″ W66°50′57.7″) were flow-regulated rivers, each with headpond reservoirs controlled by bottom-draw dams operated by New Brunswick Power at their origin. Sites on regulated rivers (Dee and Serpentine) were located either close to the dams or several kilometers downstream (D1 is 0.4 km, D3 is 16.0 km, S1 is 1.3 km, and S3 is 10.3 km downstream from their respective dams). Further physical descriptions of the Tobique basin study rivers can be found in Nafziger et al. (2017a) and Flanagan (2003).

In the Miramichi basin, embryos were incubated at three sites in each of four river reaches (Fig. 1) over two consecutive study winters (2013–2014 and 2014–2015). Catamaran Brook Lower Reach (CBL; N46°52′41.9″ W66°06′34.6″), Catamaran Brook Gorge Reach (CBG; N46°51′27.52″, W66°09′35.23″; 2014–2015 only), and Otter Brook (OB; N46°52′39.8″, W66°02′12.5″) are tributaries of the Little Southwest Miramichi River, and Rocky Brook at Big Eddy (RB; N46°42′58.9″, W66°38′53.9″) is a tributary of the Southwest Miramichi River. Further physical descriptions of the Miramichi Basin study rivers can be found in Lavery (2017) and Lavery and Cunjak (2019).

2.2 Field Methods

The field studies were conducted with approval from Fisheries and Oceans Canada (license # SG-RHQ-13-188 and SG-RHQ-14-145) and the University of New Brunswick's Animal Care Committee (AUP # 12044, 13045, and 14044).

The field methods used in each year of the study were broadly similar, but differed in some details, as outlined in Table 1 and Figs. 2 and 3. The river incubation sites were prepared prior to embryo fertilization and placement. At the top of a riffle at each site, three artificial redds were constructed with depressions dug immediately upstream to simulate natural salmon redds, according to dimensions outlined in Crisp and Carling (1989) and Bardonnet and Baglinière (2000). Holes were dug 30 cm into the gravel in the tailspill of each artificial redd, and were held open by

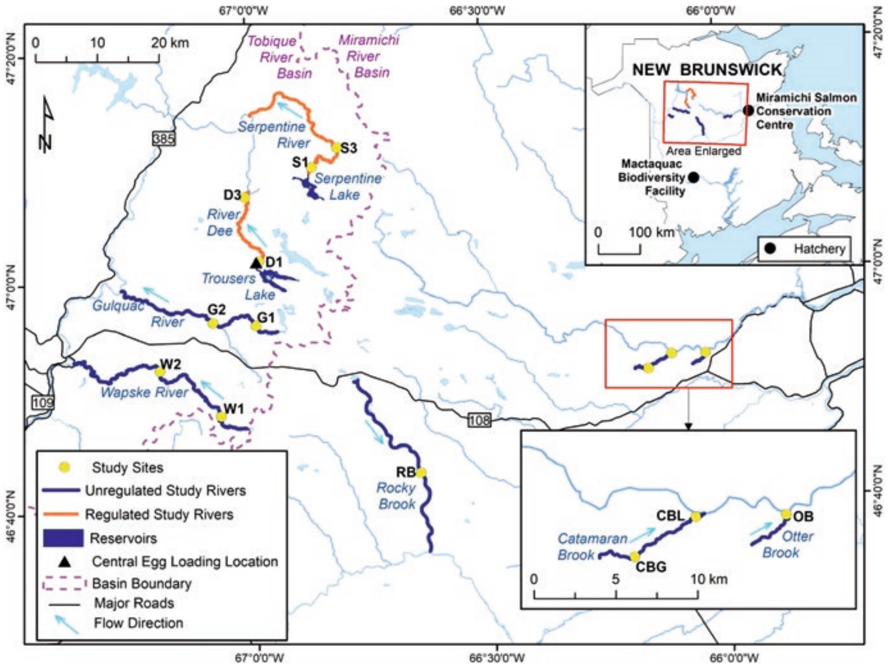

Fig. 1 Location of study rivers and study sites in the Tobique River and Miramichi River basins in north-central New Brunswick, Canada. Four rivers were studied in the Tobique River basin over one winter, two of which were subject to flow regulation for hydropower production. Four rivers or three rivers were studied in the Miramichi River basin, all of which were unregulated. Each marker in the Miramichi River basin represents three sites

burying 30 cm tall sleeves in the holes, which were made from plastic buckets with their bottoms removed.

In the autumn, Atlantic salmon embryos were obtained from the home hatchery for that basin (Table 1). Hatchery staff harvested the eggs and milt and the eggs were fertilized, disinfected, and water hardened according to hatchery protocols. Fertilized embryos were transported to the study areas and then placed into prepared, sanitized plastic (polystyrene #478) Jordan-Scotty incubator trays (each holding 200 salmon embryos in individual compartments) using the manufacturer supplied loading rays (Table 1). When buried in the substrate, Jordan-Scotty incubators—widely used in conservation and research—are thought to mimic natural incubation conditions as closely as possible while still allowing the retrieval of live embryos for sampling purposes (Lavery and Cunjak 2019). Two or three incubator trays (Table 1) were bolted together as a set and then buried in the pre-dug holes, with the long axis of the incubator tray placed vertically. The sleeves holding the holes open were removed, and the gravel was carefully pushed back into the hole, burying the incubator trays. Each set of buried, bolted trays is hereafter called a “redd.”

Table 1 Details of differences in methods between the sample basins

	Tobique Basin (2012–2013)	Miramichi Basin (2013–2014 and 2014–2015)
Home hatchery (Fig. 1)	Mactaquac Biodiversity Facility (MBF): operated by the Department of Fisheries and Oceans of Canada in French Village, New Brunswick.	Miramichi Salmon Conservation Centre (MSCC): operated by Miramichi Salmon Association, Inc. in South Esk, New Brunswick.
Broodstock	"Wild-exposed" captive broodstock: had been hatched at MBF, released into the river system as unfed fry and then re-captured as either parr or smolts and held captive until adulthood.	Wild-captured adult broodstock from three distinct Miramichi tributary stocks (Cains River, Rocky Brook, Little Southwest Miramichi River), temporarily held at MSCC.
Dates of fertilization	Nov. 2012	Oct. 2013 and Oct. 2014
Egg picking after water hardening	Embryos that appeared dead or unfertilized (opaque and whitish) were discarded from the batch, typically this is ≤5%.	No eggs discarded from the batch at time of fertilization.
Hatchery incubated embryos sampled	Yes	None
Transportation of embryos to field	Water-hardened, disinfected embryos were transported to the study area in large disinfected plastic bottles filled with hatchery water, placed inside water-filled disinfected coolers for cushioning during transport by vehicle.	Water-hardened, disinfected embryos were transported to study sites in 500 mL disinfected plastic bottles filled with hatchery water placed inside drybags during transport by vehicle.
Embryo preparation and loading into incubator trays and transport to site	Embryos were pooled at a central location (Fig. 1) in a large disinfected trough filled with water from Trousers Lake. Filled incubator trays were transported to each of the sites (up to 70 km away) by truck and on foot inside covered plastic buckets filled with water from Trousers Lake.	Bottles of embryos were taken directly to each study site and loaded into incubator trays directly beside incubation locations.
No. of incubator trays bolted together	3	2
No. embryos placed at each site	1800	1200
Time between fertilization and placement	24–31.5 h	7.25–12.5 h
Retrieval dates	February to March 2013: 102–134 days after fertilization	March 2013 and 2014: 145–169 days after fertilization
No. embryos per sample	3–12	5–20

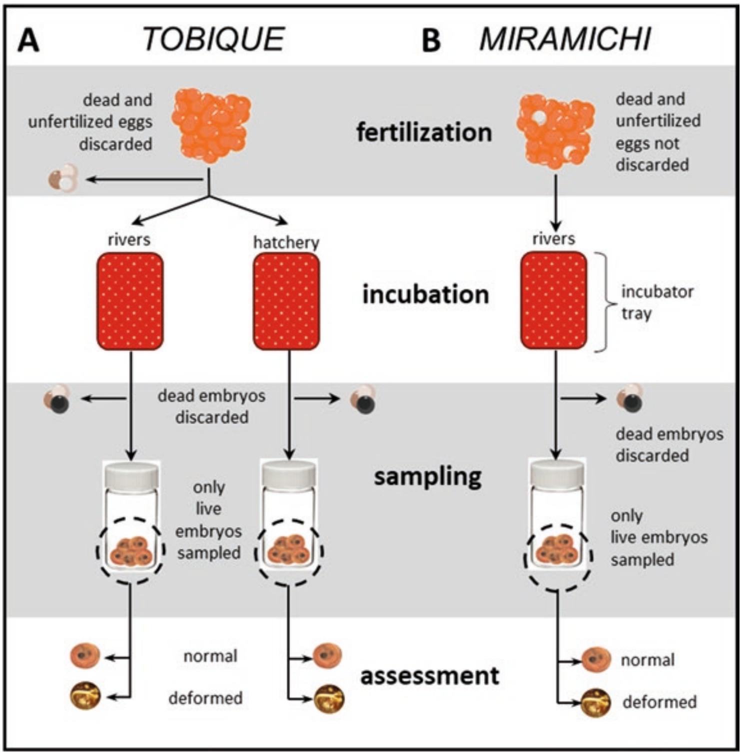

Fig. 2 Conceptual diagram outlining the sequence of events from fertilization to deformity assessment that occurred in the Tobique and Miramichi basins, with specific reference to what type of embryos were sampled and the makeup of the source embryo population

The incubator trays were retrieved from the river in mid-winter, when river ice and flow conditions allowed, and timed with the aim to sample embryos once they were "eyed." During retrieval, the incubators were removed from the river and placed in waterproof bags inside coolers, filled with river water and transported by snow machine and truck (for a maximum of ~70 km) to a heated area, to protect the large number of embryos from freezing during the sampling process. Of the embryos that appeared alive (defined as translucent and orange in color), a random sample of 3–20 embryos was taken from each incubator tray (Fig. 2). Dead embryos were not sampled because they were often affected by fungus and partially decayed. Sampled embryos were preserved in glass vials of Stockard's solution (5 parts formaldehyde, 4 parts glacial acetic acid, 6 parts glycerin, and 85 parts distilled water by volume; Velsen 1980). In total, 527 embryos were sampled from the Tobique sites and 1224 hatchery-reared embryos were sampled from the MBF facility; 529 embryos were sampled from the Miramichi sites in 2013–2014 and 954 embryos in 2014–2015. The remainder of the embryos present in incubators were either re-buried in a

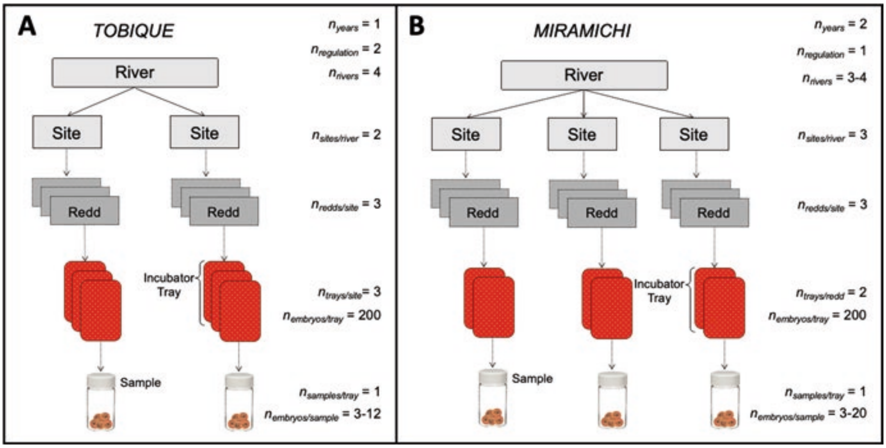

Fig. 3 Conceptual diagram outlining the hierarchical study design implemented in each of the two study basins (**a**: Tobique, **b**: Miramichi). At each study site in each study river, Atlantic salmon (*Salmo salar*) embryos were planted in three artificial redds. Within each artificial redd, two or three Jordan-Scotty incubator trays (each containing 200 embryos) were buried vertically to 30 cm below the substrate. A random sample of between 3 and 20 live embryos was taken from each of the trays

nearby hole in the streambed for conservation purposes or were dead upon examination.

Temperatures of the surface and hyporheic water (at 30 cm below the riverbed) were measured at each site in both basins at 1–15 min intervals using Vemco Minilog-II-T sensors (published accuracy ±0.1 °C, measured maximum error: ±0.056 °C) or HOBO TidbiTv2 sensors (published accuracy ±0.2 °C, measured maximum error: ±0.102 °C). The temperature data were corrected for instrument drift at 0 °C using a graphical approach as described by Nafziger et al. (2013). Additional information on the water temperatures and other environmental conditions over the study period can be found in Nafziger et al. (2017a), Lavery (2017), and Lavery and Cunjak (2019). Measured incubation temperatures, for example, sites are shown in Fig. S1.

2.3 Lab Methods

Preserved embryos were examined and dissected in the lab from 2015 to 2019. All dissections took place on a petri dish filled with distilled water. Chorions were removed from each embryo by making small incisions with a Feather 72044-11 scalpel blade and peeling with fine-tipped forceps. Excess perivitelline fluid was removed by slicing along the embryo with a scalpel. Embryos were examined using a Leica MZ16 A or Unico ZM194T stereomicroscope.

Each embryo was assessed against the embryo deformity classification tool of Bartlett et al. (2022), which describes Atlantic salmon embryo deformity types based on the deformed body part (i.e., spine, eye, yolk, multiples, or other) and presents possible subtypes of each deformity. To reduce observer bias, the same researcher (ADB) assessed all embryos. The observer was aware of the basin from which a given sample derived (Tobique vs. Miramichi), but was otherwise blind to identifying site information. Each embryo was coded 1) as "deformed" or "normal" and 2) if deformed, with the type(s) of deformity observed; single embryos may have exhibited more than one type of deformity. Deformity subtypes were also recorded as a note for each embryo.

A small number of eggs were considered alive at the time of sampling (i.e., they appeared orange and translucent, not opaque and white) but upon microscopic examination were found to not contain a developing embryo. This included 21 embryos sampled across both basins (9 from the Miramichi and 12 from the Tobique: a maximum of 3 at a given study site, and 6 from the hatchery-raised embryos). These embryos were removed from the dataset because they did not represent "normal" or "deformed" embryos, but rather an unknown state.

2.4 Statistical Methods

We defined deformity prevalence as the percentage of sampled embryos that exhibited one or more deformity types. The statistical methods used align with the hierarchical nature of the study design (Fig. 3). General linear models (GLMs) were used to investigate differences in deformity prevalence. To satisfy model assumptions, data were logit-transformed (Warton and Hui 2011) and residuals were assessed via graphical inspection. A first model (Model 1) was run on the whole dataset, with Basin as a fixed effect, average incubation temperature and hours between fertilization and placement as covariates, and a suite of random effects reflecting the hierarchical nature of the study design (Fig. 3), including Year nested in Basin; River nested in Year and Basin; Site nested in River, Year, and Basin; and Redd nested in Site, River, Year, and Basin. A second model (Model 2) was run on only data from the Tobique basin to investigate the potential effect of regulation, which was not possible using the whole dataset, due to it being skewed by the number of unregulated rivers in the Miramichi basin. In Model 2, Regulation Type was a fixed effect, average incubation temperature and hours between fertilization and placement were covariates, and a suite of random effects reflecting the hierarchical nature of the study design were included: River; Site nested in River; and Redd nested in Site and River. Analyses were not performed on data broken down by type of deformity, because embryos often exhibited more than one type. Linear regressions were also used to specifically investigate possible relationships between deformity prevalence and average incubation temperature in both basins, as well as between deformity prevalence and hours between fertilization and placement (as a measure of transport-related handling) in the Tobique basin. Analyses were

Table 2 Summary of GLM analyses of the whole dataset and Tobique basin data, where deformity prevalence was the dependent variable. Effects with *p*-values <0.05 are indicated in bold

Fixed effect/Covariate	DF	$DF_{denominator}$	*F* ratio	*p* value
Model 1: Miramichi and Tobique basins				
Basin	**1**	**1.946**	**23.305**	**0.043***
Average incubation temperature	1	0.912	0.118	0.793
Hours between fertilization and placement	1	1.309	0.344	0.643
Model 2: Tobique basin only				
Regulation	1	2.347	3.125	0.200
Average incubation temperature	**1**	**2.078**	**27.381**	**0.032***
Hours between fertilization and placement	1	3.362	0.011	0.920

performed using R (R Core Team 2020) and JMP (v.16, SAS Institute Inc) statistical software. For all analyses, significance was determined at alpha = 0.05.

3 Results

Overall, there was a higher prevalence of deformed embryos at sites in the Tobique River basin than at sites in the Miramichi River basin (GLM: Model 1, $F = 23.31$, df = 1,1.946, $p = 0.043$, Table 2). Of the 527 embryos sampled from the Tobique sites, 54% showed some form of deformity whereas, in the Miramichi sites, only 1.5% of 529 embryos and 1.8% of 954 embryos showed deformities in 2013–2014 and 2014–2015, respectively. However, considerable variation in deformity prevalence was also explained by the nested, random effects of River (GLM: Model 1, Wald $p = 0.003$) and Site (GLM: Model 1, Wald $p = 0.004$). The prevalence of deformed embryos at each site is shown in Table 3 and further broken down by deformity type in Fig. 4.

All types of deformities were more common in embryos from sites in the Tobique basin than those from the Miramichi (Fig. 4). The most common deformity in the Tobique basin sites was “yolk” (min: 0% of embryos at S1, max: 95.7% at Site S3, Fig. 4), yet this deformity was not observed in any embryos from the Miramichi. “Spine” deformities were the next most prevalent deformity type in the Tobique (min: 0% at S1, max: 47.9% at G1, Fig. 4) and this type of deformity was observed in embryos from the Miramichi, but at a far lower prevalence (up to 7.7% of embryos from OBU in 2014–2015, Fig. 4). “Eye” and “multiples” deformities were observed at similar and very low prevalence across both basins and in hatchery-reared embryos (<3% in all cases, Fig. 4). “Other” deformities were rare (Table 3), occurring in the Tobique at a low prevalence (min: 0% of embryos at S3, max: 9.9% at G1, Fig. 4) and the Miramichi at a very low prevalence (<3.5% in all cases, Fig. 4). Notes describing “other” deformities included: “abnormal growth near vent,” “malformed, blob-like body, almost no discernable features,” and “misshapen head.”

Table 3 Prevalence of deformed Atlantic salmon (*Salmo salar*) embryos sampled from incubators in the Tobique and Miramichi Rivers in New Brunswick, Canada between 2012 and 2015. A total of 3234 embryos were sampled and classified

Basin	Sample year	Regulation	River	Site	Number of embryos sampled	% Deformed
Tobique	2012–2013	Regulated	River Dee	D1	79	8.9
				D3	63	87.3
			Serpentine	S1	72	1.4
				S3	69	95.7
		Unregulated	Gulquac River	G1	71	88.7
				G2	74	70.3
			Wapske River	W1	68	48.5
				W2	31	32.3
		n/a	Mactaquac Biodiversity Facility	HY	1224	1.1
Miramichi	2013–2014	Unregulated	Catamaran Brook Lower Reach	CBLU	73	0.0
				CBLM	65	0.0
				CBLD	50	4.0
			Otter Brook	OBU	41	2.4
				OBM	89	3.4
				OBD	60	0.0
			Rocky Brook	RBU	57	0.0
				RBM	94	2.1
	2014–2015	Unregulated	Catamaran Brook Gorge Reach	CBGU	90	4.4
				CBGM	89	2.2
				CBGD	70	0.0
			Catamaran Brook Lower Reach	CBLU	88	1.1
				CBLM	88	2.3
				CBLD	81	1.2
			Otter Brook	OBU	39	7.7
				OBM	90	1.1
				OBD	88	1.1
			Rocky Brook	RBU	55	0.0
				RBM	90	1.1
				RBD	86	1.2

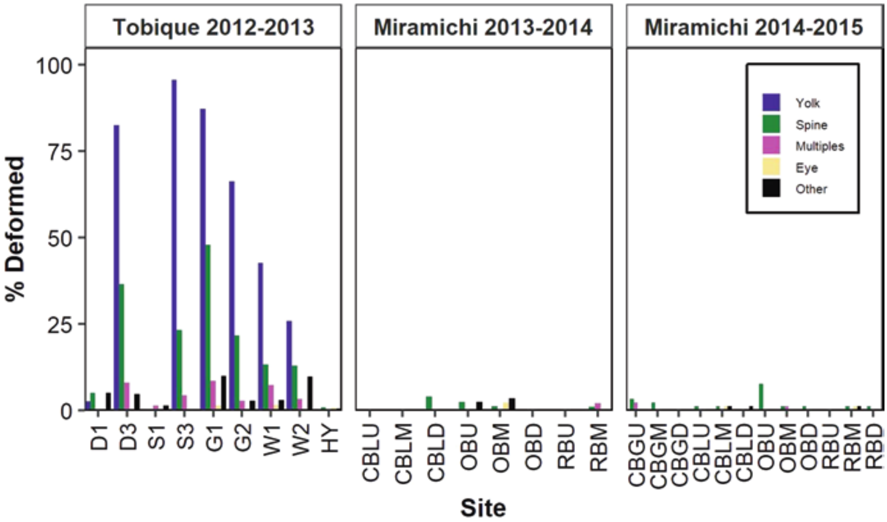

Fig. 4 Prevalence of different types of deformities (see Bartlett et al. 2022) found in Atlantic salmon (*Salmo salar*) embryos sampled from various study sites in the Tobique and Miramichi Rivers in New Brunswick. The abbreviation "HY" denotes embryos raised at the Mactaquac Biodiversity Facility hatchery

Within the Tobique basin, incubation temperature predicted deformity prevalence (GLM: Model 2, $F = 27.381$, df = 1,2.078, $p = 0.032$); while, interestingly, flow regulation did not (Table 2). Linear regression revealed a statistically significant trend ($p = 0.040$, $R^2 = 0.475$) of increasing deformities with decreasing temperature (Fig. 5), such that sites with warmer incubation temperatures (Sites D1 and S1, those closest to the dams: Figs. 1 and 4) produced considerably fewer deformed embryos than those farther downstream with colder temperatures (Sites D3, S3) or sites in unregulated rivers within the same basin that also exhibited colder temperatures (e.g., W and G sites). In contrast, in the Miramichi basin deformity prevalence was consistently low regardless of incubation temperature observed (Fig. 5): linear regressions revealed no pattern in 2013–2014 ($p = 0.729$, $R^2 = 0.022$) and a small but statistically significant ($p = 0.038$, $R^2 = 0.36$) trend of increasing deformities with higher temperatures in 2014–2015.

4 Discussion

Because the embryos were collected as part of other studies not designed to determine the cause of the deformities, several potential hypotheses deserve future testing. These are summarized in Table 4, with the three that we consider priorities for future work discussed below, including (1) differences in handling or transportation

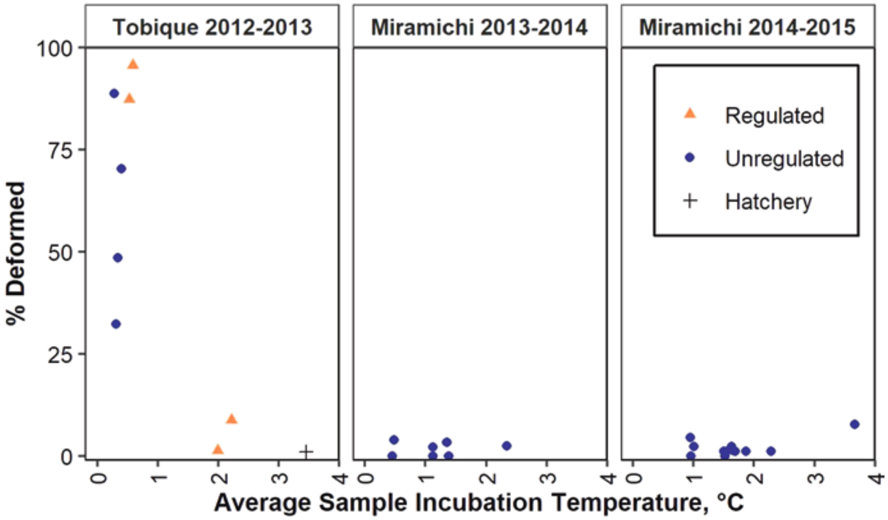

Fig. 5 Deformity prevalence in field- or hatchery-reared Atlantic salmon (*Salmo salar*) embryos from sites in north-central New Brunswick, Canada versus the time- and depth-averaged water temperature they experienced during incubation

methods between river basins could have caused deformities; (2) broodstock effects could have driven differences in deformity prevalences between basins; and (3) relatively warmer incubation temperatures at sites nearest to the bottom-draw dams on regulated rivers in the Tobique might have protected embryos from the impacts of stressors (e.g., handling, parental effects, temperature, hypoxia, and toxic compounds).

4.1 *Handling and Transport*

Given the differences in the time between fertilization and placement between basins and method of incubator tray loading and transport (Table 1), some aspect of handling and/or transport (e.g., duration and severity) experienced by embryos before incubation might be related to the deformity prevalences observed. In terms of timing, all embryos in both basins were placed within the 48-hour period recommended by others (e.g., Burrows 1949; Leitritz and Lewis 1976; Piper 1982; Jensen and Alderdice 1983), and there was no significant effect of the number of hours between fertilization and placement on deformity prevalence in either Model 1 or 2 (Table 3), nor did a linear regression reveal a predictive relationship between time to placement and deformity prevalence within the Tobique basin (Fig. 6; $p = 0.362$, $R^2 = 0.12$). This suggests that how long we took to place the embryos in their incubation sites did not impact our observations of deformities.

Table 4 Summary of additional suggested hypotheses about embryo deformity prevalence not discussed in text, relating specifically to known differences between groups of sampled embryos

Hypothesis	Rationale	References
Wild salmon choose spawning sites with optimal conditions for successful embryo incubation, but humans cannot replicate an optimal choice of spawning sites.	Sites in the Miramichi basin were selected based on direct observations of wild salmon spawning, whereas sites on the Tobique were selected based on hydraulic and geomorphic features that match typical spawning locations, since no local knowledge was available to indicate where salmon would choose to spawn. It is therefore possible that salmon select spawning sites based on different criteria than those we used in the Tobique basin and that these criteria are related to conditions that ensure successful embryo development.	Crisp and Carling (1989) Kondolf and Wolman (1993) Bardonnet and Baglinière (2000) Coulombe-Pontbriand and Lapointe (2004) McHugh and Budy (2004)
Suboptimal levels of dissolved oxygen during development due to transient ice events and/or groundwater discharge can cause sublethal damage to embryos that manifest as developmental deformities.	Hypoxia during embryo incubation has been linked to spine deformities and mortality. The presence of anchor ice at the colder sites could have caused an increase in the groundwater-to-surface-water ratio in the hyporheic zone, thus decreasing the dissolved oxygen content of the incubation environment. This could also occur due to groundwater discharge. The present study can identify one site at which groundwater is known to discharge (site OBU), but lacks the statistical power to detect an effect.	Sánchez et al. (2011) Wood et al. (2020) Lavery and Cunjak (2019) Nafziger et al. (2017b) Malcolm et al. (2003)
Relative to those in the Miramichi basin, sites in the Tobique basin have higher concentrations of salmonid embryo deformity-relevant heavy metals leaching into the hyporheic zone.	Both basins drain land underlain by mineral deposits of Ag, Au, Cu, Fe, Mo, Pb, Sn, and Zn, but geological mapping indicates these deposits may be more common in the headwaters of the Tobique sites. It is thus possible that these deposits result in higher heavy metal levels in those sites. In particular, Cu, Pb, and Zn (as well as Cd, Cr, and Hg) are known to cause deformities in both fish embryos and larvae.	New Brunswick Department of Energy and Resource Development (2020) Weis and Weis (1991) Jezierska et al. (2009) Sfakianakis et al. (2015)

(continued)

Table 4 (continued)

Hypothesis	Rationale	References
Historical insecticides that cause salmonid embryo deformities exist in headpond sediments and are somehow transported downstream during winter incubation periods.	Northern New Brunswick has historically been subject to insecticide use for forestry, including the application of dichlorodiphenyltrichloroethane (DDT), phosphamidon, and fenitrothion. As recently as 1999, surface water from headwater lakes in the region had elevated levels of DDT. The River Dee, Serpentine River, and the Gulquac River each have their headponds/source water ponds within the historical DDT application area. DDT is toxic to juvenile Atlantic salmon and can have sublethal effects on juveniles that are exacerbated by winter temperatures. Insecticide data was not collected as part of the original studies, so effects on observed deformity prevalence are unknown.	Kurek et al. (2019) Elson (1967)
Herbicides currently in use in New Brunswick can cause salmonid embryo deformities.	Glyphosate is currently applied to conifer plantations across New Brunswick. The effects of glyphosate on Atlantic salmon embryos are unknown, but preliminary studies in zebrafish suggest that exposed embryos may be adversely affected. Herbicide data was not collected as part of the original studies, so effects on observed deformity prevalences are unknown.	Adams et al. (2007) Zhang et al. (2017)

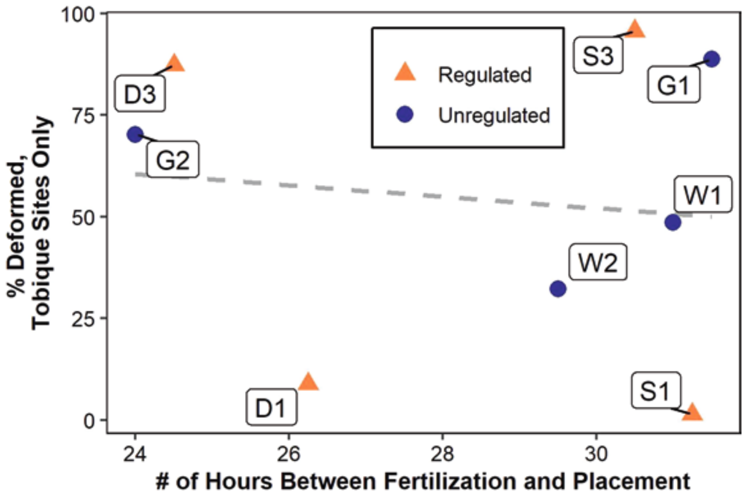

Fig. 6 Percentage of deformed Atlantic salmon (*Salmo salar*) embryos field-reared in the Tobique River system, New Brunswick, Canada versus the amount of transport handling (expressed as the number of hours between embryo fertilization and placement at study sites) to which they were exposed. There was no statistically significant trend in deformities with increasing transport handling (linear regression, $p = 0.362$, $R^2 = 0.12$, dashed gray line)

However, we do not have a measure of the magnitude of mechanical shock that embryos may have experienced due to different incubator loading and transport methods (Table 1). Transporting embryos together in water is the method recommended by fish culturist guidelines (e.g., Burrows 1949; Staff 1983) and tested by Barnes et al. (1999), and Wagner et al. (2006) found that transportation of cutthroat trout *(O. clarkii*) embryos in water coolers by truck had no effect on survival. Whether jostling in water against the individual compartments of the Jordan-Scotty incubator trays (as happened for embryos in the Tobique basin; see Table 1) has any effect on embryos has yet to be tested, though handling and mechanical shock can have an effect on salmonid embryo survival (Jensen and Alderdice 1983; Roberts and White 1992; Dwyer et al. 1993; Lavery and Cunjak 2019). However, the effects of mechanical shock on embryo deformity prevalence and type have not yet been explored, except in unrelated species at different periods of development (e.g., as for milkfish [*Chanos chanos*]: Hilomen-Garcia 1998).

4.2 Broodstock Effects

The origin of the broodstock from which the assessed embryos were harvested is also worth considering. Most study sites across both basins experienced incubation temperatures <2 °C (Fig. 5). Miramichi broodstock were of wild origin (only held captive for a few weeks in the MSA hatchery: Table 1) and would have incubated as embryos in similarly cold conditions. In contrast, the Tobique broodstock, despite being wild-exposed as juveniles, were derived from embryos incubated at warm MBF hatchery temperatures ≳3 °C over multiple generations. Importantly, parental identity and experience have been linked to cold tolerance in salmonids, either via genetic or epigenetic changes. For example, Murray et al. (1990) found that coho salmon (*O. kisutch*) from colder rivers produced embryos that could withstand colder incubation temperatures, indicating that different populations of the same species may be adapted to their respective local thermal habitats. Further, shorter-term temperature adaptations may extend across multiple generations, because incubation temperatures have been shown to affect gonadal mass, egg mass, and timing of adult return for spawning (Jonsson et al. 2014; Jonsson and Jonsson 2016, 2018). It is thus possible that Miramichi broodstock have become cold-adapted over multiple generations, producing embryos better suited to cold incubation temperatures (possibly via altered lipid content, as for sperm from thermally acclimated trout: e.g., Labbé and Maisse 1996) and thus less at risk of sublethal damage and deformity. This a fascinating hypothesis for future research, since the effect of parental temperature experience on embryo deformities remains uninvestigated.

4.3 Incubation Temperature

Limited experimental work on cold shock has shown that drops in temperature from 8 °C to 1 °C can produce spine deformities and internal abnormalities in salmonid embryos (Takle et al. 2005), and a short-duration drop from 7 °C to 0.2 °C can change the expression of thousands of genes and alter the embryonic methylome (Moghadam et al. 2017). However, the temperature regimes in the Tobique basin sites did not necessarily mimic cold shock experiments, because the decreases in temperature were more gradual and periods of colder temperatures lasted longer (see Fig. S1). Also, sites in both basins experienced similar incubation temperatures (Fig. 5) but did not exhibit similar deformity prevalences (Fig. 4); therefore, cold temperatures *per se* do not alone account for the significantly higher prevalence of deformities at colder Tobique sites. It is instead possible that cold temperatures represent one of several stressors the embryos experienced in the Tobique basin sites: several studies have identified that multiple stressors can have additive, or even synergistic, effects on incubating salmonid embryos (in terms of survival/mortality: e.g., Alderdice et al. 1958, Greig et al. 2005, Lavery and Cunjak 2019). For deformities specifically, Eriksen et al. (2006) found that they can be caused by maternal stress that is exacerbated by incubation at non-optimal temperatures. Thus, it is possible that sublethal damage from handling and transportation and/or broodstock temperature experience (or indeed another stressor as yet uncharacterized: e.g., Table 4) acted in tandem with cold temperatures to produce the deformities observed, such that warmer incubation temperatures offered embryos a degree of "protection" from deformity. This protection may be related to temperature effects on cell membrane fluidity: low temperatures may affect processes that depend on controlled changes in membrane fluidity, such as cell division and migration (e.g., Pajor et al. 1989; Los and Murata 2004). Whether certain incubation temperatures offer embryos protection from the sublethal impacts of stressors is unknown, and presents opportunities for future research in the lab and field.

5 Conclusion

Herein, we report on the high number of embryo deformities observed in samples collected for other studies. Embryo deformities were much more prevalent in the Tobique River basin than in the Miramichi River basin; within the Tobique basin, deformities were less prevalent at sites that experienced warmer incubation temperatures. Though the conditions in the Tobique resulted in an unusual number of deformities, methodological limitations meant that the cause of these deformities could not be conclusively determined. However, differences in incubation temperature, broodstock origin, handling of embryos, or other relevant factors, such as water quality, could have contributed to the high number of deformities observed at cold temperature sites in the Tobique basin. We encourage lab, field, and hybrid studies that are designed to capture the impact of additive or synergistic stressor effects on natural incubation. But regardless of which future experiments are undertaken, furthering our understanding of how embryo deformities contribute to the winter “bottleneck” of Atlantic salmon survival is important for the species’ conservation, as well as the preservation of associated commercial and cultural interests.

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Environmental Determinants of Spawning Location, and Density and Size of Age-0 Brown Trout *Salmo trutta* in a Small Boreal Stream

Leif Asbjørn Vøllestad

Abstract Brown trout *Salmo trutta* populations are common in small boreal streams in Scandinavia. Populations are often small and isolated. In this chapter, I summarized studies conducted for 8 years on a population of small-sized brown trout living in a small Norwegian boreal stream exposed to harsh winters (>5 months of ice cover) and low water levels during summer. Subsequently, I evaluated factors influencing local use of spawning areas and the distribution of age-0 individuals during autumn in a contiguous 1.4 km portion of the stream. Finally, I analyzed the local and temporal variation in individual length of the age-0 individuals during late fall and related distribution of age-0 brown trout to habitat qualities, including fish density and environmental factors varying at the catchment scale (i.e., discharge and temperature) or at the local scale (i.e., habitat characteristics summarized using principal component analysis and presence/absence of competitors). Spawning occurred throughout the stream, indicating that female brown trout were able to find small patches of suitable spawning habitat in most study sections. Age-0 brown trout were also found in all sections of the stream, with large variation among sections. General linear mixed effects models, with year as a random effect, indicated that variation in the second principal component was the main factor determining density of both mature and age-0 brown trout. However, the effect was in opposite direction for the two groups. Variation in length of age-0 brown trout was substantial, and associated with most of the measured parameters. There was a significant negative density effect, and this effect was exacerbated by the presence of alpine bullhead *Cottus poecilopus*. Both mature brown trout and age-0 juveniles utilized the full extent of the study area, leading to substantial phenotypic variation.

Keywords Density dependence · Climate · Temperature · Habitat · Interactions

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1 Introduction

The brown trout *Salmo trutta* is one of the most widely distributed salmonid fishes in the world (Elliott 1994; Jonsson and Jonsson 2011; Lobón-Cerviá and Sanz 2018; Keeley 2019). The species is well documented; a search on the Web of Science using the search topic "Salmo trutta" OR "brown trout" on March 18, 2022, returned 10,271 hits. Most of the studies pertained to fisheries, and marine and freshwater biology. This suggests extensive interest in the species, mainly because of its value for recreational fishers but also historically as a commercial species. The brown trout is phenotypically very plastic, leading to a large number of life history types and morphologies, and broad variation in individual behavior. Consequently, controversies have arisen regarding species definitions and boundaries, evolutionary history, and ultimately, conservation and management of populations (Bernatchez 2001; Kottelat and Freyhof 2007; Jonsson and Jonsson 2011; Sanz 2018; Muhlfeld et al. 2019; Whiteley et al. 2019).

Brown trout have been translocated across the globe, and generally, the introductions have been successful (Elliott 1994; McIntosh et al. 2011). The species is phenotypically plastic, and the large growth plasticity throughout life seems to facilitate success as an invader (Budy et al. 2013). This plasticity is also evident within the native range, and even at very small geographic scales. Extensive translocation and stocking of brown trout and other salmonid fishes, present management challenges at a variety of spatial scales (Young et al. 2018; Hansen et al. 2019).

Brown trout are the most common freshwater fish in Norway (Huitfeldt-Kaas 1918), as anadromous sea trout along the coast, as lacustrine-adfluvial (lake dwelling/tributary spawning) populations in numerous lakes across the landscape, and as a large river- or small stream fluvial (river dwelling/spawning) and fluvial-adfluvial (river dwelling/tributary spawning) populations. Human translocations, starting more than 1000 years ago, have resulted in numerous populations at high elevations. In many small low-order headwater streams, isolated populations of small-sized brown trout are common. These populations are isolated by natural and anthropogenic barriers to migration (Jones et al. 2021). The dendritic nature of the riverscape, and the numerous barriers to dispersal, facilitate the development of genetically differentiated populations (Morrissey and de Kerckhove 2009; Vøllestad 2018).

This chapter is focused on brown trout in a small boreal headwater stream, commonly found in Norway. The brown trout population is isolated from the population in the downstream river by a semipermeable barrier (small waterfall) to upstream migration, and the stream is fed by an upstream bog–wetland system. Individuals are small and rarely exposed to harvesting (angling). However, these headwater populations of brown trout may contain large genetic diversity that has evolved over millennia, and understanding their population dynamics is important. My focus will be on the environmental factors that determine the choice of spawning location, habitat utilization by young-of-the-year (age-0) brown trout, and the factors affecting juvenile growth during their first summer.

2 The Study System

Brown trout were sampled extensively over a 1504-m portion of the small stream Bellbekken, during 2002–2009 (Fig. 1). Twenty-five contiguous sections were sampled annually. Sample section length varied from 32 to 96 m (mean section length = 60.2 m). Habitat varied from slow flowing, relatively deep sections to steeper (high gradient) areas with large rocks/boulders and substantial habitat heterogeneity (Table 1).

The stream has been used for the transport of timber (similar to most Norwegian streams and rivers) for generations and was historically modified for that use. Timber transport on this stream and most other Norwegian waterways was discontinued during the 1970s, and the stream has subsequently reverted to pre-transport conditions through natural geomorphological processes. Timber has been harvested from the catchment at regular intervals.

A small waterfall between Sections 1 and 2 prevents upstream migration of brown trout under most environmental conditions. Below the waterfall, the stream enters the larger river Julussa. In the upper part of the stream (above section 25), the stream enters a wetland and bog area. Brown trout may use this upstream area, but due to sampling limitations, these upper reaches were not included in the study. Previous studies suggested a weak, but statistically significant, genetic differentiation between brown trout upstream and downstream of the waterfall (Taugbøl 2008;

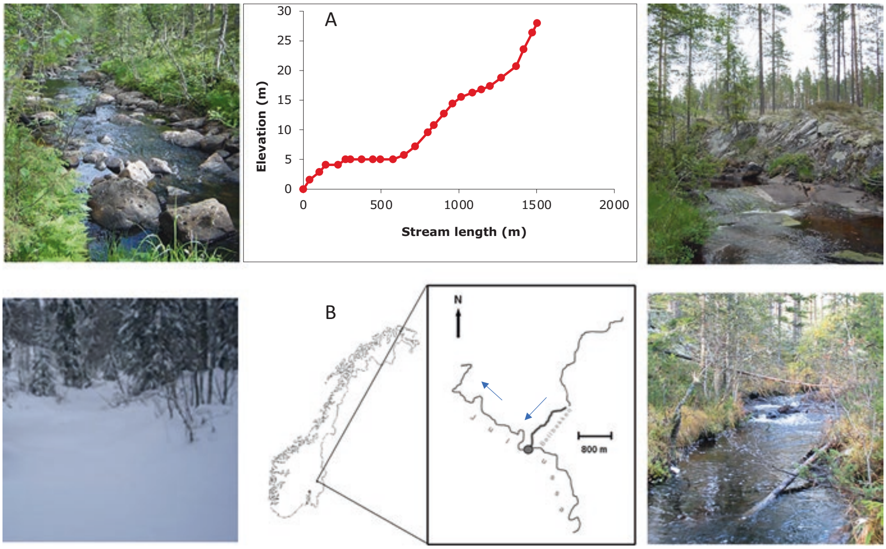

Fig. 1 The stream Bellbekken. (**a**) Stream profile of the sampled area of the stream Bellbekken. (**b**) Map of Norway, the stream Bellbekken and the larger downstream Julussa River. Arrows indicate the direction of streamflow, and the bold part of the stream Bellbekken indicates the sampled area. The pictures provide examples of stream sections, including a picture from winter when the stream is completely covered by ice and snow

Table 1 Habitat characteristics for the 25 contiguous sections of the stream Bellbekken (see Fig. 1), from the downstream to upstream section. PC1–PC3 are the mean loadings of the first three principal components from a principal component analysis. All habitat characteristics were measured at low streamflow in August 2004

Section	Length (m)	Slope	Transects (n)	Wetted width (m)	Mean depth (cm)	Exposed boulders (%)	Cover (%)	Undercut banks (%)	Underwater vegetation (%)	Substrate	Area (m^2)	Wetted area (m^2)	PC1	PC2	PC3
1	40	0.040	5	5.30	23.73	33.24	3.20	6.22	34.12	10.56	212.0	141.5	1.87	−1.06	0.73
2	64	0.020	8	4.63	17.70	30.61	18.39	20.51	36.93	8.86	296.0	205.4	0.68	0.37	0.32
3	40	0.030	5	3.80	30.88	9.82	14.48	19.20	27.92	8.88	152.0	137.1	−0.17	−0.66	−0.94
4	80	0.000	10	3.95	35.06	15.40	21.74	14.31	5.81	5.14	316.0	267.3	−1.58	−0.60	−0.19
5	48	0.020	6	4.75	26.03	17.97	17.62	19.95	15.80	6.62	228.0	187.0	−0.68	−0.32	0.38
6	32	0.000	4	4.13	52.08	0.00	23.93	37.45	0.00	4.85	132.0	132.0	−3.35	−0.62	−0.49
7	72	0.000	9	4.28	24.08	13.52	28.06	26.30	0.77	5.14	308.0	266.4	−1.96	0.36	0.19
8	72	0.000	9	4.50	29.03	20.88	19.62	19.66	0.00	4.12	324.00	256.36	−1.69	−0.07	0.52
9	48	0.000	6	3.75	25.00	14.50	14.85	30.25	0.00	4.00	180.00	153.90	−1.92	0.62	−0.36
10	80	0.000	10	4.15	17.59	24.39	19.39	20.33	0.57	4.24	332.00	251.03	−1.27	0.65	0.34
11	72	0.010	9	5.11	21.49	27.67	26.72	19.59	0.20	5.04	368.00	266.19	−1.34	0.28	1.30
12	72	0.020	9	5.22	14.12	18.38	5.41	11.54	35.12	8.57	376.00	306.90	1.28	−0.75	0.46
13	80	0.030	10	5.15	15.18	21.67	2.29	9.98	33.00	9.25	412.00	322.72	1.55	−0.81	0.42
14	40	0.030	5	4.80	14.62	18.78	1.20	17.58	32.92	9.56	192.00	155.94	1.35	−0.40	−0.01
15	64	0.030	8	7.88	14.11	24.85	2.44	10.83	39.90	8.71	504.00	378.76	1.66	−0.14	−0.54
16	56	0.030	7	4.29	13.67	28.69	1.57	17.27	38.79	8.79	240.00	171.15	1.48	0.18	−0.21
17	56	0.020	7	3.43	21.30	29.66	11.46	21.20	28.63	6.94	192.00	135.06	0.09	0.68	−0.68
18	72	0.010	9	3.67	16.69	11.90	23.26	23.26	11.70	5.93	264.00	232.58	−1.12	0.53	−0.53
19	56	0.010	7	3.93	21.90	18.17	15.66	22.60	0.54	5.74	220.00	180.02	−1.16	0.33	−0.16
20	56	0.010	7	3.79	13.87	13.21	8.93	14.47	11.76	7.21	212.00	183.99	0.05	−0.08	−0.60
21	72	0.020	9	3.83	10.89	20.49	5.46	14.43	37.60	7.98	276.00	219.45	1.14	0.12	−0.68
22	96	0.020	12	4.50	12.21	27.52	8.25	15.45	34.82	7.95	432.00	313.13	1.07	0.17	0.13

Section	Length (m)	Slope	Transects (n)	Wetted width (m)	Mean depth (cm)	Exposed boulders (%)	Cover (%)	Undercut banks (%)	Underwater vegetation (%)	Substrate	Area (m^2)	Wetted area (m^2)	PC1	PC2	PC3
23	48	0.060	6	4.42	16.75	29.15	3.65	16.27	48.32	9.17	212.00	150.20	1.65	−0.04	−0.18
24	56	0.050	7	4.07	19.01	36.51	5.96	17.00	35.69	9.07	228.00	144.75	1.26	0.35	−0.17
25	32	0.050	4	4.25	20.33	40.08	2.63	15.88	49.50	10.30	136.00	81.50	2.02	0.16	−0.16

Vøllestad et al. 2012). In fact, brown trout sampled in section 1 were more closely related to the brown trout in the river Julussa than to those upstream of the waterfall. Detailed genotypic analysis of several cohorts of brown trout suggested that a small number of individuals were immigrants from the downstream river Julussa (Serbezov et al. 2012b).

Individuals in the population are small, rarely reaching ages >6 years and lengths >20 cm (fork length, FL) (Olsen and Vøllestad 2003; Vøllestad et al. 2012). Fish density and individual growth rates are relatively low (Vøllestad et al. 2002). Analysis of long-term mark-recapture data for brown trout aged 1^+ have shown that density and temperature interact to control growth performance, and growth was more affected by density for younger than older brown trout (Bærum et al. 2013). Data also suggested that growth in general is resource limited, and individual growth variation, particularly in the early years of life, had a relatively high heritability (h^2 varying from 0.16 to 0.31, with significant maternal and paternal effects; Serbezov et al. 2010b). Slow-growing brown trout are small at maturity (Olsen and Vøllestad 2005). For example, males were predicted to mature at 3.1 y and 142 mm (FL); females were generally older and larger at first maturation (3.5 y and 147 mm, FL). Larger individuals within an age group had a higher probability of being mature (Olsen et al. 2014).

Long-term mark-recapture data have suggested that survival rate is density dependent, but survival is also influenced by density-independent and stochastic factors (Olsen and Vøllestad 2001; Carlson et al. 2008). Further, there was no strong evidence for the “big-is-better” hypothesis that suggests that survival is higher for larger fish. Rather, there was a tendency for survival to be better for the average sized fish within each age class (Carlson et al. 2008). However, we found that both mating and reproductive success increased with increasing body size for both males and females (Serbezov et al. 2010a). We used both genetic and demographic data to evaluate the effective population size (Ne) of the population, using a variety of methods (Serbezov et al. 2012a, b). Most estimates of Ne were around 100, indicating that the population is relatively small. However, the data also suggested some gene flow from the larger population in the downstream Julussa River into the Bellbekken population.

3 General Methods

3.1 Fish Sampling

Brown trout were sampled using the same backpack electrofishing apparatus and methods during all years. Here, I analyze samples collected during September–October each year in the period 2002–2009. September–October is a period where individual growth is strongly reduced (Vøllestad et al. 2002), but not necessarily zero, due to the low water temperature. Sampling was conducted just prior to the spawning season, to avoid disturbing the fish during the actual spawning. I assumed that most mature brown trout had moved to or toward their selected spawning location during that period. This assumption is based on a set of observations. During some additional sampling periods later in autumn, mature female and male trout were observed throughout the stream. We also observed post-spawned females distributed throughout the stream. Further, during early summer (June) small-sized juveniles were observed throughout the stream (Vøllestad, unpublished observations). For three cohorts, we used the observation of where potential parental fish (all genotyped) were observed during spawning, together with observation of where genotyped offspring were found the next autumn, to infer the dispersal during the first summer of life (Vøllestad et al. 2012). The results indicated a weak, but significant, downstream dispersal during the first summer. Taken together, I am confident that spawning happened throughout the length of the stream.

All sections within the stream Bellbekken were usually sampled within 1 week. Environmental conditions were stable (i.e., low streamflow and no/limited precipitation) during sampling. However, the stream drains a catchment containing bogs, wetlands, and coniferous forests leading to leaching of humic substances. The brownish-colored water and low transparency reduced visibility and led to reduced catchability, particularly for small brown trout.

On a given sampling occasion, brown trout were collected in each section using electrofishing from the downstream to the upstream limit at least three times (i.e., the removal method; White et al. 1982, Bohlin et al. 1989). Capture probabilities for age-0 individuals are generally low and variable in this and similar streams (see Lund et al. 2003; Carlson et al. 2008), and therefore, they were not included in the density estimates. Number of captured age-0 individuals per section can, however, be used as a relative measure of abundance. All fish were returned to the section of capture when all passes were completed. The relative density of age-0, and mature males and females was estimated as the total number captured within a section divided by the wetted area of the section (n m^{-2}).

Brown trout were the most abundant species present in each section. However, during some years a small number of alpine bullhead *Cottus poecilopus* were observed in some sections. In a previous study in a nearby river, we documented a significant overlap in diet for the alpine bullhead and the brown trout (Holmen et al. 2003), leading to the potential for negative competitive interactions (Vøllestad et al. 2002). Presence or absence of alpine bullhead was therefore used as a predictor variable in statistical analyses (see later).

Fork length of all fish was measured (nearest mm), and after handling, individuals were allowed to recover and were subsequently released within the section of capture. The age-0 individuals could usually be differentiated from the older fish based on length alone. A small number of scales were removed from larger fish (> 6 cm) for later age analysis in the laboratory. The sex of the mature fish could be easily distinguished during the spawning season based on external characteristics and presence of running milt and mature eggs (often clearly discernible).

3.2 Habitat Characteristics

Several habitat variables potentially important for the distribution and performance of the brown trout were measured in each section (Table 1). To get a general description of each section, transects (n = 188) were placed at 8-m intervals along the studied stream. At each transect, a measuring tape was stretched perpendicular to the streamflow to record total wetted width. Each transect was divided into 50-cm long sample stations. Depth was measured to the nearest cm at the middle of each sample station.

For each 50-cm sample station, a quadrate with a size 50 times 50 cm was visually inspected and an estimation was made of the following habitat characteristics:

1. The percentage of substrate, such as large boulders that were not submerged in water, hereafter called "exposed boulders." This reduces the overall available habitat within a section, but may also act as security habitat for fish.
2. The percentage of cover that is composed of undercut banks, hereafter called "undercut banks."
3. The percentage of the area covered by a canopy or large instream woody debris (such as large trees and branches), hereafter called "cover."
4. The percentage of the substrate covered with underwater vegetation (mosses and algae).
5. The dominant substrate type was classified according to a modified Wentworth scale (following Heggenes 1988).

For each of the 25 sections, the average slope was calculated as the total vertical displacement within a study section (m) divided by the total length of the section (m). The slope parameter provided an approximate idea of the water velocity in that section. The steepest part of the stream had a slope of 6%, whereas some sections had a slope of 0% (see Table 1).

The habitat classification was only performed once (in August 2004), at a time when the water level was low and stable. Means were estimated for all habitat characteristics in each of the 25 sections (Table 1). Many of the habitat characteristics measured in Bellbekken are strongly correlated (Table 2), indicating that they could not all be included as predictor variables in statistical analyses. To have a set of uncorrelated parameters describing the habitat in each section, I performed a principal component analysis (PCA). I extracted the three first principal components from the PCA which explained in total 73.3% of the habitat variability in the stream (Table 3). The loading matrix suggested that most parameters were associated with the first principal component (PC1; Table 3); therefore, it was not possible to extract one or two particular parameters that could easily convey information on important habitat characteristics. I therefore decided to use the mean loadings of the three first principal components for each section as predictors in subsequent statistical analyses.

Table 2 Correlation matrix for the measured habitat parameters is used for describing the habitat in the different sections. The average values for each section were used. Significant correlations are indicated in bold

	Wetted width (m)	Mean depth (m)	Exposed boulders (%)	Cover (%)	Undercut banks (%)	Underwater vegetation (%)	Substrate
Slope	0.239	−0.381	**−0.653**	**−0.756**	**−0.534**	**0.873**	**0.878**
Wetted width (m)		−0.222	−0.218	−0.316	**−0.461**	0.302	0.320
Mean depth (m)			**0.515**	**0.567**	**0.601**	**−0.528**	**−0.459**
Exposed boulders (%)				**−0.497**	**−0.538**	**0.610**	**0.536**
Cover (%)					**0.661**	**−0.828**	**−0.819**
Undercut banks (%)						**−0.610**	**−0.663**
Underwater vegetation (%)							**0.927**

Table 3 Principal component analyses for the habitat characteristics for the stream Bellbekken. Eigenvalues and eigenvector loadings for the three first principal components are given

	PC1	PC2	PC3
Eigenvalue	3.006	1.086	1.036
Percent	42.944	15.508	14.797
Eigenvectors			
Mean depth (cm)	−0.3763	−0.4752	−0.0661
Width (m)	0.0797	−0.3586	0.8628
Exposed boulders (%)	0.2888	0.5825	0.4166
Cover (%)	−0.4477	0.1792	0.1576
Undercut banks (%)	−0.3129	0.5081	−0.0331
Underwater vegetation (%)	0.4858	−0.0450	−0.1860
Substrate	0.4841	−0.1185	−0.1308

3.3 Water Temperature and Streamflow

Water temperature directly and indirectly influences fish growth and development (Kamler 1992; Wootton 1998). In the stream Bellbekken, the mean daily water temperature was estimated from readings taken 8–10 times a day with submerged HOBO loggers from May–October during 2002, 2004, and 2005. For the remaining years, direct measurements of water temperature were not available; however, mean monthly air temperature measurements at a weather station located approximately 4 km from the stream (at Rena city; data supplied by the Norwegian Meteorological Institute) and water temperature during June–September 2002, 2004, and 2005 were found to be positively correlated ($r^2 = 0.85$, $P < 0.001$). Therefore, I used air temperature as a proxy for average water temperature during the brown trout growth season. Mean monthly air temperature predictably became positive in April, reaching a maximum between 12 and 20 °C during July, and decreased to below zero again in November (Fig. 2), but interannual air temperature varied substantially during the study period. In particular, variation was greatest during July, the month when discharge normally reached base-streamflow conditions.

Discharge has not been measured directly in Bellbekken; therefore, I accessed daily discharge measurements ($m^3 s^{-1}$) from a stream in the same vicinity (the river Frya) to serve as a proxy for variation in discharge in Bellbekken. Data were available through the Norwegian Water Resources and Energy Directorate (www.nve.no). From these data, I annually extracted the maximum discharge during spring (usually May) as an index of the size of the spring flood (primarily snow-melt) and minimum discharge during the summer season (June–August) as an index of drought severity (Vøllestad and Olsen 2008). Mean summer discharge served as a metric describing habitat availability during summer and potential transport of drifting food items (Table 4).

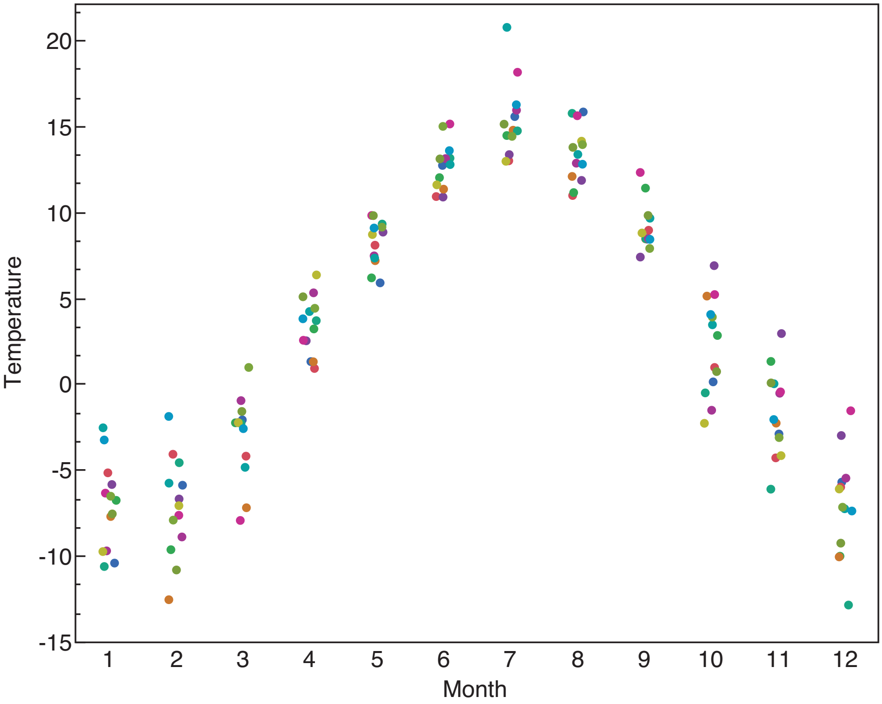

Fig. 2 Mean monthly air temperature (°C) at the Rena meteorological station, 2002–2009. Different years are in different colors

Table 4 Variation in streamflow ($m^3 s^{-1}$), based on measurements in river Frya (data from www.nve.no). Estimated mean and minimum summer streamflow, and maximum streamflow during spring are presented

Year	Mean summer streamflow	Minimum summer streamflow	Maximum spring streamflow
2002	0.92	0.04	11.85
2003	1.42	0.05	14.95
2004	1.03	0.04	14.87
2005	0.80	0.01	14.62
2006	1.44	0.02	14.62
2007	0.68	0.04	8.54
2008	1.37	0.02	15.54
2009	1.20	0.03	13.55

3.4 Analyses

I used a general linear mixed model (glmm) approach with model selection to evaluate the effects of environmental variables measured at different temporal and spatial scales on the observed variation in density of mature (males and females) and age-0 brown trout, and length of the age-0 individuals. To assess variation in the distribution of mature brown trout, I first tested for the variation in numbers among sections, using year as random variable. In a subsequent model, I then included section as a fixed effect. Finally, I evaluated which factors at the local scale best described the distribution by exchanging the section effect with various covariates. The full model included several fixed effects describing each section: slope ($m \cdot m^{-1}$) and the mean of the three first principal components. No interaction effects were included in the analyses. Year was included in all three analyses as a random variable to account for some unmeasured variation.

Variation in number of age-0 individuals at the end of the season was evaluated using the same approach as for the mature brown trout. After having identified the best model (see below), I assessed the effect of density of mature trout on the density of age-0 individuals. Finally, I assessed the influence of Alpine bullhead (presence-absence) on age-0 brown trout density.

The effect of environmental variables on length of the age-0 brown trout at the end of the growth season was evaluated using variables measured either at the annual scale (streamflow and water temperature) or at the specific section scale (habitat characteristics: PC1–3, slope, brown trout density, and presence/absence of alpine bullhead in a given section during a given year). Only the interaction between brown trout density and presence/absence of alpine bullhead was included in the modelling, and year was included as a random factor to account for among-year variation not accounted for by the predictor variables. Before doing the main analyses, I evaluated what would be the best descriptor of the influence of streamflow and brown trout density. Streamflow was estimated at the annual scale, as either minimum or mean summer streamflow, or maximum observed streamflow (during April–May) (Table 3). Density was either estimated as the total number of brown trout per section or per area (wetted area), or total number of age-0 brown trout per section. I determined the appropriate explanatory variables and the best model explaining variation in age-0 brown trout size using standard model selection (Burnham and Anderson 1998). I started with the full model, comparing all potential combinations of response variables.

All statistical modelling was performed in the JMP statistical environment (SAS Institute Inc. 2020–2021). I used the Akaike Information Criterion adjusted for small sample size (AIC_c) (Akaike 1974) for the model selection, following Burnham and Anderson (1998). The model giving the lowest AIC_c value was selected as the most parsimonious and was used for inference.

4 Results and Discussion

4.1 Mature Fish

During the 8 years of study, the total number of spawning brown trout in the study area in stream Bellbekken varied between a low of 101 and a high of 215 individuals. The male–female ratio varied around 1:1; females dominated some years, and males were most abundant in other years. Mean length of mature females (± SE) was 151 ± 1 mm, and males averaged 168 ± 1 mm (Fig. 3), and differences were statistically significant (ANOVA; $F_{1,\,1016} = 159.3$, $P < 0.001$). Mean length of males was also more variable than that of the females (Levene's test, $F_{1,\,1294} = 44.9$, $P < 0.001$). Despite a relatively small range in length for mature individuals of both sexes, sexual selection driven by female mate choice and male–male competition has been documented in this population (Serbezov et al. 2010a).

During spawning, female brown trout choose spawning locations based on availability of suitable spawning substrate (i.e., clean gravel; see review by Jonsson and Jonsson 2011) and subsequently she build a redd with a variable number of nests for egg deposition (Fleming 1998; Esteve 2005). Small-sized brown trout like those found in the stream Bellbekken spawn between 112–330 eggs (Olsen and Vøllestad 2003, Vøllestad unpublished data), and these eggs may be deposited in 1–3 nests (Fleming 1998) over 1–3 days. In the stream Bellbekken, the number of males and females in a given section was positively correlated ($r = 0.76$, $P = 0.03$), suggesting that the males may distribute themselves depending on the availability of females. However, because the females may complete actual spawning in just a few days and males may be sexually active for weeks (Fleming 1998; Esteve 2005; Jonsson and Jonsson 2011), the males may reposition repeatedly during the spawning season.

The number of mature brown trout varied among sections (Fig. 4), and the glmm model with section as fixed effect explained approximately 39% of the variation. Although suitable spawning sites were available throughout the study area, some sections with a greater than average density of mature fish did occur. For example, in section 19 there was a relatively large area with suitably-sized gravel and greater

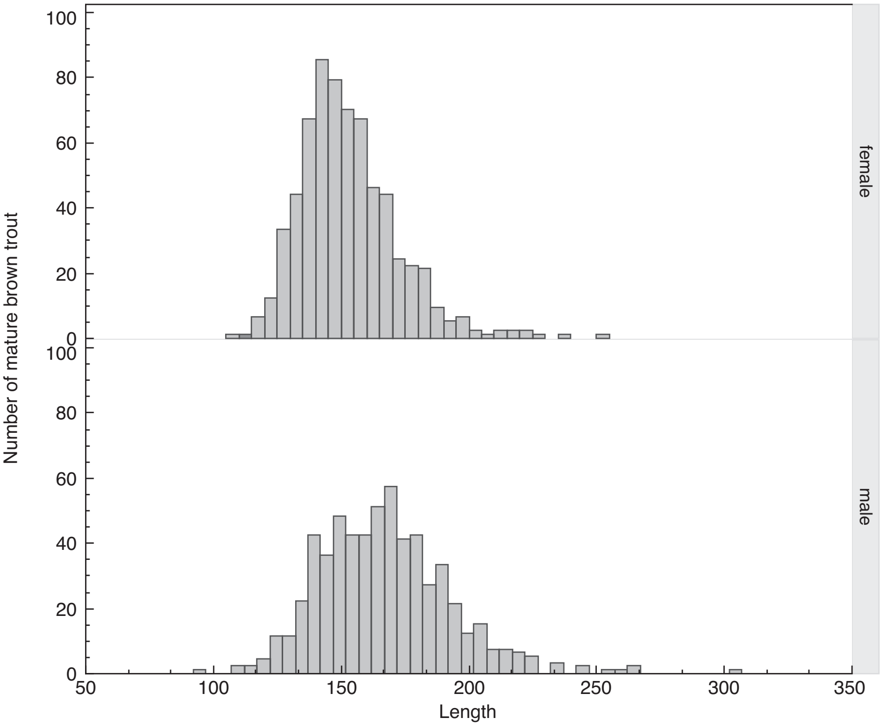

Fig. 3 Length distribution (fork length; mm) of mature male and female brown trout sampled in the stream Bellbekken during autumn (September–October) 2002–2009

than average number of mature fish. Although this type of gravel occurred throughout the stream, it was usually limited to small patches.

The best model for explaining the variation in number of mature brown trout had PC2 as the only explanatory variable, and the next best model also included the effect of slope (Table 5). Density of mature fish increased significantly with increasing values of PC2 (Fig. 5). PC2 was positively correlated with proportion underwater vegetation (various mosses; Bryophyta) and exposed boulders (not submerged) and negatively correlated with depth (Table 3). Results suggested that the brown trout selected shallow areas with cover (often underwater vegetation, see Mäki-Petäys et al. 1997) and structure; however, this model explained only 18.5% of the variation in density of mature brown trout. In contrast, the glmm with only section as fixed effect explained more of the variation (adjusted $R^2 = 0.39$; see above).

Results suggested that there is a suitable spawning habitat throughout the stream. This was supported by observations made while sampling, where small patches of suitable gravel and reasonable streamflow were observed throughout the stream. Furthermore, the generally small size of the male and female brown trout suggests that relatively small gravel in small patches will be adequate for digging redds and depositing the relatively few eggs (Ottaway et al. 1981; Gauthey et al. 2017). Indeed,

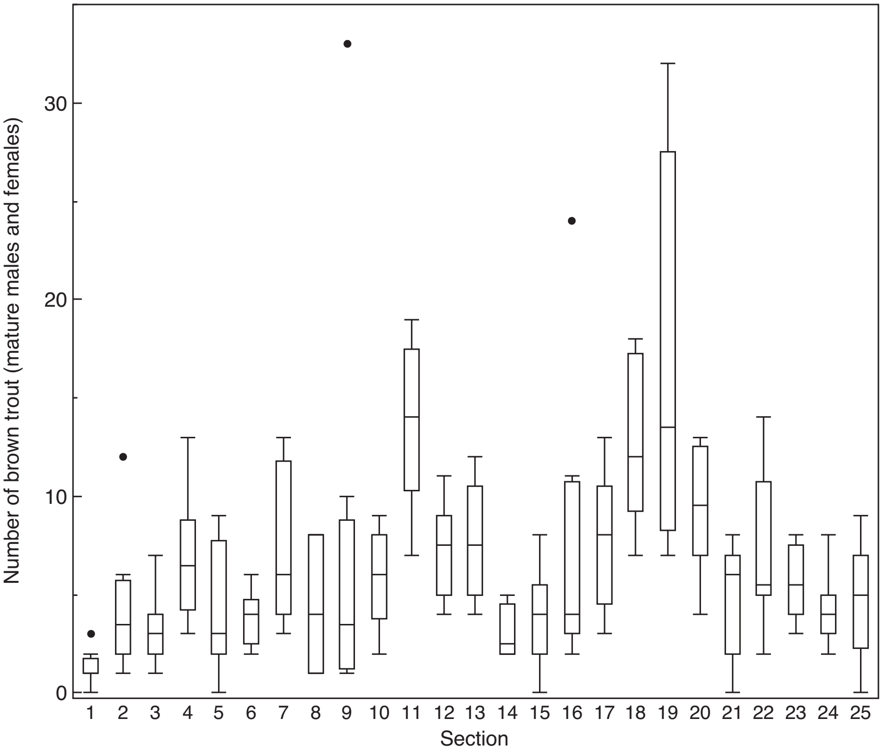

Fig. 4 Number of mature brown trout (female and male) in the different sections of the stream Bellbekken

Table 5 Selection of the best model explaining variation in the density of mature brown trout (males and females) in the stream Bellbekken. (a) The full model and the five best models are presented, with the best model given in bold. The best model is the one with the lowest AIC$_c$-value. AIC$_c$, ΔAIC$_c$, and rank are given. Year was always included as a random variable. Year was used as a random effect. (b) Parameter estimates (± SE) for the best model; R^2 = 0.162 adjusted R^2 = 0.185, n = 200, the random year effect accounted for 5.11% of the total variance

(a) Model selection

Parameters	AIC$_C$	ΔAIC$_C$	Rank
Slope + PC1 + PC2 + PC3	−814.0	22.7	6
PC2	**−836.7**	**0**	**1**
PC2 + PC3	−827.2	9.5	3
PC1 + PC2	−824.4	12.3	4
Slope + PC2	−832.2	4.5	2
Slope + PC1 + PC2	−824.0	12.7	5

(b) Parameter estimates

Parameter	Estimate	SE	DF	*t*-ratio	P
Intercept	0.034	0.003	7.02	11.511	<0.001
PC2	0.019	0.004	191	4.91	<0.001

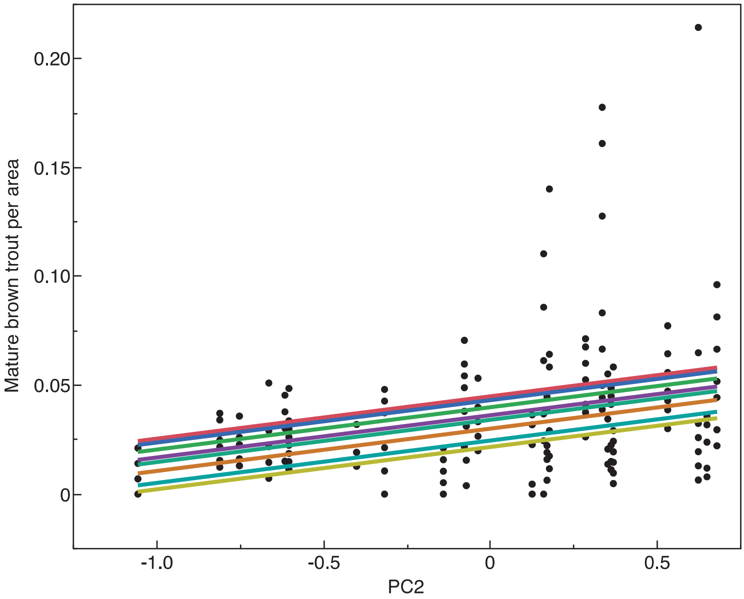

Fig. 5 Relationship between the number of mature brown trout (males and females) and proportion of undercut banks and exposed boulders (as summarized in PC2; see Tables 1 and 3 for details). The regression lines are for the different years (2002–2009), based on a random year effect (random intercept) in a general linear mixed model

average fecundity of a female brown trout in Bellbekken is approximately 280 eggs (Olsen and Vøllestad 2003). This limited number of eggs may be deposited in a small number of nests (batches), probably within the same redd (see Jonsson and Jonsson 2011). We never observed spawning directly, and these small-sized fish probably spawn at dusk or dawn to reduce predation risk (Jonsson and Jonsson 2011). Apparently, brown trout captured in this study were sheltering close to spawning sites.

4.2 Young of the Year Brown Trout—Variation in Numbers

Density of young-of-the-year (age-0) brown trout was generally low, and relative density varied spatially from a mean of almost zero in section 9, to 4–5 individuals per 100 m^2 in section 1 and 12. A glmm model with section as fixed effect and year as random effect explained 34.5% of the variation in density of age-0 brown trout.

Density of age-0 brown trout can be influenced by numerous habitat quality metrics. However, the best glmm model explaining the variation in density only comprised the second principal component as an explanatory variable (Table 6). The density of age-0 brown trout was negatively related to PC2, in direct opposition to

Table 6 Selection of the best general linear model explaining variation in the density of age-0 brown trout in the stream Bellbekken. (a) The full model and the five best models are presented, with the best model given in bold. The best model is the one with the lowest AIC_c-value. AIC_c, ΔAIC_c, and rank are given. Year was always included as a random variable. Year was used as a random effect. (b) Parameter estimates (± SE) for the best model; $R^2 = 0.189$, adjusted $R^2 = 0.158$ $n = 200$, the random year effect accounted for 14.36% of the total variance

(a) Model selection

Parameters	AIC_C	ΔAIC_C	Rank
Slope + PC1 + PC2 + PC3	−837.1	22.7	6
PC2	**−862.0**	**0**	**1**
PC3	−853.6	8.4	4
Slope	−860.6	1.4	2
Slope + PC1	−851.9	10.1	5
Slope + PC2	−857.7	4.3	3

(b) Parameter estimates

Parameter	Estimate	SE	DF	*t*-ratio	*P*
Intercept	0.021	0.004	7.01	45.11	0.001
PC2	−0.011	0.004	191	3.15	0.002

the result found for the distribution of mature brown trout. This may indicate that small-sized juvenile trout avoid areas with large numbers of larger fish, either to avoid competition for space or because of different preferences during this time. To assess the influence of mature brown trout on the density of age-0 brown trout, the number of mature individuals was included as an explanatory variable in the model; however, it was not statistically significant (parameter estimate: 0.016 ± 0.067, $P = 0.617$). Similarly, the presence/absence of the Alpine bullhead was not a statistically significant explanatory variable in the model (parameter estimate −0.003 ± 0.003, $P = 0.332$).

Habitat selection by juvenile brown trout can be both dynamic and relatively flexible (Heggenes 1996, 2002). We have earlier observed that juvenile brown trout disperse from the redd location during the first summer (Vøllestad et al. 2012), and habitat requirements vary according to life stages of brown trout (Jonsson and Jonsson 2011). Thus, habitat use just prior to the spawning season may be different than habitat use during other seasons.

4.3 *Young of the Year Brown Trout—Variation in Size*

During the 8-year study, the mean length of the age-0 brown trout at the end of the growth season (September–October) varied from a low of 42 ± 7 mm to a high of 51 ± 5 mm and differences were statistically significant (ANOVA, $F_{7,\,813} = 17.5$, $P < 0.001$). More specifically, individuals varied from <35 mm to >60 mm (Fig. 6);

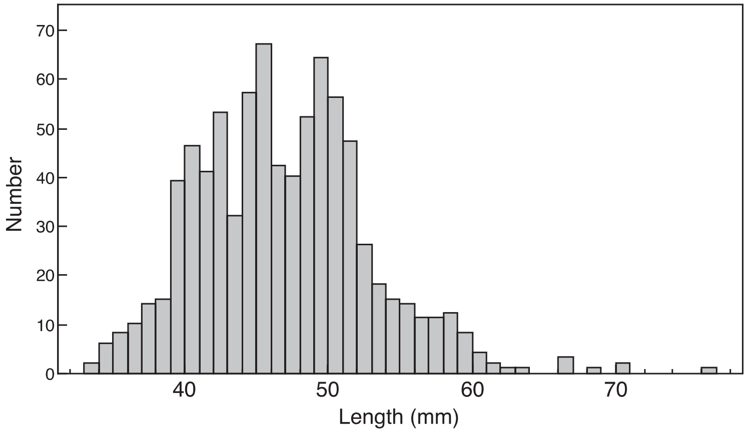

Fig. 6 Length distribution (fork length; mm) of age-0 brown trout (all years pooled) sampled in the stream Bellbekken during autumn (September–October) 2002–2009

however, individuals >65 mm may actually be age-1 brown trout that were erroneously classified as age-0 (however, included in further analyses).

Juvenile growth, and thus length at the end of the growth season, may be affected by numerous factors at a variety of scales. For example, broad-scale factors, such as streamflow (m^3 s^{-1}) and temperature, are relevant at the stream scales. Further, growth may also depend on environmental factors relevant to microhabitats utilized by individuals.

At the section scale in the present study, individual brown trout were assumed to have lived most of the first summer relatively close to the location of capture (in the same section). The effect of section slope (proxy for water velocity), the three first principal components (PC1–3) based on the habitat measures, brown trout density, and the presence or absence of alpine bullhead were tested in a glmm. Year was always used as a random factor (random intercept) in the analyses to account for among-year variation in unmeasured factors influencing growth (such as variation in primary and secondary productivity).

First, I evaluated mean summer flow, minimum summer flow, and maximum spring flow in a glmm to determine which discharge metric explained the most of among-year variation in individual age-0 length. Based on the AIC_c-criterion, minimum summer flow was the better fit to data ($\Delta AIC_c < 6.0$ units than for the two other metrics) and were thus used in the final modelling.

Second, I used a glmm with year as a random effect to assess metrics for brown trout density as a predictor, comparing density estimated as the total number of brown trout or total number of age-0 per section, or density as the number of age-0 juveniles per m^2. The total number of brown trout (all age classes) per section was the best explanatory factor with a ΔAIC_c value <16.0 units than for the two other metrics. The best model explained 17.9% of the variation in age-0 length.

Table 7 Selection of the best model explaining variation in the length of age-0 brown trout in the stream Bellbekken. (a) The full model and the five best models are presented, with the best model given in bold. The best model is the one with the lowest AIC$_c$-value. AIC$_c$, ΔAIC$_c$, and rank are given. Year was always included as a random variable. (b) Parameter estimates (± SE) for the best model is presented; $R^2 = 0.316$, adjusted $R^2 = 0.309$ $n = 811$, the random year effect accounted for 13.66% of the total variance

(a) Model selection

Parameters	AIC$_C$	ΔAIC$_C$	Rank
N(trout)*Sculpin + Streamflow + Temperature + PC1 + PC2 + PC3 + Slope	4902.6	2.4	2
N(trout)*Sculpin + Streamflow + Temperature + PC2 + PC3 + Slope	**4900.2**	**0**	**1**
N(trout)*Sculpin + Streamflow + PC1 + PC2 + PC3 + Slope	4906.1	5.9	4
N(trout)*Sculpin + Streamflow + Temperature + PC2 + PC3	4906.2	6.0	5
N(trout)*Sculpin + Streamflow + PC2 + PC3 + Slope	4903.7	3.5	3

(b) Parameter estimates

Parameter	Estimate	SE	DF	*t*-ratio	*P*
Intercept	18.57	16.81	5.30	1.10	0.317
Trout density	−0.14	0.02	802.0	−6.62	<0.001
Alpine bullhead (absent)	0.14	0.44	800.6	0.32	0.752
Trout density * alpine bullhead (absent)	0.09	0.02	799.8	4.19	<0.001
Streamflow	111.39	71.28	5.1	1.56	0.178
Slope	12.85	16.40	799.8	0.78	0.434
PC2	−1.653	0.41	799.0	−3.69	<0.001
PC3	1.84	0.40	799.8	4.63	<0.001
Temperature	2.29	1.187	5.3	1.96	0.104

The full model included numerous potential explanatory variables (Table 7). In addition to the random year effect, an interaction effect between alpine bullhead presence/absence and brown trout density was included because results from prior studies have suggested competitive interaction occurs between alpine bullhead and brown trout (Vøllestad et al. 2002; Holmen et al. 2003). The model that best fit the data, based on the AIC$_c$-criterion, contained all parameters except PC1 (Table 7a), but several of the explanatory variables were not significant (Table 7b). The full model was the second-best model, and a model without temperature and PC1 was the third-best model. The best model explained 30.9% of the variation in age-0 length. The random year effect accounted for 13.8% of the variance.

Length (and thus growth over the summer) of brown trout differed depending on habitat quality at the section scale (Table 7). Length increased with increasing stream width (PC3) and decreased with increasing proportion of cover and exposed boulders (PC2). Another interesting result from this analysis was the significant interaction between the presence/absence of alpine bullhead and brown trout density. Length was negatively correlated with brown trout density, and density

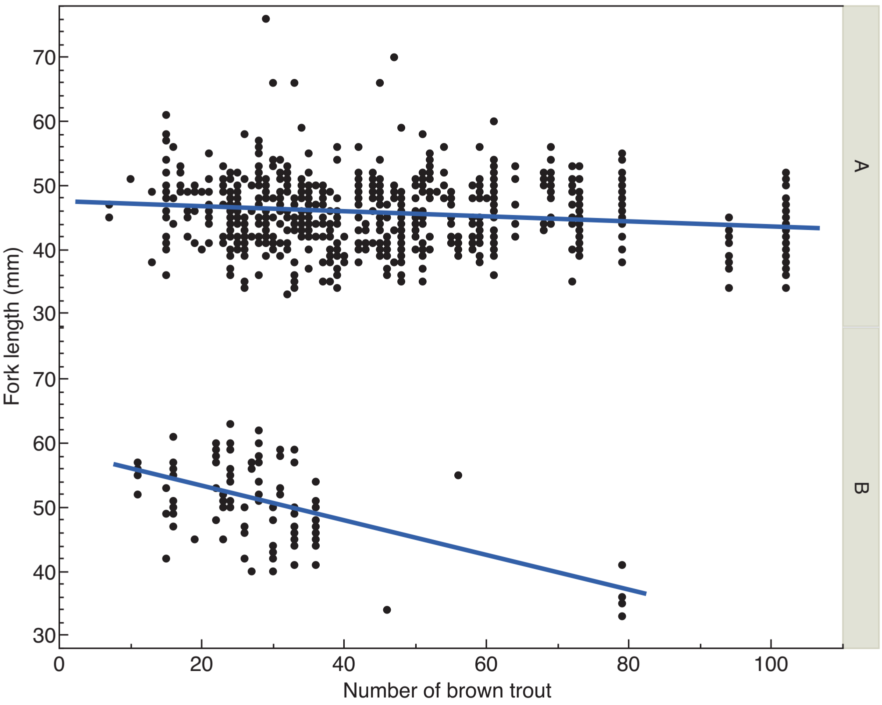

Fig. 7 Relationship between fork length (mm) of age-0 brown trout during autumn (September–October) and the total number of brown trout per section, for sections and year combinations without (**a**) or with (**b**) alpine bullhead present. Regression lines are given

dependence was significantly stronger in the presence of the alpine bullhead than when the alpine bullhead was not present (Fig. 7).

The observation that size of age-0 brown trout was smaller in sections with alpine bullhead than in sections without suggests an overall competitive interaction between the alpine bullhead and brown trout. Brown trout fry may avoid microhabitats with bullhead. For example, behavioral avoidance reactions have been documented in experimental situations (Gaudin and Heland 1984; Bardonnet and Heland 1994; Gaudin and Caillere 2000). Furthermore, evidence suggests that the alpine bullhead and brown trout compete for food, and potentially also for space (Olsen and Vøllestad 2001; Holmen et al. 2003). In addition, bullhead may be predators of small brown trout (Andreasson 1980). Taken together, the alpine bullhead may have a strong negative effect on the juvenile brown trout.

The degree to which observed size differences are important for population growth rate and resilience is poorly understood. For example, previous research has documented that early size does not have a predictable consequence for early survival of brown trout (Lund et al. 2003; Carlson et al. 2008). However, if the size differences established during the first summer are retained later in life, then these differences may translate into divergences in individual fitness. Moreover, fast-growing fish may mature at a younger age, or at a larger size (Olsen and Vøllestad 2005; Olsen et al. 2014). A long-term study on small-sized and stream-dwelling brook trout *Salvelinus fontinalis* has documented that the size distribution determined in early life is indeed maintained throughout life (Letcher et al. 2011). Results from previous research have revealed a strong maternal effect on juvenile size, in addition to measurable heritability (additive genetic effect) (Serbezov et al. 2010b). This suggests that maternal decisions as to when to mature and where to spawn may affect fitness. A significant paternal effect on juvenile length was also apparent, presumably manifested through male mate choice (Serbezov et al. 2010b). In general, therefore, the stream Bellbekken appears to have substantial capacity for retaining phenotypic variation in juvenile size (and thus growth). The weak and variable strength and direction of selection, both driven by differences in survival and growth, may help maintain phenotypic and genotypic variation. Maintaining habitat heterogeneity is probably a prerequisite for maintaining this diversity, and thus for population resilience (see Young et al. (2018) for a discussion).

5 Concluding Remarks

In this small boreal stream, mature and age-0 brown trout were distributed throughout most of the stream, and were thus exposed to fine-scale variation in environmental conditions. Such fine-scale environmental diversity can result in variation in phenotypic traits, such as growth and size, at broader spatial scales, and associated diversity in survival, maturity, and fecundity. More generally, phenotypic and genotypic variation contribute to population resilience and persistence of small populations (low effective population size).

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Density-Dependent Growth in Salmonids: A Meta-analysis

Gary D. Grossman, Daniel B. Warnell, and Keith B. Gido

Abstract The Salmonidae comprise a large group of ecologically and economically valuable species. We surveyed the published literature relating growth to density in salmonids, to perform a meta-analysis that tested for density-dependence. We obtained data from 45 studies that included 125 data sets for eight salmonids including Arctic Char, Atlantic Salmon, Brook Char, Rainbow Trout, Steelhead Trout, Brown Trout, Lahontan Cutthroat Trout, and Chinook Salmon. The random effects meta-analysis for species pooled showed an overall significant effect of density on growth (correlation = 0.58, $z = -15.18$, $p < 0.0001$) although there was some heterogeneity among species ($\tau^2 = 0.141$, 95% CI −0.0660 – −0.1657). Individual species effects were all significant (95% CI for parameter estimates did not overlap zero), but the effect of density on the growth of Chinook Salmon was weaker than other species. Our analysis confirms previous work that density-dependent growth is common in members of the Salmonidae; a finding that should be incorporated into both management and conservation plans.

Keywords Population dynamics · Trout growth · Salmon growth · Trout · Char · Salmon

1 Introduction

Stream fish populations are affected by both density-dependent and density-independent processes (Grossman et al. 1998), and both intraspecific and interspecific competition and predation may affect populations in a density-dependent

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manner. In fact, both types of competition require density-dependent processes to be operating. Density-dependence within populations is such a general phenomenon that it serves as the foundation for theory in ecology as well as the basis for harvesting models for both fisheries and wildlife sciences. Consequently, the importance of such studies cannot be overestimated. In recent reviews of density-dependence in salmonid fishes both Grossman and Simon (2020) and Matte et al. (2020) stressed that density-dependent relationships within this economically and recreationally important family are complex and multifaceted.

The very thorough review of density-dependence in growth and survivorship by Matte et al. (2020), examined 155 studies including field observational studies, field experiments, and lab experiments. Matte et al. (2020) found that research methodology had a significant effect on findings of density-dependence with field studies showing that density-dependent survival was stronger than growth and lab studies showing the opposite. Grossman and Simon (2020) did not conduct a statistical analysis in their review, mainly because they wanted to include as many potential demographic factors that could potentially display density-dependence as possible (growth, mortality, fecundity, and recruitment) and much of the available data was not amenable to a meta-analysis. In the current analysis, we use meta-analytic tools to ask whether density-dependent growth is common in salmonids as well as estimate the strength of this phenomenon.

2 Methods

Our analysis was based on a total of 45 studies that included 125 data sets for eight salmonid species and included 33 studies containing 94 data sets not examined by Matte et al. (2020).

We analyzed data for eight species including Arctic Char (*Salvelinus alpinus*), Atlantic Salmon (*Salmo salar*), Brook Char (*Salvelinus fontinalis*), Rainbow Trout (*Oncorhynchus mykiss*), Steelhead Trout, Brown Trout (*Salmo trutta*), Lahontan Cutthroat Trout (*Oncorhynchus clarkii*), and Chinook Salmon (*Oncorhynchus tshawytscha*).

2.1 Meta-analysis

We used correlation coefficients (r) to relate growth metrics [growth rates ($n = 24$), lengths ($n = 34$), or weights ($n = 67$)] to population density as a measure of effect size in our meta-analysis (Nakagawa and Cuthill 2007). If possible, we extracted data directly from tables, text, or from figures. If r values were not presented, GraphGraber (ver 2.0.2; https://www.quintessa.org/software/downloads-and-demos/graph-grabber-2.0.2) software was used to extract data from figures and calculate r as well as N. We considered data sets from different sample locations or from non-overlapping time periods from the same site as independent samples. If a study reported growth data for individuals within a sample we calculated a mean value for that sample and used that in analyses. Consequently, N was reduced to the number of sample locations or time periods in the study to avoid over-weighting non-independent samples.

We tested for density-dependent effects on growth by testing for a correlation between metrics of growth and population size using a random effects model. This analysis accounts for both within and between sources of error in the data set (Borenstein et al. 2010) and weights data for calculations, based on estimates of marginal variances for each study. We used the Sidik and Jonkman (2005) method to estimate model error variance (τ^2), which is appropriate for situations where estimates of τ^2 are moderate to large (Sidik and Jonkman 2006). Funnel plots were employed to test for potential publication bias by quantifying the relationship between sample effect size and sample variance (Egger et al. 1997). Between group (species) differences in effect sizes were tested with Cochran's Q (Cochran 1954), which is based on a weighted sum of square deviance of each subgroup from the pooled mean effect size. The observed Q value is compared to its expected value assuming a $\chi2$ distribution. When the observed value of Q is substantially larger than expected, the p-value of the Q test can be considered significant and indicative of differences in the true effect sizes among subgroups. The function "metacor" in the "meta" package (Schwarzer et al. 2015) in the R Statistical Package (R Development Core Team 2018) was used for the above analyses.

3 Results

Our data and forest tree diagram are presented in Appendix 1.

The association between the study relative standard error and deviance from the overall mean effect size approximated the expected "funnel" pattern of greater deviance from the mean effect size for samples with greater relative standard error (Fig. 1). Although there was a slight bias toward greater effect size (i.e., negative density dependence) of samples with intermediate error variance, this appears to be offset by a slight bias toward lesser effects for samples with low error variance. Overall, we conclude there was minimal bias associated with variable sample sizes across studies.

The random effects meta-analysis for species pooled showed a strong and significant effect of density on growth (Fig. 2, correlation = −0.58, $z = -15.18$, $p < 0.0001$). Nonetheless, there was significant heterogeneity among species ($\tau^2 = 0.141$, 95% CI 0.0660–0.1657), and the overall test for between group differences was significant ($Q = 18.46$; df = 7, p-value = 0.010). The main species affecting heterogeneity in the data set was Chinook Salmon, which showed a weaker effect of density dependence (overall $r = -0.33$) than other species (Fig. 2). All individual species effects were significant (95% CI for parameter estimates did not overlap zero; Fig. 2). This finding suggests that the overall general relationship

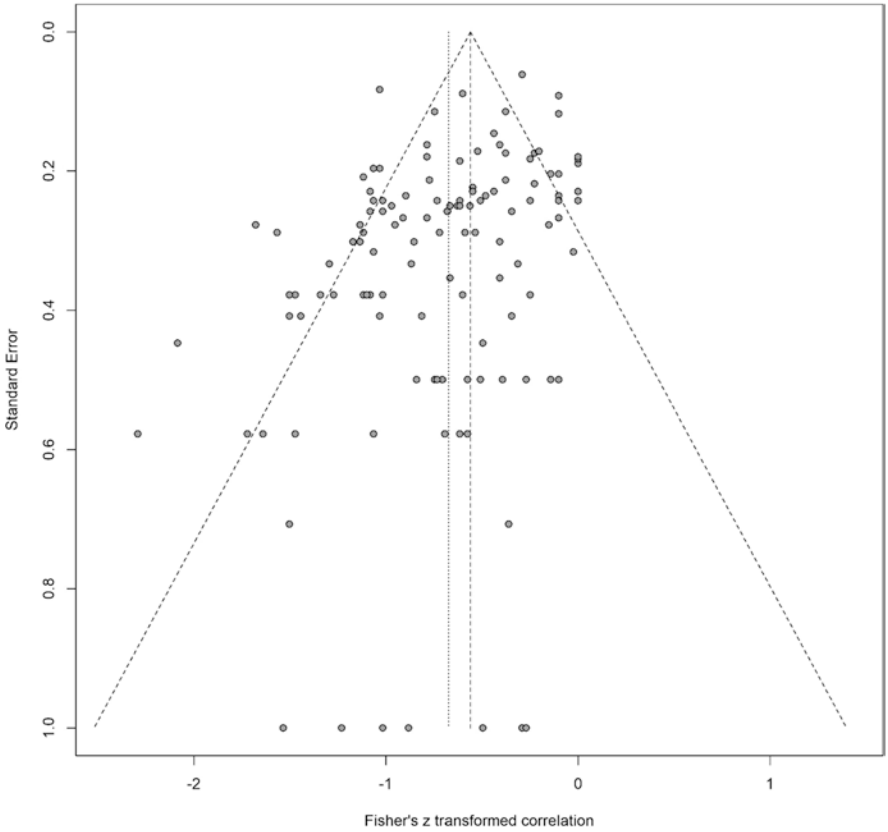

Fig. 1 Funnel plot illustrating the association between effect size (*x*-axis) and relative standard error for each study (*y*-axis). Studies with large sample sizes and low estimated relative standard error are expected to be closer to the overall mean effect size (vertical dashed line) and those with higher estimated standard error are expected to deviate more from the overall mean effect size

between density and growth is both strong and may potentially be extrapolated to other salmonid species. With the exception of Chinook Salmon, weighted correlation coefficients were similar across species ranging from −0.47 for Steelhead to −0.75 for Arctic Char. In a post-hoc analysis (random effects model) we found that migratory populations in our data set displayed a significantly lower overall negative correlation between density and growth (−0.489) than non-migratory populations (−0.664), Appendix 1. The 95% confidence intervals of these estimates do not overlap and there was a significant effect of subgroup (*P*-value = 0.0018).

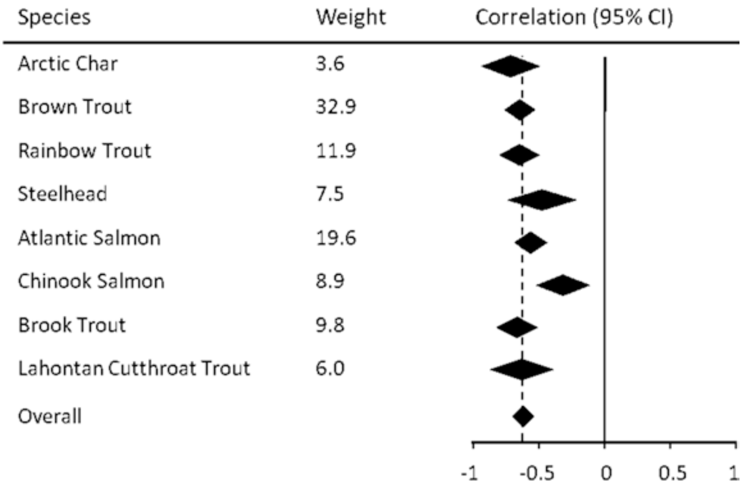

Fig. 2 Summary statistics for each salmonid species including the mean correlation coefficients (± 95% confidence intervals), overall mean and weights in the meta-analysis. Diamonds on right side of the graph represent the data for each species included in the meta-analysis. Weights of each species in the overall meta-analysis are provided as well as the overall mean and 95% CIs. Vertical dashed line is the overall weighted mean correlation across all studies and vertical solid line marks the zero correlation line

4 Discussion

Our analysis demonstrates the strong and consistent effect of density on growth in members of the Salmonidae; a finding of interest to researchers studying population dynamics as well as those involved in both management and conservation of this group. There were no significant differences in the strength of density-dependence for seven of the eight species we examined, and all displayed negative linear relationships between density and growth. Nonetheless, non-migratory populations displayed a significantly lower correlation between density and growth than non-migratory populations. This is not surprising, given that individuals in migratory populations move through multiple habitats (i.e., lotic systems small to large, lakes and oceans) and likely are subjected to more and different agents of mortality than individuals that are non-migratory.

Our overall mean correlation for non-migratory populations was similar to that obtained by Matte et al. (2020) in an additional meta-analysis of density-dependence in salmonid populations, which suggests that a value approximating −0.60 likely could be used as a general value for non-migratory populations of salmonids in modelling efforts. Nonetheless, there remains a paucity of studies on density-dependence involving other important demographic characteristics of salmonids, such as fecundity, recruitment, and mortality (Grossman and Simon 2020). This shortcoming may affect the accuracy of modeling efforts for management, reintroduction, and conservation purposes.

It is true that almost any process that affects resource availability, especially food availability also will affect density–growth relationships (David et al. 2016). This emphasizes the importance of including both environmental and demographic data in population modeling for salmonid management. Nonetheless, the strong density–growth relationships in salmonids, bodes well for management and conservation of these species (Andersen et al. 2017; Rose et al. 2001) because it suggests that salmonid populations are resilient and will be able to respond to both environmental challenges and overexploitation in a compensatory manner. In addition, growth affects many other demographic processes that are important to population persistence and resilience, including fecundity and survivorship (Andersen et al. 2017).

In general, our findings support those of Matte et al. (2020) and extend the database to 33 studies and 94 additional data sets not examined by those authors. Nonetheless, we did not examine the frequency of non-linear versus linear relationships and restricted our analysis to methods that only are capable of detecting the latter type of relationship. Matte et al. (2020) have shown that both exponential and logarithmic density-dependent relationships can be found in some salmonid species.

Although Matte et al. (2020) focused on territoriality as a mechanism producing density-dependence in growth, simple intraspecific interference competition without territoriality also is capable of producing the relationships identified in the Salmonidae. Interference competition is a simpler explanation because it requires no fixed spatial component to the interaction, although there is little difference between "personal space" territoriality and intraspecific interference competition. Evidence supporting the contention that simple intraspecific competition is a causal mechanism for the observed linear density-dependent relationships is that negative linear curves do not have an asymptotic phase that would occur when densities are sufficiently low that open territories are present because habitat saturation has not occurred. This is supported by the finding that negative linear relationships were most common in both descriptive and experimental field studies (Matte et al. 2020). Finally, Matte et al. (2020) also found no difference in the frequency of density-dependent growth relationship between lentic and lotic populations of salmonids, but our database comes almost exclusively from lotic populations of salmonids.

In conclusion, our results confirm the presence of density-dependent growth in a taxonomically broad range of salmonid species (eight), occurring over a wide geographic range, and suggest that a mean correlation coefficient of −0.60 can be used to characterize the negative relationship between density and growth for modeling, management, and conservation purposes.

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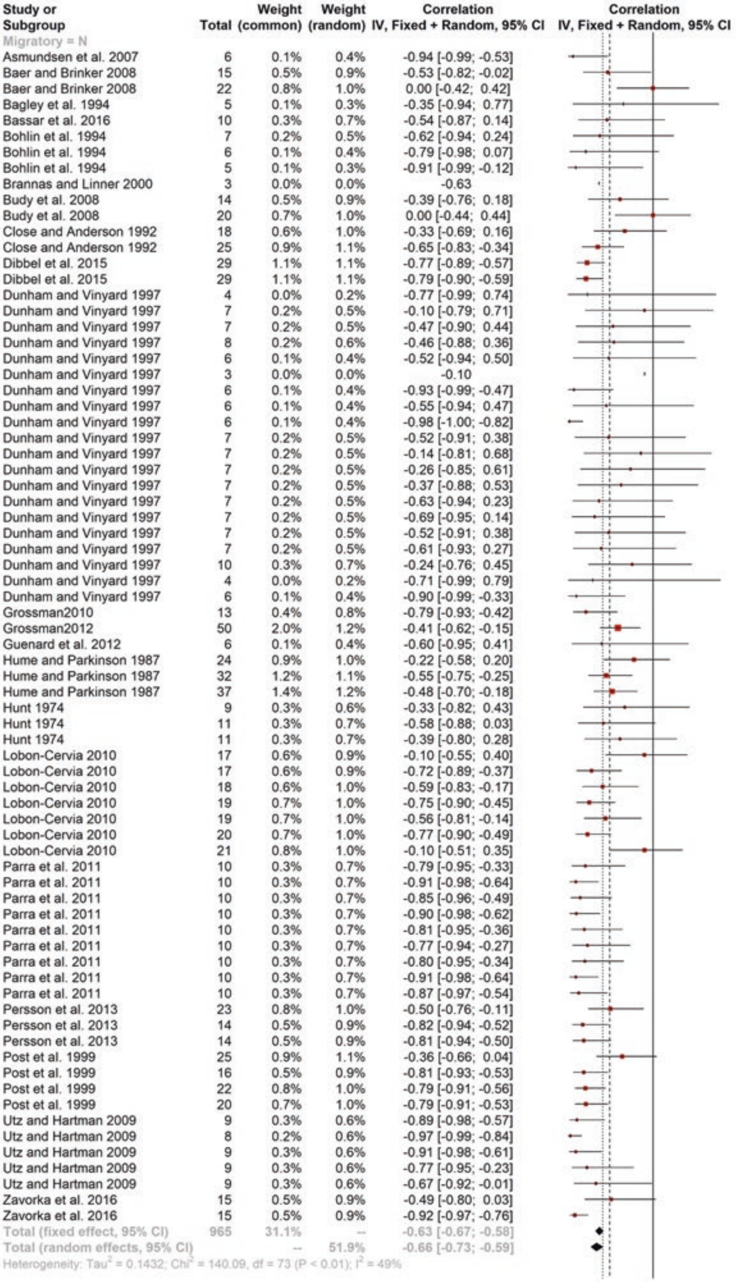
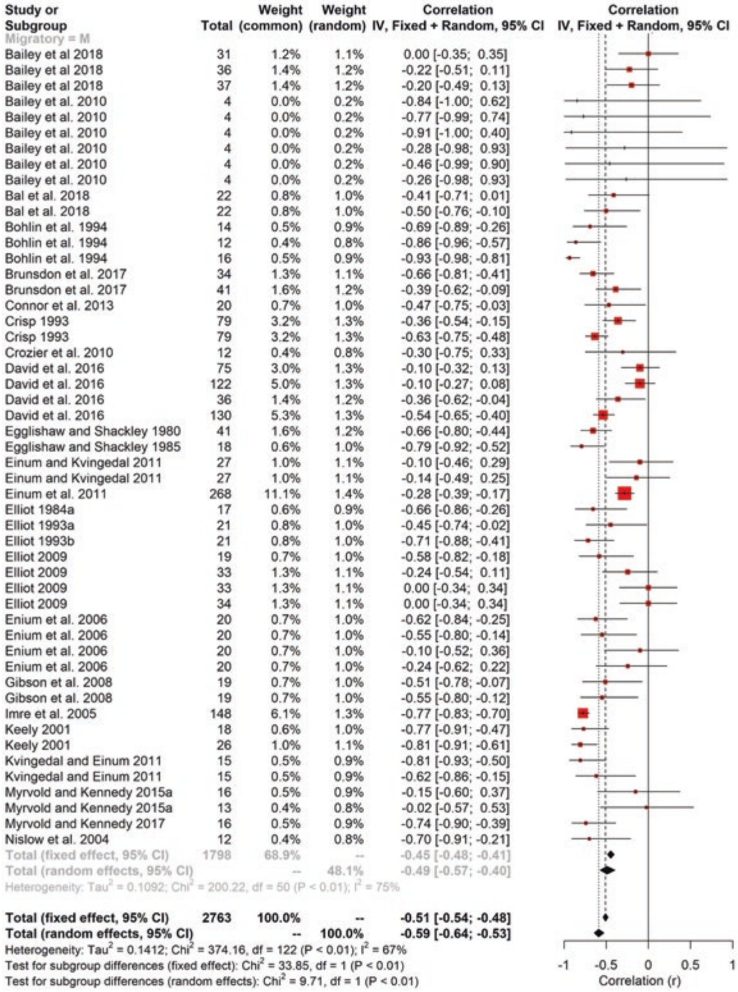
Appendix 1

The forest tree diagram of all papers used in this study is grouped by family. The photo can be opened and expanded for better visibility. Presented are the number of data sets in each study (sample size), the overall weight of the study and the correlation coefficient ± 95% CI.



Study or Subgroup	Total	Weight (common)	Weight (random)	Correlation IV, Fixed + Random, 95% CI
Migratory = N				
Asmundsen et al. 2007	6	0.1%	0.4%	-0.94 [-0.99; -0.53]
Baer and Brinker 2008	15	0.5%	0.9%	-0.53 [-0.82; -0.02]
Baer and Brinker 2008	22	0.8%	1.0%	0.00 [-0.42; 0.42]
Bagley et al. 1994	5	0.1%	0.3%	-0.35 [-0.94; 0.77]
Bassar et al. 2016	10	0.3%	0.7%	-0.54 [-0.87; 0.14]
Bohlin et al. 1994	7	0.2%	0.5%	-0.62 [-0.94; 0.24]
Bohlin et al. 1994	6	0.1%	0.4%	-0.79 [-0.98; 0.07]
Bohlin et al. 1994	5	0.1%	0.3%	-0.91 [-0.99; -0.12]
Brannas and Linner 2000	3	0.0%	0.0%	-0.63
Budy et al. 2008	14	0.5%	0.9%	-0.39 [-0.76; 0.18]
Budy et al. 2008	20	0.7%	1.0%	0.00 [-0.44; 0.44]
Close and Anderson 1992	18	0.6%	1.0%	-0.33 [-0.69; 0.16]
Close and Anderson 1992	25	0.9%	1.1%	-0.65 [-0.83; -0.34]
Dibbel et al. 2015	29	1.1%	1.1%	-0.77 [-0.89; -0.57]
Dibbel et al. 2015	29	1.1%	1.1%	-0.79 [-0.90; -0.59]
Dunham and Vinyard 1997	4	0.0%	0.2%	-0.77 [-0.99; 0.74]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.10 [-0.79; 0.71]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.47 [-0.90; 0.44]
Dunham and Vinyard 1997	8	0.2%	0.6%	-0.46 [-0.88; 0.36]
Dunham and Vinyard 1997	6	0.1%	0.4%	-0.52 [-0.94; 0.50]
Dunham and Vinyard 1997	3	0.0%	0.0%	-0.10
Dunham and Vinyard 1997	6	0.1%	0.4%	-0.93 [-0.99; -0.47]
Dunham and Vinyard 1997	6	0.1%	0.4%	-0.55 [-0.94; 0.47]
Dunham and Vinyard 1997	6	0.1%	0.4%	-0.98 [-1.00; -0.82]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.52 [-0.91; 0.38]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.14 [-0.81; 0.68]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.26 [-0.85; 0.61]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.37 [-0.88; 0.53]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.63 [-0.94; 0.23]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.69 [-0.95; 0.14]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.52 [-0.91; 0.38]
Dunham and Vinyard 1997	7	0.2%	0.5%	-0.61 [-0.93; 0.27]
Dunham and Vinyard 1997	10	0.3%	0.7%	-0.24 [-0.76; 0.45]
Dunham and Vinyard 1997	4	0.0%	0.2%	-0.71 [-0.99; 0.79]
Dunham and Vinyard 1997	6	0.1%	0.4%	-0.90 [-0.99; -0.33]
Grossman2010	13	0.4%	0.8%	-0.79 [-0.93; -0.42]
Grossman2012	50	2.0%	1.2%	-0.41 [-0.62; -0.15]
Guenard et al. 2012	6	0.1%	0.4%	-0.60 [-0.95; 0.41]
Hume and Parkinson 1987	24	0.9%	1.0%	-0.22 [-0.58; 0.20]
Hume and Parkinson 1987	32	1.2%	1.1%	-0.55 [-0.75; -0.25]
Hume and Parkinson 1987	37	1.4%	1.2%	-0.48 [-0.70; -0.18]
Hunt 1974	9	0.3%	0.6%	-0.33 [-0.82; 0.43]
Hunt 1974	11	0.3%	0.7%	-0.58 [-0.88; 0.03]
Hunt 1974	11	0.3%	0.7%	-0.39 [-0.80; 0.28]
Lobon-Cervia 2010	17	0.6%	0.9%	-0.10 [-0.55; 0.40]
Lobon-Cervia 2010	17	0.6%	0.9%	-0.72 [-0.89; -0.37]
Lobon-Cervia 2010	18	0.6%	1.0%	-0.59 [-0.83; -0.17]
Lobon-Cervia 2010	19	0.7%	1.0%	-0.75 [-0.90; -0.45]
Lobon-Cervia 2010	19	0.7%	1.0%	-0.56 [-0.81; -0.14]
Lobon-Cervia 2010	20	0.7%	1.0%	-0.77 [-0.90; -0.49]
Lobon-Cervia 2010	21	0.8%	1.0%	-0.10 [-0.51; 0.35]
Parra et al. 2011	10	0.3%	0.7%	-0.79 [-0.95; -0.33]
Parra et al. 2011	10	0.3%	0.7%	-0.91 [-0.98; -0.64]
Parra et al. 2011	10	0.3%	0.7%	-0.85 [-0.96; -0.49]
Parra et al. 2011	10	0.3%	0.7%	-0.90 [-0.98; -0.62]
Parra et al. 2011	10	0.3%	0.7%	-0.81 [-0.95; -0.36]
Parra et al. 2011	10	0.3%	0.7%	-0.77 [-0.94; -0.27]
Parra et al. 2011	10	0.3%	0.7%	-0.80 [-0.95; -0.34]
Parra et al. 2011	10	0.3%	0.7%	-0.91 [-0.98; -0.64]
Parra et al. 2011	10	0.3%	0.7%	-0.87 [-0.97; -0.54]
Persson et al. 2013	23	0.8%	1.0%	-0.50 [-0.76; -0.11]
Persson et al. 2013	14	0.5%	0.9%	-0.82 [-0.94; -0.52]
Persson et al. 2013	14	0.5%	0.9%	-0.81 [-0.94; -0.50]
Post et al. 1999	25	0.9%	1.1%	-0.36 [-0.66; 0.04]
Post et al. 1999	16	0.5%	0.9%	-0.81 [-0.93; -0.53]
Post et al. 1999	22	0.8%	1.0%	-0.79 [-0.91; -0.56]
Post et al. 1999	20	0.7%	1.0%	-0.79 [-0.91; -0.53]
Utz and Hartman 2009	9	0.3%	0.6%	-0.89 [-0.98; -0.57]
Utz and Hartman 2009	8	0.2%	0.6%	-0.97 [-0.99; -0.84]
Utz and Hartman 2009	9	0.3%	0.6%	-0.91 [-0.98; -0.61]
Utz and Hartman 2009	9	0.3%	0.6%	-0.77 [-0.95; -0.23]
Utz and Hartman 2009	9	0.3%	0.6%	-0.67 [-0.92; -0.01]
Zavorka et al. 2016	15	0.5%	0.9%	-0.49 [-0.80; 0.03]
Zavorka et al. 2016	15	0.5%	0.9%	-0.92 [-0.97; -0.76]
Total (fixed effect, 95% CI)	965	31.1%	--	-0.63 [-0.67; -0.58]
Total (random effects, 95% CI)		--	51.9%	-0.66 [-0.73; -0.59]

Heterogeneity: $Tau^2 = 0.1432$; $Chi^2 = 140.09$, df = 73 ($P < 0.01$); $I^2 = 49\%$



Study or Subgroup	Total	Weight (common)	Weight (random)	Correlation IV, Fixed + Random, 95% CI
Migratory = M				
Bailey et al 2018	31	1.2%	1.1%	0.00 [-0.35; 0.35]
Bailey et al 2018	36	1.4%	1.2%	-0.22 [-0.51; 0.11]
Bailey et al 2018	37	1.4%	1.2%	-0.20 [-0.49; 0.13]
Bailey et al. 2010	4	0.0%	0.2%	-0.84 [-1.00; 0.62]
Bailey et al. 2010	4	0.0%	0.2%	-0.77 [-0.99; 0.74]
Bailey et al. 2010	4	0.0%	0.2%	-0.91 [-1.00; 0.40]
Bailey et al. 2010	4	0.0%	0.2%	-0.28 [-0.98; 0.93]
Bailey et al. 2010	4	0.0%	0.2%	-0.46 [-0.99; 0.90]
Bailey et al. 2010	4	0.0%	0.2%	-0.26 [-0.98; 0.93]
Bal et al. 2018	22	0.8%	1.0%	-0.41 [-0.71; 0.01]
Bal et al. 2018	22	0.8%	1.0%	-0.50 [-0.76; -0.10]
Bohlin et al. 1994	14	0.5%	0.9%	-0.69 [-0.89; -0.26]
Bohlin et al. 1994	12	0.4%	0.8%	-0.86 [-0.96; -0.57]
Bohlin et al. 1994	16	0.5%	0.9%	-0.93 [-0.98; -0.81]
Brunsdon et al. 2017	34	1.3%	1.1%	-0.66 [-0.81; -0.41]
Brunsdon et al. 2017	41	1.6%	1.2%	-0.39 [-0.62; -0.09]
Connor et al. 2013	20	0.7%	1.0%	-0.47 [-0.75; -0.03]
Crisp 1993	79	3.2%	1.3%	-0.36 [-0.54; -0.15]
Crisp 1993	79	3.2%	1.3%	-0.63 [-0.75; -0.48]
Crozier et al. 2010	12	0.4%	0.8%	-0.30 [-0.75; 0.33]
David et al. 2016	75	3.0%	1.3%	-0.10 [-0.32; 0.13]
David et al. 2016	122	5.0%	1.3%	-0.10 [-0.27; 0.08]
David et al. 2016	36	1.4%	1.2%	-0.36 [-0.62; -0.04]
David et al. 2016	130	5.3%	1.3%	-0.54 [-0.65; -0.40]
Egglishaw and Shackley 1980	41	1.6%	1.2%	-0.66 [-0.80; -0.44]
Egglishaw and Shackley 1985	18	0.6%	1.0%	-0.79 [-0.92; -0.52]
Einum and Kvingedal 2011	27	1.0%	1.1%	-0.10 [-0.46; 0.29]
Einum and Kvingedal 2011	27	1.0%	1.1%	-0.14 [-0.49; 0.25]
Einum et al. 2011	268	11.1%	1.4%	-0.28 [-0.39; -0.17]
Elliot 1984a	17	0.6%	0.9%	-0.66 [-0.86; -0.26]
Elliot 1993a	21	0.8%	1.0%	-0.45 [-0.74; -0.02]
Elliot 1993b	21	0.8%	1.0%	-0.71 [-0.88; -0.41]
Elliot 2009	19	0.7%	1.0%	-0.58 [-0.82; -0.18]
Elliot 2009	33	1.3%	1.1%	-0.24 [-0.54; 0.11]
Elliot 2009	33	1.3%	1.1%	0.00 [-0.34; 0.34]
Elliot 2009	34	1.3%	1.1%	0.00 [-0.34; 0.34]
Enium et al. 2006	20	0.7%	1.0%	-0.62 [-0.84; -0.25]
Enium et al. 2006	20	0.7%	1.0%	-0.55 [-0.80; -0.14]
Enium et al. 2006	20	0.7%	1.0%	-0.10 [-0.52; 0.36]
Enium et al. 2006	20	0.7%	1.0%	-0.24 [-0.62; 0.22]
Gibson et al. 2008	19	0.7%	1.0%	-0.51 [-0.78; -0.07]
Gibson et al. 2008	19	0.7%	1.0%	-0.55 [-0.80; -0.12]
Imre et al. 2005	148	6.1%	1.3%	-0.77 [-0.83; -0.70]
Keely 2001	18	0.6%	1.0%	-0.77 [-0.91; -0.47]
Keely 2001	26	1.0%	1.1%	-0.81 [-0.91; -0.61]
Kvingedal and Einum 2011	15	0.5%	0.9%	-0.81 [-0.93; -0.50]
Kvingedal and Einum 2011	15	0.5%	0.9%	-0.62 [-0.86; -0.15]
Myrvold and Kennedy 2015a	16	0.5%	0.9%	-0.15 [-0.60; 0.37]
Myrvold and Kennedy 2015a	13	0.4%	0.8%	-0.02 [-0.57; 0.53]
Myrvold and Kennedy 2017	16	0.5%	0.9%	-0.74 [-0.90; -0.39]
Nislow et al. 2004	12	0.4%	0.8%	-0.70 [-0.91; -0.21]
Total (fixed effect, 95% CI)	1798	68.9%	--	-0.45 [-0.48; -0.41]
Total (random effects, 95% CI)		--	48.1%	-0.49 [-0.57; -0.40]
Heterogeneity: $Tau^2 = 0.1092$; $Chi^2 = 200.22$, df = 50 ($P < 0.01$); $I^2 = 75\%$				
Total (fixed effect, 95% CI)	**2763**	**100.0%**	**--**	**-0.51 [-0.54; -0.48]**
Total (random effects, 95% CI)		**--**	**100.0%**	**-0.59 [-0.64; -0.53]**

Heterogeneity: $Tau^2 = 0.1412$; $Chi^2 = 374.16$, df = 122 ($P < 0.01$); $I^2 = 67\%$
Test for subgroup differences (fixed effect): $Chi^2 = 33.85$, df = 1 ($P < 0.01$)
Test for subgroup differences (random effects): $Chi^2 = 9.71$, df = 1 ($P < 0.01$)

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The Ghost of Density-Dependence: Environmental (Hydrological) Factors Drive the Numerical Changes of Young Migratory Trout *Salmo trutta* in a Lake District Stream (UK), 1966–1996

Javier Lobón-Cerviá and Gorm Rasmussen

Abstract Finding empirical support for the “paradigm of density-dependence” has been a major focus of ecological and fishery research. Quantifying relationships between the abundance of spawners and the subsequent recruitment is essential for testing the key prediction of density-dependent population regulation: that the number of recruits is mechanistically, but non-linearly, dependent on the number of reproducing individuals. Long-term data are required to explore such relationships, but such data are rare. Elliott and colleagues used a 30-year study of brown trout, *Salmo trutta* L. in a small UK stream to construct a stock–recruitment relationship suggesting remarkably severe density-dependent mortality of recruits at high spawners’ abundance. In marked contrast, more recent studies on other brown trout populations, suggest environmental (hydrological) factors play a principal role in driving variation in recruitment. These disparate results underscore the more general controversy regarding the relative roles of density-dependent *versus* density-independent population regulation. The objective of this study was to revisit and re-analyze the data reported by Elliott in light of recent results from other trout populations. The results suggest that variation in stream discharge soon after emergence drives variation in recruitment and early survival rates, and produces the same two-phase, threshold-like recruitment patterns observed in other brown trout populations. These results cast doubt on the original interpretation of the data, and add to a growing body of evidence that environmental (hydrological) factors are the principal drivers of recruitment variation in stream-rearing salmonids.

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Keywords Stream-rearing salmonids · Population regulation · Recruitment · Density-dependence · Density-independence · Stream discharge · Hydrological variability

1 Introduction

Identifying the causes of temporal fluctuations in animal populations is a central goal of ecology and fishery research. The fundamental challenge is to understand the relative importance of density-dependence (Nicholson 1933) *versus* density-independent or environmental drivers (Andrewartha and Birch 1954). Therefore, finding empirical support for the "paradigm of density-dependence"—that the populations are regulated by density-dependent feedback loops—has been a major focus of ecological research for decades (Coulson et al. 2004).

Fishes provide useful systems for exploring mechanisms of population regulation. Fish populations are typically characterized by high mortalities rates following hatching and emergence (Bradford and Cabana 1997), so the number of recruits is generally dramatically lower than the number of eggs produced by spawners, and the magnitude of recruitment is deemed to be set at, during or soon after that time period (Cushing 1996). Identifying the factors responsible for mortality during the egg-to-recruit stage is thus essential for understanding fish population dynamics (Houde 1989; Hilborn and Walters 1992; Chambers and Trippel 1997; Walters and Martell 2004). Nevertheless, distinguishing between the roles of density-dependent *versus* density-independent factors in driving recruitment remains a sufficiently elusive "*enigma*" (Frank and Leggett 1994) to warrant calls for a "*Science of Recruitment in Fish Populations*" (Cushing 1996).

The key quantitative basis of the "paradigm of density-dependence" is that the number of recruits is mechanistically but not linearly linked to the abundance of the reproductive component of the population. It follows that regardless of the factors causing mortality during the egg-to-recruit stages, the number of spawners is the principal predictor of recruitment (Trippel et al. 1997). Therefore, exploring relationships between the number of spawners and the subsequent recruitment is an essential tool for testing population regulation hypotheses.

Long-term data series with accurate estimates of the parental (ST) and recruitment (RC) abundances are required to meaningfully quantify such stock-recruitment relationships (Walters and Martell 2004). Such data are rare, but an exceptional example is a 30-year study on Brown Trout, *Salmo trutta* L. inhabiting a small UK stream. The analyses of these data by Elliott (1984, 1985, 1987, 1989, 1993, 1994), Elliott et al. (1997) and Elliott and Elliott (2006) provide evidence for remarkably dramatic density-dependent mortality in the youngest juveniles at high spawners abundance. The dome-shaped stock–recruitment curve is one of the most influential and widely cited empirical examples of density-dependent population regulation in the ecological and fishery literature (citations compiled by major scientific literature databases corroborate this statement). Nevertheless, studies based on similar spawner–recruit time series from other stream-rearing brown trout populations in Spain (Lobón-Cerviá and Rincón 2004; Lobón-Cerviá 2006, 2007; Lobón-Cerviá et al. 2017), France (Cattanéo et al. 2002) and Denmark (Lobón-Cerviá and Mortensen 2005) point rather to the primacy of environmental (hydrological) factors in driving recruitment variations. Such results are seemingly at odds with the stock–recruitment relationships highlighted by Elliott and colleagues and, in combination, obscure more than clarify the long-standing controversy on the relative roles of density-dependence *versus* density-independence underpinning population growth, persistence, and resilience in stream salmonids and other fish populations.

This study re-visits the data from Black Brows Beck described by Elliott and colleagues. The results bring into doubt the importance of the density-dependent mechanisms in driving variation in recruitment. Instead, these new analyses suggest that stream discharge operating during or soon after emergence drives variation in recruitment, a pattern consistent with those observed in other stream-rearing brown trout populations.

2 The Study Population and Data Collection

Demographic data on brown trout inhabiting a stream section of Black Brows Beck was reported by Elliott (1984, 1985, 1987, 1989, 1993, 1994), Elliott et al. (1997) and Elliott and Elliott (2006). This small stream enters Dale Park Beck, a tributary of the River Leven in northern England, and is a highly productive nursery for sea-migratory trout (Elliott 1984). Over three decades, the number of recruits was quantified at the end of May or early June in a 75 m long (60 m^2) section of the stream. The number of fertilized eggs as a proxy of the spawners' abundance, was estimated in a 45-m long (32 m^2) section downstream of the recruitment section. Further details of the study site and methods are given in Elliott (1984).

Parental density and recruitment were reported in two different studies. Elliott (1984, 1985) presents data from the 1966–1983 cohorts as eggs and recruits m^{-2}, or as the total number of eggs and recruits at the 60-m^{-2} study site. The second data set includes 13 additional cohorts (1984–1996) to complete 30 years from 1966 to 1996 and was reported in figures by Elliott et al. (1997). For this study, Figs. 1 and 2 in Elliott et al. (1997, p. 1232–1233) were scanned with an image analyzer. The data from 1966 to 1983 obtained *via* image analyzer matched the data reported by Elliott (1984, p. 340) and Elliott (1985, p. 620), confirming the accuracy of the method.

Stream discharge data were obtained from a local gauging station that recorded daily flows in m^3/s over the entire study period. The identification of this station and the corresponding data set is: National River Flow Archive; Database, nrfa_public name; Station: 73010; name: "Leven at Newby Bridge, FMS". Grid reference SD367863. Daily data were used to calculate the cumulative stream discharge over the 30 days of April. Spring rainfall data were reported by Elliott et al. (1997, Fig. 1) as the total spring rainfall with March, April and May pooled together.

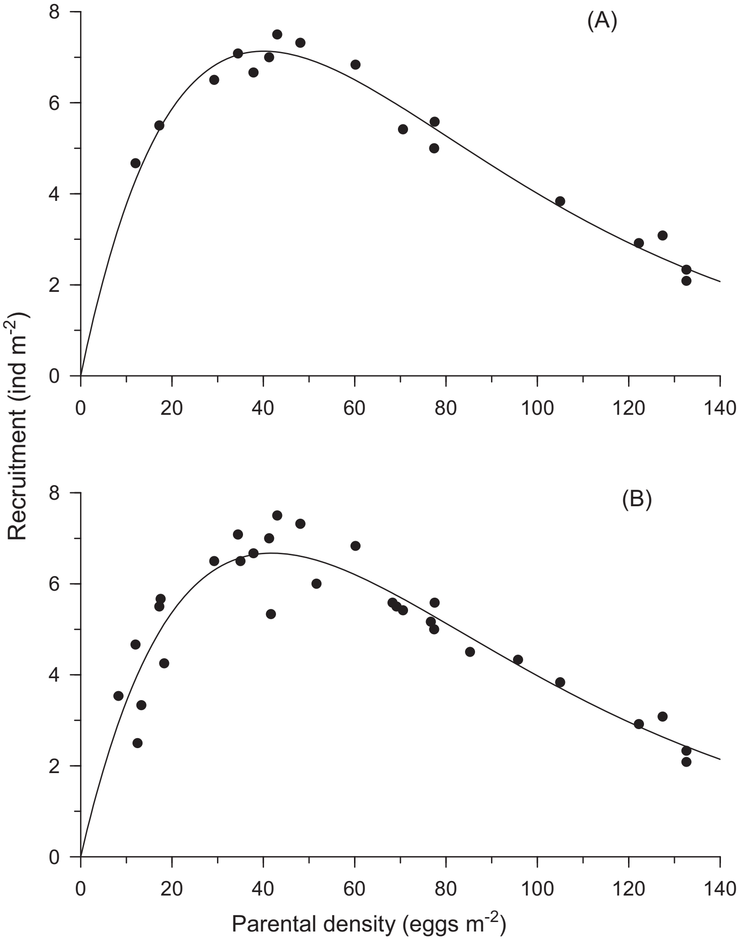

Fig. 1 Stock–recruitment relationships for Black Brows Beck brown trout with a Ricker model fitted to data. Redrawn from Elliott (1984, 1985) and Elliott et al. (1997). (**a**) Recruitment of the 1966–1983 cohorts with constants and variance explained: $A = 0.49$, $B = 0.025$ and $R^2 = 0.997$. (**b**) Recruitment of the complete data set (1966–1996) with a Ricker model fitted to data with constants and variance explained: $A = 0.042$, $B = 0.0004$ and $R^2 = 0.87$. All significant at $p < 0.001$

3 Results

3.1 Elliott's Findings: Density–Dependent Recruitment Regulation

During the 1966–1996 study period, recruitment in May/early June (stage R1 in Elliott 1985), varied between 2.1 and 7.5 m^{-2}, which is equivalent to approximately 125–450 individuals in the 60 m^{-2} study section. Spawners' density varied between

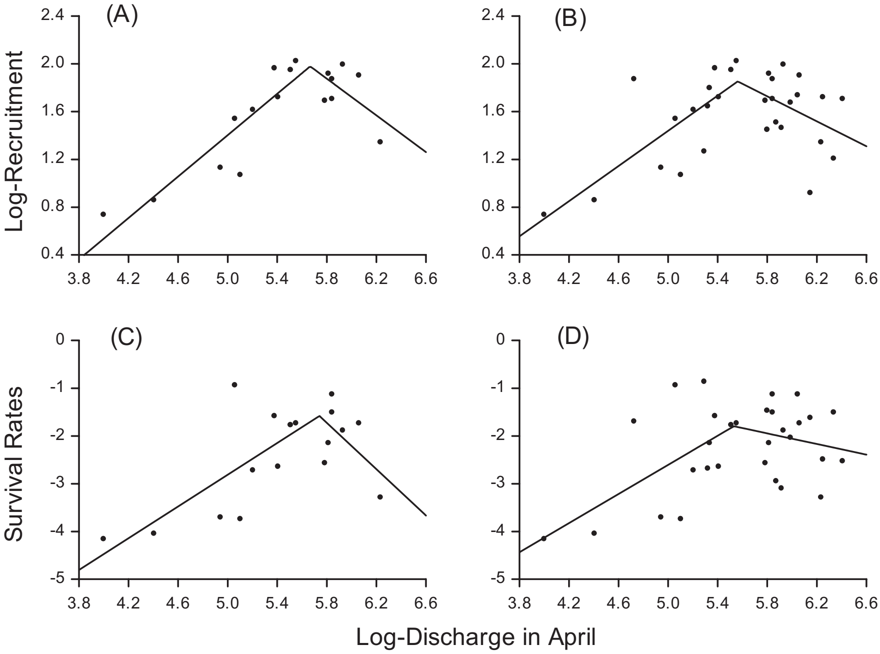

Fig. 2 Log-transformed recruitment RC, ind m^{-2} and survival rates SR = Log (RC/ST) *versus* log-transformed discharge in April (m^3/s) with two-phase linear regressions fitted to data: (**a**) Log-transformed recruitment for the 1967–1983 cohorts. Constants, variance explained and significance levels: $A = -2.92$, $B = 0.87$, $X = 5.67$ and $K = -0.77$; $R^2 = 0.81$, $p < 0.001$. (**b**) Log-transformed recruitment for the complete data set (1967–1996), with constants, variance explained and significance levels: $A = -2.24$, $B = 0.74$, $X = 5.56$ and $K = -0.52$; $R^2 = 0.45$, $p < 0.01$. (**c**) Survival rates for the first data set, 1967–1983, with constants, variance explained and significance levels: $A = -11.1$, $B = 1.66$, $X = 5.74$ and $K = -2.42$ ($R^2 = 0.53$, $p < 0.001$). (**d**) Survival rates for the complete data set (1967–1996), with constants, variance explained and significant level: $A = -10.2$, $B = 1.53$, $X = 5.53$ and $K = -0.56$; $R^2 = 0.30$, $p < 0.01$

5 and 140 eggs m^{-2}. Elliott (1984, 1985, 1987, 1989, 1993, 1994), Elliott et al. (1997) and Elliott and Elliott (2006) constructed parental density (ST)—recruitment (RC) relationships using a Ricker model (Ricker 1954) of the form:

$$\mathrm{RC} = a\,\mathrm{ST}\,e^{-b\mathrm{ST}}$$

The result was a strikingly dome-shaped relationship indicative of strong density-dependent mortality during the egg-to-recruit life stage. For the first part of the study (1966–1983, Fig. 1a), Elliott (1984) reported that the Ricker model explained essentially all the variation in recruitment ($R^2 = 0.997$). For the extended data set (1966–1996), Elliott et al. (1997) reported that the model still explained a remarkable amount of recruitment variation ($R^2 = 0.87$) (Fig. 1b).

3.2 New Insight: Stream Discharge Explains Recruitment Variation

Based on evidence from other stream-rearing brown trout populations (Lobón-Cerviá 2006, 2007; Lobón-Cerviá and Rincón 2004, Lobón-Cerviá and Mortensen 2005, Lobón-Cerviá et al. 2017), we explored whether variation in recruitment in Black Brows Beck was related to stream discharge in April, a critical month covering hatching, emergence and recruitment settlement.

A visual exploration of the relationships between recruitment (RC, ind m^{-2}) *versus* discharge in April (henceforth, DIS, m^3/s) for the two data sets 1967–1983 and 1967–1996 highlighted strongly consistent patterns (Fig. 2). For the first data set, log-transformed recruitment *versus* log-transformed discharge demonstrated a continuous ascend/descent pattern over the whole range of discharge values. Recruitment was low in years of low discharge, increased with increased discharge up to a maximum, and then declined with further increases in April discharge (Fig. 2a). The complete data set (1967–1996) followed the same pattern (Fig. 2b). Similar two-phase, threshold relationships between the survival rates, calculated as SR = ln (RC/ST), and discharge suggest the relationship between recruitment and discharge is mechanistic (Fig. 2c, d).

We quantified these patterns using split-line, two-phase linear regressions of the form:

$$\mathrm{RC} = a_1 + b_1\,\mathrm{DIS}\left(\mathrm{DIS} \le k\right) + a_2 + b_2\,\mathrm{DIS}\left(\mathrm{DIS} > k\right)$$

with the restriction for continuity $a_1 + b_1 * k = a_2 + b_2 * k$ at the threshold point k,where the slope changes direction. For computational purposes this two-phase regression can be re-written as:

$$\mathrm{RC} = \left(a_1 + b_1\,\mathrm{DIS}\right)\left(\mathrm{DIS} \le k\right) + \left(a_1 + \left(b_1\,k + b_2\,\mathrm{DIS} - b_2\,k\right)\right)\left(\mathrm{DIS} > k\right)$$

This re-formulation has the advantage that only one intersect "a", the positive and negative slopes "b_1 and b_2", and the threshold "k", upon which the trajectory changes direction from positive to negative, need to be estimated.

For the first data set (1967–1983), the two-phase regression was highly significant ($p < 0.001$); April discharge explained 80% of the variation in recruitment (Fig. 2a). For the full data set (1967–1996) the two-phase model was still significant ($p < 0.01$), but April discharge explained less of variation in recruitment ($R^2 = 0.45$, Fig. 2b). Importantly, the same model applied to the survival rates (SR) *versus* log-transformed discharge also showed highly significant fits (Fig. 2c, d).

A very small stream like Black Brows Beck might be extremely sensitive to rainfall episodes. Therefore, I explored how spring rainfall (March, April and May pooled together as reported by Elliott) might be related to stream discharge and recruitment. Before exploring potential effects of spring rainfall on recruitment, I examined whether spring rainfall was a good predictor of discharge in April. During the study years, spring rainfall varied widely (110–570 mm). However, a rainy spring with high discharge does not necessarily imply a rainy April with high discharge. In any given year, rainy *versus* dry months may alternate with each other so that a rainy month with high discharge may be preceded or followed by a dry month with low discharge thus, yielding a spring of intermediate conditions. This complexity is revealed by plotting discharge in April *versus* spring rainfall (Fig. 3). For example, the 2 years with the lowest April discharge, 1974 and 1982, were associated with relatively dry and wet springs. Despite such variability, discharge in April was significantly related to the total spring rainfall over the study period ($R^2 = 0.29$, $p = 0.002$, Fig. 3).

Recruitment plotted *versus* spring rainfall also demonstrated a consistent ascending/descending relationship, but the outliers highlight the role of April discharge in driving recruitment (Fig. 4). Recruitment in 1982, is unexpectedly low because it corresponds to one of the lowest discharge in April recorded over the 30 study years (Fig. 2). Alternatively, the 1984 recruitment is unexpectedly high, because that year had the driest spring but a more moderate April discharge (Figs. 2 and 4). After omitting these 2 years, the data conformed to a two-phase relationship that explained 44% of the variation in recruitment ($p < 0.05$). Consequently, both discharge in April and spring rainfall appeared to drive variation in recruitment over the study

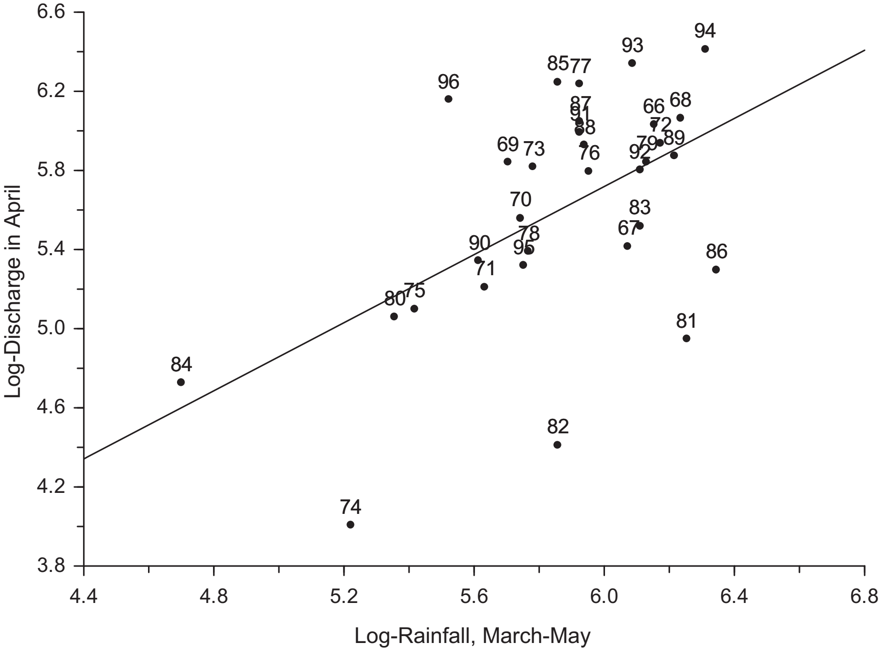

Fig. 3 Positive linear relationship between log-transformed discharge in April (m^3/s) *versus* log-transformed rainfall (mm) over the spring months (March, April and May pooled together). Constants for the linear regression, variance explained and significant level: $A = 0.55$, $B = 0.86$, $R^2 = 0.30$, $p = 0.002$

period. Collectively, these relationships offer compelling evidence to support a major role of rainfall/discharge conditions soon after emergence as a major determinant of recruitment abundance.

We applied the corrected Akaike's Information Criterion (Burham and Anderson 2002; Motulsky and Christopoulos 2004) to explore the relative strength of the Ricker (spawners) *versus* two-phase (environmental) models. The AICc values were calculated for each model (AICc_1 and AICc_2). The differences between the two AICc values (ΔAIC) provide an estimate of how many times more likely a particular model is. Overall, the model with a lower AICc score is more likely to be correct. The difference between the AICc scores can be further used to calculate the probability that a model is correct. A difference $\text{AICc}_2 - \text{AICc}_1$ =/0 indicates that the two models have an equal probability of being correct. A difference $\text{AICc}_2 - \text{AICc}_1 = 2$ indicates a 73% probability and those between 5 and 10 indicate 90–100% probability that the preferred model is correct.

For the first data set (1967–1983), the ΔAIC scores were $\text{AIC}_{\text{RC}} = -37.47$ and $\text{AIC}_{\text{DIS}} = -43.9$, and as a consequence, $\Delta\text{AIC} = 6.9$, indicating a > 90% probability that the two-phase discharge model is the most plausible. For the whole data set, 1966–1996, the AICc scores were $\text{AIC}_{\text{RC}} = -22.59$ and $\text{AIC}_{\text{DIS}} = -69.32$ and as a

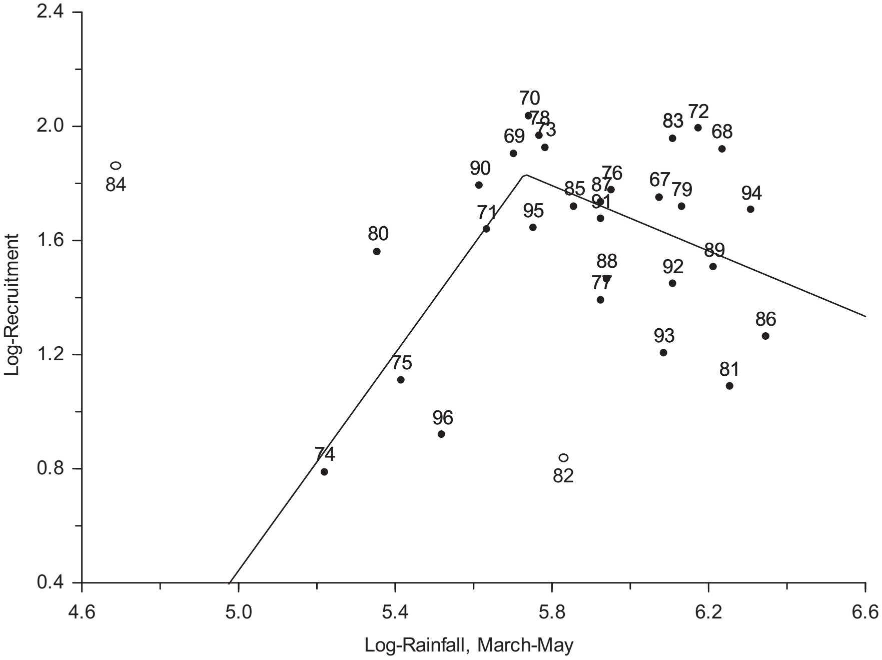

Fig. 4 Ascent/descent relationship depicted by log-transformed recruitment (ind m^{-2}) *versus* log-transformed spring rainfall (March, April and May pooled together) with a two-phase regression fitted to data. After omitting the 1982 and 1984 observations (open circles), the constants, variance explained and significant level are: $A = -9.07$, $B1 = 1.9$, $K = 5.72$ and $B2 = -0.57$, $R^2 = 0.42$, $p < 0.01$

consequence, ΔAIC = 46.7, demonstrating the discharge-dependent recruitment model is far more likely to be the most plausible than the density-dependent model.

3.3 *Elliott's Findings Revisited*

Evidence that environmental conditions drive variation in recruitment and survival rates requires a critical re-evaluation of the stock–recruitment relationships reported by Elliott and colleagues. It is seriously questionable that the operation of two, essentially opposing and for most incompatible factors as discharge- and density-dependence may operate simultaneously to generate two different and contradictory patterns. How can we cope with this serious discrepancy?

Inherent in the stock–recruitment relationships reported by Elliott (Fig. 1) is that: (1) recruitment is density-dependent; it follows that (2) recruitment is largely independent of the large variation in the environmental (hydrological) conditions, particularly at high parental density; (3) at low spawners abundance, recruitment increases with increased parental density up to a threshold assumed to be the carrying capacity. (4) The carrying capacity that sustains maximum recruitment magnitudes is constant over time. However, (5) along the right-side wing, recruitment attains values far below the threshold upon which recruitment declines abruptly with increased parental density and (6) the slope of the right-side wing is sufficiently steep to predict that a minor increase in parental density would result in population extirpation (i.e. RC = 0). Based on the preceding re-analysis of Elliott's original data, we consider the following points in turn:

Elliott (1984) argued that recruits are highly territorial. In other words, the youngest juveniles compete for and defend territories after emerging from the gravel and moving across the water column in search of feeding positions. Even if the territories were exclusive, their number likely depended on discharge soon after emergence, which varied from 54.9 m^3/s to 610 m^3/s during the study period. If habitat availability drives competition and fry mortality, it is unclear how recruitment was similar (i.e. 2.0–3.5 recruits m^{-2}) in 1993 and 1996. when the parental density was lowest, with only 13 and 12 eggs m^{-2} but discharge was highest with 567.5 and 471.7 m^3/s and, at the opposite extreme, in 1974, 1975, 1981 and 1982, when the parental density was ten times higher with 122.2, 127.4 and 132.6 eggs m^{-2} but the discharge was an order of magnitude lower. Such inconsistency is explained by a simple visual inspection of the two-phase, discharge-dependent recruitment relationships (Fig. 2), in which the years located at the opposing extreme of discharge with very low *versus* very high discharge conditions result in similarly low recruitment levels including exactly 1974, 1975, 1981, 1982, 1993 and 1996.

A similar argument applies to the temporal persistence of the carrying capacity. This can be defined by the amount of suitable space capable of sustaining a maximum number of recruits (assuming sufficient food availability). This being the case, the carrying capacity might necessarily be mediated, once more, by the discharge conditions offering an overwhelming variability of space suitable for recruits over the study years. This is, unequivocally demonstrated by (1) the discharge-dependent recruitment relationships where the annual-specific discharge in April represents the annual-specific carrying capacity to sustain recruits and eventually determines an annual-specific recruitment strength. Concurrently, (2) the 10 years of maximum recruitment in the stock-recruitment relationships are exactly those matching intermediate discharge conditions within the range, log (discharge) 5.2–6.1 or between 200 and 450 m^3/s (see Fig. 1 *versus* Fig. 2). That is, the highest recruitment recorded during the study years did not maximize at a temporally persistent carrying capacity *vis-a-vis* appropriate levels of parental densities but, on the contrary, when the space suitable for recruits maximize in years of intermediate discharge.

In regards to issue #6, the right-side wing of the fitted stock–recruitment curve is steep enough to predict that a small increase in the parental density would result in population extirpation. A line drawn over the declining subset of data (Fig. 5) predicts an intersection (i.e. RC = 0) at a parental density of little more than 10,000 eggs. Given female fecundity ranges from 500 to 1800 eggs (Elliott 1984, 1994), this right-side wing predicts serious risks for the population if the parental density increases with the simple addition of one large-sized (spawning, for example 1800 eggs) or two medium-sized females (spawning, for example 2000 eggs).

At the opposite extreme, the recruitment of the seven cohorts located at the left-side wing is associated with parental densities below 1000 eggs (or <30 eggs m^{-2} in Fig. 1). Again, given the fecundity range reported by Elliott (1984, 1994) implies that recruitment of those cohorts may well derive from the successful spawning of just one female. This observation is actually documented in Elliott et al. (1997, Fig. 2, p. 1233) and Elliott and Elliott (2006, Fig. 18.2) where the surviving females in November/December (life stage R_5 in his key-factors analysis) are exactly one female in 6 years and two females in 3 years.

Apparently, during the 30 years of study, the population of Black Brows Beck persisted when only one or two females successfully reproduced, whilst, at opposite extreme, the single extra female predicted to drive recruitment to zero never materialized. The question still remains as to which mechanism, other than the innate upstream migratory behaviour of sea trout, may actually guarantee the temporally persistent "en route" colonization of just one or two females to spawn successfully at the study site. The discharge–recruitment relationship contains no such inconsistency; whatever number of females spawn successfully at the study site, the subsequent recruitment is determined by the discharge conditions.

4 Discussion

The relationship between rainfall/discharge and recruitment/survival rates elucidated in this study for Black Brows Beck brown trout provide compelling evidence that environmental (hydrological) conditions drive recruitment and combined with

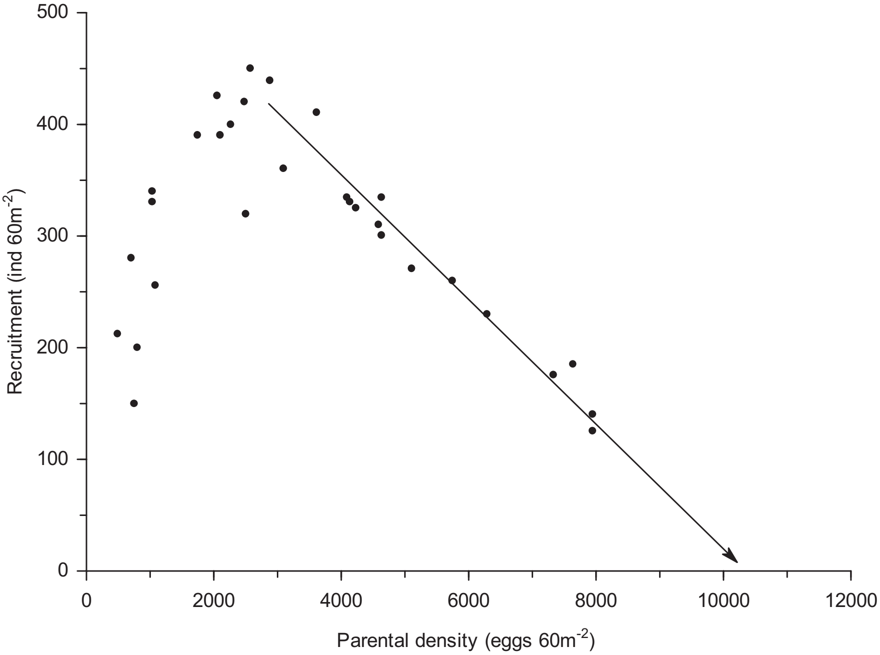

Fig. 5 Re-calculated and redrawn from Fig. 1b. A linear line drawn over the declining recruitment values of the stock–recruitment relationship indicates an intersect at the parental stock-axe of 10,300 eggs 60 m^{-2}

the biological inconsistencies of the stock–recruitment curves, cast doubt on the interpretations offered by Elliott and colleagues.

Interestingly, Elliott focused on the stock–recruitment relationships but also considered rainfall/discharge conditions on several occasions. In an early study, Elliott (1984, p. 329) concluded that, over the summer (June to August), "*rainfall and hence the discharge remained fairly constant from 1966 to 1982*". Later on, Elliott (1985, p. 630) explored relationships between recruitment and spring rainfall, and stated that: "*Neither water temperature nor rainfall significantly affected loss-rates except those for 1+parr …*". More assertively, Elliott et al. (1997, p. 1233) stated that "*the densities for 0+ parr in late May or early June* (i.e., recruitment in this study), *could be affected by spring droughts for the period March to May but this did not occur".*

Clearly, for one or another reason, Elliott overlooked the effects of the rainfall/discharge conditions in April, the critical time of fry emergence. This oversight together with the re-analysis of the stock-recruitment relationships makes the proposed dramatic density-dependent regulation of recruitment in Black Brows Beck most unlikely.

In contrast, the rainfall/discharge-recruitment relationship for Black Brows Beck matches patterns previously found in other stream-rearing brown trout populations

(Lobón-Cerviá and Rincón 2004; Cattanéo et al. 2002; Lobón-Cerviá and Mortensen 2005; Lobón-Cerviá 2007; Lobón-Cerviá et al. 2017). All these studies emphasize the "*modus operandi*" of a single environmental (hydrological) factor on recruitment, and further highlight that the effects of rainfall/discharge describe the very same, ascent/descent pattern where recruitment strength is weaker in the driest years of lowest discharge, higher in years of increased discharge up to a threshold in years of intermediate discharge, and lower again in years of highest discharge.

Nevertheless, environmentally determined recruitment is not incompatible with the operation of density-dependence in post-recruitment stages. For example, recent investigations have reported density-dependent mortality in adults, but not in juveniles in contrasting populations of brown trout (Lobón-Cerviá 2012). This appears also the case in North-American stream-rearing salmonids (Grossman et al. 2010, 2012; Kanno et al. 2015). However, even if density-dependence operates on post-recruitment stages over the lifetime, its role as a "Nicholsonian population regulator" might be minor, irrelevant or non-existent; simply because whatever number of spawners survive to the operation of density-dependence, the subsequent recruitment will be determined by the discharge conditions soon after emergence. And, given that recruitment is the major determinant of year-class strength (Lobón-Cerviá et al. 2011), the population size will fluctuate once more, tracking the vagaries of the rainfall/discharge conditions over time.

In perspective, these environmentally-determined recruitment patterns clash with the "paradigm of density dependence" and, more specifically, with the temporal stability expected to occur under the operation of density-dependence in the form of stock-recruitment relationships. Instead, these patterns offer evidence that stream-rearing salmonid populations vary through time due to density-independent variation in recruitment. Such temporal instability is consistent with the notion of non-equilibrium populations that fluctuate temporally tracking the environmental/climatic randomness (Andrewartha and Birch 1954) and further adds to the Krebs (2002)' claim: "*The assumption that we can uncover invariant relationships between population growth rate and some other variables is an "article of faith". Numerous commercial fishery applications have failed to find invariant relationships between stock and recruitment as predicted by the density paradigm"* and *"Environmental variation is the rule, and non-equilibrium dynamics should force us to look for the mechanisms of population change"*.

Ackowledgements Comments and suggestions of numerous individuals were instrumental in completing an early draft. John Armstrong provided environmental data; Thomas Jenkins, Kyle Young, Gorm Rasmussen, Gary Grossman, Phaedra Budy, Nigel Milner and Asbjorn Vollestad revised point by point and improved substantially the English style. Their efforts and unlimited patience are warmly acknowledged.

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Long-Term Recruitment Patterns of 0+ Brown Trout in the River Maine, Northern Ireland

Richard Kennedy, Robert Rosell, and Michelle Allen

Abstract Lough Neagh is the largest freshwater lake in the UK and Ireland (392 km^2) and has a stock of lake migrating brown trout which recruit/spawn in the influent tributaries and mature in the lake. Potamodromous trout are exploited commercially in Lough Neagh with total landings ranging from c. 0.3 to 29.4 tons year^{-1} between 2001 and 2020. The recruitment of 0+ trout has been assessed annually on the River Maine, a large tributary of Lough Neagh, across an extensive and consistent network of Semi-Quantitative electric fishing sites between 2002 and 2020. The annual trout recruitment index for the River Maine was analysed against a range of potential explanatory variables including estimates of adult trout migration into the river, the commercial landings from the lake, electric fishing indices of Atlantic salmon (*Salmo salar* L.) recruitment and various discharge metrics. A stock–recruitment relationship was evident between the run of adult trout measured through the River Maine fish counter and subsequent 0+ recruitment measured in the following year.

Keywords Discharge, Potamodromy · Stock–recruitment · *Salmo trutta*

1 Introduction

Stream dwelling brown trout, *Salmo trutta* L., can display marked diversity in morphology and life history (Ferguson et al. 2017) with up to five different life history-migratory strategies possible (Ferguson et al. 2019). Some *S. trutta* stocks are characterised by a potamodromous life history strategy in which lacustrine–adfluvial movements may occur involving migrations between a lake and an influent river (Northcote 1997). The freshwater environment in Northern Ireland is

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dominated by two large lake catchments, Lough Neagh (surface area 396 km^2) and Lower Lough Erne (surface area 109 km^2). The influent streams on these lake systems support extensive stocks of potamodromous trout which in turn sustain important recreational fisheries across both catchments and a significant commercial fishery in Lough Neagh (Kennedy et al. 2021). The River Maine is a major tributary of Lough Neagh and is noted for its strain of lake running brown trout, known locally as dollaghan trout. A fishery monitoring programme was initiated in the River Maine in 2001–02 with a routine, semi-quantitative (SQ) electric fishing survey (Crozier and Kennedy 1994) conducted annually at 199 sites throughout the range of migratory salmonids across the river (Kennedy et al. 2014). A fish counter was also commissioned on the lower river in 2001 to provide an assessment of adult spawning runs.

The recruitment success of 0+ salmonids is influenced by a diverse range of biological and environmental parameters that may function in synergy (Imre et al. 2002; Armstrong et al. 2003). Milner et al. (2003) further outlined that juvenile trout abundance in streams can be regulated by density-dependent mechanisms (e.g. territorial competition) and/or density-independent factors (e.g. climate). Elliott (1989), for example demonstrated that population size in an anadromous *S. trutta* stock in the English lake district was regulated by density-dependent mortality operating over a relatively short critical period (c. 30–70 days) following the emergence of fry from the redds. The importance of density-independent factors has also been clearly illustrated for other stream dwelling brown trout stocks, with high flows during emergence significantly limiting subsequent 0+ densities in French rivers (Cattanéo et al. 2002).

The current study tabulated the long-term electric fishing data from the River Maine for the period 2002–2020, documenting and describing annual variations in recruitment of 0+ trout in the catchment. This enabled an investigation of relationships between the annual 0+ trout recruitment index and a panel of available explanatory biological and environmental variables, to define potential factors regulating recruitment.

2 Materials and Methods

2.1 Study Area

The River Maine is 45 km in length, has a catchment area of >200 km^2, average daily discharge of c. 24 m^3/s and flows into the northeast section of Lough Neagh in Northern Ireland (Fig. 1). The River Maine has three major tributaries including the Kellswater, Braid and Cloghwater and hosts a number of local angling clubs which mainly target the migratory ‘dollaghan’ brown trout. The other fish fauna common in the River Maine includes Atlantic salmon, *Salmo salar* L., eel, *Anguilla anguilla* L., minnow, *Phoxinus phoxinus* L., stickleback, *Gasterosteus aculeatus L.* and

Fig. 1 Location of River Maine catchment in Northern Ireland and insert showing distribution of individual electric fishing sites (black dots)

Stoneloach, *Barbatula barbatula L.* The River Maine catchment has a predominately agricultural (pastoral) land use, the underlying geology is granite and the river was subject to a historical arterial drainage scheme in the 1970s (Essery and Wilcock 1990).

2.2 *Monitoring Data*

Juvenile salmonids were monitored on the River Maine by a semi-quantitative (SQ) electric fishing programme, conducted across a standard network of 199 sites over a 19-year period (2002–2020). SQ survey sites were typically undertaken in shallow (<30 cm) nursery habitats, with a site located every 500–1000 m of channel length throughout all the tributaries and the main channel of the river. The survey design ensured complete coverage of the catchment and included all areas accessible to migratory fish (Kennedy et al. 2014). The SQ surveys were undertaken during the high summer (15th July–15th September) with the same locations, equipment and as far as possible the same survey staff used each year. The SQ sampling is a Catch-Per-Unit-Effort technique and involves electrofishing each site for a fixed time of 5 min using a single anode, portable backpack electrofishing apparatus and a single catcher (Crozier and Kennedy 1994). The SQ technique was designed specifically for 0+ salmonids and relies on standardisation of effort and high capture efficiency. Any 'missed' fish that are observed to evade the catcher are noted and any site where capture efficiency drops below 60% is discarded and re-visited at a later date (Crozier and Kennedy 1994). All fish caught during the survey were anaesthetised using Tricaine methanesulphonate (MS-222), identified and measured for fork length L_F (mm) before being returned alive to the river. A subsample of fish had scale samples removed for age determination and salmonid species were split between 0+ and >0+ age classes according to L_F. The catch data for each site was expressed as a catch-per-unit-effort (CPUE) index detailing the number of fish (by species and age class) captured per 5 min (e.g. number 0+ trout/5 min). The SQ electric fishing survey data were tabulated each year with the catchment divided into 18 geographically sequenced sections (Table 1). The mean CPUE index for 0+ trout was calculated for each section and then the overall catchment-scale recruitment index was determined as the mean of the 18 sections (Table 1).

Upstream migrant salmon and trout in the River Maine are monitored using an Aquantic (™) 2100C resistivity fish counter, installed into the fish pass at a weir situated c. 3 km from the confluence with the lake. The weir feeds an adjacent hydroelectric side channel which diverts a portion of the river flow and ensures that the fish pass is the main upstream passage route for migratory trout ascending the river. The counter is known to detect a number of Atlantic salmon which are larger than the migratory trout and contribute to the total upstream count each year. Calibration work was undertaken at the fish counter site using CCTV imaging, direct sampling and length frequency analysis to differentiate between upstream trout and salmon movements. Trout were observed to consistently compose the bulk

Table 1 Example of semi-quantitative electric fishing survey results for 0+ age class trout collected from the River Maine in 2011

Sub-catchment	Sub-catchment section	E-Fishing survey site nos.	No. sites completed (2011)	CPUE (no 0+ /5 min)
Kellswater	Kells Top	1–14	14	8.29
Kellswater	Kells Upper	15–22	8	7.75
Kellswater	Kells Middle	23–33	7	5.22
Kellswater	Kells Bottom	34–47	5	3.00
Kellswater	Kells Minor Tribs	10	10	9.78
Braid	Braid Upper	1–11	11	8.36
Braid	Braid Middle	12–24	13	5.17
Braid	Braid Bottom	25–35	11	2.60
Braid	Braid Minor Tribs	16	12	5.73
Clough	Clough Upper	1–10	10	4.30
Clough	Clough Middle	11–20	10	3.90
Clough	Clough Bottom	21–31	11	5.67
Clough	Clough Tribs	10	10	5.20
Cloughmills	Cloghmills Upper	1–8	8	8.83
Cloughmills	Cloghmills Lower	9–17	9	4.57
Killagan	Killagan	1–13	2	4.55
Maine	Main 1	1–12	4	5.00
Maine	Main 2	13–20	8	2.67
Total sites surveyed 2011			163	
Mean catchment CPUE index (no. 5 min^{-1})				*5.59*

of the count (>90%) and a size threshold was established for application to the counter detections to separate the annual salmon count. The counter has been operational on the river since 2001. A flow gauging station is also available on the River Maine close to the fish counter site at Randalstown and the mean daily river discharge (m^3/s) was tabulated for the period 2000–2020.

2.3 Analysis

Annual 0+ trout recruitment indices were investigated against a panel of potential explanatory biological and environmental time series. Explanatory biological variables included estimates of adult abundance from the previous year represented by the adult trout count (yr^{-1}) and the total commercial catch of dollaghan from Lough Neagh (yr^{-1}). Additional parameters considered included electric fishing derived SQ indices of >0+ trout parr and 0+ salmon abundance in the same year (yr). Discharge data measured at the flow gauging station on the River Maine were also considered and mean daily flow records were tabulated to determine Mean Monthly Flow (MMF), mean flow during the adult migratory season (Aug–Oct) and mean flow over the ova to fry development phase (Nov–Apr) prior to each 0+ monitoring year. The number of high flood events (>Q 1 flows) that occurred during the development of each 0+ cohort (previous Nov–Apr) were also considered as a potential explanatory variable.

The individual time series were assessed for autocorrelation. Each time series, with the exception of the trout parr index, were stationary. Applying first-order differencing to the >0+ trout parr index time series induced stationarity. A cross-correlation analysis was conducted to investigate the potential association between the various input time series, which for the >0+ trout parr index was the first-ordered differenced time series, and the output time series which was 0+ juvenile trout recruitment. All time series analyses were conducted using R (R Core Team 2021).

Emergence of 0+ trout from spawning redds typically occurs sometime between early April to mid-May across the River Maine. The impact of discharge on recruitment was investigated specifically at this critical time and the 0+ recruitment index was compared against the river discharge in April and May earlier that year.

In order to consider the role of density dependence on the River Maine stock the annual 0+ trout recruitment indices were modelled against the adult fish count from the previous year (yr^{-1}) to explore any possible relationship between stock (fish counter estimates) and recruitment (SQ 0+ indices). Two classic stock–recruitment models were applied to the dataset including the Ricker model (Ricker 1954);

$$R = a\,\mathrm{S}\exp^{-b\mathrm{S}}$$

where S = Breeding stock [count yr^{-1}], R = recruitment [SQ index yr], a and b are constants. Secondly the Beverton-Holt model was applied (Beverton and Holt 1957);

$$R = a^* S / \left(1 + b^* s\right),$$

where S = Breeding stock [count yr^{-1}], R = recruitment [SQ index yr], a and b are constants.

Each stock–recruitment model was tested against an alternative density-independent model describing the mean recruitment values for the dataset. The Akaike Information Criterion (AIC) and the extra sum-of-squares test were used to compare the respective S–R model against the density-independent model. The amount of variation explained by each non-linear model was calculated as the pseudo-r^2, that is the correlation between the observed and fitted values squared. The analyses were conducted using *R* (packages FSA, dplyr, magrittr, plotrix, nlstools, lsmeans, magrittr, nlstools plotrix and qpcR).

3 Results

The juvenile (0+) trout recruitment index for the River Maine, monitored by the SQ survey programme and expressed as a relative abundance index (mean no. 0+ trout 5 min^{-1}), has varied from 5.6 (2011) – 14.7 0+ trout 5 min^{-1} (2020) across the time series (Fig. 2). The mean relative abundance was 10.5 0+ trout 5 min^{-1} and the coefficient of variation was 3.3 indicative of fair variation across the available time series. Older trout parr (>0+) were less abundant in the surveys and ranged from 1.3

Fig. 2 Mean annual abundance indices (no. fish/5mins) for 0+ and >0+ brown trout, developed from semi-quantitative electric fishing surveys across the River Maine catchment between 2002 and 2020

(2010) – 3.7 > 0+ trout 5 min^{-1} (2019) (Fig. 2) with a mean level of 2.4 > 0+ 5 min^{-1} and showed a lower coefficient of variation of 2.9.

The abundance of returning adult trout, as quantified by the resistivity fish counter on the Lower River Maine, varied markedly from 390 (2010) to 4461 (2018) (Fig. 3). Landings of dollaghan trout from the commercial fishery in Lough Neagh, included fish originating from all the influent lake tributaries including the Maine, were also highly variable across the time series and catch returns varied from 334 kg (2004) to 29,441 kg (2015) (Fig. 3).

Prior to cross-correlation analysis the response and explanatory time series' were assessed for autocorrelation. Each of the time series, with the exception of the >0+ trout parr index dataset, was stationary. Applying first-order differencing to the >0+ trout parr index time series induced stationarity. A significant positive cross-correlation was observed between the 0+ trout recruitment index time series and the salmon fry index ($r = 0.68$). No other significant relationship was evident although weak positive correlations were evident between the 0+ trout recruitment index and both the adult count and commercial landings from Lough Neagh from the previous season (Fig. 4). Spring discharge on the River Maine, co-incident with 0+ trout emergence, has varied extensively across the time series with mean April flows ranging from 5.1 m^3/s (2020) to 24.0 m^3/s (2009) and mean May flows ranging from 2.7 m^3/s (2020) to 22.8 m^3/s (2012) (Fig. 5). The mean 0+ trout recruitment index was explored against river discharge levels in April and May and no linear, parabolic or polynomial relationships were evident (Fig. 6).

The 0+ trout recruitment index was further investigated for possible density-dependent relationships against a measure of adult trout abundance (fish counter) from the previous year. The Beverton-Holt model provided an improvement over the density-independent model (extra sum-of-squares test, sum of squares =5.38,

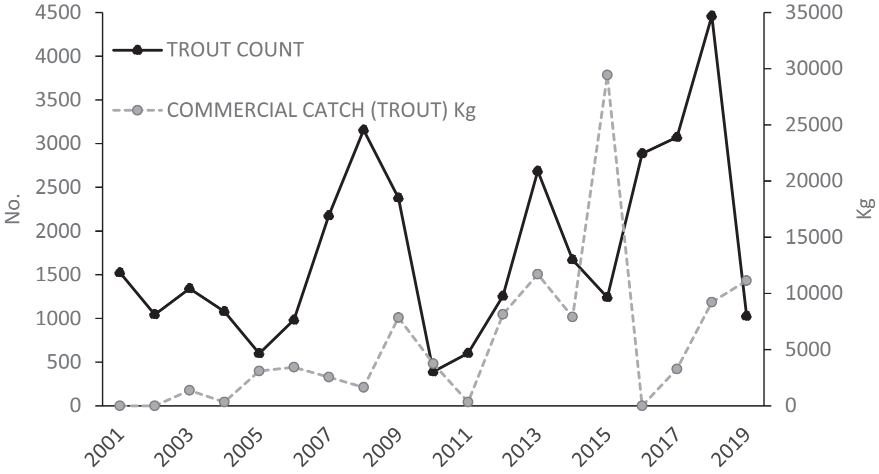

Fig. 3 Annual count of dollaghan trout from the River Maine resistivity fish counter and the total commercial landings of trout from Lough Neagh 2001–2019

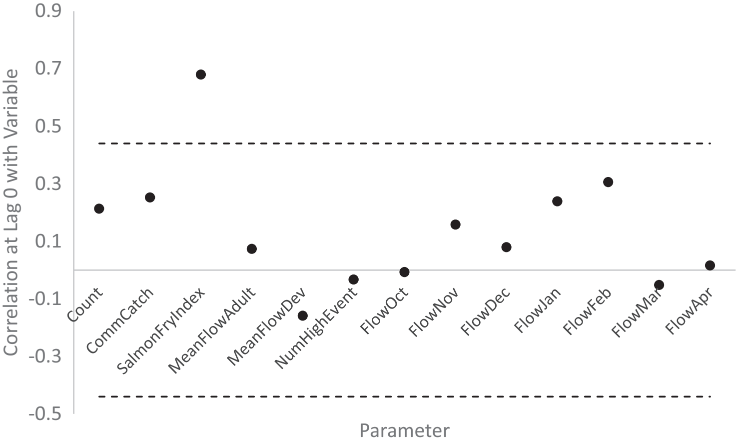

Fig. 4 Cross-correlation analysis of 0+ trout recruitment index against a panel of potential influential biological and environmental variables. Note; MeanFlowAdult = Mean discharge over the period August–October; MeanFlowDev = Mean discharge over the period November–April. The 95% confidence intervals are indicated by dashed lines

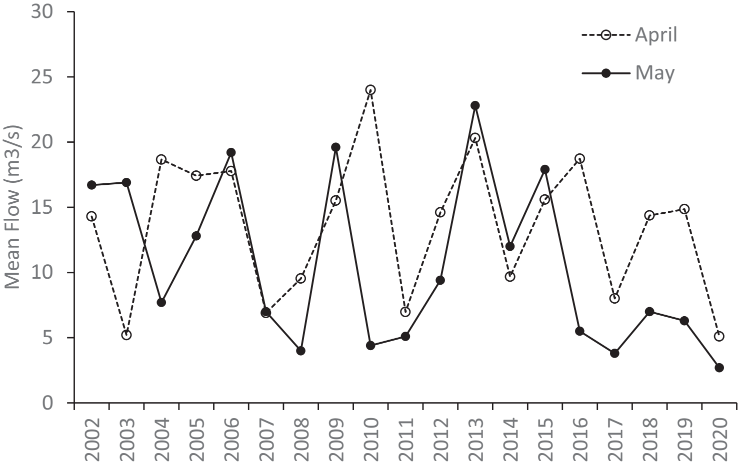

Fig. 5 The mean discharge (m^3/s) for April and May, measured at the River Maine gauging station, 2002–2020

$F_{(1,\,17)} = 67.89$, $P < 0.001$). The Akaike Information Criterion (AIC) for the density-independent and Beverton-Holt density-dependent models were 38.18 and 9.63, respectively.

The Ricker model also provided an improvement over the density-independent model (extra sum-of-square test, sum of squares = 5.30, $F_{(1,\,17)} = 63.22$, $P < 0.001$). Comparing the AIC for both models, which were 38.18 and 10.71 for the density-independent and for Ricker models, respectively, further confirmed the Ricker

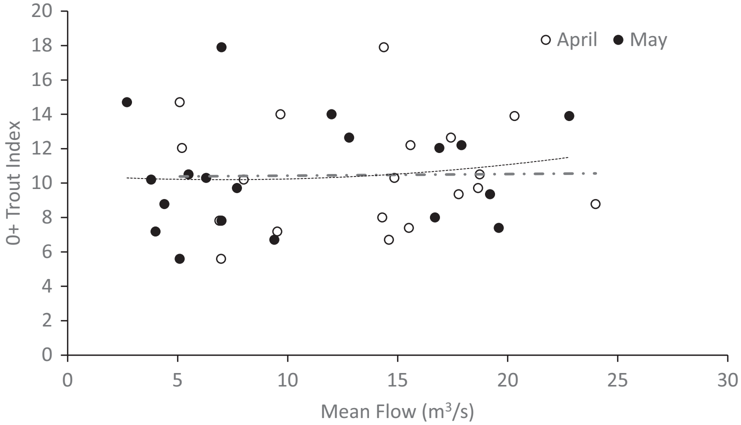

Fig. 6 0+ trout recruitment index plotted against mean monthly discharge in the preceding spring (April, May) across the monitoring period 2002–2020

model was an improvement over the density-independent model. The Akaike weights were 0, 0.37 and 0.63 for the density-independent, Ricker and Beverton-Holt models, respectively. The relative likelihood of the density-independent model was zero times and the Ricker model was 0.58 times as probable as the Beverton-Holt model to minimise information loss. The Beverton-Holt exhibited a pseud-r^2 value of 0.14 and the model constants were $a = 42.2$; $b = 3.4$ (Fig. 7a). The Ricker model had a pseudo-r^2 value of 0.13, parameters were $a = 17.3$; $b = 0.5$, and it indicated that the adult spawning stock (S_M) that yielded maximum recruitment was 1996 fish whilst the stock level that provided the maximum surplus production (S_G) was 1721 fish (Fig. 7b).

4 Discussion

Recruitment is the fundamental determinant of brown trout year-class strength and the identification of significant recruitment drivers represents a major research goal in fisheries science (Lobón-Cerviá et al. 2017). The influence of density-independent and density-dependent processes in 0+ trout recruitment has been investigated, compared and debated across a range of European case studies (Nicola et al. 2008; Lobón-Cerviá et al. 2017). Grant and Imre (2005) postulated that the regulation of stream dwelling salmonid populations was primarily driven by mortality and emigration at higher densities through interference competition, and by density-dependent growth via exploitative competition for food at lower densities. The impact of density dependence on individual growth is particularly important and has been well documented in a number of previous studies (Bohlin et al. 2002; Lobón-Cerviá 2005). Grossman and Simon (2020) reviewed 199 datasets across 21

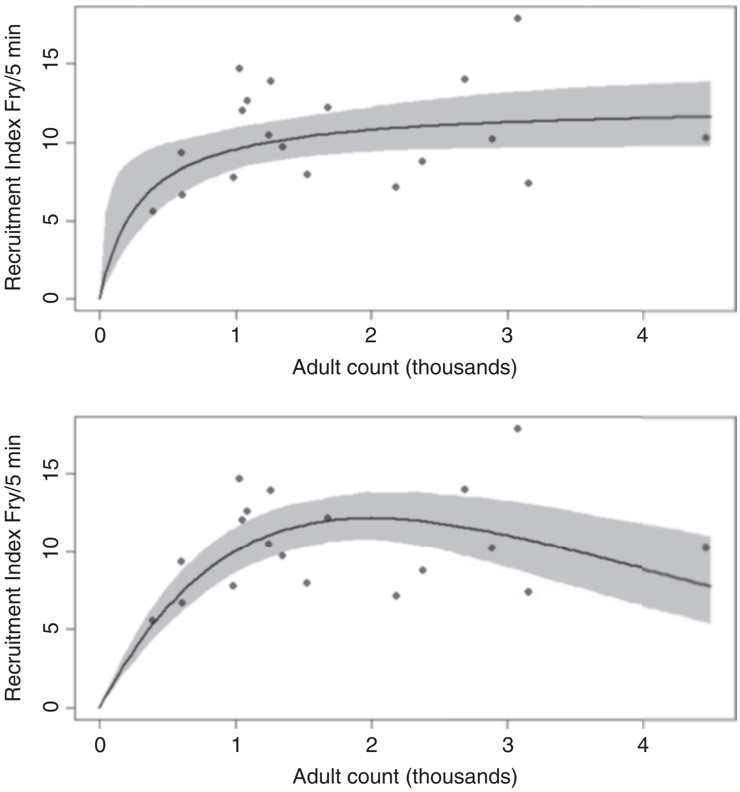

Fig. 7 Stock–recruitment curves fitted for River Maine brown trout, stock (adult count y^{-1}) and recruitment (semi-quantitative 0+ abundance index) datasets; grey shading indicates 95% confidence intervals; **a** (top) Beverton-Holt model; **b** (bottom) Ricker model

salmonid species and found that 71% showed density dependence in growth, whilst (Matte et al. 2020) indicated that density-dependent growth was stronger than survival in laboratory studies.

The River Maine data reflected a tentative stock–recruitment relationship. This was perhaps surprising since the recruitment measurement was based on a non-quantitative CPUE index of 0+ recruits instead of the more usual estimate of subsequent filial smolt or adult production. The S–R relationship on the River Maine was also surprising given that the stock estimate (adult count) was limited entirely to the migratory portion of the stock (e.g. the lake running dollaghan trout) and did not account for the potential contribution of sexually mature river resident trout. In anadromous trout populations, S–R relationships can often be confounded by the unknown effect of river resident brown trout spawners (Kennedy et al. 2017). Although resident brown trout may have contributed to fry recruitment across the River Maine monitoring network, the survey targeted areas accessible to, and dominated by, migratory dollaghan trout. In trout stocks with a migratory component, the migratory females are generally larger than con-specific residents and able to contribute more to overall ova production. Milner et al. (2006), for example suggested that migrant female sea trout were likely to be the dominant source of total egg production in most rivers with a migratory trout component.

Dome-shaped stock–recruitment curves have been described for some trout populations in Europe (Nicola et al. 2008; Elliott and Elliott 2006) whilst an asymptotic S-R model provided a better fit for a sea trout stock on the lacustrine Burrishoole catchment in Western Ireland (Poole et al. 2006). Many previous studies investigating the effects of density dependence on salmonid populations did so using stock–recruitment relationships of adult spawners against subsequent recruits (either smolts or adults) to infer density-dependent regulation on juvenile life stages (Marco-Rius et al. 2013). The monitoring of trout recruitment in the present study (0+ trout fry) occurred during the first summer and represented the earliest practical audit point in the life cycle to reflect recruitment, as soon as possible after the critical post-emergence regulatory density dependent period between 33 and 70 days (Elliott 1989). This early audit point may therefore better reflect the underlying S–R dynamic more closely than in later life stages after density-independent influences may have exerted further effects on the recruiting cohort (Kennedy et al. 2017).

A limitation with inferred studies can result from the sampling area being mismatched against the spatial range of the study species, such that the density estimate may not provide an adequate measure of competitive pressure, particularly if individuals can simply relocate from the limiting area to a new area (Berryman 2004). Previous work on the River Maine has shown that marked 0+ salmon were able to disperse extensively downstream by the following season (Kennedy et al. 2014) thus demonstrating the ability of young-of-year salmonids to relocate between habitats. Solomon (2006) postulated that dome-shaped S–R relationships were unlikely to be functional at a larger basin scale given the catchment-wide diversity of optimal and sub-optimal habitats available for dispersal and recruitment. Ray and Hastings (1996) furthermore suggested that the identification of functional density-dependent processes is more often hindered by inadequate spatial scaling than time series duration or test power. An advantage of the present study was that the extensive survey design exhaustively covered the total range available to migratory trout within the entire catchment and thus reflected recruitment status at the absolute maximum spatial scale. The fit of a dome-shaped model at the overall catchment scale was perhaps unexpected given the wide geographical range covered and the intrinsic ability of young trout to disperse within the river and therefore potentially ‘escape’ from density-dependent regulation. The survey design in the current study, although wide-ranging, located sampling sites sequentially on suitable shallow nursery habitats such that deeper adjacent sub-optimal habitats were not fully accessed. Ironically, despite the geographically exhaustive sampling regime, it may still be possible that the survey was not spatially exhaustive and that sub-optimal unsurveyed habitats could still have provided a refugia from density-dependent regulation. The (albeit inferred) existence of density-dependent-based regulation on the River Maine trout stock is still compelling, however, given the lack of alternative predictive relationships associated with the other available explanatory variables. A major anthropogenic pressure on the Maine stock is due to the commercial fishery which has harvested up to 30 tons of dollaghan from the lake each year. Although no significant relationship was evident between 0+ trout recruitment and commercial catch it is possible that the harvest may have decreased adult returns in some years, increasing the range and variability in spawner return rates and therefore stimulating the apparent S–R relationship observed in the stock.

Density-independent factors such as river discharge can also influence brown trout recruitment (Armstrong et al. 2003). Interestingly, a significant positive correlation was observed between 0+ trout and 0+ salmon recruitment on the River Maine, perhaps suggestive of common environmental conditions influencing the success of emergent salmonid cohorts? A distinct parabolic relationship has been documented elsewhere between the flows evident upon alevin emergence and subsequent trout recruitment, in which low and high flows corresponded with reduced recruitment whilst medium flows tended to associate with better recruitment. This phenomenon has been observed in brown trout populations across a number of other countries and throughout the natural range of the species (Cattanéo et al. 2002; Richard et al. 2015; Lobón-Cerviá et al. 2017). The ecological mechanisms underlying such a parabolic relationship between recruitment and spring flows may be linked to reduced habitat quantity for young-of-year juveniles in drought years and wash-out of emergent fry in high discharge years (Heggenes and Traaen 1988). Lobón-Cerviá et al. (2017) argued that the consistent identification of stream discharge as a predictor of annual recruitment, across many different stream types and life history strategies, provided compelling evidence for it to be considered as the main underlying 'modus operandi' for trout recruitment. The River Maine lacked any clear association between trout recruitment and river discharge, particularly for the flows experienced by emerging juveniles in April or May. The climate in Northern Ireland is mild and wet with high exposure to rain bearing winds off the Atlantic Ocean and average annual rainfall totals of between 800 and 2000 mm (UK Met Office). A consequence of these consistent rainfall patterns is that true drought periods, evident in other regions, are highly unusual in Northern Ireland. When dry spells do occur in Northern Ireland they are generally in summer, outside the key period between spawning and emergence of salmonids, and being on the northeast Atlantic seaboard of Europe, high summer river temperatures threatening to salmonid fish are as yet extremely rare. Recruitment limitation, consequential to low stream flow conditions post-alevin emergence, was not observed on the River Maine. In fact, the highest trout recruitment years recorded in the Maine catchment (2017, 2020) actually resulted from the driest springs, confounding a parabolic relationship between discharge and recruitment. It should be noted however, that the River Maine was subject to extensive anthropogenic pressures, including the commercial fishery, but also a major arterial drainage scheme in the 1970–1980s which modified the channel topography and hydrology (Essery and Wilcock 1990). It is entirely possible that the modified post-drainage channel morphology and discharge patterns may have altered, weakened or unnaturally influenced the relationship between trout recruitment and flow on the river.

5 Conclusions

The current study illustrates the benefit of long-term monitoring programmes which provide an important basis for describing and understanding short-term fluctuations and trends (Euzenat et al. 2006). The work also indicates the potential of resource-efficient semi-quantitative electric fishing methods to build long-term recruitment monitoring datasets. Traditional, quantitative, depletion electric fishing methods are resource heavy in comparison to the semi-quantitative method which is rapid, portable and can facilitate up to 15 sites per day using a two-person crew (Crozier and Kennedy 1994). A large river catchment like the River Maine can thus potentially be fully surveyed using SQ techniques in c. 2 weeks per year. The recruitment index of 0+ trout on the River Maine was linked to the previous adult spawning cohort through a S–R relationship rather than environmental parameters such as spring flows. The S–R relationship outlined in the River Maine case study may have been heavily influenced or even generated by local, anthropogenic factors and this will require further targeted investigation and assessment.

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Spatial Patterns of Synchrony in Recruitment of Trout Among Streams

Troy Zorn and Jan-Michael Hessenauer

Abstract Synchronous recruitment has been documented among salmonid populations in streams draining mountainous regions, and to a lesser degree in low-gradient, groundwater-fed streams. Relatively little is known about the spatial extent of recruitment synchrony among trout populations in low-gradient streams. We mapped Brook Trout *Salvelinus fontinalis*, Brown Trout *Salmo trutta*, and Rainbow Trout *Oncorhynchus mykiss* populations in low-gradient Michigan, USA streams whose recruitment dynamics were synchronous based on correlations in annual densities of age-0, age-1, and age-2 fish, and used maps of correlated populations to estimate the spatial extent of synchrony. Significant correlations indicative of synchronous recruitment occurred for all three species. The maximum spatial extent of synchronous recruitment observed for each species was greater than in many studies to date. Most Rainbow Trout populations were adfluvial, resulting in our documenting synchrony in steelhead recruitment. The persistence of synchronous patterns in year-class strength among older age groups of trout highlights the importance of recruitment to trends in trout abundance among streams within a region. By controlling for spatial variation among sites through time, use of index sites enables a coherent picture of synchronous patterns in recruitment to emerge at the regional scale and better positions fishery managers to evaluate influences of local-scale factors and larger-scale processes on local stream trout populations.

Keywords Brook trout · Brown trout · Rainbow trout · Steelhead · Recruitment · Synchrony · Rivers · Streamflow

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1 Introduction

Abiotic processes often play a driving role in population dynamics of stream-dwelling salmonids. Recruitment has been found to be synchronous among trout populations in high-gradient streams in many areas of the world, including the United States, Spain, and France (e.g., Strange et al. 1993; Nehring and Anderson 1993; Cattanéo et al. 2002; Lobón-Cerviá and Rincon 2004), with reproductive success negatively affected by high flow conditions that influence eggs and fry in redds or salmonid fry after they emerge from redds. Synchronous recruitment of Brook Trout and Brown Trout in low-gradient, groundwater-fed streams has also been documented the Great Lakes region of North America, being governed by similar mechanisms noted in more mountainous regions (Nuhfer et al. 1994; Zorn and Nuhfer 2007a). As age-0 trout disperse and age, biotic factors may become important (Elliott 1994; Bret et al. 2016), though the initial effects of stochastic factors (e.g., flow or current velocity at fry emergence) often persist even as year-classes reach maturity (Strange et al. 1993; Lobón-Cerviá 2007; Zorn and Nuhfer 2007b; Bret et al. 2016; Kanno et al. 2016).

The spatial extent to which recruitment synchrony occurs among salmonid populations has been described for mountainous regions. Lobón-Cerviá (2004) observed synchrony in Brown Trout recruitment among Spanish stream sites less than 30 km apart and concluded that similarities in streamflow levels among sites during or just after emergence were responsible for synchrony observed in Brown Trout population dynamics. Gowan and Fausch (1996) observed synchronous changes in adult trout abundance among six Colorado streams up to 60 km apart. Copeland and Meyer (2011) noted recruitment synchrony among salmonid populations spaced up to 330 km apart.

Less is known about the spatial extent of synchrony in salmonid population levels in groundwater-fed, low-gradient streams. For low-gradient (e.g., 0.1–0.2% gradient) streams draining glacial drift deposits in Michigan, synchrony in recruitment of Brook Trout and Brown Trout was noted for populations up to 140 km apart (Zorn and Nuhfer 2007a). Zorn and Nuhfer (2007a) observed that peak spawning and estimated swim-up periods for Brown Trout were synchronous among several streams in the northern Lower Peninsula of Michigan and that temporal patterns in average May discharge (associated with fry emergence) were synchronous for streams across much of Michigan, but corresponding biodata to evaluate trout population trends and synchrony were lacking. Likewise, Kanno et al. (2016) highlighted the lack of information characterizing the spatial extent of synchronous population dynamics for wide-ranging species such as Brook Trout.

Initiation of Michigan’s statewide inventory program in 2002 resulted in the establishment of over 30 salmonid population index sites throughout the state (Hayes et al. 2003), providing a spatially dispersed network of locations for assessing synchrony in recruitment of stream salmonids. These sampling locations include streams with resident Brook Trout and Brown Trout and reaches hosting naturally reproducing populations of adfluvial or resident Rainbow Trout. Negative effects of

Pacific salmonids on Brook Trout and Brown Trout populations, and of Brown Trout on Brook Trout, have been documented in Michigan and elsewhere (e.g., Waters 1983; Nuhfer et al. 2014; Zorn et al. 2020), and the extent to which such effects might obscure synchrony was unknown.

The goal of this study was to describe and better understand synchrony in Brook Trout, Brown Trout, and Rainbow Trout recruitment in low-gradient cold-water streams in the Great Lakes region of North America using data collected at these index sites in Michigan since 2002. Our specific objectives were twofold. First, we conducted a landscape-scale evaluation of whether synchrony in trout recruitment was greater for streams within a region than among regions by comparing correlations in density of trout age-classes. Second, we identified and mapped locations of trout populations whose recruitment dynamics appeared to be synchronous based on correlations between annual densities of age-0, age-1, and age-2 fish at sites, and used mapped patterns of synchronous recruitment to estimate the potential spatial extent of synchrony of recruitment in Michigan streams.

2 Methods

2.1 Study Area

Michigan, in the Great Lakes region of North America (Fig. 1), has an estimated 47,535 km of stream reaches capable of supporting salmonids (Zorn et al. 2018). Streams in this relatively flat region of North America support trout populations year-round due to high inflows of groundwater entering stream channels located downslope of coarse-textured glacial moraines and outwash features (Wiley et al. 1997; Zorn et al. 2002, 2020).

Michigan streams host an array of trout and salmon species, most of which are not native to the state (Zorn et al. 2018). Resident stream trout populations are largely self-sustaining, consisting of Brown Trout and Brook Trout. Brown Trout was first introduced into Michigan (and North America) in 1884, while Brook Trout is native to Michigan's Upper Peninsula and the northern tip of the Lower Peninsula (Zorn et al. 2020). Both species were widely stocked into Lower Peninsula streams during the late 1800s, resulting in widespread establishment of Brown Trout and substantial range expansion for Brook Trout (Zorn et al. 2020). Both species spawn in fall, with data from several Michigan streams indicating synchrony in periods when peak spawning and fry emergence occur (Zorn and Nuhfer 2007a).

Adfluvial populations of Rainbow Trout became established in Michigan within 20 years of the species introduction in 1876 (Michigan Department of Natural Resources (MDNR) 1974). Chinook Salmon and Coho Salmon were initially introduced in 1966 and 1967 to reduce nuisance-level populations of invasive Alewife *Alosa pseudoharengus* (Zorn et al. 2020). Adfluvial populations of these three species in the Great Lakes represent a combination of naturally reproduced and hatchery fish, with the contributions from each source varying by location (Zorn et al. 2020).

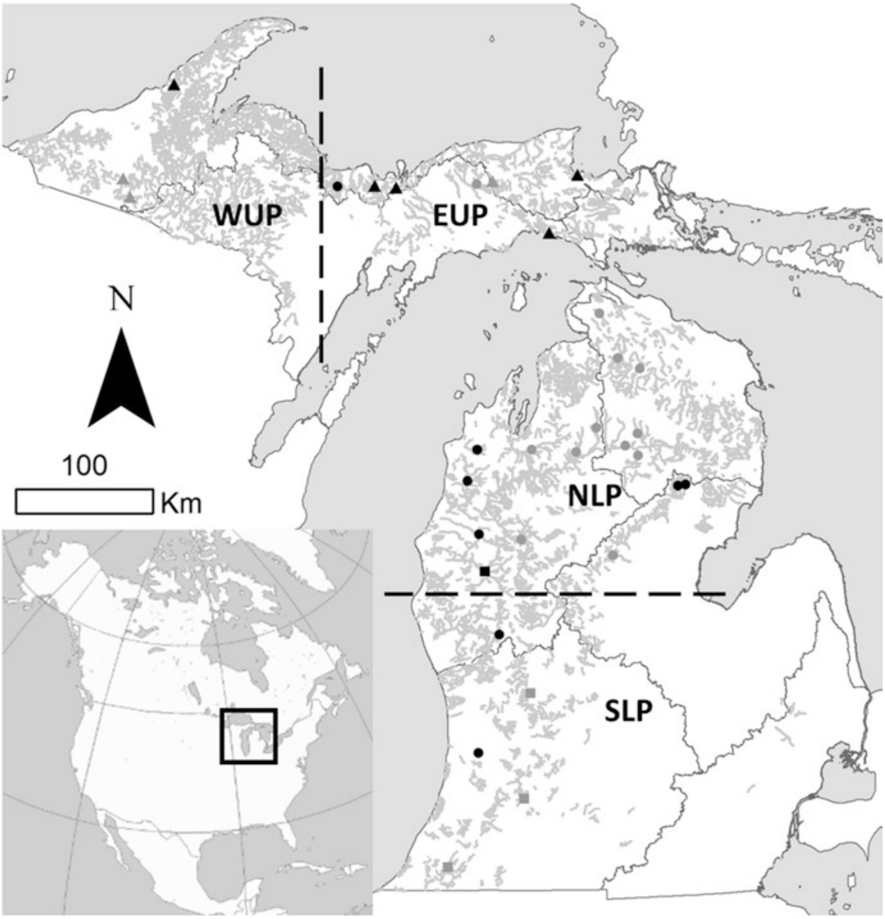

Fig. 1 Locations of index reaches on cold-water streams (gray lines) in Michigan, indicating Great Lakes accessibility and resident trout species present. Sites accessible to Pacific salmonid species are black and inaccessible (land locked) sites are gray. Possible combinations of resident trout species at sites were both Brook Trout and Brown Trout (circles), only Brook Trout (triangles), and only Brown Trout (squares). Dashed lines separate study regions Eastern and Western Upper Peninsula (EUP and WUP), and the Northern and Southern Lower Peninsula (NLP and SLP)

Fish population data were obtained from 32 long-term population index reaches (fixed sites) sampled from 2002 to 2019 under MDNR Fisheries Division's Status and Trends Program (Hayes et al. 2003). Fixed sites are geographically representative, providing a range of sizes, with some having Great Lakes access and others not (Table 1; Fig. 1). Most fixed sites were established at the initiation of the Status and Trends Program in 2002, with a few sites being added or discontinued since (Zorn et al. 2020). Trout populations in each stream are sustained entirely by natural reproduction and are representative of quality trout waters in that area of the state (Zorn et al. 2020).

Table 1 Attributes of study reach including region, stream name, site coordinates, trout species present indicated by "X" (BKT = Brook Trout, BNT = Brown Trout, RBT = Rainbow Trout), sampling rotation (1 or 2), with Great Lakes accessible (G Lks) reaches indicated with "Y". List is sorted by region (Fig. 1) and latitude of the reach sampled on a river (R) or creek (Cr)

Region	Stream	Latitude	Longitude	BKT	BNT	RBT	Rotation	G Lks
WUP	Elm R	47.02689	−88.85787	X		X	2	Y
WUP	Two Mile Cr	46.39431	−89.31069	X			2	
WUP	Middle Branch Ontonagon R	46.27693	−89.23872	X			1	
EUP	Naomikong Cr	46.46127	−84.98575	X		X	2	Y
EUP	Tahquamenon R	46.42391	−85.79789	X			1	
EUP	East Branch Fox R	46.40467	−85.94731	X	X		1	
EUP	Rock R	46.39078	−86.91258	X		X	1	Y
EUP	Chocolay R	46.38406	−87.26437	X	X	X	1	Y
EUP	North Branch Valley Spur	46.38060	−86.70893	X		X	2	Y
EUP	Davenport Cr	46.08248	−85.26009	X		X	2	Y
NLP	West Branch Maple R	45.55113	−84.79639	X	X	X	2	
NLP	West Branch Sturgeon R	45.25537	−84.63091	X	X	X	2	
NLP	Pigeon R	45.18495	−84.42838	X	X	X	1	
NLP	Manistee R	44.80001	−84.84069	X	X		1	
NLP	North Branch Au Sable R	44.75737	−84.45760	X	X		2	
NLP	Au Sable R	44.67992	−84.57599	X	X	X	1	
NLP	Platte R	44.65955	−85.94386	X	X	X	1	Y
NLP	Boardman R	44.65733	−85.43771	X	X		1	
NLP	North Branch Manistee R	44.64122	−85.02698	X	X		1	
NLP	South Branch Au Sable R	44.61379	−84.45641	X	X		1	
NLP	Bear Cr	44.45612	−86.03139	X	X	X	2	Y
NLP	Gamble Cr	44.41485	−84.02862	X	X	X	2	Y
NLP	Houghton Cr	44.40824	−84.09631	X	X	X	1	Y
NLP	Little Manistee R	44.10448	−85.92491	X	X	X	1	Y
NLP	Pine R	44.06974	−85.54030	X	X	X	2	
NLP	North Branch Tobacco R	43.95969	−84.70352	X	X		1	
NLP	Pere Marquette R	43.86023	−85.87194		X	X	1	Y
SLP	Bigelow Cr	43.44592	−85.74408	X	X	X	2	Y
SLP	Bear Cr	43.05770	−85.46510		X		2	
SLP	Silver Cr	42.66847	−85.93237	X	X	X	1	Y
SLP	Spring Brook	42.36344	−85.52986		X		1	
SLP	Pokagon Cr	41.91440	−86.20560		X		1	

2.2 Sampling Methods

Fish populations at fixed sites were sampled during 2002–2019. Fixed sites are generally sampled in 3 years on 3 years off rotations which enables broader spatial coverage (for a fixed level of sampling effort) of Michigan while allowing estimation of annual survival of resident trout age-classes in 2 of the 3 survey years at a site (Wills et al. 2006; Zorn et al. 2020). About 90% of electrofishing reaches were 305 m, with longer or shorter survey reaches (from 229 to 488 m in length) occurring for some sites to match reaches historically sampled prior to 2002 (Zorn et al. 2020).

Population estimate surveys were typically conducted at the same time of year for an individual reach, with the low-flow month of August being the target period for surveys across all fixed sites in Michigan (Zorn et al. 2020). Salmonid population estimates were made via mark–and–recapture electrofishing (without block nets) using 240-volt DC tow-barge or backpack electrofishing units. The number of anodes used ranged from one to three across all survey locations, varying with stream size, but was consistent through time at each survey reach (Zorn et al. 2020). Fish sampling began at the downstream end of the study area and proceeded upstream. Resident trout and Pacific salmonids captured on the marking run received a small caudal fin clip to identify them on the recapture run; clips were regenerated between years (Zorn et al. 2020). Recapture collections were typically made 1–2 days after marking. Population estimates were computed for 25-mm length groups of resident trout using the Chapman modification of the Petersen mark–recapture method (Ricker 1975). Scales were taken from up to 10 trout per 25-mm length group and the aging results were used to apportion population estimates by length groups into estimates by age-class (Zorn et al. 2020). Additional detail on field and population estimation methods occurs in Wills et al. (2006) and Zorn et al. (2020).

Population estimates were reasonably precise with the standard deviation about non-zero estimates for age-0, age-1, and age-2 trout being within 18.5%, 13.4%, and 19.1% of the estimate value, based on 550, 530, and 276 population estimate surveys, respectively (Zorn and Hessenauer, unpublished data). Field survey measurements, scale aging data, and population estimates from all surveys are stored in a centralized database. We queried species and age-class-specific population estimates for each fixed site survey from this database for our analysis.

2.3 Statistical Analysis

Synchrony within regions vs. between regions—We expected synchrony to be greater among populations within a region than populations between regions, so tested the hypothesis that mean correlations for pairs of sites within a region would be more positive than those based on pairings of sites among regions. We divided the state into four regions (Fig. 1) having similar spatial extent and watershed-based boundaries generally corresponding to existing MDNR fisheries management units, the Southern Lower Peninsula (SLP), Northern Lower Peninsula (NLP), Eastern Upper Peninsula (EUP), and Western Upper Peninsula (WUP). We focused on age-0, age-1, and age-2 Brown Trout, Brook Trout, and Rainbow Trout, analyzing each age-species combination separately and combining results for the two sampling rotations. For each species-age combination, we obtained Pearson correlations for all pairs of sites within the region and did the same for all pairs of sites representing each combination of regions. We then calculated the mean and standard error for all correlations within and between regions. We did not report values for regions where there were insufficient pairs of sites for computing a standard error value. These criteria eliminated WUP sites from the analysis.

Identifying pairs of synchronous populations—We examined correlations among age-class densities to identify pairs of sites where trout populations appeared to be synchronous, restricting our selection of potentially synchronous sites as follows. For sites having at least 5 years of paired population estimates, we identified pairs of sites whose Pearson correlation coefficients for a given species and age-class were positive and significant at $P < 0.05$. We limited our selection to pairs of sites having at least 5 years of observations to minimize the likelihood of spurious correlations due to low sample sizes and excluded significant correlations for pairs of sites when zeros made up the large majority (e.g., all but one or two) of the density estimate values for a location.

For each species and age-class studied, pairs of sites showing synchrony were mapped using lines to connect significantly correlated sites. Visual analysis of spatial patterns in significant correlations provided insight into the potential spatial extent of synchronous recruitment patterns for each species in Michigan.

3 Results

Synchrony within regions vs. between regions—Summary of 923 correlation coefficients indicated synchrony in age-class densities was generally greater among streams within a region than between streams in neighboring regions for Brown Trout and Brook Trout, but not Rainbow Trout (Table 2). For each age-class of Brown Trout, mean correlation coefficients from all pairings of sites within the NLP and SLP were higher than mean correlation values when NLP and SLP sites were paired, though considerable variation occurred around each mean value (Table 2). The same was true for Brook Trout, except that the mean correlation coefficient for age-1 brook trout in NLP stream pairings was lower than that from NLP-EUP pairings. For Rainbow Trout, mean correlation coefficient values from between region pairings of sites were greater than those from within region pairings of sites, except for age-1 fish in the EUP (Table 2). Several regions were not included due to limited occurrence of a species (e.g., Brown Trout in EUP and WUP; Brook Trout in SLP)

Table 2 Mean, standard error, and number (*n*) of Pearson correlations by fish species and age-class (1, 2, or 3) within and between different regions of Michigan. Regions are Northern Lower Peninsula (NLP), Southern Lower Peninsula (SLP), and Eastern Upper Peninsula (EUP). Region category with "-" between regions represents correlations for pairs of sites where one site was in each of the regions shown

	Mean correlation			SE			*n*		
Region	0	1	2	0	1	2	0	1	2
Brown trout									
NLP	0.119	0.147	0.274	0.051	0.045	0.039	70	81	81
NLP-SLP	−0.134	−0.040	−0.106	0.057	0.068	0.063	45	48	48
SLP	−0.040	0.018	0.125	0.320	0.157	0.094	4	4	4
Brook trout									
EUP	0.014	0.176	0.355	0.154	0.148	0.100	9	9	9
EUP-NLP	−0.035	0.170	−0.039	0.061	0.057	0.062	50	59	50
NLP	0.053	0.035	0.009	0.070	0.054	0.065	43	69	43
Rainbow trout									
EUP	0.023	0.444	−0.356	0.115	0.061	0.138	2	2	2
EUP-NLP	0.063	0.314	0.090	0.073	0.072	0.079	24	27	25
NLP	0.013	0.200	−0.117	0.059	0.074	0.059	32	46	37

or a lack of sites or sites within a rotation needed for calculating within region standard errors (e.g., all species in WUP; Rainbow Trout in WUP and SLP).

Identifying pairs of synchronous populations—We identified 66 significant positive correlations indicative of synchrony in recruitment between pairs of stream sites from 1252 correlations examined. Significant positive correlations in fish density occurred for age-0 Brook Trout at 9 pairs of sites, age-1 fish at 10 pairs of sites, and age-2 fish at 8 pairs of sites (Fig. 2). Correlated sites were up to 430 km apart (based on straight-line distance between sites), often spanning Great Lakes drainage divides and sometimes the Upper and Lower peninsulas of Michigan.

Brown Trout year-classes showed considerable synchrony at age-0 and as year-classes aged. Significant positive correlations in fish density occurred for age-0 Brown Trout at 8 pairs of sites, age-1 fish at 10 pairs of sites, and age-2 fish at 10 pairs of sites (Fig. 3). An additional 8 pairs of sites were approaching significance, having P values <0.10. Significant positive correlations in density occurred for sites that were up to 350 km apart.

The extent of synchrony in Rainbow Trout densities among streams seemed to differ with the age-class examined. Significant positive correlations in age-0 Rainbow Trout density occurred for only one pair of sites, but significant positive correlations occurred for 10 pairs of sites when analyzing age-1 fish, with an additional 4 pairs of sites approaching significance having *P* values <0.10 (Fig. 4). No pairs of sites had significant positive correlations in density of age-2 Rainbow Trout. Rainbow Trout in nearly all study reaches were from adfluvial populations, so age-2 fish may often have out-migrated to the Great Lakes prior to sampling, confounding

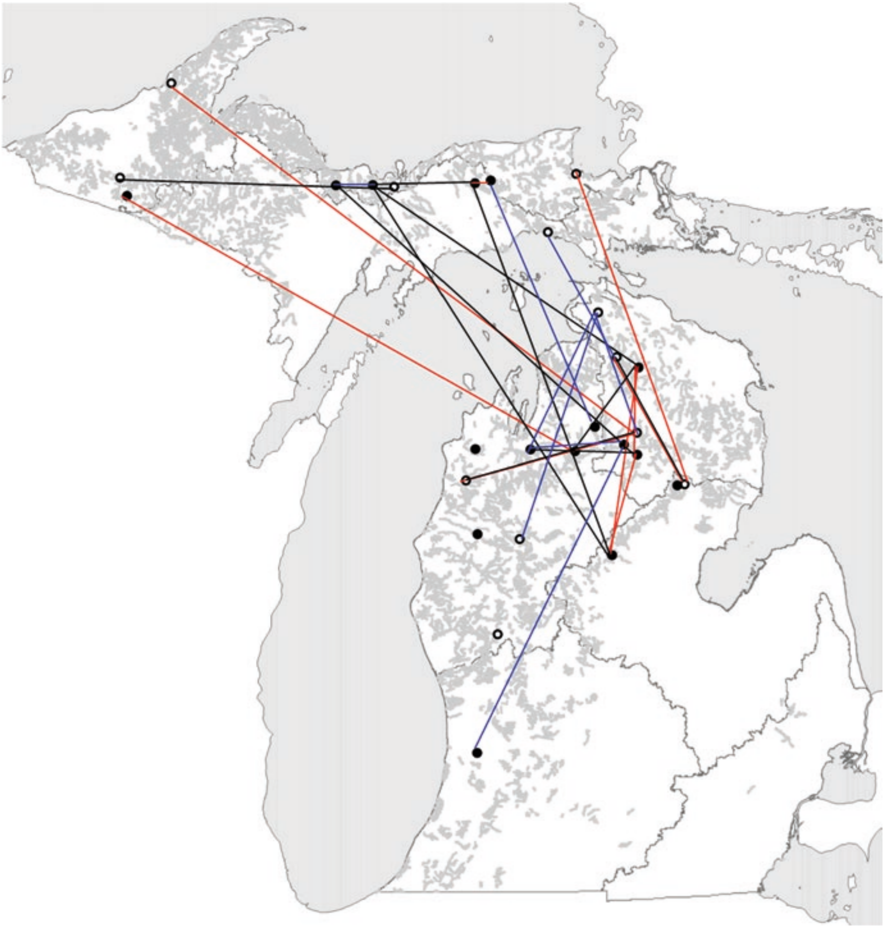

Fig. 2 Map of index sites on Michigan streams showing sampling rotation (open vs. closed circles) with lines connecting sites where densities of age-0 (red lines), age-1 (black lines), or age-2 (blue lines) Brook Trout were significantly correlated ($P < 0.05$) over time. Correlations could not be calculated between sites in different sampling rotations

detection of year-class synchrony at age-2. For sites where Rainbow Trout occurred, 54% of age-2 density values were zero while only 30% of age-0 density values were zero. Of the three species studied, age-class density values of zero occurred most often for Rainbow Trout (34% of values), followed by Brook Trout (22%) and Brown Trout (6%). Significant positive correlations in density of Rainbow Trout occurred for sites up to 260 km apart.

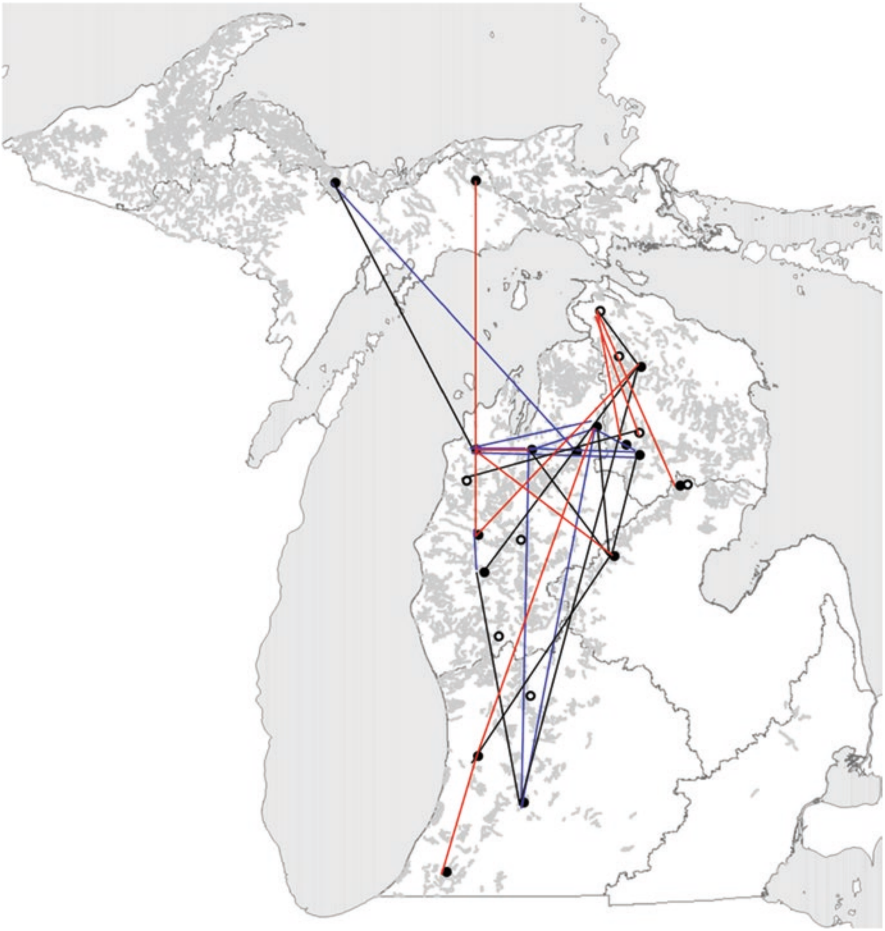

Fig. 3 Map of index sites on Michigan streams showing sampling rotation (open vs. closed circles) with lines connecting sites where densities of age-0 (red lines), age-1 (black lines), or age-2 (blue lines) Brown Trout were significantly correlated ($P < 0.05$) over time. Correlations could not be calculated between sites in different sampling rotations

4 Discussion

Our findings of stronger patterns of synchronous recruitment of Brown Trout and Brook Trout within regions compared to between regions were consistent with previous studies highlighting synchronous recruitment at relatively small spatial scales. For example, Gowan and Fausch (1996) observed synchrony in abundance of adult Brown Trout, Brook Trout, and Rainbow Trout across a 60-km area, Lobón-Cerviá (2004) noted synchrony among Brown Trout in Spanish streams less than 30 km apart, and Myers et al. (1997) suggested a scale of less than 50 km for freshwater

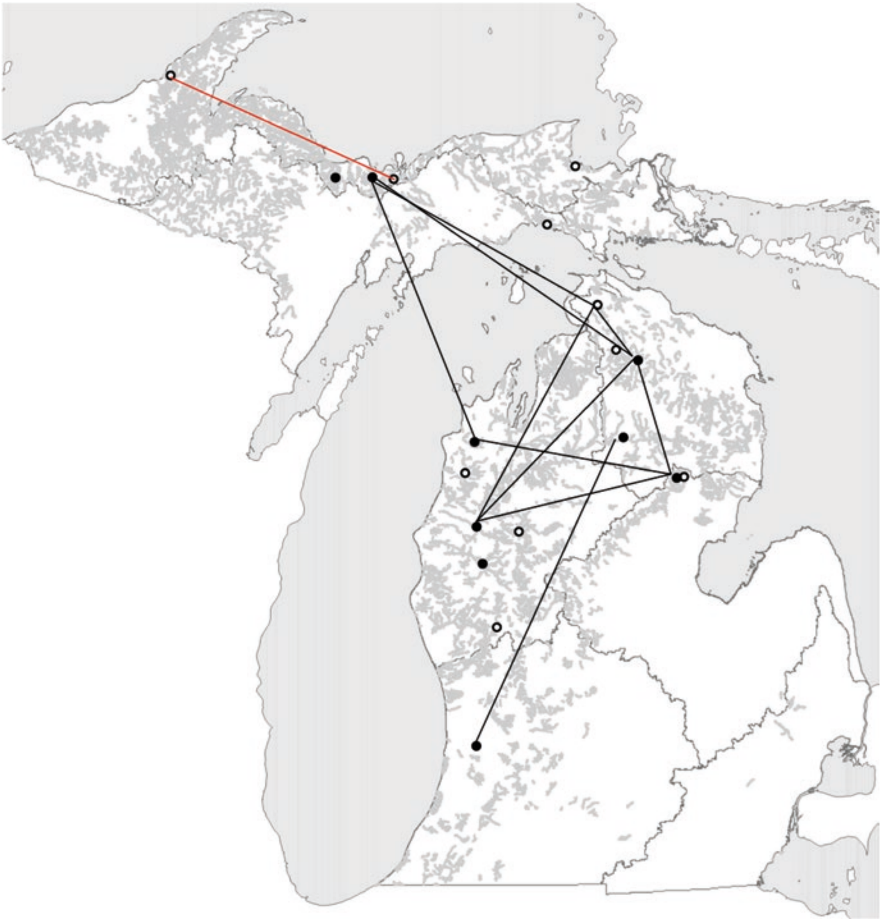

Fig. 4 Map of index sites on Michigan streams showing sampling rotation (open vs. closed circles) with lines connecting sites where densities of age-0 (red lines), age-1 (black lines), or age-2 (blue lines) Rainbow Trout were significantly correlated ($P < 0.05$) over time. Correlations could not be calculated between sites in different sampling rotations

fish. Consistent with our findings, Bergerot et al. (2019) found that synchrony among Brown Trout populations in France did not occur across the entire country but was more localized and likely to occur among streams whose streamflow patterns were synchronous, especially during periods critical for trout reproduction.

The maximum spatial extent of synchronous population dynamics we noted (430 km for Brook Trout, 350 km for Brown Trout, and 260 km for Rainbow Trout) was greater than estimates in most studies to date. Copeland and Meyer (2011) noted synchrony of six salmonid species, including steelhead and Brook Trout, across a 330 km region of Idaho. Bret et al. (2016) noted strong synchrony in Brown Trout year-classes for streams less than 75 km apart and strong synchrony in flows at emergence across distances over 200 km. The broader spatial extent of synchrony we noted likely relates to the greater sampling extent of our study and similarities in seasonal stream discharge patterns among streams in the Great Lakes region due to its relatively flat topography and uniform climate (Albert 1995). For example, Zorn and Nuhfer (2007a) documented significant correlations in May discharge among Michigan streams spanning several 100 km, many of which support trout and were included in this study.

Correlations in fish densities observed among fixed sites during 2002–2019 were consistent with findings of analyses of long-term trout population data from seven Michigan streams (Zorn and Nuhfer 2007a). As in their study, we saw significant correlations in Brook Trout and Brown Trout age-class densities for rivers in northern portion of Michigan's Lower Peninsula (Figs. 2 and 3). We also observed numerous significant correlations in Brook Trout densities between pairs of sites in Michigan's Lower and Upper peninsulas, with fewer pairs for Brown Trout since they are less widely distributed in the Upper Peninsula (Figs. 2 and 5; Table 1). Likewise, significant correlations in Brook Trout and Brown Trout density occurred between sites in northern and southern portions of the Lower Peninsula. Such correlations align with spatial correlations in spring discharge on trout streams throughout Michigan (Zorn and Nuhfer 2007a), suggesting similarity in spring flow conditions within regions help to synchronize trout year-class strength and abundance trends (Zorn and Nuhfer 2007b) over time across the region.

In contrast to the positive mean correlations we typically observed, the mean correlations for age-0 and age-2 brown trout densities between sites in the NLP and SLP were negative, having absolute values greater than 0.1 (Table 2). Opposing

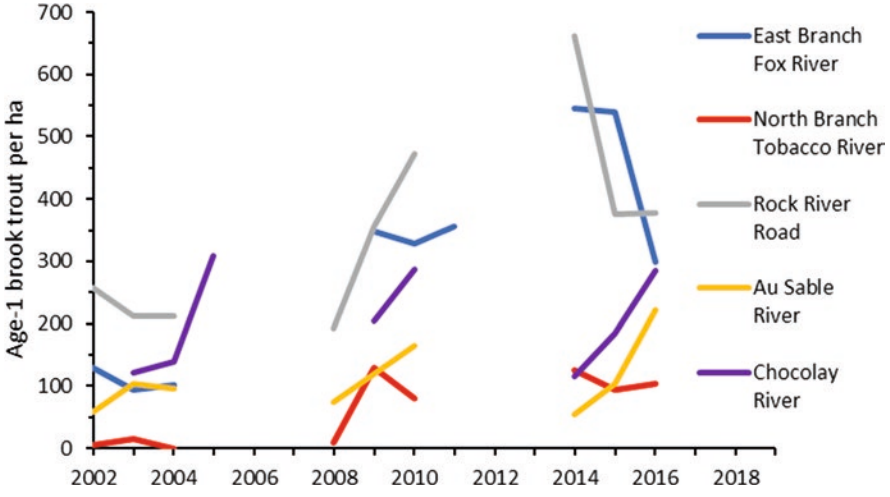

Fig. 5 Densities of age-1 Brook Trout at two fixed sites in Michigan's Upper Peninsula lacking Brown Trout (East Branch Fox River and Rock River) and three sites having both Brown Trout and Brook Trout, one in the Upper Peninsula (Chocolay River) and two in the Northern Lower Peninsula (North Branch Tobacco and Au Sable rivers)

long-term trends in spring discharge between these regions of the state (Hodgkins et al. 2007) may contribute to contrasting trends in trout recruitment, but other factors may be responsible as well.

Given the many correlations examined, one might expect a portion of them to be statistically significant due to chance. We estimated that 31 positive correlations might be statistically significant due to chance (using a two-tailed significance level of 0.05) if the 1252 correlations we examined were normally distributed. Despite our use of additional criteria to restrict selection of significantly correlated pairs of sites for mapping (Figs. 2–4), the 66 pairs we mapped represented over twice the number of significant positive correlations than would be expected by chance. In addition, correlation analyses of longer-term age-class abundance data for brook trout and brown trout at several of these sites provide further evidence of synchronous recruitment (Zorn and Nuhfer (2007a). While some correlations may be significant by chance, we conclude that most indicate populations showing synchronous patterns of recruitment.

Our study provides scarce documentation of recruitment synchrony in wild steelhead because adfluvial populations occurred at all fixed sites with Rainbow Trout, except the land-locked Au Sable and Pine river sites. Most naturally reproducing steelhead spawn in Michigan rivers between late February and early May, with peak spawning usually in April (M. Tonello, Michigan Department of Natural Resources, personal communication). Fry typically emerge in late spring or early summer and are likely similarly vulnerable to high flows as fry of Brook Trout and Brown Trout (Zorn and Nuhfer 2007a). Gowan and Fausch (1996) observed concordance in adult trout abundance in a Colorado study that included Rainbow Trout and three other trout species, but none of their study populations were adfluvial. In his study of wild steelhead population dynamics in British Columbia rivers, Smith (2000) identified flow-induced mechanisms capable of increasing juvenile mortality, loss of low-velocity refuge habitat for parr (Fausch 1993) during years of high flows and the premature flushing of juveniles out of suitable habitat or the river by high flows (Nehring and Anderson 1993; Latterell et al. 1998).

We observed significant correlations in age-1 steelhead density between distant streams in Michigan's Upper and Lower Peninsulas (Figs. 4 and 6). The relatively high level of synchrony we observed among age-1 steelhead (Table 2) may relate to the short-term nature of their interactions with resident trout (Copeland and Meyer 2011). There may also be fewer stock-recruitment influences on juvenile steelhead abundance, compared to those for stream-dwelling Brown Trout or Brook Trout (Zorn and Nuhfer 2007b), since spawning habitats in study reaches may regularly be saturated with eggs from highly-fecund female Rainbow Trout that grew to maturity in Great Lakes habitats (Chapman 1966; Nuhfer et al. 2014).

The occurrence of synchronous steelhead recruitment in Michigan streams (e.g., Fig. 4) is notable given earlier studies suggesting the considerable contribution of stocked fish to spawning runs. For example, Bartron and Scribner (2004) estimated an average of 40% of spawners in Lake Michigan tributaries in Michigan during 1998–1999 being from stocking. While our study streams were not stocked, other streams and the Great Lakes are, so the ability to detect synchrony in age-0 or age-1

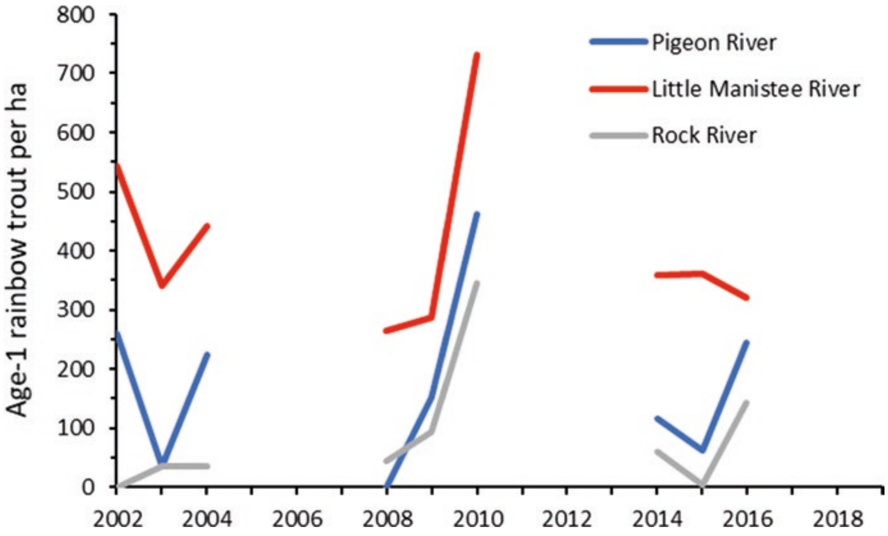

Fig. 6 Densities of age-1 migratory Rainbow Trout at one fixed site in Michigan's Upper Peninsula (Rock River) and two Northern Lower Peninsula fixed sites (Little Manistee and Pigeon rivers)

Rainbow Trout densities between some study streams could potentially be affected by spatial or temporal changes in steelhead stocking elsewhere that affect adult run size and egg deposition in study reaches.

We saw little synchrony for age-0 Rainbow Trout, but the size of age-0 fish may likely differ among rivers and years, which could influence their vulnerability to electrofishing sampling in late summer. This could limit comparability of age-0 Rainbow Trout densities among sites and years, and ultimately assessment of synchrony for age-0 fish.

We noticed that pairs of sites significantly correlated for one age-class of a species were often not correlated for other age-classes of that species. This does not necessarily indicate that synchrony does not persist between pairs of sites and may instead be indicative of immigration or emigration of fish resulting from differences between reaches in amounts of suitable habitat for each age-class of fish. Fish may stay within a reach if provides adequate habitat as they grow older and larger, but oftentimes they move elsewhere seeking food resources and habitats better suited to their changing needs. Such source-sink dynamics and differences between reaches in habitat and food resources available for a species and age-class can mask occurrence of synchrony. Thus, an apparent lack of reproductive synchrony between some nearby streams may more often relate to occurrence of habitat conditions that fish repeatedly migrate to or from than a lack of shared temporal patterns in the timing of trout spawning, incubation temperatures, or spring flow conditions (Zorn and Nuhfer 2007a).

4.1 Limitations

Some aspects of the data used in this study limit our findings, with a primary limitation being relatively small number of observations at sites. While our study covers a nearly 20-year period, streams were only sampled in half of the period due to the sampling rotation. Rotational sampling was chosen to enable greater spatial coverage of fixed sites for the limited sampling effort that was available for this work, with the understanding that it would result in fewer samples at each site over time. While this leads to greater uncertainty regarding the extent of synchrony between sites, previous documentation of synchrony among populations in some of these rivers from longer-term analysis (Zorn and Nuhfer 2007a) suggests that significant patterns of synchrony we observed in this analysis may often persist and increase in statistical significance over time as sampling continues.

While the rotational sampling enabled field crews to sample more fixed sites within their management unit, this approach sometimes hindered evaluation of synchrony between nearby fixed sites because crews often alternated annual surveys between them (i.e., their rotations differed). This issue could be addressed by periodically sampling nearby sites that were on different rotations during the same year, though this would be extra work for field crews unless scheduled sampling at other fixed sites was cancelled.

In some situations, low densities of a species at a location complicate our ability to document synchrony with certainty. Low densities of a species age-class at a site could relate to unsuitable habitat (e.g., Raleigh et al. 1986; Zorn et al. 2011), interspecific interactions that reduce the amplitude of temporal variation in abundance (Waters 1983; Nuhfer et al. 2014; Zorn et al. 2020), or other factors. To overcome this issue, we limited the selection of significant correlations to pairs of sites having densities greater than zero in most years for the species and age-class of interest. However, more years of paired observations are needed to further clarify synchrony between some pairs of sites for specific species and age-class combinations.

Deterministic processes, particularly interspecific and intraspecific interactions, are known to influence abundance of trout age-classes and can obscure effects of factors favoring synchrony in recruitment (Strange et al. 1993). In general, one might expect density-dependent survival to reduce the relative abundance of strong year-classes over time and increase the abundance of weak year-classes. Interspecific competition and predation will also alter the abundance of year-classes from levels initially “set” by flow conditions during critical periods. For example, in the relatively benign environments provided by Michigan’s groundwater-fed streams, intraspecific effects have been documented for Brown Trout and Brook Trout (Zorn and Nuhfer 2007b; Grossman et al. 2012), and interspecific effects observed for Brown Trout on Brook Trout (Zorn and Nuhfer 2007b; Zorn et al. 2020), Rainbow Trout on Brown Trout (Kocik and Taylor 1995; Nuhfer et al. 2014) and Pacific salmonids on Brown Trout and Brook Trout (Zorn et al. 2020).

4.2 Management Implications

The persistence of synchronous patterns in year-class strength to older ages highlights the importance of flow-related effects on trout recruitment and population abundance trends. The positive correlations we observed for older age-classes are consistent with previous studies with Brook Trout, Brown Trout, and migratory Rainbow Trout suggesting year-class strength effects carry through from early ages to adulthood in these species (e.g., Smith 2000; Lobón-Cerviá 2007; Zorn and Nuhfer 2007a, b). That the previous year's abundance of an age-class was often the best predictor of its abundance the following year was especially notable given significant influences of other habitat factors and inter- and intraspecific effects on age-specific densities of these species in Michigan (Zorn and Nuhfer 2007b; Nuhfer et al. 2014; Zorn et al. 2020). We suspect the propagation of recruitment and synchrony effects to older age-classes likely occurs elsewhere, given the results of trout population dynamics studies in other regions of the world (e.g., Strange et al. 1993; Elliott 1994; Gowan and Fausch 1996; Lobón-Cerviá 2007; Copeland and Meyer 2011).

By controlling for site-scale variation, our index site sampling approach enables a coherent picture of synchronous patterns in temporal variation in fish populations to emerge at the regional scale. Such temporal patterns can readily be overwhelmed by variation due to site- or stream-scale conditions when sampling locations change from year to year. For example, analysis of long-term data from four Michigan streams (i.e., mainstem Au Sable River, North and South branches Au Sable River, and South Branch Paint River) showed 50% changes in Brown Trout biomass density could be detected with 3, 3, 4, and 9 years, respectively, of pre- and post-data from the index site, while more than 15 years of pre- and post-data would be needed to detect the same change if one of these index sites was randomly chosen for sampling each year (Wills et al. 2006). Such findings highlight the need for index sites in trend monitoring programs for streams.

In addition to being of ecological interest, understanding spatial extent of synchrony has management utility. Since the waters sampled provide representative coverage of trout streams around the state, understanding the spatial extent of regional trends in trout recruitment and population synchrony better positions fishery managers to evaluate relative influences of local-scale factors and larger-scale climatic and hydrologically driven processes on trout abundance levels (Zorn et al. 2023). For example, the identification of asynchronous patterns among typically synchronous sites (e.g., low recruitment at a site during a period of high recruitment in the region) suggests local-scale factors may be affecting trout reproductive success at the site. Understanding current trout population levels is of considerable interest to anglers, fishery managers, interest groups, and individuals, so making such data publicly available is desirable. To satisfy these interests in a user-friendly manner, trout population data from fixed sites in Michigan are available online via MDNR's Stream Fish Population Trend Viewer (Zorn et al. 2023).

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The Use of Net Energy Intake Models to Predict Microhabitat Selection by Drift-Feeding Fishes: Are Common Assumptions Warranted?

Bryan B. Bozeman and Gary D. Grossman

Abstract Net energy intake (NEI) models are useful for quantifying mechanisms driving habitat selection in drift-feeding stream fishes; nonetheless, their complexity has limited their application in conservation. We evaluated the validity of assumptions and the performance of multiple variants of an exemplar NEI model for juvenile Chinook Salmon (*Oncorhynchus tshawytscha*), Dolly Varden Char (*Salvelinus malma*), and Arctic Grayling (*Thymallus arcticus*) in interior Alaska. We tested model assumptions that: (1) drift concentration, (2) fish visual reaction area, and (3) swimming cost do not vary meaningfully within the range of focal velocities occupied by drift-feeding stream fishes and can therefore be treated as constants or ignored. We then compared the predictive success of complex and simplified model variants. Comparisons of literature and field data indicated model assumptions were: (1) plausible, (2) plausible, and (3) implausible, respectively. Simplified model variants generally performed as well or better than the complex model. Drift concentration, visual reaction field, and swimming cost are important components of drift-feeder habitat selection; however, the difficulty of accurately estimating these variables may currently limit the utility of complex NEI models. Simplified NEI models are pragmatic tools for addressing urgent conservation needs and can guide development of complex NEI models as estimation techniques improve.

Keywords Habitat · Optimal foraging · Stream fishes · Net energy intake · Focal position · Velocity

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1 Introduction

Rivers and streams are important habitats for many aquatic organisms, including the highly diverse fish assemblages of North America (Abell et al. 2008; Grossman et al. 1990; Poff et al. 2001). Many fishes in these lotic systems—including many if not most salmonids—feed on prey drifting downstream in the water column for all or a part of their lifetime and are known as drift-feeders (Quinn 2018). Drift feeding is a distinct foraging strategy whereby: (1) individuals occupy a fixed focal position facing upstream, (2) pursue and intercept prey flowing downstream, and (3) return to their initial focal position after attack. The suite of physical and biological characteristics in the immediate vicinity (~ m^2) of a fish's focal position comprise its microhabitat (Grossman and Freeman 1987; Piccolo et al. 2014; Grossman 2014).

Given that streams are heterogeneous in space and time, the ability to discern and select favorable microhabitats from the mélange of available options within the broader habitat matrix has important implications for individual fitness (Vannote et al. 1980; LaPerriere 1981; Hughes 1992). Studies of the mechanisms affecting microhabitat choice of drift-feeders have long been of interest to ecologists, because of their relevance to community and behavioral ecology, habitat and population management, and conservation (Jenkins 1969; Everest and Chapman 1972; Grossman et al. 1998). Correlative habitat selection studies comparing abundance to physical and chemical habitat characteristics are common but are generally unable to identify specific characteristics that drive habitat use (Boyce and McDonald 1999). Mechanistic models are a promising alternative to correlative studies because they quantify habitat characteristics relevant to a target species' physiology and behavior (e.g., energy balance) and, ultimately, fitness (Grossman 2014; Rosenfeld et al. 2014; Naman et al. 2019).

Mechanistic net energy intake (NEI) models are useful tools that quantify the energetic benefits and costs associated with microhabitat use by drift-feeding stream fishes and then predict focal position selection or potential growth or abundance based on energy optimization criterion (Hayes et al. 2007, 2016; Wall et al. 2015). By quantifying the energetic benefits and costs associated with a given focal position, NEI models can identify optimal focal positions where the difference between the energetic benefits and costs is the greatest (Fig. 1). Drift-feeders are good candidates for mechanistic habitat use studies because they have been shown to preferentially select focal positions on the basis of energy optimization by occupying the stream position that affords the greatest energy intake that they can successfully defend in competitive hierarchies (Fausch 1984; Hughes 1998; Rosenfeld et al. 2014). Most NEI models assume drift-feeders maximize fitness by selecting focal positions that optimize energy intake (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993); however, newer models have begun incorporating elements of survival (e.g., predation risk) in addition to strict energy optimization (Railsback et al. 2021).

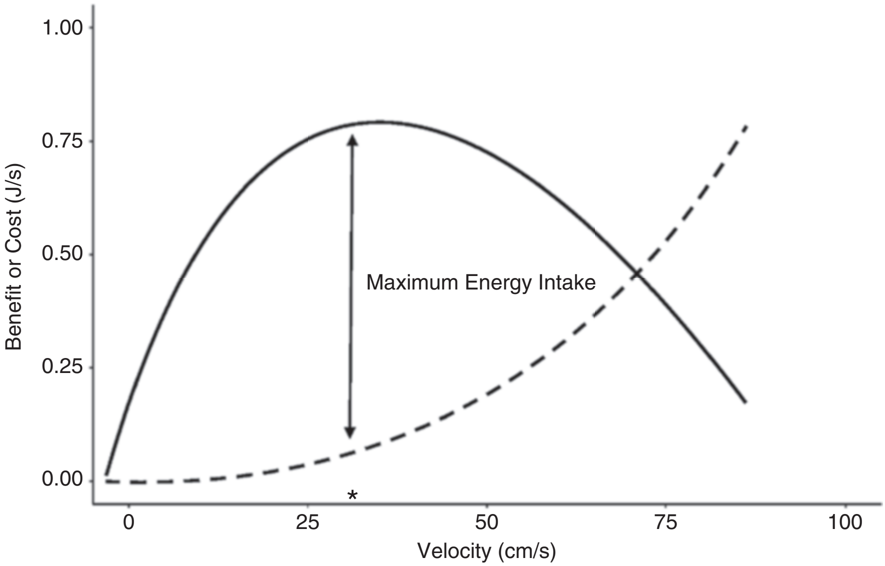


Fig. 1 Conceptual depiction of a cost–benefit NEI model for microhabitat use (via focal position velocity). The broken line is energetic cost; the solid line is energetic benefit. The maximum difference between cost and benefit lines is the optimal focal position velocity (denoted with an asterisk) where NEI is maximized

1.1 NEI Model Background

NEI models are grounded in optimal foraging theory, which connects habitat choice and foraging to fitness via energy optimization within the heterogeneous environmental matrix of a stream (MacArthur and Pianka 1966; Pyke et al. 1977; Schoener 1971). The many NEI models that have been developed and refined in the decades since Fausch's (1984) original model vary in predictive goals, information requirements, complexity, and realism (Piccolo et al. 2014; Rosenfeld et al. 2014). NEI models with different predictive goals have different input requirements and different sensitivities to potential biases of those inputs. Models that predict instantaneous microhabitat selection rank stream positions by their relative energetic potential (e.g., Guensch et al. 2001; Grossman et al. 2002). Therefore, slightly biased estimates of microhabitat energetic potential—via inaccurate estimates of input variables or structural errors in how the model estimates NEI—may still produce accurate predictions of optimal focal point velocities as long as the relative ranking of microhabitats is correct. Conversely, models that predict drift-feeder growth or abundance over entire stream reaches or fish lifespans (e.g., Hayes et al. 2000, 2007; Wall et al. 2015) are dependent on accurate input variable estimates (e.g., drift abundance, swimming costs) to produce accurate estimates of absolute NEI. Therefore, NEI models that predict instantaneous microhabitat selection based on relative energetic potential may be more easily and appropriately simplified and generalized than NEI models which rely on more complete characterizations of absolute NEI to predict potential growth or carrying capacity at a given site.

NEI models also differ in terms of the variables they use to quantify energetic benefits and costs to predict habitat use. Variables associated with energetic gain include prey energy content, density of prey in the drift, and prey encounter and capture rates (e.g., Grossman et al. 2002; Jenkins and Keeley 2010; Naman et al. 2019). Energetic cost variables include metabolic cost of swimming at focal positions, maneuvering costs for prey pursuit and capture, and prey processing costs, which often are estimated via equations from bioenergetic models for different species (Hughes and Kelly 1996; Hayes et al. 2000, 2016). Finally, NEI models with both instantaneous and long-term predictive goals frequently incorporate environmental and behavioral variables hypothesized to influence fish energetics, including velocity, depth at fish focal position, fish visual reaction area, foraging time, turbidity, presence of competitors, and amount of woody material (Harvey and Railsback 2009; Wall et al. 2017; Kalb et al. 2018).

The variables included in a given NEI model are largely dependent upon the predictive goals of the model, the species or system it is to be applied to, and insights gained from previous modeling and parameter estimation efforts. Most contemporary NEI models are built on the shoulders of one or more foundational models (Piccolo et al. 2014). For instance, Dodrill et al. (2016) developed an NEI model based on a previous model adapted by Hayes et al. (2000) from one of the earliest NEI models (Hughes and Dill 1990). The development of new NEI models is an incremental process incorporating more recent information, such as variable estimates or measurements that previously were held constant or neglected. For example, Hayes et al. (2016) incorporated the effects of velocity and turbidity on prey capture success, as well as prey pursuit costs across velocity gradients, which were not included in an earlier iteration of the model (Hayes et al. 2007). In general, mechanistic drift-foraging NEI models are better predictors of drift-feeder growth than correlative models and newer, more realistic NEI models ostensibly should be better predictors of drift-feeder habitat selection than their predecessors (Grossman 2014; Naman et al. 2019). However, empirical comparisons of the performance of incrementally progressive NEI models are rare (Hughes and Dill 1990; Naman et al. 2019; Jowett et al. 2021). Model parsimony generally is desirable, and more work is needed to assess how NEI models with differing amounts of complexity and biological realism perform in comparative studies with the same data.

In all modeling applications, there is tension between ease of parameterization and use, and biological realism. Simplified NEI models contain few input variables and are relatively easy to parameterize and test. For instance, an NEI model that uses the relationship between prey capture success and velocity to predict optimal focal point velocity is easily parameterized via laboratory experiments that characterize this relationship (e.g., Hill and Grossman 1993). However, the mechanistic insight and predictive value of these simplified models may be limited because they do not incorporate all variables that potentially influence focal position selection, such as the amount of available prey in the drift, metabolic costs of swimming and pursuing prey, or fish visual reaction area. This fact necessitates evaluation of simplified models under varying conditions and with varying species.

Conversely, complex NEI models incorporate a range of biological and physical variables to more accurately characterize biological reality. Because complex models may more closely approximate the actual habitat conditions and foraging processes that determine drift-feeder focal position selection, they potentially have greater ability to explain habitat use, growth or carrying capacity than simplified models. However, the predictive ability success of complex NEI models is dependent upon our ability to estimate input variables precisely and accurately. Each variable incorporated into a complex model has both a value and an error term; if variable error terms are large, models that incorporate greater realism may actually exhibit reduced ability to predict optimal focal velocities, growth, or reach-specific abundances. Furthermore, the high spatial and temporal heterogeneity of complex variables, such as macroinvertebrate drift dynamics, further complicates our ability to incorporate these processes in NEI models in useful ways (Brittain and Eikeland 1988; Naman et al. 2016).

Species-specific data for some complex NEI model variables is limited, so researchers sometimes substitute data from different species to parameterize models. For example, Brett and Glass' (1973) swimming cost equations for Sockeye Salmon (*Oncorhynchus nerka*) and Rao's (1968) model of oxygen consumption of Rainbow Trout (*Oncorhynchus mykiss*) frequently are used to estimate some or all of the metabolic costs associated with drift-feeding for other salmonid species (e.g., Hayes et al. 2000; Hughes and Dill 1990; Rosenfeld and Taylor 2009) or are extrapolated beyond the range of temperatures, masses, and velocities to which the original models were fit. Species-borrowing is not inherently bad, but even closely related species can exhibit substantively different metabolic rates (Trudel and Welch 2005). Therefore, the utility of complex NEI models that incorporate greater biological realism may be limited or negated by practical constraints associated with uncertainty regarding the quality and error of parameter estimates, or a lack of empirical data.

Simplified predictive models sometimes emerge when modelers, who set out to explain a natural phenomenon with as much biological realism as is practical, observe that one or a few model parameters exert disproportionate effects on model output, and condense the model to highlight those influential parameters. Hill and Grossman (1993) attempted to build a complex NEI model to explain focal position selection of Rainbow Trout (*Oncorhynchus mykiss*) and Rosyside Dace (*Clinostomus funduloides*) as a function of standard and active metabolic rate (data from Facey and Grossman 1990), food utilization efficiency, prey capture success, and prey abundance in a North Carolina stream. This model described focal position selection in terms of focal velocity, which is the velocity at the focal position as measured from the nose of the fish. They found, however, that prey capture success contributed disproportionately to the output of the complex model, and that the point at which prey capture success declined most rapidly with increasing velocity (i.e., the minima of the third derivative of the prey capture success-velocity function) was a better predictor of focal velocities occupied by these species in the stream than the complex model.

Consequently, Grossman et al. (2002) developed and field tested a simplified NEI model for four cyprinid species based solely on the negative logistic relationship between focal velocity and prey capture success (Fig. 2). The original, more complex version of their model included energy content of prey in the drift, fish visual reaction area, and swimming costs. However, many drift-feeding species in the study system (a fifth order stream in the Southern Appalachian Mountains) occupied focal positions within a relatively small range of low velocities (~5–20 cm/s; Grossman and Freeman 1987; Facey and Grossman 1992; Hill and Grossman 1993), and previous work in the same system suggested there was little variation in energetic costs at these velocities (Facey and Grossman 1990). This observation led to the removal of swimming costs, fish visual reaction area, and energy content of prey in the drift from the full model under the assumption that they varied minimally across the low and narrow range of velocities occupied by these drift-feeders, and could be considered constant (Facey and Grossman 1990, 1992; Grossman et al. 2002).

The simplified Grossman et al. (2002) NEI model has been field tested on nine species in systems ranging from the Southeastern US to Alaska. The model has successfully predicted optimal habitat selection (via focal position velocity) for seven species, displayed marginal success for interior Dolly Varden Char, and failed to

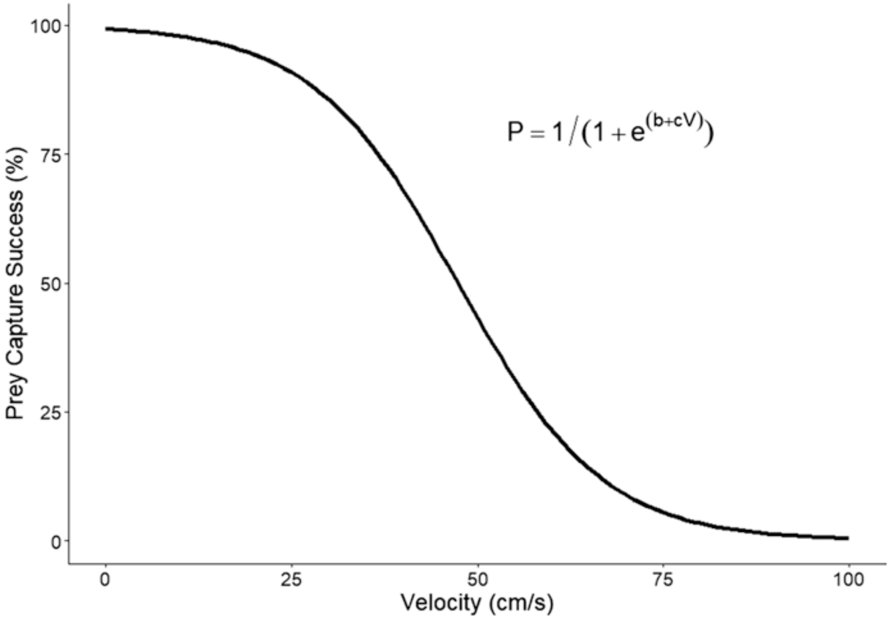


Fig. 2 The negative logistic relationship between prey capture success and velocity with Hill and Grossman's (1993) equation that describes the relationship between prey capture success and velocity (Eq. 3)

predict microhabitat selection by juvenile Chinook Salmon (Grossman et al. 2002; Donofrio et al. 2018; Bozeman and Grossman 2019a, b; Sliger and Grossman 2021). Despite its success at predicting focal position velocities, the validity of the simplified Grossman et al. (2002) model assumptions has not been assessed, and the simplified version of the model has not been tested against the full, more complex version.

To our knowledge, there has not been a review, comparison, and field test of simplified and complex versions of an NEI model to assess potential differences in predictive abilities. The lack of understanding of the influence of complex variables on NEI model output—as well as the validity of simplifying assumptions—is a potential blind spot that hinders our ability to determine the utility and generality of these models. Consequently, we used full and simplified variants of the Grossman NEI models, empirical data, and data from the literature to evaluate the validity of model assumptions and compare predictive success of models with differing levels of complexity.

1.2 NEI Model Variants

Conceptually, the full NEI model explains focal position energetics for drift-feeders as a function of energy intake

$$I_x = \left(E_x \times P_x\right) - S_x \tag{1}$$

where I is the net energy intake, E is the prey encounter rate, P is the proportion of prey captured that enter the visual field of the fish, and S is the swimming cost, all at microhabitat x (Grossman et al. 2002). Thus, net energy intake is a function of the number of prey that a fish encounters, pursues, and successfully captures at a specific focal position, minus the metabolic cost of maintaining that focal position.

Prey encounter rate, E, at a given microhabitat x, is expressed as

$$E_x = D_x \times A_x \times V_x \quad \left(\text{Hughes1998}\right) \tag{2}$$

where D is the abundance of prey in the drift converted to energy density (J/m^3), A is the visual reaction area of the fish (m^2), and V is the velocity (m/s). The proportion of prey captured that enter the visual field of the fish (P) at a given microhabitat can be expressed as

$$P_x = \frac{1}{\left(1 + e^{\left(b + cV_x\right)}\right)} \quad \left(\text{Hill and Grossman1993}\right) \tag{3}$$

where b and c are curve-fitting constants as estimated by nonlinear least squares regression for the relationship between P and V at microhabitat x.

Therefore, given Eqs. (1), (2), and (3), net energy intake (I) at microhabitat x is mechanistically estimated via

$$I_x = \left\{ \left(D_x \times A_x \times V_x \right) \times \left[\frac{1}{\left(1 + e^{\left(b + cV_x \right)} \right)} \right] \right\} - S_x \tag{4}$$

Equation (4) is the full NEI model.

After simplifying the full NEI model based on the assumption that *D*, *A*, and *S* vary minimally across the range of drift-feeder focal velocities and thus can be dropped from the equation (Facey and Grossman 1990, 1992; Grossman et al. 2002), we obtain

$$I_x = V_x \times \left[\frac{1}{\left(1 + e^{\left(b + cV_x \right)} \right)} \right] \tag{5}$$

which is solved iteratively to predict the velocity (*V*) at optimal microhabitat *x* (i.e., optimal focal velocity) where net energy intake (*I*) is maximized by a drift-feeder. Equation (5) is the simplified NEI model, which is dependent only on the relationship between prey capture success and velocity (Fig. 2).

The velocity term in the simplified NEI model reflects the velocity at which the prey are traveling when captured (as driven by treatment velocities in the experimental stream flume). However, drift-feeding stream fish are known to occupy slower focal velocities and capture prey in nearby faster velocities (Hughes and Dill 1990). Therefore, we used the experimentally derived relationship between focal and foraging velocities to adjust the simplified NEI model output reflect observed differences in focal and foraging velocities; this is the adjusted NEI model (Sliger and Grossman 2021). The third derivative of the negative logistic relationship between prey capture success and velocity (Fig. 2) is the rate of increase of acceleration of prey capture success as velocity increases. We calculated the minima of the third derivative function—which is the maximum point of deceleration of the *P*–*V* curve—for each of our study species (Hill and Grossman 1993). This is the third derivative NEI model.

1.3 Study Objectives

We had two study objectives: (1) to assess the validity of the assumptions made by the simplified NEI model (Eq. 5)—that energy content of prey in the drift, fish visual reaction area, and swimming cost terms from the full model could be omitted; and (2) to compare the optimal focal velocity predictions of the full, simplified, adjusted, and third derivative NEI models. To satisfy these objectives, we used empirical field data and data from the literature to address the following questions: (1) Are energy content of prey in the drift, fish visual reaction area, and swimming cost correlated with focal position velocities occupied by juvenile Chinook Salmon (*Oncorhynchus tshawytscha*), Dolly Varden Char (*Salvelinus malma*), and Arctic Grayling (*Thymallus arcticus*) from interior Alaskan streams? (2) What is the range of focal position velocities occupied by drift-feeding fishes as reported in the literature? (3) Does the published literature reveal consistent correlations between commonly occupied focal velocities and energy content of prey in the drift, fish visual reaction area, and swimming cost? and (4) What is the comparative performance of the original Grossman et al. (2002) full NEI model, simplified NEI model, adjusted NEI model, and third derivative model with respect to predicting optimal focal velocities?

2 Methods

We tested for correlations between energy content of prey in the drift (*D*), visual reaction area (*A*), and swimming cost (*S*) and focal velocities of juvenile Chinook Salmon, Dolly Varden Char, and Arctic Grayling using field observations and laboratory experiments. We also reviewed the primary literature to summarize the range of focal velocities commonly occupied by drift-feeders and the reported relationships between *D*, *A*, *S*, and stream velocity, within and beyond the range of common focal velocities. Finally, we used these data to evaluate the validity of simplified NEI model assumptions and parameterize and compare output of four NEI model variants.

2.1 Study Species and Systems

We studied populations of juvenile Chinook Salmon in the Chena River, Dolly Varden Char in Panguingue Creek, and Arctic Grayling in the Richardson Clearwater River in Alaska's Yukon River Drainage. Additional site and species information may be found in Donofrio et al. (2018), and Bozeman and Grossman (2019a, b). These three species are ecologically, economically, and culturally important in interior Alaska. Chinook Salmon populations in the Chena River have been studied and monitored for several decades, and are in decline in some parts of the state (Barton 1986; Schindler et al. 2013). Similarly, Arctic Grayling populations in the Richardson Clearwater River have been monitored for many years (Ridder 1988; Gryska 2001). Comparatively, little is known about the Dolly Varden Char population in Panguingue Creek or other interior populations of this species within its native range in the Pacific Northwest (Washington Department of Fish and Wildlife 2000; Bozeman and Grossman 2019b). Interior Dolly Varden Char are widely but patchily distributed throughout much of Alaska (Armstrong and Morrow 1980). We chose these system-species combinations because they were representative of ideal habitats for the respective study species and had water clarity permitting extensive video observations.

2.2 *Field Observations*

We conducted field observations during summer (June–August) of 2015 and 2016 in the Chena River (juvenile Chinook Salmon), Richardson Clearwater River (Arctic Grayling), and Panguingue Creek (Dolly Varden Char and Arctic Grayling). Mean standard length (± SD) of fish observed in the field for foraging behavior data collection was 4.7 cm (±1.0) for juvenile Chinook Salmon ($N = 24$), 17.6 cm (±2.8) for Dolly Varden Char ($N = 32$), and 42.4 cm (±4.5) for Arctic Grayling ($N = 29$). Field data were obtained by identifying drift-feeding individuals via streamside observation, placing paired underwater video cameras near drift-feeding positions, and recording drift-feeding activity once fish had resumed normal foraging behavior, and then capturing videoed individuals via hook and line once videography data was collected for length and mass measurements and diet content analysis. Turbidity was low in study systems (visibility >1 m, see: https://www.youtube.com/watch?v=BJokgZrAi84&t=15s), and not dissimilar to conditions in the experimental flume (see: https://www.youtube.com/watch?v=RXcn1ew3KuM).

2.2.1 Energy Density in the Drift (*D*)

We estimated energy density in the drift (D, J/m^3) by placing fine mesh (100 μm, 47.7 × 29.2 cm opening, Chena River only), coarse mesh (243 μm, 49.5 × 29.5 cm opening), and ultra-coarse mesh (500 μm, 32 × 32 cm opening, 2016 Richardson Clearwater River only) drift nets in our study sites in habitat that contained drift-foraging fish. We measured velocity (m/s, electronic velocity meter) and water depth (straightedge, m) at net placement sites. We placed drift nets as close as possible (straight upstream or downstream) to drift-feeding fish without disturbing them (3–20 m away) for an average of 45 min (range: 10–186 min). After we removed drift nets from the stream, we split captured prey into 1 mm size classes (1–10 mm) and estimated energy content based on prey identity and published length-mass regressions (e.g., Rogers et al. 1977; Benke et al. 1999; Sabo et al. 2002). We used the length and width of the net openings (m^2) along with water velocity measurements (m/s) at drift-net placement positions to measure the volume of water filtered per sampling time. We estimated prey drift concentration (items/m^3) using the maximum observed value for either the fine or coarse net for each taxon to account for backwash bias (J. Neuswanger pers. comm.). Finally, we multiplied mean prey energy content (J) by prey drift concentration (items/m^3) for each size class and then summed across size classes to estimate energy content of prey in the drift (D, J/m^3) for use in analyses.

2.2.2 Visual Reaction Area of the Fish (*A*)

We used videos of juvenile Chinook Salmon in the Chena River, Dolly Varden Char in Panguingue Creek, and Arctic Grayling in the Richardson Clearwater and VidSync 3D video analysis software to estimate several metrics of fish reaction distance (VidSync.org; Neuswanger et al. 2016). We reviewed field video footage for each of our study species and recorded the distance between a drift-foraging individual and a prey item when the fish first oriented toward the prey item to initiate a discrete foraging attempt. Reaction distance measurements were linear (cm) in three-dimensional space (i.e., straight line distance from fish snout to prey item in any direction). We used the 95th percentile of fish lateral reaction distance (i.e., cross-stream plane) as the radius to calculate a circular reaction area (cm^2) perpendicular to the direction of stream flow (Hughes and Dill 1990) for use in our analysis. We truncated the circular reaction area when the radius was greater than the distance from fish focal position to the surface and/or stream bottom. Reaction distance values for each individual observed (juvenile Chinook Salmon $N = 24$, Dolly Varden Char $N = 32$, Arctic Grayling $N = 29$) were based on an average of 103 measurable foraging attempts (range: 46–180) per individual. Mean lengths (± SD) of prey items consumed during foraging attempts were 2.3 mm (±0.4) for juvenile Chinook Salmon, 3.9 mm (±0.6) for Dolly Varden Char, and 6.0 (±0.9) for Arctic Grayling.

2.2.3 Swimming Cost (*S*)

We estimated the total metabolic costs of drift feeding as the sum of standard metabolic rate, swimming activity at the focal position, and foraging maneuvers to capture prey. We estimated standard metabolic rate as a function of temperature and mass using models parameterized for species closely related to our study species; Baikal Grayling (*Thymallus baicalensis*; Hartman and Jensen 2017) for Arctic Grayling, Bull Trout (*Salvelinus confluentus*; Mesa et al. 2013) for Dolly Varden Char, and an *Oncorhynchus* spp. model that is widely used for Chinook Salmon (Stewart et al. 1983; Stewart and Ibarra 1991). We used a mass- and swimming speed-dependent equation from Trudel and Welch (2005) parameterized for Sockeye Salmon (Brett and Glass 1973) to estimate swimming cost associated with holding a fixed focal position in the stream. Finally, we used a maneuver model (Neuswanger et al. in preparation) to estimate the metabolic cost of maneuvering to capture prey in the drift and returning to the focal position. Accounting for standard metabolic rate, swimming cost, and foraging maneuvers likely is a more accurate characterization of metabolic costs incurred by drift-feeders than steady swimming costs alone (Hughes and Kelly 1996).

2.2.4 Focal Position Velocity (V)

We quantified focal velocity using in situ stream velocity measurements at fish focal positions and field videos and VidSync. Focal velocity is the velocity at the nose of a drift-feeding stream fish. For juvenile Chinook Salmon in the Chena River, Dolly Varden Char in Panguingue Creek, and Arctic Grayling in the Richardson Clearwater, we estimated focal velocities by observing drift-feeding individuals via the cameras and releasing pre-soaked, neutrally buoyant Israeli cous-cous upstream of the individual. During video analysis, we used the cous-cous particles as velocity tracers and averaged the velocities of the six tracers nearest to the drift-feeding fish. For Arctic Grayling in Panguingue Creek, we identified drift-feeding individuals ($N = 25$) in the camera viewfinders, observed each individual pursue and capture at least five prey items and return to the same fixed focal position between foraging attempts, and then measured focal position velocity with a Marsh McBirney Model 201 electronic flow meter.

To evaluate the assumption that energy content of prey in the drift (D), visual reaction area (A), and swimming cost (S) could be held constant across the range of velocities occupied by drift-feeders, we regressed values of A and S against focal velocities from each species-stream combination. Because D was sampled in locations that did not necessarily correspond to stream fish focal positions, we regressed values of D with velocities taken at drift-net placement positions, which were well within the range of focal velocities occupied by drift-feeders in the same stream. We used a t-test to test the null hypothesis that the slope of the regression line does not differ significantly from zero.

2.3 *Laboratory Experiments*

We captured specimens for laboratory experiments from the same streams and in the same seasons as field observations and shipped them to the University of Georgia for prey capture success—velocity experiments (Fall 2014–Fall 2016). Mean standard length (± SD) of fish used in laboratory experiments was 6.2 cm (± 1.1) for juvenile Chinook Salmon ($N = 43$), 16.5 cm (±2.4) for Dolly Varden Char ($N = 20$), and 16.8 cm (±3.0) for Arctic Grayling ($N = 40$). A full description of laboratory experiment protocol can be found in Donofrio et al. (2018) and Bozeman and Grossman (2019a, b).

We fed individual subjects 9 prey (frozen bloodworms, 8.8 ±1.4 mm) per specimen per velocity treatment (10–70 cm/s in 10 cm increments) in an experimental stream flume and recorded the proportion of those prey captured (prey capture success, P). We also measured the velocity at the focal position occupied by the subject during the trial to assess potential differences in treatment velocity in the stream flume (V) and focal velocity. Turbidity in the stream flume was negligible (Bozeman and Grossman 2019b). We then used nonlinear least squares regression (package “nlstools” in R; Baty et al. 2015) to estimate species-specific curve-fitting constants *b* and *c* to best describe the negative logistic relationship between prey capture success (*P*) and treatment velocity in the stream flume (*V*) (Fig. 2; Eq. 3).

2.4 Literature Review

We reviewed the published literature to quantify the patterns of focal velocities occupied by drift-feeders as well as patterns in relationships between *D*, *A*, and *S* and stream velocity. We searched Google Scholar and Web of Science for relevant papers using combinations of the terms "microhabitat," "stream fish," "habitat use," "stream velocity," "fish metabolism," "focal position," "reaction area," and "energy content of prey in the drift." We also identified relevant papers by checking the reference sections of published NEI studies and other articles identified in the review. In our review of focal velocities, we only included sources that reported focal velocities measured in situ directly at a drift-feeder's focal position following observations of active, undisturbed feeding. We did not include information from sources that reported average velocities at locations where fish were collected or embedded focal velocities within PCA or habitat suitability curves instead of reporting them directly.

2.5 Parameterizing and Testing NEI Model Variants

We parameterized and tested: (1) the full NEI model that includes data for *D*, *A*, and *S* (Eq. 4), (2) the simplified NEI model (Eq. 5), (3) the adjusted NEI focal model, and (4) the third derivative NEI model. To parameterize and run the simplified NEI model, we used nonlinear least squares regression in R package "nlstools" (Baty et al. 2015) to estimate species-specific *b* and *c* values for the relationship between prey capture success and velocity (Eq. 3). We then solved Eq. (5) iteratively to produce the optimal foraging velocity prediction of the simplified NEI model. Note that the simplified NEI model is based on the relationship between velocity and prey capture success as characterized in the experimental stream flume, where velocity refers to the speed prey were traveling at when captured. Therefore, the simplified NEI model predicts optimal foraging velocities, which may or may not be different from focal velocities, depending on the species and system. The simplified NEI model is the variant tested by Donofrio et al. (2018), and Bozeman and Grossman (2019a, b).

Because drift-feeders are known to select focal positions at slower velocities and forage for prey in nearby faster velocities (Fausch and White 1981; Fausch 1984), we used the experimentally derived relationship between foraging velocities (i.e., water velocity treatment levels in stream flume experiments) and focal velocities (generally less than foraging velocity, see Bozeman and Grossman 2019a, b) to predict the optimal focal velocity. We ran a simple linear model to characterize the relationship between focal and foraging velocities from our laboratory experiments and used model coefficients and the simplified NEI model prediction to obtain the optimal focal velocity prediction of the adjusted NEI model.

To test the third derivative model, we calculated the third derivative of our experimentally derived prey capture success-velocity relationship and identified the minima of the resulting function—the maximum point of deceleration of the curve describing the negative logistic *P*–*V* relationship—as the optimal velocity predicted by the third derivative model. Finally, we used a combination of nonlinear least squares and simple linear regression to parameterize and solve the full NEI model (Eq. 4): we related model variables *D*, *A*, and *S* (*P* already is incorporated as a function of *V* with curve-fitting constants *b* and *c* estimated in parameterization of the simplified NEI model) to fish focal position velocity via regression and then identified the focal position velocity at which *I* was maximized.

The Grossman NEI model was developed in a system where predation and competition were not important drivers of microhabitat selection (Grossman et al. 1998), and drift-feeders were assumed to select focal positions solely based on NEI maximization (Hill and Grossman 1993; Grossman et al. 2002). Accordingly, we tested NEI model variants by comparing model predictions with the velocities of focal positions occupied by fish in their respective study streams. If model predictions fell within the 95% confidence interval of field focal position velocities, we considered them successful. Predictions that fell outside of this interval were considered unsuccessful.

2.6 Statistical Analyses

All statistical analyses were performed in R statistical software (R Core Team 2018; www.R-project.org) and alpha for frequentist statistics was 0.05. Potential outliers in regression analyses were identified via a combination of Cook's Distance and studentized and standardized residuals (R package "olsrr," Hebbali 2020). We removed outliers with a Cook's Distance value greater than 4× the mean of Cook's Distance and an absolute studentized and standardized residual greater than two (Kutner et al. 2005). To limit data loss, we removed outliers identified during evaluation of the full data set, but not during subsequent evaluation of the data (i.e., new outliers were not identified after removal of outliers from the full data set). This outlier removal protocol resulted in the removal of no more than two data points in any species/system-variable combination.

3 Results

3.1 Literature Review of Drift-Feeder Focal Velocities

Our search of the literature for focal velocity measurements for drift-feeders revealed 21 peer-reviewed articles containing 50 independent reports of focal velocity from 7113 individual records encompassing a wide range of age classes, seasons, geographic locations, and seasons (Table 1). Our literature review indicated that mean focal velocity for drift-feeding stream fish species was 16.5 cm/s (±8.5 SD) (Fig. 3). More than 75% of stream fish held position at velocities below 20 cm/s, and more than 90% occupied microhabitats with velocities below 35 cm/s. The assumptions of the simplified NEI model state that D, A, and S can be considered constant across the range of focal velocities occupied by most stream fishes (Grossman et al. 2002). Consequently, we evaluate our NEI model assumptions in the context of this summary of common drift-feeder focal point velocities.

3.2 Energy Content of Prey in the Drift (D)

3.2.1 Empirical Analysis: Energy Content of Prey in the Drift (*D*)

There were no significant relationships between drift-net velocity and energy density of prey in the drift for any of the three systems observed (Fig. 4, $p = 0.33$ (a), 0.96 (b), 0.10 (c), respectively). Linear models described only a small proportion of the variation of D ($R^2 < 0.15$). The relationship between drift-net velocity and energy density in the drift generally was negative for the Chena River and Richardson Clearwater; there was no relationship observed between these variables in Panguingue Creek. The three species occupied focal velocities over the lower range of drift-net velocities.

3.2.2 Literature Review, Energy Content of Prey in the Drift (*D*)

Our literature review revealed a generally positive relationship between velocity and drift. Multiple studies have shown that various measures of drift abundance (e.g., concentration, rate, proportion) increase across velocities of 10–80 cm/s (Elliott 1971; Townsend and Hildrew 1976; Ciborowski 1983; LaPerriere 1983; Smith and Li 1983; Brittain and Eikeland 1988; Gibbins et al. 2010). This encompasses the range of focal velocities occupied by most drift-feeders (8.0–25.0 cm/s) and argues for inclusion of drift abundance metrics in microhabitat models.

However, the drift-velocity relationship is complex and mediated by several other factors. Macroinvertebrate drift mechanics are driven by a combination of hydraulics (i.e., passive drift) and behavior (i.e., active drift), the balance of which

Table 1 Sources, species, age classes, seasons, reported focal velocities (mean ± SD, cm/s), and sample sizes from literature review of focal velocities of drift-feeding stream fishes. Season abbreviations are as follows: Sp, Spring; Su, Summer; Fa, Fall. Sources with no focal velocity standard deviation did not directly report a measure of precision with mean focal velocity

Source	Species	Age class	Season	Focal velocity (cm/s)	*N*
Baltz et al. (1987)	Rainbow Trout (*Oncorhynchus mykiss*)	Adult	Su/Fa	14.7 (14.0)	137
	Hardhead (*Mylopharodon conocephalus*)	Adult	Su/Fa	19.6 (14.0)	27
	Sacramento Pikeminnow (*Ptychocheilus grandis*)	Adult	Su/Fa	12.6 (11.8)	56
Baltz et al. (1991)	Rainbow Trout (*O. mykiss*)	YOY	Su/Fa	5.0 (7.7)	166
		Juvenile	Su/Fa	8.0 (9.0)	101
		Adult	Su/Fa	13.0 (11.9)	32
Bozeman and Grossman (2019a)	Arctic Grayling (*Thymallus arcticus*)	Adult	Su	36.7 (8.7)	20
				24.3 (7.8)	25
Bozeman and Grossman (2019b)	Dolly Varden Char (*Salvelinus malma*)	Adult	Su	27.1 (5.8)	29
Donofrio et al. (2018)	Chinook Salmon (*Oncorhynchus tshawytscha*)	Adult	Su	12.0 (4.9)	28
Enders et al. (2005)	Atlantic Salmon (*Salmo salar*)	Juvenile	Su	36.4 (8.7)	8
Facey and Grossman (1992)	Rainbow Trout (*O. mykiss*)	Adult	Sp/Su	14.8 (40.7)	94
	Rosyside Dace (*Clinostomus funduloides*)	Adult	Sp/Su/Fa	10.6 (46.2)	347
Fausch and White (1981)	Brook Trout (*Salvelinus fontinalis*)	Juvenile	Su	16.6 (11.8)	96
		Adult	Su	16.4 (9.5)	18
Grossman et al. (2002)	Rosyside Dace (*C. funduloides*)	Adult	Su	14.7 (18.6)	214
	Warpaint Shiner (*Luxilus coccogenis*)	Adult	Su	15.3 (13.2)	44
	Tennessee Shiner (*Notropis leuciodus*)	Adult	Su	16.0 (7.3)	25
	Yellowfin Shiner (*Notropis lutipinnis*)	Adult	Su	11.0 (10.0)	38
Hayes and Jowett (1994)	Brown Trout (*Salmo trutta*)	Adult	Su	23.5	189
Healy and Lonzarich (2000)	Coho Salmon (*O. kisutch*)	Juvenile	Su	5.0	80
Heggenes (2002)	Brown Trout (*Salmo trutta*)	All	Su	14.0 (11.0)	1598
Hill and Grossman (1993)	Rainbow Trout (*O. mykiss*)	Juvenile	All	14.7 (20.4)	85
		Adult	All	19.3 (19.2)	133
	Rosyside Dace (*C. funduloides*)	Juvenile	All	13.2 (16.0)	441
		Adult	All	13.2 (16.3)	319
Hillman et al. (1987)	Chinook Salmon (*O. tshawytscha*)	Juvenile	Su	11.7 (6.0)	281
			Fa	9.5 (3.5)	120

(continued)

Table 1 (continued)

Source	Species	Age class	Season	Focal velocity (cm/s)	*N*
Hughes and Dill (1990)	Arctic Grayling (*T. arcticus*)	Adult	Su	37.5 (17.6)	8
Moyle and Baltz (1985)	Rainbow Trout (*O. mykiss*)	YOY	Su/Fa	7.3 (8.6)	82
		Juvenile	Su/Fa	19.4 (16.1)	108
		Adult	Su/Fa	28.6 (18.0)	108
	Sacramento Pikeminnow (*P. grandis*)	Juvenile	Su/Fa	12.1 (13.0)	149
		Adult	Su/Fa	18.3 (14.5)	49
	Hardhead (*M. conocephalus*)	Juvenile	Su/Fa	14.0 (14.0)	81
		Adult	Su/Fa	21.7 (17.9)	57
	Tule Perch (*Hysterocarpus traskii*)	Juvenile	Su/Fa	7.4 (6.0)	12
		Adult	Su/Fa	6.1 (5.8)	19
Naman et al. (2022)	Rainbow Trout (*O. mykiss*)	Juvenile	Su	17.3 (16.6)	92
	Bull Trout (*S. confluentus*)	Juvenile	Su	10.8 (13.0)	60
Nielsen (1992)	Coho Salmon (*O. kisutch*)	Juvenile	Su	14.0 (3.3)	107
				12.0 (1.3)	216
Rimmer et al. (1984)	Atlantic Salmon (*Salmo salar*)	YOY	Su	16.8	501
			Fa	7.8	117
		Juvenile	Su	29.8	218
			Fa	9.4	48
		Adult	Su	38.4	146
			Fa	7.1	28
Rincón and Lobón-Cerviá (1993)	Brown Trout (*Salmo trutta*)	Adult	All	22.8	193
Sliger and Grossman (2021)	Brook Trout (*S. fontinalis*)	Adult	Su	17.0 (8.6)	26

shifts as a function of environmental conditions and species-specific traits (Naman et al. 2016). Positive relationships between drift and flow observed between streams or habitat types (pools, riffles, runs) may disappear at smaller spatial and temporal scales (e.g., within a single habitat type in a single stream) relevant to drift-feeder ecology and habitat use (LaPerriere 1983; Leung et al. 2009). Numerous studies have shown that in addition to velocity, drift processes are dependent upon many interacting factors including: season; time of day; macroinvertebrate species, body size and origin (terrestrial or aquatic); presence of predators; stream alkalinity; and substrate type (Everest and Chapman 1972; Wankowski and Thorpe 1979; Ciborowski 1983; Brittain and Eikeland 1988; Hoover and Richardson 2010).

Drift-flow relationships vary based on which metrics of flow are considered; increases in drift concentration may be positively correlated with increasing velocity, a linear measurement, and concurrently negatively correlated with increasing discharge, a volumetric measurement, via dilution (LaPerriere 1981, 1983). Heavy rainfall events that cause flows to increase at a given stream station may result in

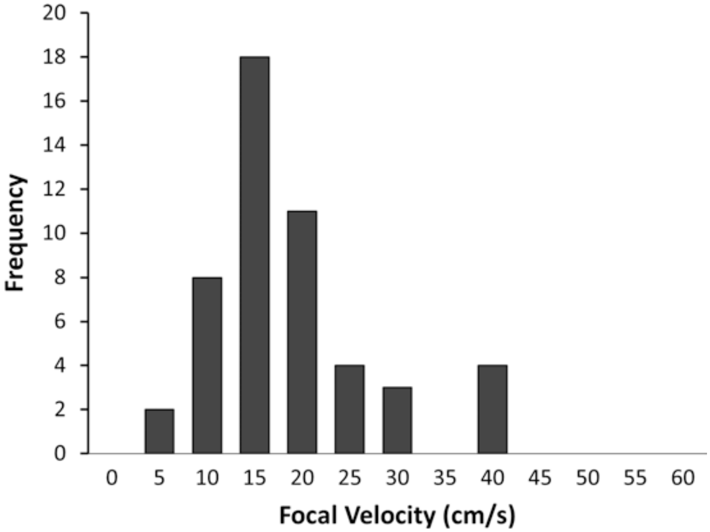


Fig. 3 Frequency distribution histogram of published focal velocities ($N = 50$ data sets representing 7113 individual measurements, Table 1) for stream fishes

lower drift concentration per flow volume, but an overall increase in drift concentration export longitudinally downstream. Drift-feeding fishes upstream also may deplete drift concentrations immediately downstream (Hughes 1992; Hayes et al. 2007). These relationships may shift at velocity extremes; at high velocities (>40 cm/s) some macroinvertebrates may reduce drift rates and shelter in substrate and at low velocities (<10 cm/s) macroinvertebrates may increase drift rates to escape drying streams (Elliott 1971; Hoover and Richardson 2010). Finally, drift rates also may depend on previous flow conditions, with taxa responding differently to the same flow conditions based on whether flow is increasing or decreasing (Gunderson 2000; Naman et al. 2016).

3.2.3 Constant Drift Versus Velocity Assumption

In summary, the relationship between metrics of drift and flow is complicated, but D and V generally appear to be positively correlated. The observed relationship depends on which metrics of drift (e.g., concentration, abundance, rate, etc.) are compared to which metrics of flow (e.g., discharge, filtered volume, velocity, etc.), in addition to other potentially correlated factors (e.g., season, time of day, macroinvertebrate species, alkalinity, drift-feeder depletion, etc.). Sampling techniques also may affect the observed relationship between drift and flow due to phenomena such as net clogging and backwash at high velocities.

Nonetheless, data from our study streams show no significant relationships between drift-net velocities and drift concentrations (Fig. 4). Despite the nuance in

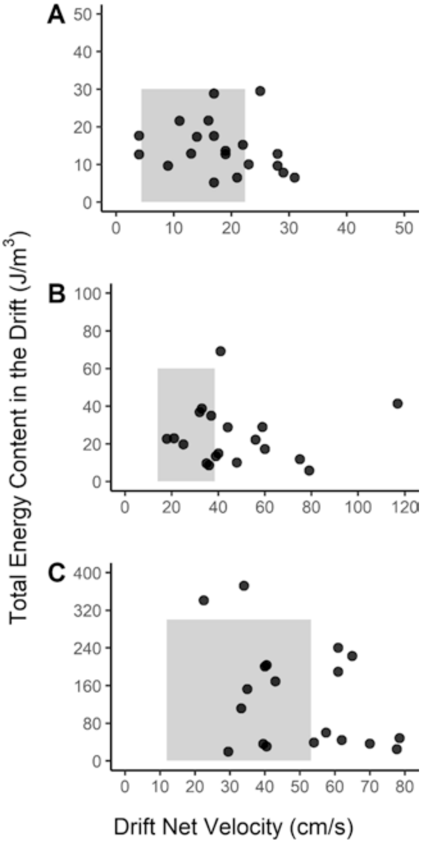
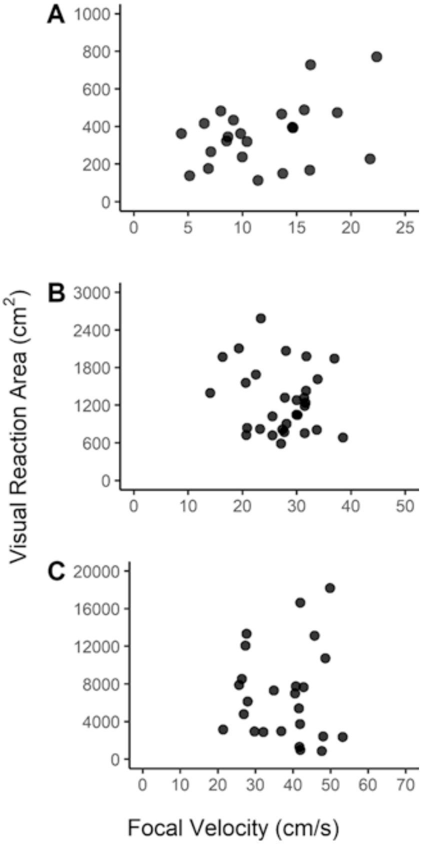


Fig. 4 Mean drift-net velocity (cm/s) versus total energy density in the drift (J/m^3) in habitats occupied by: (**a**) juvenile Chinook Salmon (Chena River), (**b**) Dolly Varden Char (Panguingue Creek), and (**c**) Arctic Grayling (Richardson Clearwater). Note differences in axis scales. The gray shaded areas are the focal velocities of the respective species in their respective streams

previously reported drift-flow relationships, the consensus in the literature is that flow and drift concentration are positively related, even at the focal velocities of 8.0–25.0 cm/s occupied by most drift-feeders (Brittain and Eikeland 1988). The discrepancy between our empirical observations and the literature may be due to the complexity and subtlety of the flow-drift relationship (e.g., mediating factors of season, daylight, species, substrate, dilution, habitat type, etc.), the fact that this relationship may become homogenized at small scales of time and space relevant to the drift-feeders in our study, or methodological issues such as net backwash or net clogging. Nonetheless, the assumption of constant *D* over the range of focal velocities occupied by drift-feeders is plausible for models predicting instantaneous microhabitat selection within many systems although in general it may be context-specific.

Fig. 5 Focal velocity (cm/s) versus visual reaction area (cm²) for: (**a**) juvenile Chinook Salmon, (**b**) Dolly Varden Char, and (**c**) Arctic Grayling. Note the differences in axis scale



*3.3 Fish Visual Reaction Area (*A*)*

3.3.1 Empirical Analysis: Fish Visual Reaction Area (*A*)

There were no significant relationships between focal velocity and visual reaction area for any of our study species (Fig. 5, $p = 0.06$ (a), 0.34 (b), and $p = 0.89$ (c), respectively). Linear models were poor fits to the data in each case (Fig. 5, all R^2 values were <0.16). Arctic Grayling reaction areas were nearly two orders of magnitude greater than those of juvenile Chinook Salmon and one order of magnitude greater than Dolly Varden Char reaction areas.

3.3.2 Literature Review, Fish Visual Reaction Area (*A*)

Our literature review revealed few papers that directly measured the relationship between *A* and velocity or prey density, and the studies that measured these variables yielded mixed results. Most studies measured reaction distance, which is the straight line distance between a drift-feeder's nose and the prey item at the moment the fish initiates prey pursuit. Godin and Rangeley (1989) observed decreases in reaction distance across velocities from 4 to 14 cm/s for juvenile Atlantic Salmon (*Salmo salar*); however, they also noted that fish oriented to prey items prior to pursuing them in faster velocities, concluding that fish minimized pursuit costs by delaying attack maneuvers at faster velocities. This implies that fish visual reaction distance remained high at fast velocities. Piccolo et al. (2008) reported declining prey detection distances across velocities ranging from 30 to 60 cm/s for juvenile Coho Salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*), which is faster than most drift-feeder focal velocities (Fig. 3). O'Brien and Showalter (1993) likewise found that the prey search window decreased with increasing velocities for Arctic Grayling; however, this decrease primarily occurred at velocities greater than 32 cm/s and was offset by increased prey encounter rates at velocities up to 46 cm/s. O'Brien et al. (2001) found that increasing velocities from 25 to 40 cm/s (near the high end of typical focal velocities) resulted in decreased location distance and efficiency for Arctic Grayling, although feeding rate remained unchanged, which suggests a trade-off between increasing prey encounter rates and reaction area. It is possible that at faster velocities, drift-feeders alter foraging strategies and intercept prey predominately by moving laterally rather than hurriedly pursuing prey upstream before returning downstream to the focal position (Wankowski and Thorpe 1979).

Early models conceptualized reaction distance as a positive function of prey size, fish size, turbidity, and light conditions (Schmidt and Obrien 1982; Sweka and Hartman 2001; Hughes et al. 2003), rather than velocity. Laboratory experiments that hold prey size, prey density, light, and turbidity constant have shown that reaction distance increases slightly from 10 to 70 cm/s or remains unchanged and is not strongly correlated with fish size (Donofrio et al. 2018; Bozeman and Grossman 2019a; Sliger and Grossman 2021). Holding prey density constant in experiments is important because prey encounter rate increases with velocity, which may confound a potential relationship between velocity and reaction distance (Fausch 1984; Hughes and Dill 1990). Are fish traveling shorter distances to capture prey because reaction area is decreased at higher velocities, or because more prey is available nearer the focal position?

3.3.3 Constant Visual Reaction Area Versus Velocity Assumption

Our field data displayed no significant relationships between focal velocity and visual reaction area for our study species, which parallels results of our past laboratory experiments (Donofrio et al. 2018; Bozeman and Grossman 2019a, b; Sliger and Grossman 2021) as well as assumptions of original reaction distance models (Schmidt and Obrien 1982; Hughes and Dill 1990; Hughes et al. 2003). The relationships reported in the literature contradict these results but are confounded by correlations with other variables (i.e., declining reaction distances at velocities greater than those commonly occupied by drift-feeders or observations of fish noticing prey prior to initiating capture maneuvers). Functionally, accounting for visual fields of drift-feeders in NEI models explains—in conjunction with *D* and *V*—the amount of prey a drift-feeder encounters at its focal position, which is important for energy intake. Our data suggest visual field does not decrease with increasing velocity. The literature suggests that visual field decreases with velocity, but drift-feeders do not exhibit concurrent decreases in prey consumption. In both circumstances, *A* values have little effect on energy intake across focal velocities generally occupied by drift-feeders. Therefore, we suggest that the assumption of constant *A* across the range of velocities occupied by drift-feeders is plausible for NEI models predicting microhabitat selection based on relative energetic potential between available focal positions.

3.4 Swimming Cost (S)

3.4.1 Empirical Analysis: Swimming Cost (*S*)

We observed a significant positive relationship between focal velocity (cm/s) and total swimming cost (J/s) for juvenile Chinook Salmon (Fig. 6a, $p = 0.01$), Dolly Varden Char (Fig. 6b, $p = 0.02$), and Arctic Grayling (Fig. 6c, $p = 0.04$). Linear models fit the data poorly (R^2 values: 0.18–0.27); however, residual patterns did not suggest that nonlinear functions would be better descriptors. Average swimming cost increased by 500%, 240%, and 150% across the range of relatively low focal velocities occupied by juvenile Chinook Salmon, Dolly Varden Char, and Arctic Grayling, respectively (Fig. 6). Note that total swimming costs increase from juvenile Chinook Salmon to Dolly Varden Char to Arctic Grayling such that swimming cost estimates differ by approximately one order of magnitude between species.

3.4.2 Literature Review, Swimming Cost (*S*)

Our literature review revealed that drift-feeder swimming costs generally are positively related to water velocity as well as fish mass and water temperature (Ware 1978; Boisclair and Tang 1993; Trudel and Welch 2005). Drift-feeder swimming costs (as estimated via equations and constants derived from oxygen consumption studies; e.g., Brett and Glass 1973) largely are exponentially related to velocity within and beyond the range of velocities occupied by drift-feeders (Rao 1968; Feldmeth and Jenkins Jr. 1973; Lee et al. 2003), though for some species and seasons this relationship is linear (Facey and Grossman 1990). Dickson and Kramer (1971) observed an asymptotic relationship between velocity and active metabolism for Rainbow Trout; however, this only occurred at velocities of 40–100 cm/s, which is greater than the range of velocities occupied by most drift-feeders (8.0–25.0 cm/s, Fig. 3) including Rainbow Trout in other natural systems (Grossman and Freeman 1987; Grossman and Ratajczak 1998).

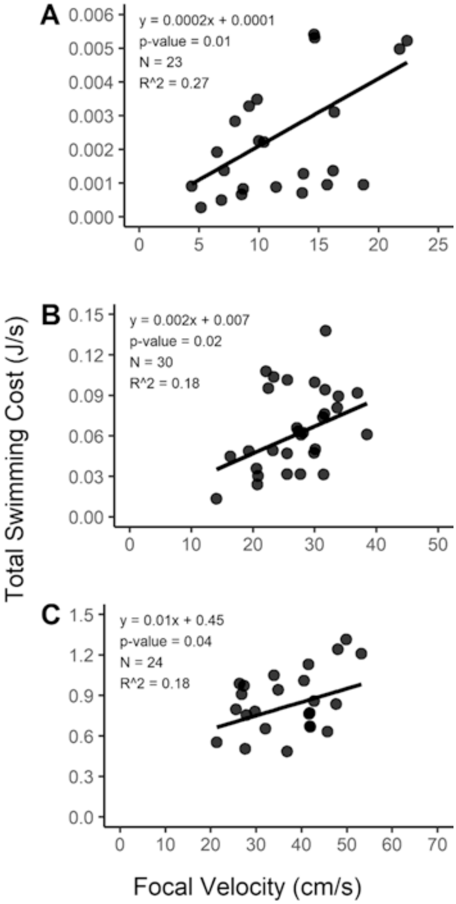


Fig. 6 Focal velocity (cm/s) versus estimated total swimming costs (J/s) for juvenile Chinook Salmon (**a**), Dolly Varden Char (**b**), and Arctic Grayling (**c**). Note the differences in axis scales

The relationship between velocity and swimming costs is mediated by many factors, including water temperature, fish mass, turbulence, and fish swimming activity (Enders et al. 2005; Trudel and Welch 2005; Jowett et al. 2021). In cooler months, swimming costs may only increase linearly with velocity, or not at all (Facey and Grossman 1990). The effects of temperature on metabolism are greatest at low velocities (i.e., < 30 cm/s where most drift-feeders are found), and temperature becomes less important relative to velocity as velocities approach critical swimming speeds (Brett and Glass 1973). Models that estimate fish metabolism based on steady swimming at a fixed velocity within flumes with no turbulence and neglect the additional costs of foraging maneuvers and prey assimilation may dramatically underestimate actual metabolic costs incurred by drift-feeders in turbulent streams with considerable velocity heterogeneity (Facey and Grossman 1990; Hughes and Kelly 1996; Tang et al. 2000). Additionally, applications that estimate swimming costs by extrapolating models beyond the ranges of fish masses, velocities, and temperatures at which they were parameterized, or those that use parameters developed for different species, may be vulnerable to bias (Trudel and Welch 2005).

3.4.3 Constant Swimming Cost Versus Velocity Assumption

Our data (Fig. 6) and the literature clearly indicate that there is a significant positive relationship between swimming costs and the range of velocities occupied by drift-feeding fish. The literature suggests this relationship generally is exponential (e.g., Lee et al. 2003). When pooled, our data show a positive exponential relationship between velocity and swimming cost, largely due to the considerable discrepancies in species-specific swimming cost estimates; however, this relationship is linear when separated by species. Drift-feeders often select focal velocities near the low (i.e., flat) end of the exponential relationship, yet may still experience potentially meaningful increases in swimming costs even at those focal velocities. Our data and the literature suggest that the assumption of constant *S* over the range of velocities occupied by drift-feeding stream fishes is not valid for NEI models predicting microhabitat selection.

3.5 NEI Model Variant Predictions

We compared model output for the four NEI models to quantify their comparative ability to predict the optimal focal velocities of juvenile Chinook Salmon, Dolly Varden Char, and Arctic Grayling in natural systems. We judged model performance by comparing predicted optimal velocities with the 95% confidence interval of velocities of focal positions occupied by drift-feeders in their respective study streams.

Model performance varied between species and model variant. The 95% confidence interval of focal velocities occupied by juvenile Chinook Salmon ($N = 24$) in the Chena River was 9.7–13.9 cm/s. All four models overestimated optimal focal velocities of juvenile Chinook Salmon in the Chena River; the adjusted NEI model was the closest to field focal velocities (<5 cm/s from the upper CI), with the other three models producing worse predictions (Table 2). The 95% confidence interval of focal velocities of Dolly Varden Char ($N = 32$) in Panguingue Creek was 25.1–29.2 cm/s. The adjusted NEI model and full NEI model each missed the 95% CI of Dolly Varden Char focal velocities in Panguingue Creek by less than one cm/s, which is well within the range of measurement error. In addition, a potential competitor (Arctic Grayling) was present in Panguingue Creek at the time of our study. Dolly Varden Char optimal microhabitat was underestimated by the third derivative NEI model and overestimated by the simplified NEI model (Table 2). Finally, the 95% confidence interval for Arctic Grayling was 34.0–42.3 cm/s in the Richardson Clearwater ($N = 29$) and 20.8–27.2 cm/s in Panguingue Creek ($N = 25$). Three of the four model variants were successful for Arctic Grayling, albeit in different contexts.

Table 2 NEI model variant optimal microhabitat predictions and field focal velocities (mean and 95% CI) for each study species. Focal velocities are mean (95% confidence interval, cm/s). Model predictions falling within the 95% CI are marked with an asterisk and those falling just outside the CI (<1 cm/s) are marked with a †

Species	Field focal velocity	Model	Prediction (cm/s)
Chinook Salmon (*N* = 24)	11.8 (9.7–3.9)	Simplified NEI	34.0
		Adjusted NEI	18.5
		Third derivative	20.7
		Full NEI	34.4
Dolly Varden Char (*N* = 32)	27.2 (25.1–29.2)	Simplified NEI	36.4
		Adjusted NEI	24.4†
		Third derivative	17.2
		Full NEI	29.5†
Arctic Grayling (*N* = 29, 25)	37.6 (34.0–41.2) (RC)	Simplified NEI	37.2*
	24.0 (20.8–27.2) (PC)	Adjusted NEI	23.0*
		Third derivative	25.1*
		Full NEI	32.5

RC, Richardson Clearwater; PC, Panguingue Creek

The simplified NEI model successfully predicted microhabitat selection of Arctic Grayling in the Richardson Clearwater, but not in Panguingue Creek, where a potential competitor (Dolly Varden Char) was present. Both the adjusted NEI model and the third derivative model successfully predicted microhabitat selection in Panguingue Creek, but not in the Richardson Clearwater (Table 2). The full NEI model prediction fell between the optimal focal velocities observed in Panguingue Creek and the Richardson Clearwater (Table 2), and thus was unsuccessful in both contexts.

4 Discussion

Investigations of the factors affecting habitat selection are essential for our understanding of how animals behave, which is a requirement for effective, science-based conservation and management. A key challenge for aquatic ecologists is identifying the fitness consequences of habitat selection. Mechanistic NEI models for drift-feeding stream fish are potentially useful tools for this task because they connect habitat use to fitness via energetics. Our evaluation of the assumptions of a simplified NEI model and comparison of complex and simplified models illuminates the mechanics of these models, highlights potential shortcomings associated with input variable estimation and parameterization, and provides important insight into how such models might be improved in the future.

Our empirical analysis demonstrated no relationships between velocity and energy content of prey in the drift or fish visual reaction area for any of our study species and a positive relationship between velocity and swimming cost for all of our study species. In conjunction with our review of the literature for each of these variables, we concluded that energy content of prey in the drift and fish visual reaction area could plausibly be considered constant within the range of drift-feeder focal position velocities, but swimming cost could not. When we parameterized and tested the four model variants, we found the adjusted NEI model was the best predictor of focal velocities occupied by the drift-feeders in this study; it was successful for Arctic Grayling in Panguingue Creek and was consistently closer to the 95% CI focal velocity window for Dolly Varden Char and juvenile Chinook Salmon than the other variants. These findings have important implications for how we theorize and estimate the various components of drift-feeder energetics and habitat use.

4.1 NEI Model Variable Estimation: Challenges and Implications

Our data suggests the Grossman et al. (2002) simplifying assumption for energy content of prey in the drift (*D*) is plausible, because we observed no significant correlations between these *D* and *V* for any of our study species. However, it is possible we did not observe a significant relationship between these variables due to high natural variability in the drift process, biased sampling techniques, or some combination of these things. The lack of observed relationship between *D* and *V* in our empirical analysis stands in contrast to the majority of the published literature, which suggests a positive relationship between velocity and metrics of drift (see Brittain and Eikeland 1988 for a review). Drift at any focal velocity is a complex function of lateral and vertical hydrodynamics, entry point (i.e., benthos, drift from upstream, or terrestrial sources), settling rate, abundance, and depletion by drift-feeders upstream. Drift processes also are influenced by macroinvertebrate species-specific traits, whereby macroinvertebrates actively enter or exit the drift based on abundance, season, time of day, and velocity (Nakano and Murakami 2001; Stark et al. 2002; Naman et al. 2016). The amount of energy in the drift available to drift-feeders is a complex function of the interaction between the abiotic dynamics of the stream and the ecological and biological characteristics of the invertebrate species themselves; any estimate of that amount is dependent on the time, place, and techniques used to sample this phenomenon.

There are a few potential biases which may have affected our estimates of energy concentration of prey in the drift. Sampling drift concentrations 3–20 m away from drift-feeders may not be reflective of drift concentrations encountered by drift-feeders at their focal positions given that drift can be highly spatially heterogeneous (Brittain and Eikeland 1988). Backwash due to net clogging and drift-net placement in the water column (the typical method of sampling macroinvertebrate drift) may underestimate drift concentrations, especially in fast velocities, which could potentially explain the negative trends observed in our data. However, removing the five fastest velocity data points from our velocity-drift concentration analyses did not change the observed relationship between drift and velocity in any of the three study systems. In addition, it possible that we did not observe a relationship between drift and velocity, because the velocity at drift-net positions potentially did not reflect flow conditions upstream that produced drift conditions.

Our field data showed no significant relationships between fish reaction area (*A*) and focal velocity, which matches results from laboratory experiments on these same species (Donofrio et al. 2018; Bozeman and Grossman 2019a, b). These results stand in contrast to the negative relationships between metrics of reaction field and velocity frequently reported in the literature. One possible explanation of these differences is that our method of recording reaction distance (for both laboratory experiments and field videos), which was the basis of our reaction area estimates, may not accurately capture the visual field of drift-feeding fish. We measure reaction distance between a drift-feeder and a prey item at the moment the drift-feeder initiates movement toward the prey. However, it is possible that drift-feeders visually observe prey prior to orienting toward it, thus decoupling the moment of prey recognition from the initiation of prey pursuit (Godin and Rangeley 1989). This phenomenon would bias our reaction area estimates such that they underestimate the true size of the visual window within which drift-feeders are foraging for prey items.

It is unclear how true visual reaction areas could be detected and measured because of the difficulties associated with discerning when a fish sees a prey item versus when it initiates pursuit of that prey item. Feeding in faster currents may necessitate that drift-feeders initiate foraging maneuvers earlier than they would in slower currents despite visually observing prey items at similar distances from their focal position. Published reports of decreased reaction distances for drift-feeders with increasing velocity either reported this relationship at velocities greater than most drift-feeders occupy (O'Brien and Showalter 1993; Piccolo et al. 2008) or observed constant or increasing prey encounter rates (O'Brien et al. 2001). Additionally, drift-feeders must discriminate between similarly sized prey items and inedible debris, the latter of which can vastly outnumber consumable prey especially for small-bodied drift-feeders (Neuswanger et al. 2014). The presence of potential competitors also may influence reaction distance, whereby drift-feeders are more likely to pursue prey on sight rather than let it drift closer and risk losing it to competition. Collectively, these dynamics make it difficult to know whether fish travel shorter distances to capture prey due to decreased prey recognition ability, large quantities of inedible debris, or increased prey availability nearer their focal position.

Original reaction distance models conceptualized reaction distance as a function of fish size, prey size, and light conditions (Schmidt and Obrien 1982; Hughes and Dill 1990; Hughes et al. 2003). Fish size was not significantly correlated with reaction distance in past laboratory experiments (Donofrio et al. 2018; Bozeman and Grossman 2019a, b) despite a wide range of experimental specimen lengths (4–27 cm) including many fish within the range of sizes at which are hypothesized to influence reaction distance (<19 cm; Hughes and Dill 1990). Light intensity may influence reaction distance (Mazur and Beauchamp 2003; Hansen et al. 2013), but it is unlikely that light conditions affected our reaction distance measurements, because laboratory measurements were conducted in a well-lit facility, and field observations were conducted during the Alaskan summer (>16 h in a day of daylight). Turbidity has been shown to be positively associated with stream velocity and negatively associated with fish reaction distance and foraging success (Vogel and Beauchamp 1999; Sweka and Hartman 2001; Hansen et al. 2013), but was negligible in our laboratory experiments (stream flume <0.001 NTUs) and low in our field observations (visibility greater than 1 m). We are hopeful that advances in underwater videography (e.g., VidSync) will continue to improve our understanding of three-dimensional fish foraging areas—including how fish visual field shifts in response to fish and prey size, light, turbidity, and presence of competitors—to address shortcomings of early foraging models (Dunbrack and Dill 1984; Neuswanger et al. 2016).

Unsurprisingly, swimming costs were positively related to focal velocities for all three species; a trend also observed in our literature review (e.g., Rao 1968; Feldmeth and Jenkins Jr. 1973). Nonetheless, several studies have shown that the incorporation of swimming costs in NEI models—a parameter that is logistically difficult to quantify and highly variable—does not necessarily improve the predictive ability of NEI models (Hughes and Dill 1990; Hill and Grossman 1993). Indeed, the full NEI model did not outperform the more simplified model variants despite being the only model containing this information. It is possible that drift-feeders occupy focal positions where energetic benefits overwhelm even considerable energetic costs, which would explain why costs did not improve the predictive ability of our full NEI model that ranks focal position based on relative energetic potential. However, this does not mean costs associated with swimming and foraging are unimportant for drift-feeder energetics modeling, because NEI models that calculate absolute NEI require accurate estimates of swimming cost even when costs are small relative to benefits.

The relative importance of energetic benefits (e.g., prey capture success) and costs in determining focal velocity selection via NEI is dependent on fish size. Jowett et al. (2021) found that swimming cost was more important for predicting optimal velocities of large fish (>96 g, 20 cm) than prey capture success, but that prey capture success was more important than costs for small fish optimal velocity predictions. It is widely known that fish metabolism is dependent on mass, especially for small fish (Trudel and Welch 2005; Rosenfeld and Taylor 2009). Finally, most NEI models that include energetic costs—including our full NEI model—estimate this variable using equations that were parameterized for different species using swimming trials in laminar flow swimming chambers (e.g., Trudel and Welch 2005), or extrapolate the models beyond the ranges of fish sizes, temperatures, or velocities for which they were parameterized. This may or may not be appropriate depending on the modeled species and the severity of the extrapolation.

Ideally, we would like to be able to quantify and include each element of swimming metabolism potentially affecting and affected by focal position choice by drift-feeders. However, the complexity and logistical difficulties of accurately and precisely measuring multi-faceted metabolic costs (e.g., standard metabolism, active metabolism, anaerobic foraging burst maneuvers, digestive costs, etc.) may limit their utility to NEI models, at least those which rank focal positions based on relative NEI. Previous studies demonstrated that estimates of swimming cost that do not incorporate the effects of turbulence or the energetic demands of burst foraging maneuvers may considerably underestimate the full energetic costs of drift-feeding in streams (Hughes and Kelly 1996; Tang et al. 2000; Enders et al. 2003). Therefore, although foraging maneuvers certainly inflate swimming costs it remains to be seen whether the inclusion of the complete energetic costs associated with drift-feeding can be incorporated in NEI models with sufficient precision to increase their predictive ability (see Facey and Grossman 1990, 1992). Clearly, more work is needed to reliably and precisely estimate swimming costs and incorporate them into NEI habitat selection models, and our results illustrate the difficulty of including accurate energetic cost data in these models.

Prey capture success is the most important determinant of output of the NEI models tested in this study. Prey capture success was the only model input variable derived from laboratory experiments, and as such, likely is the most precise variable included in the models. Nonetheless, there are several potential biases associated with our protocol for estimating prey capture success that could influence the output of each of our NEI model variants.

The experimental stream flume we used to measure prey capture success differed from natural stream environments in serval important ways. The stream flume received consistent lighting during all experiments, and contained very little visual complexity, outside of a small clump of bamboo placed at the upstream end of the flume to facilitate fish orientation. We regularly cleaned the stream flume to minimize debris and turbidity, and only presented prey items to fish one at a time. Each of these departures from the natural stream environment were necessary to facilitate laboratory experiments (whose scope extended beyond simple prey capture success measurements) and keep fish healthy; however, these simplifications of the stream environment potentially result in prey capture success being overestimated at a given velocity. Clearly, this would have serious implications for model output given the importance of the prey capture success-velocity function to the formulation of the NEI models. However, this bias has not apparently been reflected in the past success of our simplified and adjusted NEI models (Grossman et al. 2002; Donofrio et al. 2018; Bozeman and Grossman 2019a, b; Sliger and Grossman 2021). Future experiments focusing purely on prey capture success (and not other processes that require flume water clarity or bright lighting, e.g., video recording for reaction distance) under more natural conditions of turbidity, turbulence, prey-like inedible debris, and variable lighting conditions may more appropriately characterize prey capture success of drift-feeders in natural systems and improve foraging models.

4.2 Implications of Simplified Versus Complex NEI Model Success

The predictive ability of the four variants of the Grossman NEI model varied among species and systems. Overall, the adjusted NEI model outperformed the other model variants by successfully predicting Arctic Grayling optimal focal velocities in Panguingue Creek, underestimating Dolly Varden Char optimal focal velocities in Panguingue Creek by less than 1 cm/s, and being the closest of the variants to the 95% confidence interval of juvenile Chinook Salmon focal velocities in the Chena River (<5 cm/s away). There was no clear-cut second-best model, with the simplified, full, and third derivative model variants performing differentially for different species. This observation indicates parameter estimates for D, A, and S did not increase the predictive ability of the full NEI model in our study.

Except for juvenile Chinook Salmon, which likely are selecting habitat for reasons other than energy optimization (e.g., predator avoidance via strong association with shelter), our NEI models performed reasonably well and were able to yield insights into the process of microhabitat focal velocity selection. The performance of the models for Dolly Varden Char and Arctic Grayling was impressive given that model predictions fell within ~10 cm/s of the 95% CI of field focal velocities for these species in the Richardson Clearwater and Panguingue Creek despite water column velocities in our study sites ranging from negligible to at least 120 cm/s. These insights are important because many NEI models have been developed in the 40 years since their inception (Fausch 1984; Piccolo et al. 2014), but few if any studies have directly assessed the predictive ability of various forms of an NEI model, and the majority of NEI models have not undergone rigorous testing with multiple species and in multiple years and seasons.

Given that the Grossman et al. (2002) NEI model was developed for systems in which interspecific competition and predation were not strong driving factors affecting microhabitat selection (Grossman et al. 1998), it is not surprising that the model and its variants performed poorly for juvenile Chinook Salmon in the Chena River (Donofrio et al. 2018). Juvenile Chinook Salmon in the Chena River typically were observed in shallow areas near or underneath shelter (e.g., within root balls of fallen trees), which suggests that the proximity to shelter from predators may be an important component of microhabitat selection (Quinn 2018). This habitat preference is evidenced by lower focal velocities and swimming costs (by one and two orders of magnitude) for Chinook Salmon compared to Dolly Varden Char and Arctic Grayling, respectively. However, this observation is unsurprising, because juvenile Chinook Salmon in this study were very small (4.7 ± 1.0 SD SL), and focal velocity typically increases with length (Everest and Chapman 1972; Grossman and Ratajczak 1998). Larger individuals often select microhabitats nearer the center of the channel with greater focal velocities and are not as vulnerable to potential predators (Hughes and Reynolds 1994; Hughes 1998; Bozeman and Grossman 2019a).

One interesting aspect of model variant performance is that the simplified NEI model successfully predicted optimal microhabitats of Arctic Grayling in the

Richardson Clearwater, whereas the adjusted NEI model (and the third derivative NEI model) successfully predicted Arctic Grayling optimal microhabitats in Panguingue Creek. We observed that these systems differ markedly in depth, velocity heterogeneity, habitat complexity, and the presence of a potential competitor (Dolly Varden Char). It is important to consider the possibility that model variants may perform differentially based on the systems in which they are applied. For instance, it is well known that drift-feeders may occupy slightly slower focal velocities adjacent to higher velocity microhabitats in which they forage for drifting prey (Everest and Chapman 1972; Fausch and White 1981; Naman et al. 2022). In systems with considerable velocity heterogeneity with potentially large differences between focal and foraging velocities (e.g., Panguingue Creek), models that predict optimal focal velocity (as discounted from foraging velocity) may outperform models that predict optimal foraging velocity. By contrast, optimal foraging velocity models may perform better in systems with less velocity heterogeneity and fewer focal and foraging velocity shears. Some NEI models address this issue by accounting for vertical or lateral velocity differentials in foraging areas (Hayes et al. 2000; Dodrill et al. 2016). Understanding how different models (or different versions of models that account for spatial velocity heterogeneity) perform in different systems is an important area of research for the development and application of future NEI models.

From a logistical point of view, it is encouraging that the simplified, adjusted, and third derivative models performed just as well or better than the full NEI model because model parsimony generally is desirable and estimates for D, A, and S are costly and difficult to obtain. However, from a NEI model development and managerial perspective, it is discouraging that our estimates of these additional variables do not improve model output given that many NEI models calculate absolute NEI, which is dependent on D, A, and S, to predict potential growth, abundance, or carrying capacity for applied management strategies. One potential explanation for the underwhelming performance by the full model is that the linear models we used to relate D, A, and S to velocity and subsequently parameterize the full model explain very little of the variation in D, A, and S due to velocity (R^2 ranged from 0.00 to 0.27). This is not a particularly robust or elegant way to parameterize the full NEI model; however, this is the first attempt to parameterize and test this model, and inspection of the data suggested that nonlinear functions would not be better descriptors than linear functions.

Another potential and related reason for underperformance of some variants is bias associated with our data collection. In each application of the model variants, the full and simplified NEI model predictions were greater than the third derivative and adjusted NEI model predictions. This pattern suggests we likely are overestimating drift-feeder NEI. Two potential sources of overestimation of NEI are underestimation of swimming costs and overestimation of prey capture success (it seems less likely that drift density and visual reaction area would be biased high). Improved estimation techniques for both of these variables, as previously discussed, will provide additional insight into the dynamics of these models.

Our NEI model comparison has important implications for NEI models with different predictive goals. For NEI models that rank instantaneous optimal microhabitat selection based on relative NEI, parsimonious models that do not account for energy content of prey in the drift, visual reaction area, and swimming cost perform reasonably well. This conclusion is supported by the finding that the full model rarely outperforms the adjusted or simplified models despite incorporating more biological realism by including additional variables.

However, parsimony is inappropriate for models that predict potential growth or carrying capacity via absolute NEI; these models require accurate estimates and arrangements of energetics variables to produce reasonable results. For instance, swimming costs may be overwhelmed by energetic benefits in NEI models that predict instantaneous habitat selection via ranking of available focal positions (Hughes and Dill 1990; Hill and Grossman 1993), but even small swimming cost estimates may be highly influential in NEI model applications that predict potential growth or carrying capacity over space or time (e.g., Hayes et al. 2016; Naman et al. 2019). Likewise, temporal (diel) and spatial (within or between habitats) variation in drift may hinder our ability to detect patterns at scales relevant to modeling of instantaneous focal position selection by drift-feeders (LaPerriere 1981; Leung et al. 2009; Naman et al. 2016). Drift density may also interact with predation risk to explain focal position selection. If predation risk is high, drift-feeders may forage in faster velocities to achieve satiation in less time compared to foraging all day in slower velocities absent predation risk (Naman et al. 2022; Railsback et al. 2021). Drift dynamics certainly are critical components of drift-feeder habitat quality given that drifting macroinvertebrates, both terrestrial and aquatic, comprise most of the food for drift-feeding fishes (Elliott 1973; Quinn 2018).

4.3 Looking Forward

Variables that regulate energetic gain (prey quantity and quality, fish visual reaction field, prey capture success) and expenditure (cost of holding a fixed focal position in the stream, cost of foraging) certainly are important determinants of drift-feeder habitat selection, ecology, and fitness. This observation is evidenced by the inclusion of these variables in the vast majority of NEI models, including the earliest and latest applications (e.g., Fausch 1984; Rosenfeld and Taylor 2009; Naman et al. 2019), and is substantiated by our review of the relevant literature. More sophisticated methods of parameter estimation for energy content of prey in the drift, visual reaction area, and swimming costs will improve our understanding of the intricacies of drift-feeder microhabitat selection and may ultimately improve the power, tractability, and utility of complex NEI models that use these and other variables to estimate absolute NEI.

Our results indicate that prey capture success is the variable with the most influence on the predictions made by our NEI model variants. Future research should parameterize prey capture success-velocity functions for additional species and age classes that could be incorporated into user-friendly habitat suitability estimation software (e.g., Naman et al. 2020) or generalized across populations. Developing prey capture success-velocity functions specific to species, age classes, or even types of systems (e.g., stream size), especially through methods that guard against overestimation of prey capture success in oversimplified stream flumes, will provide important insight into model formulation and drift-feeder foraging behavior for absolute and relative NEI models alike. Understanding species-specific foraging performance also will help us predict how species may respond in the face of shifts in habitat quality or quantity, or the presence of competitors (e.g., Nakano et al. 1999).

Global climate change and other anthropogenic stressors necessitate that we develop practical conservation and management strategies to mitigate threats to freshwater biodiversity (Dauwalter et al. 2011; Williams et al. 2011; Jenkins et al. 2015). One of the most promising aspects of NEI models is their potential ability to be linked to hydrodynamic models to predict microhabitat quality and quantity at broader spatial scales (Hayes et al. 2007; McHugh et al. 2017; Railsback 2016), or incorporated into software that can readily estimate absolute NEI based on user-selected fish species, mass, water depth, velocity, and other variables (Hayes et al. 2020; Naman et al. 2020). Global climate change will affect drift-feeder habitat quality and quantity through many mechanisms, including altering metabolic rates (Trudel and Welch 2005) and availability of prey in the drift. Although simplified variants of NEI models can be linked to climate modeling based on predicted changes in flow, complex NEI models that predict absolute NEI will be necessary to capture the full suite of effects of climate change on drift-feeder populations.

In conclusion, our results demonstrate that energy content of prey in the drift and fish visual reaction area potentially can be considered constant across the range of velocities occupied by drift-feeders, but swimming cost cannot. Nonetheless, we found that simplified variants of an NEI model based on the prey capture success-velocity function performed as well or better than a more complex NEI model, which is more difficult to parameterize. In the short term, this is encouraging because we can use simplified NEI models to predict instantaneous habitat selection by drift-feeders. However, complex NEI models that predict potential growth, abundance, or carrying capacity via absolute NEI ultimately are needed for robust management and conservation applications. We support the continued improvement of complex habitat variable estimation techniques, as well as the parameterization of species-specific prey capture success-velocity functions to advance our understanding of drift-feeding foraging behavior and our ability to evaluate stream fish habitat quality and quantity in an uncertain future.

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Understanding Stream-Resident Salmonid Movements in Groundwater-Fed Streams of the Driftless Area (USA)

Douglas J. Dieterman, Loren M. Miller, and R. John H. Hoxmeier

Abstract Fish movements have been extensively studied and variously described for many years and several conceptual frameworks have since been proposed to help organize and understand these movements. Frameworks include ecological scale, the restricted movement paradigm, partial migration, dynamic landscape model, and riverscape approach. We blended reviews of selected frameworks and past studies in the Driftless Area of the upper Midwestern United States to advance an understanding of stream-resident salmonid movements. Past studies examined feeding and exploratory, seasonal migration and dispersal movements using underwater videography, radiotelemetry, capture–recapture method, and genetics method at various spatiotemporal and ontogenetic scales. Movements were complex and changed over the course of ontogeny. Most movement was at the youngest ages and smallest sizes and again at very large sizes as a result of exploratory behavior and feeding movements to seek better physical habitat conditions (e.g., deeper pool habitat) or to avoid competitive or predatory interactions with other salmonids. In between, adult-sized salmonids were mostly sedentary as suggested by the restricted movement paradigm. Restricted movement was likely due to ideal environmental conditions provided by a combination of groundwater-fed springs supporting good baseflow and cold temperatures, productive streams with abundant invertebrate prey, and diverse physical habitat conditions in a small spatial area. Thus, there was little evidence of seasonal migration to fulfill seasonal resource needs as predicted by the dynamic landscape model. Rather, a more general riverscape model best describes the partial migration of Driftless Area salmonid populations. In this

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model, stream reaches provide adequate seasonal habitat facilitating mostly sedentary adults, but with some inter-reach dispersal at juvenile ages and at the largest adult sizes.

Keywords Brown trout · *Salmo trutta* · Brook trout · *Salvelinus fontinalis* · Movement · Driftless Area

1 Introduction

Many conceptual frameworks have been proposed to help synthesize and advance our understanding of ecology. Whereas several early concepts focused on discrete spatial areas, as in succession, or the autecology of specific species, as in the niche concept, subsequent concepts evolved to note the importance of ecological scale and animal and energy movements among spatially and temporally heterogeneous environments (Real and Brown 1991). In particular, concepts such as landscape ecology (Forman and Godron 1986) and metapopulation ecology (Hanski 1999) developed to highlight the importance of animal movements and led to analogous developments in stream fish ecology.

Stream fish movements have been studied for a long time and been variously described. Fishes have been marked by many methods since at least the 1800s and subsequent recaptures provided inferences on how far and where and when fishes moved, as in early observations of Danish (Rasmussen and Pedersen 2018) and Scottish (W.L.C 1937) salmon and sea trout. After more than a century of such observations, many types of fish movements have been described with some excellent reviews published (e.g., Dingle and Drake 2007; Ferguson et al. 2019). Saint-Pe (2019) summarized fish movements into four broad categories that vary based in large part on spatiotemporal scale: prospecting/exploratory movements, feeding movements, migration, and dispersal. Exploratory and feeding movements generally happen over short time periods, from a few hours to a full day, and usually within small spatial areas or over short stream distances. Feeding movements were distinguished from exploratory movements by specifically identifying movements to feed. Migrations encompass larger spatial-scale movements that take longer to complete, such as across seasons or a year, and include movements toward some spatial area and then a return to an original location (Dingle and Drake 2007). Ferguson et al. (2019) identified several forms of such migrations for feeding, reproduction, or temporary refuge that included anadromy and three types of potamodromous (freshwater) migrations; fluvial-adfluvial (movements between smaller tributaries and mainstem rivers), lacustrine-adfluvial (movement between a lake feeding area and an upstream spawning tributary), and allacustrine (movement from a lake feeding area to a downstream river-outlet spawning area). Finally, dispersal was defined as movements from one spawning location to a separate location where the fish spawns again, typically in a separate year. Such dispersal movements could be made at any age and are associated with reproduction and gene flow that can ultimately determine spatial patterns in genetic structure (Saint-Pe 2019).

To assess fish movements, a wide variety of methods and analyses have been developed since the earliest mark–recapture studies (Pine et al. 2012; Aarestrup et al. 2018). In addition to traditional marking studies using some form of external mark, such as a floy tag or fin clip, many studies began to use either radiotelemetry (e.g., Alp et al. 2018) or acoustic telemetry to assess movement, including use of more comprehensive acoustic telemetry arrays (e. g., Barry et al. 2020). Recent advances in tag development included tags that lasted longer, offered better retention and still allowed identification of individuals, such as passive integrated transponder (PIT) tags. When PIT tags are used in conjunction with stationary antenna arrays, they allow almost continuous monitoring of movements among pre-defined stream areas for several years as demonstrated in Cucherousset et al. (2005). Genetics have also been used to infer movements, often over large spatial areas and long time periods, as in basic studies of genetic structure among spatially separate populations. Such studies have contributed to our understanding of the evolutionary history of species and important sub-species (e.g., Meraner and Gandolfi 2018). More definitive movements over smaller spatial and shorter temporal scales have been assessed with genetic assignment studies that identify immigrant individuals within a population and where they may have originated (Berry et al. 2004; Wood et al. 2018). Even more recent, and becoming more common, are the use of stable isotopes and otolith microchemistry to infer individual fish origins and movements across a range of spatial and temporal scales (Elsdon et al. 2008; Hoffman 2016).

Fisheries managers in the Driftless Area of the upper Midwestern United States have long speculated on the importance of fish movement for conservation and management of recreationally important salmonids. Most speculation has arisen following infrequent observations from a range of studies conducted to assess specific management needs. These studies included limited mark–recapture sampling, radiotelemetry projects, and genetics studies. However, no one has attempted to synthesize these studies and place them in conceptual frameworks to facilitate comprehensive understanding and more effective management. In this chapter, we (1) review selected conceptual frameworks to help organize and describe salmonid movements, (2) describe environmental conditions of the Driftless Area which may influence salmonid movement, (3) review Driftless Area studies (published and unpublished) documenting potamodromous movements of stream salmonids (primarily brown trout and brook charr), and (4) synthesize these movements in the context of the conceptual frameworks.

2 Conceptual Frameworks for Understanding Salmonid Movement

Several conceptual frameworks have been proposed to aid our understanding of stream fish movements. These frameworks evolved from early descriptions of organismal scales and physical habitat needs of key life stages to recognition of other factors that regulated populations including connectivity and movement among habitats. Selected frameworks include ecological scale, the five-component approach, restricted movement paradigm, partial migration, dynamic landscape model, and riverscape approach. Perhaps the most unifying framework underpinning most ecological concepts is hierarchical scale, or more specifically, spatial, temporal, and organismal scales (Levin 1992). Ecological scaling acknowledged that larger-scale items are composed of a number of smaller-scale items nested within them and that space and time are inextricably linked. For example, ecologists long recognized that the organismal scale of communities was composed of species, with each species composed of several populations, each in turn, composed of individuals. Even individuals were recognized as developing through a series of ontogenetic life stages (e.g., egg, alevin, juvenile, and adult) with each life stage being regulated by genes within each individual. Early ecologists often studied the habitat needs, with an emphasis on physical habitat of key life stages to better understand how to conserve or increase populations.

Later stream ecologists applied the concept of ecological scaling to understand how physical habitat features important to these life stages were created and maintained. These ecologists noted that stream habitat features were the result of distinct interactions between water and land over several spatial and temporal scales (Allan 1995). Large spatial-scale features of streams, such as river valleys and floodplains, operate at long temporal scales, taking hundreds of years to form and change. Conversely, very small-scale habitat features such as sand particles on the stream bed change every second.

Other stream ecologists noted that this hierarchical scaling of stream habitat focused principally on the physical nature of habitat and failed to explicitly recognize other factors influencing stream biota. An alternative framework of five components was simultaneously proposed to help organize the myriad factors influencing all aspects of stream biota: hydrology, water quality, physical habitat/geomorphology, biotic interactions, and connectivity (Rabeni and Jacobson 1999; Annear et al. 2004) (Fig. 1). Hydrology encompassed effects of floods and droughts, whereas water quality included factors such as dissolved oxygen, turbidity, and agricultural chemicals. The physical habitat/geomorphology component grouped traditional habitat features such as pool depths, water velocity, and fish cover as well as the geomorphic processes that create, maintain, or change these features. Biotic interactions included predator–prey, competition, and disease factors. The connectivity component included the importance of energy flow in stream food webs but was later revised to incorporate the emerging importance of fish movement.

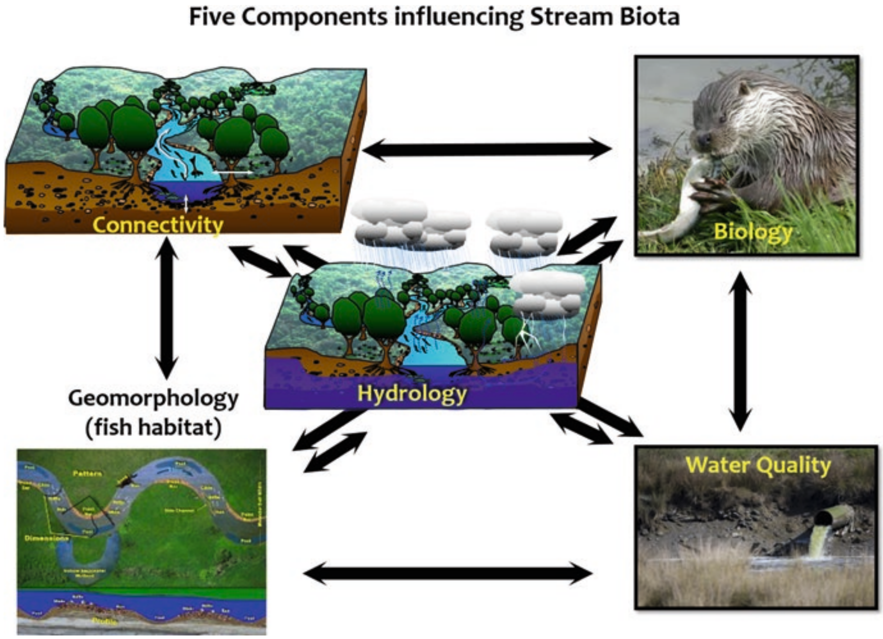

Fig. 1 The five components of streams that influence stream biota, including salmonid populations (figure adapted from L. Aadland, Minnesota Department of Natural Resources)

The five components were not developed to replace the importance of ecological scale, but rather, the components are integrated with scale. For example, a chemical spill will have an impact on a small spatial area in a stream and last for only a few days before being diluted. Fishes may perform short-term exploratory movements to avoid the area before returning. Conversely, climate change may increase water temperatures that result in large spatial-scale changes in distribution that can last for decades or even centuries. The five-component framework is especially useful for organizing and understanding important aspects of stream fish ecology, such as recognition of which factors promote fish movement or conversely, support sedentary behavior.

Many early salmonid movement studies documented a lack of movement that generated considerable debate. Several studies published prior to 1994 report limited salmonid movement, but that restricted movement paradigm was challenged in part, because of the mark–recapture methods used (Gowan et al. 1994). It was argued that the numerous marked individuals that were never recaptured, often >50%, were evidence of larger-scale movements out of study areas. Since then, methodological and analytical approaches to better quantify salmonid movements were advanced (e.g., Rodríguez 2002). These approaches recognized that mobile and sedentary populations do not have to be mutually exclusive, but rather, a single population can have both mobile and sedentary individuals, a notion that contributed to subsequent research on the importance of individuality in movement studies

(Rasmussen and Belk 2017; Spiegel et al. 2017). Application of these approaches resulted in better quantification of sedentary and mobile portions of populations, a pattern often termed partial migration (Chapman et al. 2012). However, many salmonid populations subsequently examined still found large majorities of sedentary individuals, in apparent support of the restricted movement paradigm (e.g., Knouft and Spotila 2002; Aparicio et al. 2018).

Schlosser and Angermeier (1995) blended increasing knowledge of fish movements and importance of stream connectivity with landscape ecology and metapopulation concepts and proposed a dynamic landscape model for stream fish populations. Landscape ecology recognized that distinct habitat patches were present on the terrestrial landscape and that habitat patches differed in terms of size, juxtaposition, and quality of habitat within them. The concept of metapopulations explicitly incorporated animal movements among these habitat patches. Schlosser and Angermeier (1995) proposed that in order for stream fishes to complete their annual life cycle they may need to be able to move among different habitat patches to complete critical life stages (Fig. 2). This included seasonal movements to and from habitat patches used for spawning, feeding, and refugia from harsh conditions such as drought [sensu migrations of Saint-Pe (2019)]. However, a corollary to this model was that fishes may not need to move if a single habitat patch fulfills the

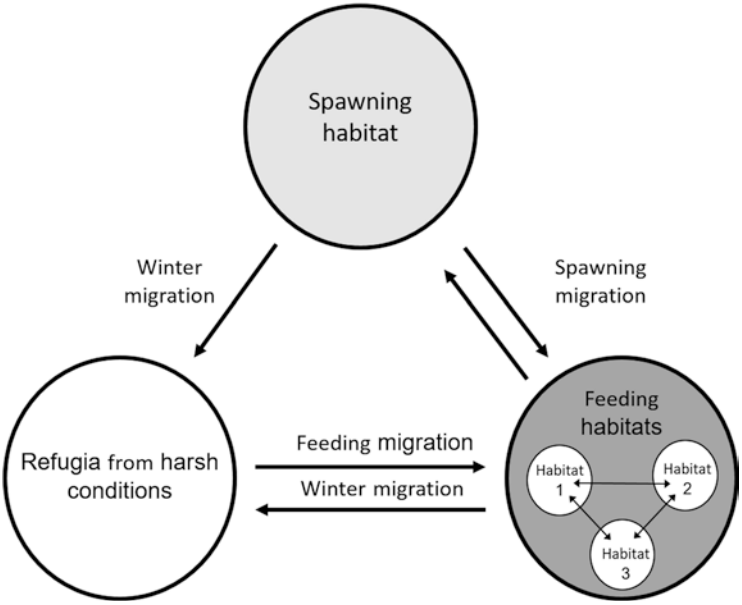

Fig. 2 Dynamic landscape model for stream fishes to complete their life cycle (modified with permission from Schlosser and Angermeier 1995 for fall-spawning salmonids). Seasonal movements among habitat patches for feeding, spawning, and refugia needs represent migratory movements as defined by Saint-Pe (2019), whereas movements among the three smaller feeding habitat patches represent feeding or exploratory movements

seasonal and ontogenetic needs of all life stages, as implied in the restricted movement paradigm.

Finally, to provide a more holistic framework that incorporated all preceding concepts and models applied to stream fish ecology, Fausch et al. (2002) proposed the riverscape approach to guide management and conservation of stream fishes. The riverscape approach expanded the dynamic landscape model to note, in part, that management and research efforts need to consider how fish movements among all heterogeneous habitat patches across the full extent of all spatial and temporal scales dictate persistence and abundance of stream fishes in any particular habitat patch at a particular time. Several methods to quantify riverscape features have since been advanced (e.g., Erős and Lowe 2019) and applied to better understand ecological patterns indicative of fish movement, such as spatial patterns in genetic structure (Davis et al. 2018).

3 Driftless Area Environmental Conditions

3.1 Geologic History and Land Use

The Driftless Area is a 62,200 km^2 area encompassing portions of four states (Minnesota, Wisconsin, Iowa, Illinois) in the upper Midwestern United States. The area is termed driftless because it lacks much of the rounded sedimentary sand, gravel, and boulders, termed glacial drift, which was transported by glaciers during the last ice age, about 10,000–30,000 years ago. Pleistocene glaciers circumvented much of the area based on examination of glacial deposits and sediments (Splinter 2019; Fig. 3). Water from melting glaciers and subsequent stream erosion carved numerous dissected valleys bordered by steep bluffs, ranging from 180 to 520 m high.

Historical land use was a mix of deciduous forest, prairie, and oak savanna but was converted for agricultural development by European settlers beginning in the early 1800s (Thorn et al. 1997). Poor land use practices, such as deforestation and row crop agriculture on steep hill sides, resulted in severe flooding, gully erosion, and subsequent sediment deposition in river valleys (Fig. 4). Various soil conservation efforts, such as contour plowing, protection of steep hill sides, and establishment of earthen dams on gullies and ravines, were implemented in the early 1900s to reduce flooding and erosion. Current land use is still primarily agricultural pasture and row crops, but these practices are limited to bluff top and river valley areas (Fig. 5). Hillsides have been reforested with mostly northern deciduous tree species, such as maple *Acer* spp., birch *Populus* spp., and oak *Quercus* spp.

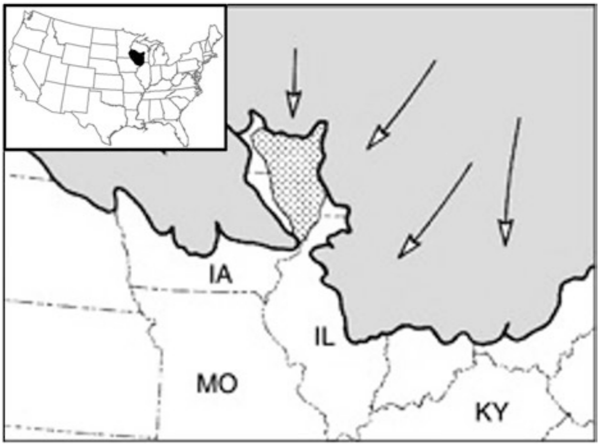

Fig. 3 Approximate extent of glacial advance in the upper Midwestern region of the United States during the late Wisconsinan glaciation 22,000 years ago. Stippled area is the approximate boundary of the Driftless Area and arrows indicate direction of ice movement. Modified from Cote, W. E., D. L. Reinertsen, and M. M. Killey, 1971. Guide Leaflet, Geological Science Field Trip, Galena Area: Jo Daviess County Illinois and Lafayette County, Wisconsin: Galena 15-Minute Quadrangle, Cuba City and New Diggings 7.5 minute Quadrangles: Illinois State Geological Survey, Guide Leaflet 1971c, 36 p. Copyright © 1971 University of Illinois Board of Trustees. Used with permission of the Illinois State Geological Survey. Inset map is Driftless Area location (black polygon) in the United States

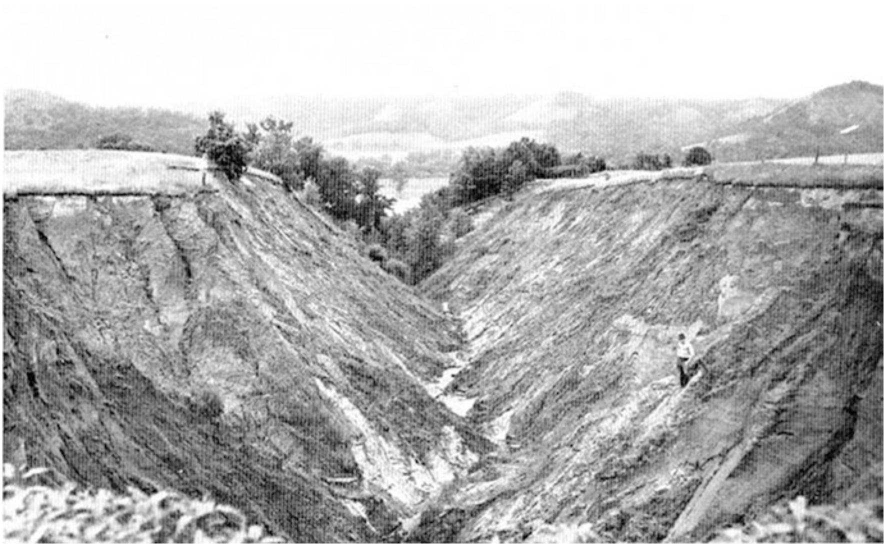

Fig. 4 Characteristic gully erosion in a Driftless Area valley in southeast Minnesota, USA, circa 1900

Fig. 5 Characteristic Driftless Area valley with a coldwater trout stream flowing through it and bordered by forested hillsides. Note the immediate riparian zone used as cattle pasture and adjacent to that, row crop agriculture practices

3.2 *The Five Components of Driftless Area Streams That May Influence Salmonid Movement*

Several aspects of the five components of streams could interact to influence salmonid movements or promote sedentary behaviors (Table 1). Driftless Area hydrology is more stable than other areas, because of its underlying geology, but streams and rivers are still subject to large floods. The area is underlain by Karst geology composed of sandstone, shale, limestone, and dolostone with many sinkholes and caves conveying surface water to underground aquifers (Splinter 2019). This cold, clear groundwater is discharged by numerous springs that support over 15,000 km of coldwater riverscape in the region, resulting in very stable baseflow conditions. Measurements conducted since the 1970s suggest that baseflows have been increasing over the past half century (Potter 2019). However, intense, but spatially variable, rainfall events result in large floods that punctuate stable baseflow conditions. Yet, relative to streams and rivers across the United States, Driftless Area stream

Table 1 Summary of selected Driftless Area environmental conditions, organized by the five stream components: hydrology (H), water quality (WQ), physical habitat and geomorphology (PH), connectivity (C), and biology (B), and potential effects on stream-resident salmonid movements

Stream component	Environmental condition	Potential movement effects
H	Occasional large floods	Promote movement to refugia or dispersal of young individuals
H	Stable baseflows	Promote sedentary behavior
WQ	Cold, stable water temperatures in most designated trout streams	Promote sedentary behavior
WQ	Larger downstream rivers with warm water in summer become colder in late autumn-winter	Promote seasonal migrations downstream to thermally variable spawning and wintering habitat
WQ	Excess nutrients such as fecal coliform and nitrate, or toxic levels of agricultural chemicals causing fish kills	Promote movement to refugia or to recolonize
PH	Spatial riverscape mosaic of important physical habitat features such as gravel substrates for spawning, deeper pools for resting or overwintering, and overhead bank or woody debris cover for protection from predators	Promote seasonal migrations to complete key life stages
C	Occasional large (5–20 m high) dams and abundant road-stream crossings with potentially improper fish passage designs	Block dispersal or recolonization movements
B	Competition and predation interactions between some salmonid species	Limit dispersal or migration
B	Abundant aquatic insect prey	Promote sedentary behavior

hydrology is classified by McManamay et al. (2014) as super-stable groundwater, characterized by very high baseflows and high stability but not necessarily with high runoff. Thus, adverse hydrologic conditions in other regions, such as droughts, are uncommon even though large floods may create environmental conditions from which stream fishes need to seek refuge.

Water quality in Driftless Area streams is considered ideal for salmonid production but occasional pollution creates harsh environmental conditions. Driftless Area streams are considered very fertile with alkalinity ranging from ≈170 to 270 mg/L $CaCO_3$ and conductivity from 425 to 860 μS/cm (Kwak and Waters 1997). Several water quality variables indicative of agricultural land use can also be high, such as nitrate levels of 14 mg/L, ammonia of 0.68 mg/L, and orthophosphate of 17.64 mg/L (Kwak and Waters 1997). Water temperature in most designated trout streams rarely exceeds 22 °C. Some stream reaches are considered impaired because they do not meet water quality standards for ammonia, fecal coliform, nitrate, nutrients, or turbidity. Fish kills are also reported occasionally, but identification of specific pollutants is rarely determined because the offending pollutant has usually been diluted by the time water samples are collected. Still, such events highlight adverse water quality conditions that stream fishes must move to avoid, or to recolonize after the pollution has abated.

The large number of streams traversing the landscape, their subsequent degradation and more recent restoration activities have created a spatial mosaic of physical habitat conditions across the Driftless Area riverscape. Although some streams originate on hill tops and are considered warm water, all streams descend to valley bottoms through steeper gradient reaches (up to 2.5% slope) with more coarse substrate, receive groundwater inputs from springs and seeps, and transition into cold-water streams with mean widths ranging from 3 to 15 m (Thorn and Anderson 1999; Vondracek et al. 2005). Most coldwater reaches eventually enter larger (mean widths >12 m) and deeper (mean depths > 0.8 m) warmwater rivers that have an abundance of silt and sand substrate. Almost all streams were degraded following European settlement, but in response, instream habitat rehabilitation efforts were begun in the 1950s (Thorn et al. 1997). Rehabilitation efforts sought to improve sediment transport by narrowing and deepening streams and sloping stream banks and later, emphasized addition of fish cover, such as overhead bank cover, instream rocks, and woody debris. A multivariate stream classification study conducted in Minnesota's portion of the Driftless Area, identified five coldwater and five warmwater stream classes (Thorn and Anderson 1999). Thus, the Driftless Area riverscape is composed of a spatial mosaic of habitat conditions that salmonids may move among to complete key life stages, such as smaller upstream reaches that provide spawning habitat or deeper downstream areas where larger adult salmonids can overwinter. Also, fisheries scientists have long speculated on how reaches with artificially improved habitat conditions influence fish movements (Roni 2019). Do such reaches provide good spawning habitat that produce excess individuals that move to supplement populations in adjacent reaches (sensu source populations)? Alternatively, do artificially improved reaches simply concentrate fishes that move into them?

There are few obvious barriers to connectivity, such as large dams blocking fish movements among coldwater stream reaches, however several subtle and seasonally variable barriers exist, such as poorly designed stream crossings and potential thermal barriers. Although government agencies identify several large, 5–20 m high dams in the Driftless Area, most such dams were placed on dry first- or second-order stream channels to control excessive flooding in the early 1900s. Only a few dams are located on mainstem coldwater streams or warmwater rivers. Perhaps more pervasive is the large number of road crossings over streams that can fragment stream habitats and impede fish movements if designed improperly (Diebel et al. 2014). Recent estimates indicate >8500 road-stream crossings exist in the Driftless Area with about 55% expected to be at least a partial barrier to some fish species or sizes (Miller 2016). Finally, warmwater rivers are considered effective thermal barriers to salmonids, prohibiting dispersal and recolonization movements among coldwater tributaries. However, such thermal barriers are only present during warm summer months (Fig. 6). As autumn air temperatures get colder, water temperatures in the warmwater rivers and coldwater tributaries become nearly identical, because

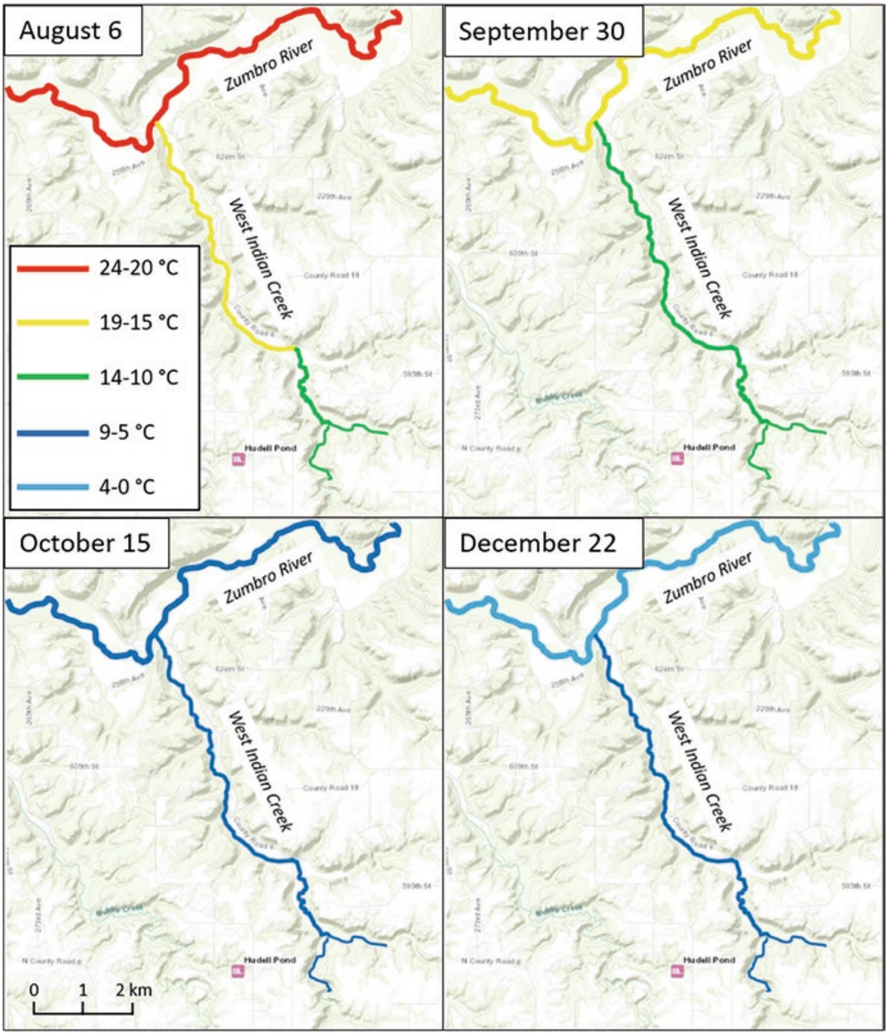

Fig. 6 Spatiotemporal changes across the thermal riverscape of a warmwater river, the Zumbro River, and one coldwater tributary, West Indian Creek from late summer to early winter in 2019

the warmwater rivers have less groundwater inputs to buffer thermal changes. By early winter, the tributaries, with more groundwater flow, become warmer than the downstream rivers that were considered warm water just a few months earlier in summer. Salmonids could use these spatiotemporal changes in the thermal riverscape of Driftless Area streams for dispersal and recolonization movements or even to make use of seasonally inhospitable habitats (i.e., the warmwater rivers) for spawning and overwintering.

Three primary salmonid species inhabit the highly productive streams of the Driftless Area. Brook charr *Salvelinus fontinalis* are the only native salmonid but naturalized, self-sustaining populations of brown trout *Salmo trutta* are the most widespread. For example, brown trout are present in over 90% of Driftless Area streams in Minnesota (Dieterman et al. 2020) and Wisconsin (Mitro et al. 2019) and over half of the streams in northeast Iowa (Kelly et al. 2021). Non-native rainbow trout *Oncorhynchus mykiss* are also present, being stocked in some streams to supplement recreational fisheries, but natural reproduction is rare. Other fishes inhabiting coldwater streams in the Driftless Area include slimy sculpin *Cottus cognatus*, mottled sculpin *Cottus bairdii*, white sucker *Catostomus commersonii*, brook stickleback *Culaea inconstans*, and minnows and dace (Family Cyprinidae). These fish communities often display longitudinal zonation with brook charr and *Cottus* spp. tending to be restricted to smaller headwater streams and rainbow trout, brown trout, and other fishes more abundant in larger, downstream reaches (Weigel and Sorensen 2001; Hoxmeier and Dieterman 2013; Kelly et al. 2021). Restriction of brook trout to headwater areas is likely a result of competitive or predatory interactions with brown trout (Hoxmeier and Dieterman 2013). As noted previously, Driftless Area streams are very fertile and support abundant aquatic insect populations that are the basis of most salmonid diets (French et al. 2016; Cochran-Biederman and Vondracek 2017). The fertile streams with abundant invertebrate prey support fast-growing salmonids. On average, brown trout reach 125–145 mm at time of first annulus formation and 215–240 mm at second annulus formation (Dieterman et al. 2004; Carlson et al. 2016). Brook charr reach 97–128 mm at first annulus formation and 165–204 mm at second annulus formation (Hoxmeier et al. 2015).

4 Review of Salmonid Movement Studies in the Driftless Area

Challenges to the restricted movement paradigm in conjunction with salmonid movement studies in other upper Midwest USA streams and observations in the Driftless Area, kindled interest in the importance of salmonid movements in the 1990s. As detailed previously, several studies (e.g., Gowan et al. 1994; Schlosser and Angermeier 1995) prompted greater consideration for the importance of stream fish movements. At the same time, movements of large (350–635 mm) brown trout were documented in other upper Midwest, USA streams in Wisconsin and Michigan (Clapp et al. 1990; Meyers et al. 1992). These studies identified long-range (7–33 km) seasonal migrations between spring-summer feeding habitat and overwintering habitat in larger, deeper stream reaches considered thermally marginal for salmonids in summer. In addition, movements exceeded boundaries of stream reaches with angling regulations designed to protect these fish. Clapp et al. (1990) also documented short-term feeding movements between daytime cover and nighttime drift-feeding sites in the middle of the stream channel. These findings inspired closer examination of salmonid movements in the Driftless Area at several ecological scales using a variety of methods including underwater videography, telemetry, capture–recapture, and genetics.

4.1 Small-Scale Feeding Movement

Only one study examined small-scale feeding movements of salmonids in the Driftless Area. Short-term feeding movements were documented using underwater videography by Grant (1999) while conducting other research. Grant (1999) determined microhabitat feeding locations (depth and velocity), prey detection distances, and maximum capture distances of brown trout and rainbow trout in one stream near the northern edge of the Driftless Area. Both prey detection distances and maximum capture distances varied depending on fish length, prey size, and velocity. Drifting and benthic prey were detected at distances that exceeded the maximum stream depth of 1.1 m and overall maximum capture distances ranged from 0.3 to 1.3 m. Grant (1999) also noted interspecific and ontogenetic differences in microhabitat feeding locations and movements with older and larger trout using deeper feeding locations with slower velocities (Fig. 7). Age 1 and 2 brown trout (100–250 mm) directed about half of feeding movements at drifting prey in the water column and the other half at benthic prey. Conversely, larger age 3+ brown trout (250–330 mm) almost never made a feeding movement between daylight hours of 0530 and 2030 PM when video cameras were operational, similar to what Clapp et al. (1990) observed in Michigan. In contrast, all ages of rainbow trout (98–320 mm) fed during daylight hours and directed 82–90% of feeding movements at drifting prey in the water column with 18% or fewer movements (depending on age group) directed at benthic prey.

4.2 Intermediate-Scale Seasonal Migration

Seasonal movements of brown trout were often studied or noted during earlier radiotelemetry studies and later by more sophisticated capture–recapture and genetics studies. Seasonal movements to overwintering areas were noted during one radiotelemetry study that examined winter habitat of large (332–562 mm) brown trout (Dieterman et al. 2018). Transmitters were implanted in 10–15 large brown trout in each of seven southeast Minnesota streams prior to winter habitat data collection (i.e., during the spawning season in late October or November; see Dieterman et al. 2018 for details on tagging and tracking). Most post-spawning trout (73%) moved to overwinter in either a single pool or group of two–four pools within the same stream used for spawning. Trout were always relocated in these pools for the duration of winter and most pools were <400 m from spawning locations. Surprisingly, 17 of 48 tagged brown trout (35%) emigrated up to 8 km downstream to overwinter in a larger, 6th–8th order river considered to be either thermally

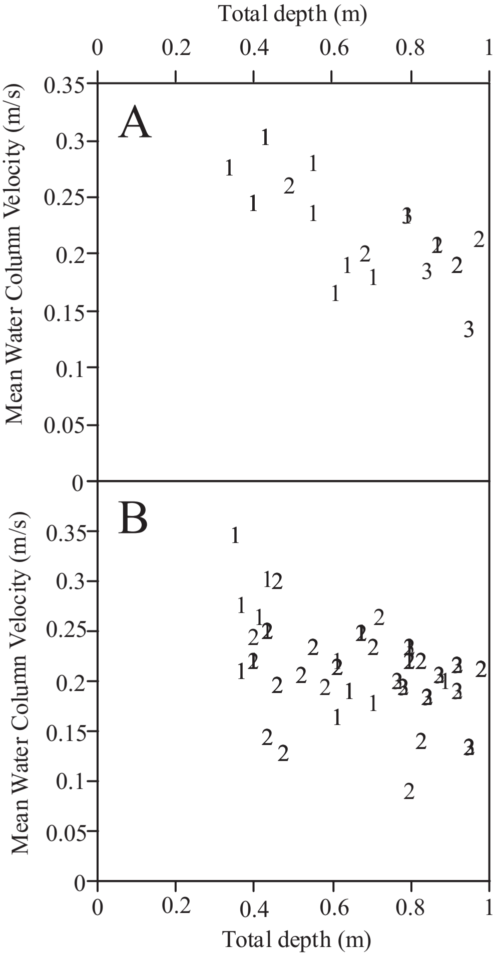

Fig. 7 Total depth and mean water column velocity of feeding locations used by (**a**) individual brown trout and (**b**) individual rainbow trout. Numbers represent the age group of each fish. Figure taken with permission from Grant (1999)

marginal or too warm for trout in summer. These downstream movements into a different river were indicative of a seasonal migration and similar to patterns identified by Clapp et al. (1990) and Meyers et al. (1992). The probability that a large brown trout would emigrate was significantly associated with fish length (-2log likelihood = 19.85, $P < 0.001$). Brown trout longer than 450 mm had more than a 50% probability of emigrating and about an 80% probability of emigrating at lengths greater than 480 mm (Fig. 8).

Weiss (2000) examined brown trout movement in conjunction with an angler creel survey conducted on two streams in 1999. He marked a large number of 203–305 mm trout (≈ age-1 to age-3) with floy tags and radio-tracked a small number of larger (≥380 mm) brown trout (four in each stream) to better quantify movement. He used the concept of turnover rate to infer immigration, where turnover rate was defined as 1—the proportion of marked individuals recaptured in each stream's

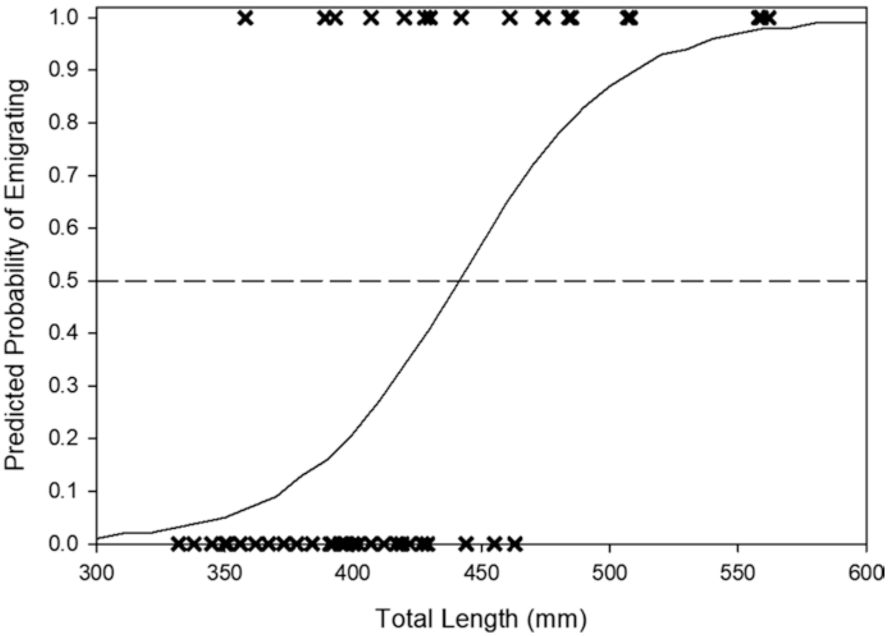

Fig. 8 Relationship (solid line) between total length and the predicted probability that large (332–562 mm) brown trout will emigrate from smaller tributaries used for spawning to overwinter downstream in a larger river or stream in the Driftless Area of Minnesota. Dashed reference line at 50% probability of emigration. Symbols are actual fish and whether they emigrated (*y*-axis = 1) or did not emigrate (*y*-axis = 0)

sampling station. Turnover rate is influenced by station length (i.e., shorter stations can have higher turnover rates; Rodríguez 2002). Sampling stations were 823 and 703 m long in each stream. Trout were first captured in March and recaptured 6 months later in October. After accounting for tag loss, angler harvest, and the estimated proportions of marked and unmarked fish present in each station, only 24 and 13% of marked brown trout were recaptured within the sampling station of their respective stream. Ten tagged trout were known to have moved because they were harvested by anglers from a pool located 23 m upstream. Based on numbers of new unmarked fish captured in October, turnover rate was estimated to be 61% (immigrants) in the 823 m station and 73% in the 703 m station, implying substantial movement over the 0.7–0.8 km spatial and 6 month temporal scales. These immigration estimates may be biased because unreported angler harvest was never estimated and actual movements were never quantified. In contrast, six of eight radio-tagged brown trout exhibited no long-range summer or fall-spawning movements. These fish inhabited just one pool between tagging in late April and recapture (to remove tags) in November, 1999. One trout moved slightly more as it alternated between two pools located 122 m apart and eventually moved 30 m downstream to spawn in early November. The eighth trout (12% of total tagged) was lost 1 week after implantation and could have represented a long-range movement.

These telemetry studies only documented migrations in specific seasons (i.e., just movements to overwintering or summer habitats) but no study had tracked trout over all seasons of the year. Wilfond and Moeckel (Minnesota Department of Natural Resources, unpublished data) radio-tagged and attempted to relocate 16 large (420–645 mm) brown trout weekly, between November 2000 and January 2002, in the Vermillion River, Minnesota. They quantified movement for five seasons: spawning (November 1–December 13), winter (December 14–March 14), spring (March 15–July 4), summer (July 5–September 19), and fall (September 20–October 31). Tagging and relocation methods followed those reported in Dieterman et al. (2018) and Weiss (2000). Fish were most active during the spawning season as fish were found at a different location in 62% of all observations, and movement was initiated when water temperatures approached 10 °C. Mean distance moved between weekly observations during the spawning season was 239 m (SD = 337 m) with maximum distances moved for each fish ranging from 27 to 5614 m. Trout moved less during winter with mean distance moved being 35 m (SD = 72, minimum = 0, maximum = 1041 m) and three of 11 trout (27%) appeared to never move, being relocated at the exact same location every week. Only three trout were tracked for the full 63 week time period encompassing two spawning and wintering seasons (other fish were harvested by anglers, lost, or died). These three fish exhibited strong site fidelity as they were located at nearly the exact same locations in the second spawning and wintering seasons as in the first year. Large brown trout moved extensively in spring (mean = 323 m, SD = 456, minimum = 0, maximum = 7303 m), with some individuals seeking refuge from flooding. Two of 11 fish (18%) moved several kilometers downstream seeking refuge in tributaries and three others moved shorter distances into slow velocity side channels that would not have sufficient depth for them during non-flood flows. Trout moved little during summer with mean movement being 7 m (SD = 13 m). Five of eight trout still alive during summer (63%) never moved and 80% of all observations relocated trout at the exact same location as the previous week, which was similar to observations made by Weiss (2000). Movement was more extensive in fall (mean = 145 m, SD = 125 m), with most movement made just before the spawning season. Wilfond and Moeckel also observed one trout moving between apparent thermal refugia in a tributary (≈ 2 °C cooler) and the main stem river when summer water temperatures were warmest. Despite some limitations, such as small sample sizes (some tagged fish died or were harvested by anglers) and observations limited to larger body sizes, this dataset provided a rare opportunity to document long-term seasonal movements. Still, a continuing need to document movements of smaller-sized individuals prompted a need for studies with other methods.

The most comprehensive Driftless Area salmonid movement studies were made by Dieterman and Hoxmeier (2011) and Hoxmeier and Dieterman (2013) using capture–recapture of PIT-tagged brown trout and brook charr. PIT tags, as opposed to radiotags, allowed assessment of movements of smaller sizes and younger ages of trout and charr for multiple years across a 6.2 km riverscape composed of multiple reaches (0.3–1.3 km in length) in three inter-connected streams. Movements were quantified on seasonal and annual temporal scales and three organismal scales: individual, life stage, and population. Life stages were age-0 juvenile trout and charr, small adults (age 1–2 brown trout and age 1 brook charr), and large adults (age 3+ brown trout and 2+ brook charr). Age-0 juvenile movements were assessed beginning before their first fall when they were large enough to be tagged. Individual movements were based on capture–recapture locations in specific pools and measured distances among all pools in the study area. Population-scale movements were estimated as the proportion of emigrants from reach-specific populations.

Most individual trout and charr were seasonally sedentary being recaptured in the same pool or the next adjacent one to two pools upstream or downstream (i.e., within about 50 m of their previous location) between 3-month sampling events (Figs. 9 and 10). The proportion of brown trout recaptured within 50 m of their previous location was 65% for age-0 juveniles, 72% for small adults, and 69% for large adults. For all brook charr, the proportion was 74%. Only a small proportion of reach-specific trout and charr populations (0–26% depending on species, life stage, and stream reach) emigrated in each season (Table 2), again indicating a majority of trout and charr were seasonally sedentary. Age-0 brown trout was the only life stage with seasonally variable emigration, with most emigrating during their second spring. Lack of seasonal effects on other life stages and species suggests that in Driftless Area streams, most brown trout and brook charr do not undertake seasonal migrations for fall spawning or overwintering.

Although only small proportions of individuals emigrated in each season emigration estimates were more substantial when calculated over an entire year (Table 2). Depending on fish species and life stage, anywhere from 0 to 70% of brown trout and brook charr emigrated annually to different reaches in this riverscape, with several factors influencing emigration. More adult brook charr emigrated away from larger downstream reaches dominated by brown trout to upstream reaches with less abundant brown trout (Hoxmeier and Dieterman 2013). When brown trout abundance was reduced in downstream reaches, brook charr reversed emigration patterns, with more charr emigrating to downstream reaches, suggesting a release from competitive interactions (Hoxmeier and Dieterman 2016).

For brown trout, physical habitat characteristics of each reach influenced movement, with trout displaying an ontogenetic emigration pattern. Increasing numbers of age-0 juvenile and age-1 and 2 small adult trout left shallow reaches with little adult cover and moved to larger and deeper reaches with more adult cover (Dieterman and Hoxmeier 2011). Similarly, reaches with the deepest pools and most adult cover had the fewest emigrants, especially for larger age-3+ brown trout (0–18% emigrated annually). In this respect, stream reaches with artificially improved instream habitat had a profound influence on ontogenetic emigration patterns as fewer brown trout emigrated from improved reaches than immigrated into them (Fig. 11). Brown trout moved to these deeper reaches with more cover, presumably to avoid predation, as survival was highest in these reaches (Dieterman and Hoxmeier 2011), whereas movement did not confer any growth benefits (Dieterman et al. 2012).

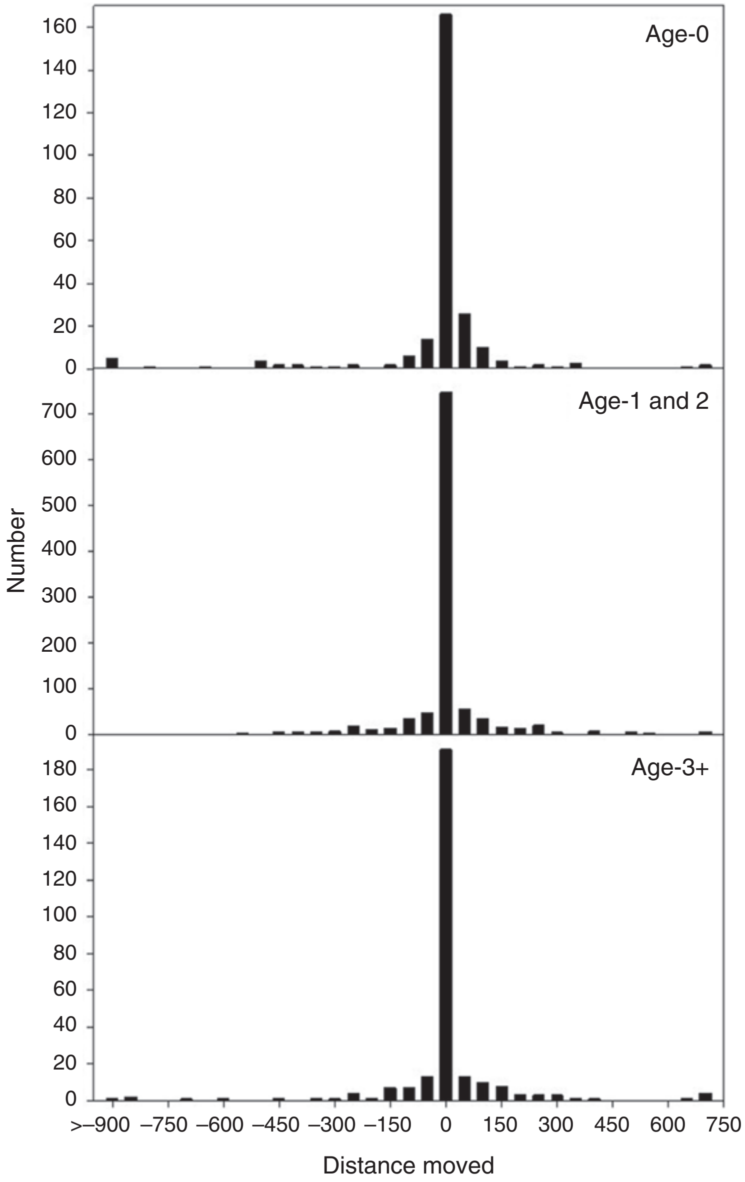

Fig. 9 Distance moved (m) by individual brown trout recaptured in consecutive 3-month seasonal sampling events for each of three age groups between September 2006 and September 2008. Data collected in three inter-connected streams in the Driftless Area of southeast Minnesota. Negative numbers are downstream movements

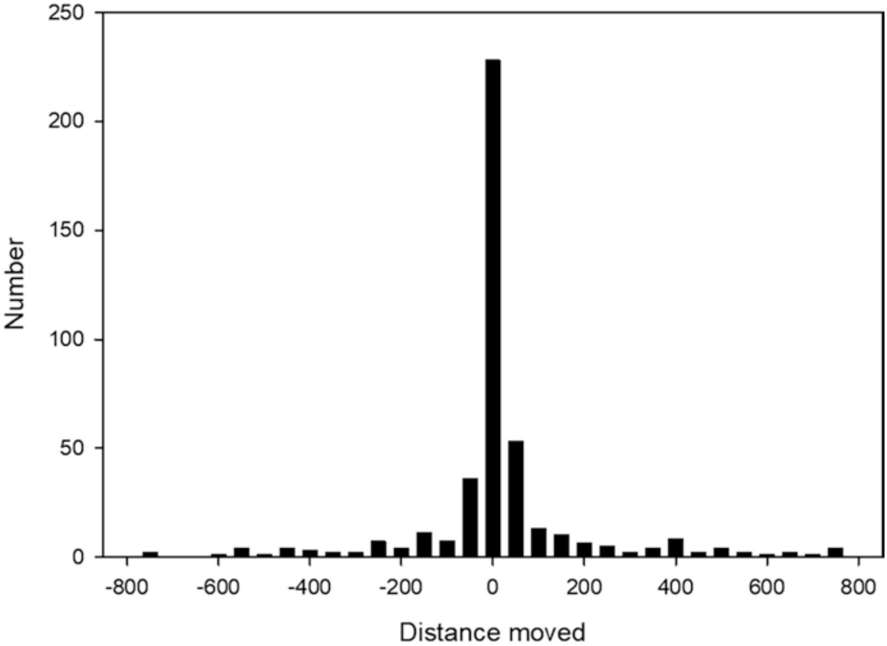

Fig. 10 Distance moved (m) by individual brook charr (ages 0–2+) recaptured in consecutive 3-month seasonal sampling events between September 2006 and September 2008. Data collected in three inter-connected streams in the Driftless Area of southeast Minnesota. Negative numbers are downstream movements

Table 2 Minimum and maximum estimates of the proportion of individual brown trout and brook charr emigrating from reach-specific populations for each season and cumulatively across a whole year. Specific emigration estimates varied depending on which reach fishes were emigrating from. Age-0 brown trout were the only life stage where emigration estimates varied by season, but not reach. Data were collected between September 2006 and September 2008 in three inter-connected Driftless Area streams in southeast Minnesota

		Seasonal time scale				
Species	Life stage	Fall	Winter	Spring	Summer	Annual time scale
Brown trout	Age-0	3%	6%	10%	n/a[a]	18%
	Age 1–2	1–26%	1–26%	1–26%	1–26%	4–70%
	Age 3+	0–5%	0–5%	0–5%	0–5%	0–18%
Brook charr	Age-0	1–14%	1–14%	1–14%	n/a[a]	4–45%
	Age-1	2–11%	2–11%	2–11%	2–11%	8–37%
	Age-2+	0–12%	0–12%	0–12%	0–12%	0–40%

[a] Emigration not estimated in this season

Assessing seasonal movement of the youngest individuals in a population is complicated by their small size, which hinders use of most tag types. Advances in otolith microchemistry, stable isotopes, and genetic methods allow examination of these types of movements (Berry et al. 2004; Pine et al. 2012). Miller et al. (2019)

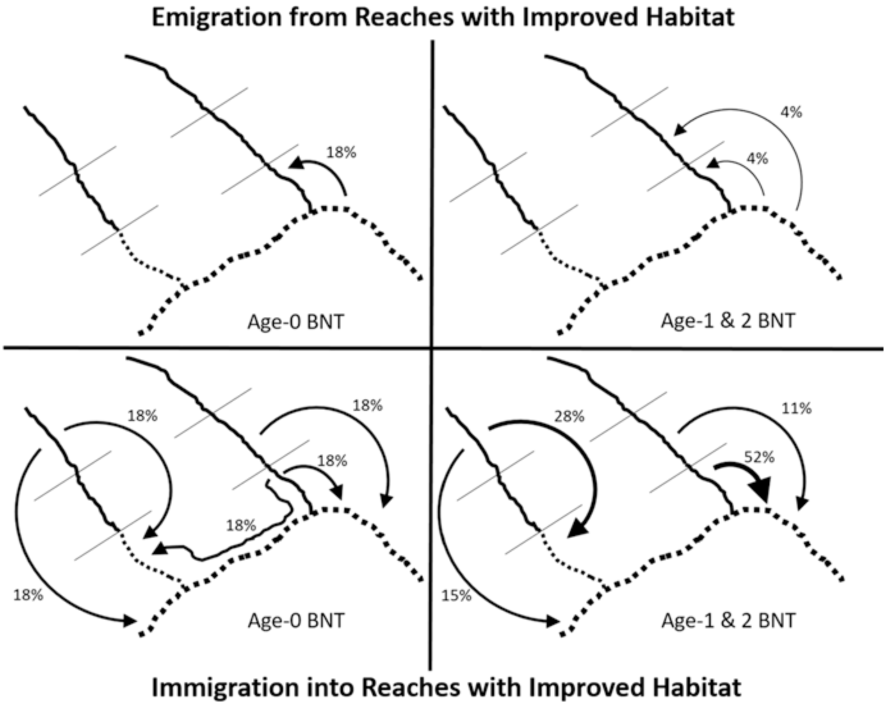

Fig. 11 Annual emigration from, and immigration into, stream reaches with artificial instream habitat improvement (dashed lines) and reaches without such habitat improvement (solid lines) for two age groups of brown trout

used a sibship and parentage genetic approach to identify family groups of brook charr in one 1.6 km Driftless Area stream in southeast Minnesota. Each pool in the entire stream was sampled independently and recorded when parents were collected during fall-spawning in October and when subsequent progeny were captured about a year later. Thus, assuming parent locations represented the approximate area where fertilized eggs were deposited, natal movement among pools over their first 6 months (i.e., between spring emergence and subsequent capture in fall) was estimated. Miller et al. (2019) found that most progeny originated from a small group of parents with probability of successful reproduction being influenced by parent size. Subsequent natal movement was variable among families, with some progeny being captured predominantly upstream of their parent locations the previous fall, some downstream, and some progeny dispersed in both directions (Fig. 12; figure derived from data in Miller et al. 2019). In particular, progeny from the largest family were captured in over half of all pools available (52%) and were scattered throughout most of the entire 1.6 km stream.

Almost all seasonal salmonid movements documented in Driftless Area streams were movements from one location to a separate location (e.g., emigration from one stream reach into another), with very few instances of a return movement to the

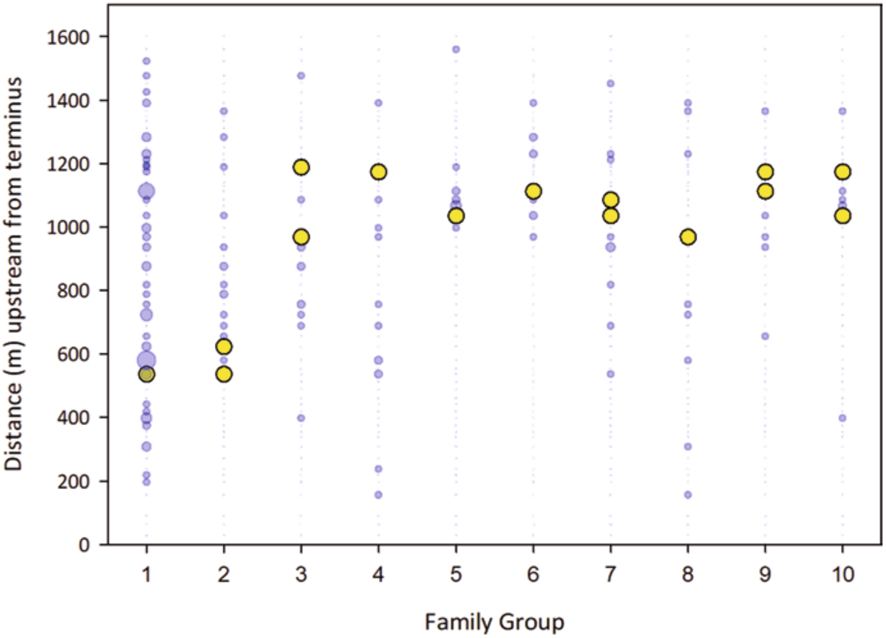

Fig. 12 Natal movement of brook charr for the ten most abundant family groups among all pools in a 1.6 km stream in southeast Minnesota based on genetic parentage assignment. Yellow circles are locations of parents collected during the 2011 fall-spawning sample and blue circles represent capture locations of their progeny a year later in fall 2012

original location. Thus, these seasonal movements do not fit the definition of migration as articulated by Saint-Pe (2019). Rather, these intermediate-scale seasonal movements probably represent a transitional succession of several smaller-scale feeding and exploratory movements made across several months that result in annual dispersal of individuals among stream habitats or reaches. Ultimately, a sequence of several such annual dispersals should result in even larger-scale dispersal to adjacent streams or drainages that may be observed in studies of genetic structure.

4.3 Large-Scale Dispersal

Population genetic structure has commonly been used to investigate phylogenetic relationships and evolutionary history, identify potential disturbance refugia, and infer post-disturbance dispersal pathways. For example, such work has been completed in the context of glacial refugia and dispersal for many European regions with native brown trout populations (Sanz 2018). In the Driftless Area, population genetic structure studies for native brook charr revealed likely disturbance refugia and complex dispersal movements (Hoxmeier et al. 2015). As noted previously, the Driftless Area was not subjected to the most recent glacial advances. However, native brook charr populations declined or were locally extirpated from most streams during more recent European settlement around 1900 by a combination of poor agricultural land use, stream degradation, and stocking of non-native brook charr hatchery strains from the eastern United States as well as brown trout and rainbow trout (Thorn et al. 1997; Hoxmeier et al. 2015). Despite these recent disturbances, genetic structuring identified three drainage-basin-scale clusters of stream populations more similar to each other than to other brook charr populations in southeast Minnesota and not associated with non-native hatchery strains of brook charr (Fig. 13). This suggests that these three drainage basins may have provided post-settlement disturbance refugia. Dispersal movements within these drainage basins could have happened within the past century via post-disturbance recolonization, although local anthropocentric dispersal cannot be excluded. If all streams in these clusters provided refugia, then dispersal could have happened centuries earlier. These populations have been termed "remnant" or "heritage strain" brook charr. Some heritage-strain brook charr populations were established by anthropogenic dispersal, based on known translocations to other streams in the 1970s and 1980s

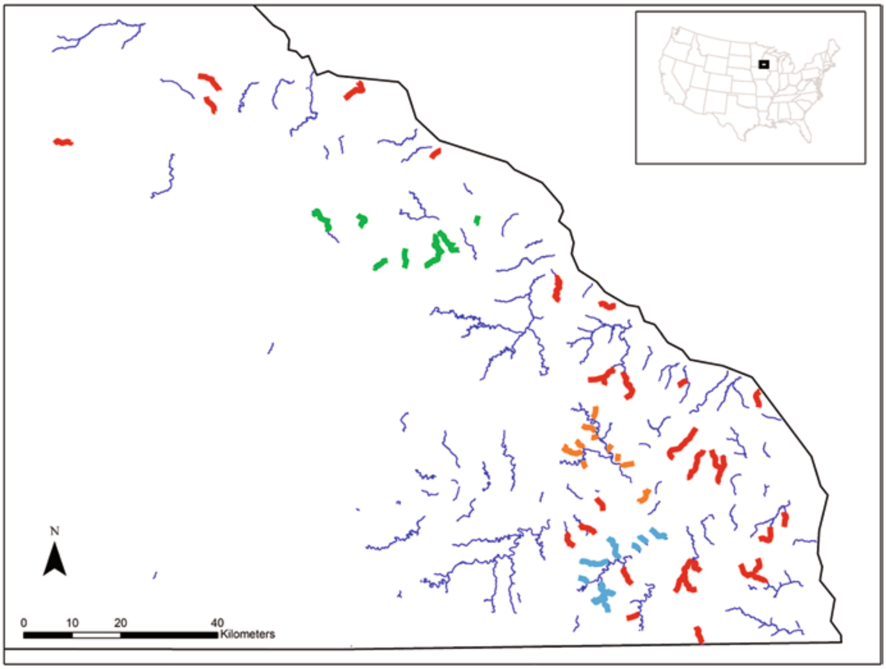

Fig. 13 Designated coldwater trout streams in the Driftless Area of southeast Minnesota with highlighted streams containing brook charr. Streams with native heritage-strain brook charr are in one of three clusters highlighted in green, orange, or light blue. Streams highlighted in red contain brook charr populations matching hatchery strains of eastern U.S. origin

(Hoxmeier et al. 2015). Some translocated populations appear to have subsequently dispersed over the past 30–40 years to additional streams located at least 8 km away.

5 An Ontogenetic Synthesis of Driftless Area Salmonid Movements

Although we reviewed Driftless Area movement studies in the context of increasing spatiotemporal scales, we synthesize those movements across ontogenetic life stages to clarify how important movements change with ontogeny and how movement of each life stage may be best described by different frameworks. Because the four broad salmonid movements of Saint-Pe (2019), namely, feeding, exploratory, seasonal migrations, and dispersal, vary based on spatiotemporal scales, they can be placed within the riverscape scales of Fausch et al. (2002) to highlight where most Driftless Area salmonid movement studies have been conducted (Fig. 14). In this context, most studies over the past three decades have investigated seasonal to annual migrations at the stream segment scale, a spatial scale which Fausch et al. (2002) noted was less studied than other spatial scales two decades ago. Although several studies were implemented to assess seasonal migrations, there was little

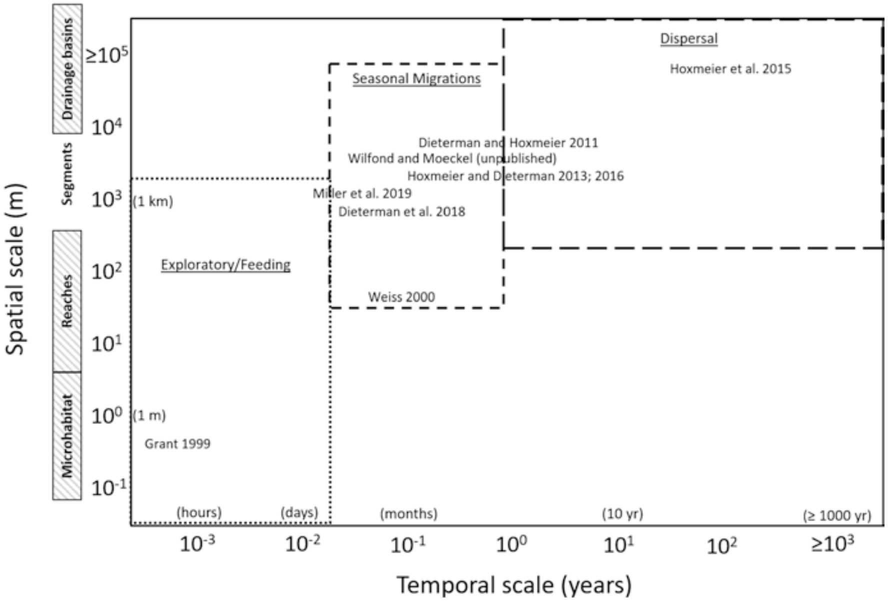

Fig. 14 Summary of Driftless Area salmonid movement studies organized by four primary movement types after Saint-Pe (2019) and in the context of Fausch et al. (2002) riverscape spatiotemporal scales. Spatial scales in boxes (*y*-axis) represent those identified by Fausch et al. (2002) as having been well studied prior to 2002

evidence that a majority of Driftless Area salmonids conducted extensive movements to fulfill seasonal resource needs as in the Dynamic Landscape Model. Instead, aspects of the five stream components influenced salmonid movements, resulting in varying levels of partial migration across ontogeny with the concepts of dispersal, restricted movement, and migration applying to different life stages (Fig. 15).

Most Driftless Area salmonid movement happens during the first year of life, between alevin emergence in spring through their first fall and winter and into the following spring. Movements in the first few months following emergence, often termed natal dispersal, can be the result of several factors including intra-cohort competition and high current velocities, as from flooding (Crisp 1993; Daufresne et al. 2005). In the Driftless Area, natal dispersal varies by family, partly depending on family size (L. Miller unpublished data). Between their first fall and subsequent spring, age-0 juveniles continue exploratory and feeding movements to adjacent stream reaches with movement dependent on physical habitat conditions (brown trout) or biotic interactions, as brook charr avoid interspecific brown trout competitors. First-year salmonid movement can be extensive and is likely an important mechanism for gene dispersal, supplementation of populations in adjacent reaches, and more generally, population recovery following episodic water quality events, such as fish kills. In summary, reach-specific populations of juvenile salmonids conduct partial migrations through exploratory and feeding movements of individuals that represent an important time of salmonid dispersal in Driftless Area streams.

Small proportions of adult trout and charr within Driftless Area populations continue to move to reaches with better physical habitat (brown trout) or lack of

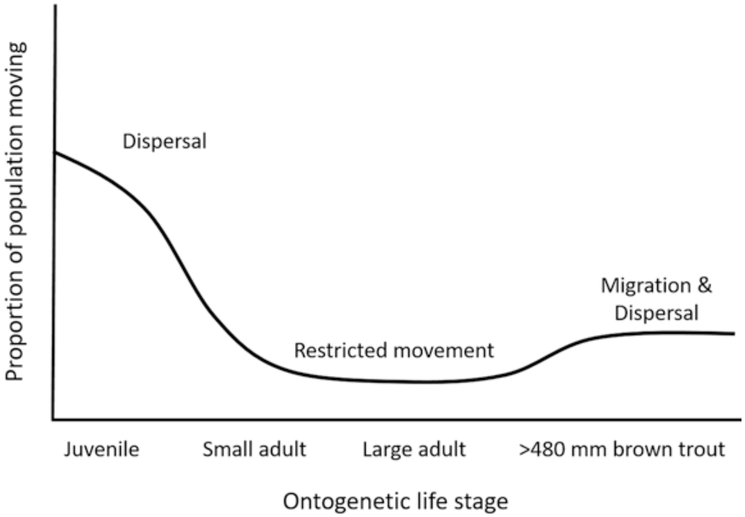

Fig. 15 Ontogenetic patterns of partial migration (proportion of population moving), and in application of selected frameworks, to stream-resident salmonid movements in the Driftless Area of the upper Midwestern United States

interspecific competitors (brook charr), but become more sedentary as they age, grow, and find pools with ideal habitat. Most Driftless Area stream reaches have sufficient food resources and habitat to fulfill feeding, spawning, and refugium needs, and this likely explains the high salmonid production in these groundwater-fed systems (Newman and Waters 1989; Kwak and Waters 1997; Hoxmeier and Dieterman 2019). We hypothesize that abundant, fertile groundwater sources and hydrologic stability of Driftless Area streams provide good quality habitat and resources to promote mostly sedentary adults, as characterized by the restricted movement paradigm and in contrast to the Dynamic Landscape Model (Fig. 16). Habitat quality is known to influence animal movement with areas with good habitat quality having fewer mobile individuals than areas with poor habitat quality (Bélanger and Rodríguez 2002; Rasmussen and Belk 2017). Galinat et al. (2020) documented less movement of brown trout after improving habitat quality in a South Dakota (USA) stream than prior to project implementation. Similarly, groundwater-fed streams flowing through limestone catchments, such as those in the Driftless Area, likely represent streams with good habitat quality because they

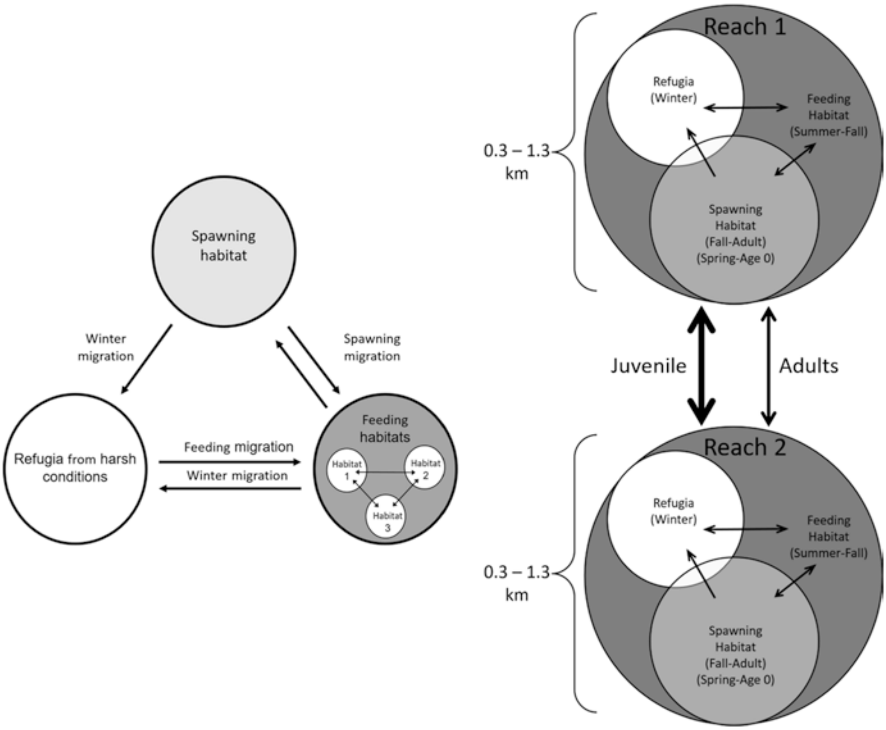

Fig. 16 Riverscape conceptual figures contrasting salmonid movement in differing stream systems. Left figure is traditional Dynamic Landscape Model where salmonids need to move to different reaches to fulfill seasonal needs. Right figure represents groundwater-fed Driftless Area streams where salmonids are able to fulfill most seasonal habitat needs within a single reach, but with some movement among reaches for juvenile and adult life stages

tend to be fertile and have stable hydrologic and thermal regimes (McFadden and Cooper 1962; Nicola and Almodóvar 2002; Nicola et al. 2009; Dermond et al. 2017). Conversely, surface-water-fed streams flowing over sandstone, shale, or granite geology have soft, infertile waters and hydrology punctuated by extreme high and low flows and more variable water temperatures. These habitat differences between fertile, groundwater-fed and infertile, surface-water-fed streams have been shown to influence salmonid recruitment, growth, mortality, and feeding (McFadden and Cooper 1962; Nicola et al. 2009; Dermond et al. 2017) and we hypothesize that these differences should influence movement as well. In less fertile, more variable surface-water-fed streams, salmonids may be expected to move more to seek less abundant food resources or to avoid habitats influenced by extreme high or low flows or water temperatures as suggested by the Dynamic Landscape model. We do not know of any studies that have specifically contrasted salmonid movements between fertile, groundwater-fed and infertile, surface-water-fed streams and suggest this may represent a future research need. Nevertheless, by age-2 or -3, most adult salmonid populations in the Driftless Area can be generally characterized by the restricted movement paradigm, with only small proportions of individuals conducting partial migration among reaches.

Finally, very large brown trout, those exceeding ≈ 480 mm, represent a life stage with entirely different habitat needs and behaviors, as large proportions of these fish moved longer distances than smaller adults. As such, this size group may represent another important life stage promoting broad population dispersal. This life stage was also the only one that demonstrated true migration with a return to former spawning and wintering locations in two separate years, although only a few trout made this movement. Specific research on the ecology and potamodromous movement of these big fish in Driftless Area and other groundwater-fed streams is scant, with mostly anecdotal observations made in conjunction with other studies summarized here. More focused studies of stream-resident large brown trout movement have been conducted in other upper Midwestern streams, but often had limited sample sizes also (e.g., Clapp et al. 1990, $n = 8$; Diana et al. 2004, $n = 11$).

Driftless Area studies of large brown trout reviewed here noted long-range movements to seek refuge from adverse environmental conditions and to overwinter in larger streams. Wilfond and Moeckel (reviewed here) observed large brown trout moving to seek refuge from excessive flooding or to apparent thermal refuge in a tributary. However, their study was conducted on a stream system in an urbanizing watershed, with likely unstable hydrology and thermally marginal waters, which is uncharacteristic of most other Driftless Area coldwater streams. Wang et al. (2003) noted increasing urbanization to be associated with altered thermal regimes, baseflows, and fish and invertebrate communities in other Driftless Area streams. Perhaps increasing watershed urbanization, with associated increases in impermeable surfaces (e.g., concrete pavement), forces streams to behave more like surface-water-fed systems than groundwater-fed systems.

Downstream movement of large brown trout from small coldwater tributaries to overwinter in larger streams may reflect a lack of physical space or habitat volume. Researchers have documented positive associations between brown trout size and stream size or discharge in European streams (several studies reviewed in Jonsson and Jonsson 2011) as well as in the Driftless Area (Dieterman et al. 2006). This suggests bigger trout need more space, presumably in the form of big pools with deep water. Conversely, seasonal water temperature changes may expand Driftless Area riverscapes, making deep pools in large streams available to large brown trout. Wilfond and Moeckel noted most radio-tagged brown trout moved in fall when water temperatures approached 10 °C. Seasonal water temperature changes create a spatiotemporally variable thermalscape across many Driftless Area streams, based in part on differing groundwater inputs to different stream reaches (Fig. 6). We

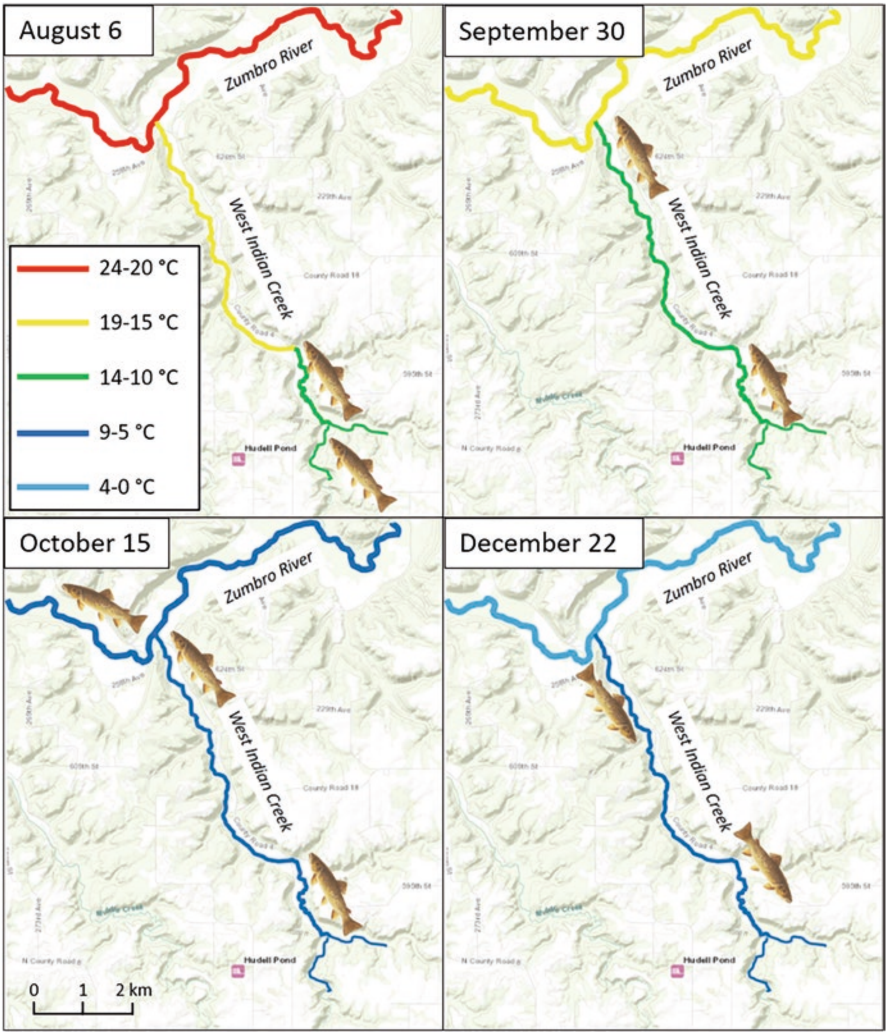

Fig. 17 Hypothesized movement of large brown trout across a spatiotemporally variable Driftless Area thermalscape

hypothesize that large brown trout may move downstream and upstream following these changing thermal boundaries across time (Fig. 17). Regardless of reason, reach-specific populations of very large brown trout exhibit fluvial-adfluvial partial migrations that have important implications for genetic and population level dispersal as well as management actions, such as angling regulations to protect them.

In addition to uncertainty about movements of the largest brown trout, movements of very large ($\geq$ 455 mm) native brook charr have not been well studied in the Driftless Area. For example, do very large brook charr move from small coldwater tributaries to overwinter in larger streams similar to large brown trout? If so, do they follow changing thermal boundaries as we hypothesized for large brown trout? If they emigrate from small tributaries, at what size do they emigrate or does competition with introduced brown trout simply limit large brook charr to headwater areas as found for other sized charr (Hoxmeier and Dieterman 2016)?

Dispersal studies at the largest spatiotemporal scales have also been limited (Fig. 14). Although Hoxmeier et al. (2015) examined genetic structure of brook trout populations to infer dispersal, similar studies have not been conducted on non-native brown trout or rainbow trout. Determining dispersal ability of brown trout in particular, could be important because they are considered one of the most invasive fish species that can negatively impact native fishes (Budy et al. 2013; Jones and Closs 2018). Increasing baseflows in the Driftless Area may facilitate brown trout expansion to new streams that support native fishes, including several species of conservation concern (Kelly 2020).

The ontogenetic movement patterns described for our Driftless Area salmonid populations are likely applicable to other stream-resident salmonid populations living in fertile, groundwater-fed streams flowing over karst geologic formations of limestone and dolomite. Globally, about 15% of the ice-free land surface is karst with over 10.6 million km^2 in temperate, cold, and polar regions where salmonids occur (Goldscheider et al. 2020). Thus, the patterns we observed could have broad applicability. Still, many other movement patterns have been documented for salmonids in a variety of environments. A complete review of such movements, and how they compare and contrast with patterns we observed, is beyond the scope of this chapter. Also, we do not know of many studies that have tried to integrate their findings over several temporal and ontogenetic scales as we have done, which makes specific comparisons difficult. We hope our integration is useful for others to make such comparisons, such as comparing between groundwater-fed and surface-water-fed systems we noted previously.

In summary, Driftless Area salmonids exhibit ontogenetic differences in degree of movement with most dispersing during their first year of life or at the oldest ages and largest sizes. Intermediate sizes and ages exhibit some movement among reaches, but a majority of individuals are sedentary as suggested by the restricted movement paradigm. Thus, the dynamic landscape model of stream fish movement has less application to Driftless Area salmonid populations than a more general riverscape model of stream reaches providing adequate seasonal habitat facilitating mostly sedentary individuals, but with some inter-reach dispersal. In this sense, Driftless Area salmonid communities are best described as exhibiting partial fluvial-adfluvial migration characteristic of a patchy metapopulation (sensu McCullough 1996).

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Trophic Flexibility of Stream-Dwelling Salmonids: Disentangling Common Ontogenetic and Seasonal Patterns

Javier Sánchez-Hernández

Abstract This review synthesises the literature on ontogenetic and seasonal changes in feeding patterns of nine genera of the family Salmonidae (*Coregonus*, *Prosopium*, *Stenodus*, *Hucho*, *Oncorhynchus*, *Salmo*, *Salvelinus*, *Brachymystax* and *Thymallus*), disentangling the general mechanisms driving those changes and the common dietary patterns. Stream-dwelling salmonids are characterised by their trophic flexibility, exhibiting consistent ontogenetic and seasonal patterns. One of the most outstanding ontogenetic dietary changes is the switch to piscivory along ontogeny. However, there is no solid evidence supporting piscivorous behaviour in riverine grayling (*Thymallus* spp.) and whitefish (*Prosopium williamsoni* and *Coregonus lavaretus*) despite been frequently shown in lacustrine populations. Other general ontogenetic patterns include allometry in prey size and a higher consumption of terrestrial invertebrates (i.e. switch to surface-foraging). This consumption of allochthonous resources is especially important during the summer in temperate territories when insect phenology maximises and thus, becomes accessible to salmonids. In addition, availability of imagoes of aquatic invertebrates (Ephemeroptera, Trichoptera, Diptera and Plecoptera) is highly related to emergence (emergence peaking around spring and early summer), but also highly dependent on climate-related geographical variability. Thus, climate influence on seasonal life-history traits of prey taxa (hatching, emergence, diapause, etc.) can strongly determine seasonal changes in feeding of salmonids through bottom-up mechanisms. Understanding global dietary patterns can be complex because the environmental conditions change broadly across salmonid's distribution as well as seasons, but still common patterns can be extended to geographic regions with similar climatic conditions.

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1 Introduction

Riverine salmonids have been useful model species in feeding studies describing ontogenetic and seasonal changes (e.g. Lowery and Beauchamp 2015; Sánchez-Hernández and Cobo 2018; Kreiling et al. 2021). However, little attention has been given to explore global dietary patterns from an ontogenetic and seasonal perspective within the family Salmonidae. Overall, stream-dwelling salmonids commonly are drift feeders that typically use "sit-and-wait" strategies to ambush prey from short distances (Rader 1997; Tunney and Steingrímsson 2012). However, this may not apply to species that have the potential to switch to piscivory very early in their development such as the huchen species (Nagy 1976; Holčík 1990) and large individuals of other salmonid species displaying more active feeding strategies to consume fish prey. In addition, diets of stream-dwelling salmonids are dependent on the availability, abundance and distribution of food resources, making them opportunistic with populations composed by individuals that can be either generalist or specialist. For example, de Crespin de Billy and Usseglio-Polatera (2002) observed that riverine brown trout (*Salmo trutta*) feed on the most accessible invertebrates which are those living in exposed microhabitats and with a high tendency to drift and aggregation. Today, there are some limitations and considerations that need to be acknowledged when attempting to explore global dietary patterns of salmonids in riverine systems. First, salmonids are distributed across a large geographical extension (northern hemispheric regions of Eurasia and North America, but several species introduced to the southern hemisphere), covering different freshwater ecoregions and climate regions (Abell et al. 2008). Thus, specific climate-related prey, habitat (stream size) and life history that broadly change among geographical areas are expected to impact on diet composition among salmonid's populations (Sánchez-Hernández et al. 2019b; Sánchez-Hernández 2020a), which may hinder the ability to identify global and common feeding patterns (here ontogenetic and seasonal patterns) for stream-dwelling salmonids. Second, stream-dwelling salmonid species have been studied, but the current knowledge are commonly biased towards some genera (*Salmo*, *Salvelinus* and *Oncorhynchus*) or some species within the same genus. In this regard, little effort has been paid to explore the feeding ecology of taimen *Hucho taimen* and Japanese huchen *Hucho perryi* compared to huchen *Hucho hucho* (Table 1). This prevents a deeper knowledge on seasonal and ontogenetic dietary shifts on the genus *Hucho* and hinders the exploration of common dietary patterns. Third, whitefishes (Coregonidae) mostly include typical lake-dwelling species (*Coregonus* spp.) and only few species are predominantly stream-dwelling such as mountain whitefish (*Prosopium williamsoni*) and Inconnu (*Stenodus leucichthys*), which constrains the information available. Still, juveniles

Table 1 Summary of the number of species and their distributions/ranges, relevant life histories and climate with respect to where diet data are available

Species	Country	Latitude	Life histories	Stream size (width)	Climate zone[a]	Data source[b]
Coregonus lavaretus	Russia	64.5	Resident	Not available	Subarctic (Dfc)	Novoselov (2014)
Coregonus clupeaformis	Canada	60	Resident	Not available	Subarctic (Dfc)	Little et al. (1998)
Prosopium williamsoni	USA	43.7	Resident	Not available	Warm-summer humid continental (Dfb)	Pontius and Parker (1973)
	Canada	50.7	Resident	Not available	Warm-summer humid continental (Dfb)	Thompson and Davies (1976)
	USA	48.4	Resident	Not available	Warm-summer humid continental (Dfb)	DosSantos (1985)
	USA	46.9	Resident	Not available	Warm-summer humid continental (Dfb)	Whiteley (2007)
Stenodus leucichthys	Russia/ Kazakhstan	46.5	Amphidromous and resident	Not available	Cold semiarid - steppe (Bsk)	Poursaeid and Falahatkar (2012)
Hucho hucho	Slovakia	49.1	Resident	Not available	Warm-summer humid continental (Dfb)	Nagy (1976)
	Slovakia	49.2	Resident	Not available	Warm-summer humid continental (Dfb)	Holčík (1990)
	Poland	49.5	Resident	Not available	Warm-summer humid continental (Dfb)	Witkowski et al. (1994)
	Serbia	44.1	Resident	3–4 m	Temperate oceanic (Cfb)	Nikcevic et al. (1998)
	Slovakia	49.2	Resident	Not available	Warm-summer humid continental (Dfb)	Šubjak (2013)

(continued)

Table 1 (continued)

Species	Country	Latitude	Life histories	Stream size (width)	Climate zone^{a}	Data source^{b}
Oncorhynchus mykiss	Japan	42.7	Resident (introduced)	Not available	Warm-summer humid continental (Dfb)	Kitano et al. (1993)
	Spain	42.8	Resident (introduced)	9 m	Temperate oceanic (Cfb)	Oscoz et al. (2005)
	USA	43.4	Anadromous (juvenile)	65 m on average	Warm and dry-summer continental (Dsb)	Godby et al. (2007)
	Argentina	–41.2	Resident (introduced)	1.5–2.5 m	Warm-summer Mediterranean (Csb)	Buria et al. (2009)
	Chile	44.3	Resident (introduced)	60–130 m	Warm-summer Mediterranean (Csb)	Arismendi et al. (2012)
	Russia	54.4	Anadromous (juvenile)	Not available	Subarctic (Dfc)	Kuzishchin et al. (2015)
	Chile	–39.4	Resident (introduced)	3.5–25 m	Warm-summer Mediterranean (Csb)	Fierro et al. (2016)
	USA	43.8	Anadromous/Resident	Not available	Warm-summer Mediterranean (Csb)	Li et al. (2016)
	USA	36.1	Anadromous/Resident	Not available	Warm-summer Mediterranean (Csb)	Rundio and Lindley (2019)
	USA	36.3	Anadromous/Resident	Not available	Warm-summer Mediterranean (Csb)	Rundio and Lindley (2021)
Oncorhynchus clarkii	USA	55.7	Resident	2–9 m	Temperate oceanic (Cfb)	Wipfli (1997)
	USA	41.3	Resident	Not available	Subarctic (Dfc)	Bozek et al. (1994)
	USA	43.8	Resident	Not available	Warm-summer Mediterranean (Csb)	Li et al. (2016)
	USA	44.6	Resident	1–3 m	Warm-summer Mediterranean (Csb)	Falke et al. (2020)

Species	Country	Latitude	Life histories	Stream size (width)	Climate zone[a]	Data source[b]
Oncorhynchus tshawytscha	Chile	–45.8	Anadromous (juvenile - introduced)	Not available	Temperate oceanic (Cfb)	Ibarra et al. (2011)
	Russia	54.4	Anadromous (juvenile)	Not available	Subarctic (Dfc)	Kuzishchin et al. (2015)
	Chile	–44.6	Anadromous (juvenile/ immature - introduced)	Not available	Temperate oceanic (Cfb)	Barca et al. (2019)
Oncorhynchus kisutch	USA	55.7	Anadromous	2–9 m	Temperate oceanic (Cfb)	Wipfli (1997)
	Russia	54.4	Anadromous (juvenile)	Not available	Subarctic (Dfc)	Kuzishchin et al. (2015)

(continued)

Table 1 (continued)

Species	Country	Latitude	Life histories	Stream size (width)	Climate zone[a]	Data source[b]
Oncorhynchus masou	Russia	54.4	Anadromous (juvenile)	Not available	Subarctic (Dfc)	Kuzishchin et al. (2015)
Salmo trutta	Ireland	53.3	Resident	Not available	Temperate oceanic (Cfb)	Kelly-Quinn and Bracken (1990)
	Scotland	57.3	Resident	Not available	Subpolar oceanic (Cfc)	Bridcut (2000)
	Spain	42.3	Resident	2.5 m	Temperate oceanic (Cfb)	Montori et al. (2006)
	Ireland	53.9	Resident	2.56–5.08 m	Temperate oceanic (Cfb)	Dineen et al. (2007)
	Italy	42.6	Resident	Not available	Warm-summer Mediterranean (Csb)	Fochetti et al. (2003, 2008)
	Spain	42.9	Resident	2–3 m	Warm-summer Mediterranean (Csb)	Sánchez-Hernández et al. (2011a, 2013)
	Chile	44.3	Resident (introduced)	60–130 m	Warm-summer Mediterranean (Csb)	Arismendi et al. (2012)
	Spain	40.3	Resident	15.7 m	Warm-summer Mediterranean (Csb)	Sánchez-Hernández and Cobo (2012, 2018)
	Finland	65.6	Resident	1.6–80 m	Subarctic (Dfc)	Syrjänen et al. (2011)
	Czech Republic	50.9	Resident	2–5 m	Temperate oceanic (Cfb)	Horká et al. (2017)
	USA	44.1	Resident (introduced)	Not available	Temperate oceanic (Cfb)	Cochran-Biederman and Vondracek (2017)

Species	Country	Latitude	Life histories	Stream size (width)	Climate zone[a]	Data source[b]
Salmo salar	Scotland	58.4	Anadromous (juvenile)	Not available	Temperate oceanic (Cfb)	Allan (1941)
	Canada	46.9	Anadromous (juvenile)	Not available	Warm-summer humid continental (Dfb)	Keeley and Grant (1997)
	Finland	69.9	Anadromous (juvenile)	4–6 m	Subarctic (Dfc)	Erkinaro and Erkinaro (1998)
	Norway	69.8	Anadromous (juvenile)	20–30 m	Subarctic (Dfc)	Gabler and Amundsen (1999)
	Scotland	57.3	Anadromous (juvenile)	Not available	Subpolar oceanic (Cfc)	Bridcut (2000)
	Norway	69.9	Anadromous (juvenile)	230 m	Subarctic (Dfc)	Amundsen et al. (2001)
	Ireland	53.9	Anadromous (juvenile)	2.56–5.08 m	Temperate oceanic (Cfb)	Dineen et al. (2007)
	USA	42.4	Anadromous (juvenile)	4.9 m	Warm-summer humid continental (Dfb)	Grade and Letcher (2006)
	Norway	69.8	Anadromous (juvenile)	Not available	Subarctic (Dfc)	Sánchez-Hernández et al. (2016a)
Salvelinus fontinalis	USA	41.4	Resident	2.1 m	Warm-summer humid continental (Dfb)	Hubert and Rhodes (1989)
	USA	38.6	Resident	Not available	Temperate oceanic (Cfb)	Webster and Hartman (2005)
	France	42.7	Resident (introduced)	5.2–6 m	Temperate oceanic (Cfb)	Cucherousset et al. (2007)
	USA	38.7	Resident	1.46–4.77 m	Temperate oceanic (Cfb)	Utz and Hartman (2007)
	Czech Republic	50.9	Resident (introduced)	2–5 m	Temperate oceanic (Cfb)	Horká et al. (2017)
Salvelinus alpinus	Canada	81.8	Resident	Not available	Polar tundra (ET)	Sinnatamby et al. (2012)
	Norway	69.8	Anadromous (juvenile)	Not available	Subarctic (Dfc)	Sánchez-Hernández et al. (2016a, b)
	Iceland	64.0	Anadromous/Resident	Not available	Subpolar oceanic (Cfc)	Kreiling et al. (2021)

(continued)

Table 1 (continued)

Species	Country	Latitude	Life histories	Stream size (width)	Climate zone[a]	Data source[b]
Salvelinus confluentus	Canada	51.6	Anadromous/Resident	Not available	Subarctic (Dfc)	Furey et al. (2015)
	USA	48.7	Anadromous/Resident	Not available	Dry-summer subarctic (Dsc)	Lowery and Beauchamp (2015)
Salvelinus malma	USA	55.7	Resident	2–9 m	Temperate oceanic (Cfb)	Wipfli (1997)
	Russia	54.4	Resident	Not available	Subarctic (Dfc)	Kuzishchin et al. (2015)
Salvelinus leucomaenis	Russia	54.4	Anadromous (juvenile)	Not available	Subarctic (Dfc)	Kuzishchin et al. (2015)
Brachymystax lenok	Korea	37.8	Resident	Not available	Monsoon-influenced subarctic (Dwc)	Yoon et al. (2013)
	Mongolia	50.3	Resident	Not available	Monsoon-influenced subarctic (Dwc)	Olson et al. (2016)
Thymallus thymallus	England	52.2	Resident	Not available	Temperate oceanic (Cfb)	Hellawel (1971)
	England	50.7	Resident	Not available	Temperate oceanic (Cfb)	Scott (1985)
	France	46.1	Resident	10–15 m	Temperate oceanic (Cfb)	Sempeski et al. (1995)
	Russia	56.4	Resident	Not available	Subarctic (Dfc)	Zuev et al. (2017)
	Poland	53.3	Resident	15–30 m	Temperate oceanic (Cfb)	Smoliński and Glazaczow (2019)
	France	47.0	Resident	20–40 m	Temperate oceanic (Cfb)	Frossard et al. (2021)
Thymallus arcticus	Mongolia	50.3	Resident	Not available	Monsoon-influenced subarctic (Dwc)	Olson et al. (2016)

[a] Climate zones according to the updated Köppen–Geiger climate classification (Kottek et al. 2006)

[b] Only included articles used in this chapter to explore common ontogenetic and seasonal patterns

of lake whitefish species commonly inhabit riverine systems (lake tributaries) showing seasonal patterns in feeding (Little et al. 1998).

Seasonal changes in prey availability may shape predator niche variation through bottom-up mechanisms and salmonids can modify their niche depending on availability of preferred resources (Sánchez-Hernández et al. 2021). Because life-history traits of aquatic invertebrates such as emergence of pupae and adults (peaking around spring and early summer) can satiate predators seasonally in temperate river systems (Sweeney and Vannote 1982; Nakano and Murakami 2001), it is reasonable to expect that seasonal variation in invertebrate communities drives changes in salmonids' diet (e.g. Hellawel 1971; Li et al. 2016; Kreiling et al. 2021). However, emergence peaks of aquatic insects, in terms of phenology (timing throughout the year) and number (unimodal or bimodal), can substantially vary among territories with different climate but also within the same riverine system (i.e. year-to-year variation) (e.g. Huryn and Wallace 2000; Baxter et al. 2005; Wipfli and Baxter 2010). Thus, the seasonal reliance of stream-dwelling salmonids on aquatic imagoes and terrestrial invertebrates can largely vary among territories in line with climate-related geographical variability along salmonids' distribution, a perspective that needs to be integrated into studies exploring common seasonal patterns in feeding. Another knowledge gaps about seasonal patterns in feeding are that most studies have occurred in specific territories (temperate regions over the four seasons and subarctic rivers over the ice-free period) and normally focussed on single river systems or local territories (e.g. Kelly-Quinn and Bracken 1990; Erkinaro and Erkinaro 1998; Amundsen and Gabler 2008; Sánchez-Hernández et al. 2016b; Kreiling et al. 2021). Thus, broad-scale patterns among stream-dwelling salmonids are not well-known.

Ontogenetic dietary shifts are also widespread in the family Salmonidae, with the switch to piscivory and surface-foraging (i.e. higher consumption of terrestrial invertebrates) along ontogeny being a common feature of many species (e.g. Nagy 1976; Mittelbach and Persson 1998; Keeley and Grant 2001). In fact, the onset of piscivory in salmonids has been suggested to occur around 310 mm in length, regardless of habitat type (Keeley and Grant 2001). However, the minimum size at which piscivory can occur has been found at much smaller lengths (85 mm) in riverine and high-competition systems (Sánchez-Hernández et al. 2011b). These ontogenetic dietary shifts can have profound ecological consequences for fish by, for example, enhancing individual growth and lifetime reproductive output or reducing the risk of mortality (Sánchez-Hernández et al. 2019b). In addition, many salmonid species include anadromous populations, which undergo profound seasonal and ontogenetic dietary shifts linked to habitat changes as a consequence of their life histories (Klemetsen et al. 2003).

Despite ontogenetic and seasonal diet variation are ubiquitous among most stream-dwelling salmonids, the delineation of global feeding patterns remains unexplored. Thus, this book chapter represents the first attempt to (1) review ontogenetic and seasonal variation in feeding of stream-dwelling salmonids and (2) uncover common ontogenetic and seasonal changes in feeding of stream-dwelling salmonids including resident populations or freshwater development stages (juveniles, smolts and immature adults) of anadromous populations. The literature review consisted of published literature (peer-reviewed papers and thesis) on ontogenetic and seasonal dietary shifts of stream-dwelling salmonids using two different search engines (Web of Science and Google Scholar). Published literature (only title and abstract) were reviewed and selected to remove any irrelevant literature. A total of 65 studies were found to provide high-quality data (Table 1). Relevant information about geographical coordinates, climate, life histories and habitat setting were extracted from literature sources. In cases of missing records of geographical coordinates (latitude and longitude) of the study area in a literature source, I digitalised the coordinates based upon assessments of location information or maps provided in the source. In this chapter, I assigned sampling sites to climate zones according to the updated Köppen–Geiger climate classification (Kottek et al. 2006), and then climate was spatially matched with fish data (literature sources) using a raster file (available in the public repository of the University of Vienna at http://koeppen-geiger.vu-wien.ac.at/present.htm) in QGIS 2.16 (QGIS Development Team 2016). This chapter is structured by genera (*Coregonus*, *Prosopium*, *Stenodus*, *Hucho*, *Oncorhynchus*, *Salmo*, *Salvelinus*, *Brachymystax* and *Thymallus*), including a total 20 species of the family Salmonidae (Table 1) and spanning –45.8° S to 81.8° N, which covers a substantial part of the salmonids' geographical range (Fig. 1). This structure enables a contextualisation of the status of knowledge at the genus level to then provide common patterns within high-rank taxa (family) based on the premise that related species are more similar in feeding compared with species that are taxonomically more distant (Sánchez-Hernández 2020b).

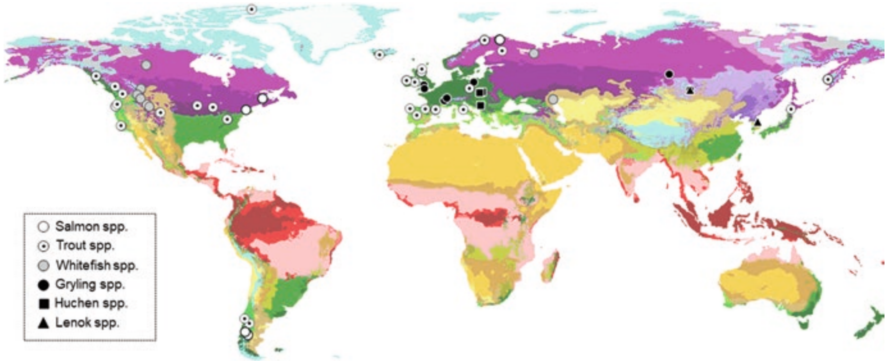

Fig. 1 World map showing the location of the literature sources used in this book chapter and climate information (Köppen–Geiger climate classification; Kottek et al. 2006). Whitefish species (*Coregonus lavaretus*, *C. clupeaformis*, *Prosopium williamsoni* and *Stenodus leucichthys*), huchen species (*Hucho hucho*), trout species (*Oncorhynchus mykiss*, *O. clarkii*, *Salmo trutta*, *Salvelinus fontinalis*, *S. alpinus*, *S. confluentus*, *S. malma* and *S. leucomaenis*), salmon species (*O. tshawytscha, O. kisutch, O. masou* and *S. salar*), lenok species (*Brachymystax lenok*) and grayling species (*Thymallus thymallus* and *T. arcticus*) are grouped for illustrative purposes (see Table 1 for species-specific information about climate)

2 Ontogenetic Changes

A knowledge of the ontogenetic changes in feeding of fish is key to understanding the processes that function at the individual, population and community levels since these dietary shifts over ontogeny can have significant consequences for the growth, survival, fecundity and recruitment of fish (Sánchez-Hernández et al. 2019a). In salmonid populations, dominant fish individuals may exclude less aggressive individuals, thereby limiting their access to resources within patches (e.g. Gotceitas and Godin 1991; Griffiths and Armstrong 2002). Thus, feeding can be modified through size-structured dominance hierarchies, where dominant and often large individuals gain access to the best patches for feeding (e.g. Nakano et al. 1999a). It is well-known that salmonid populations exhibit ontogenetic shifts in their diet and habitat use: (1) preferring deeper and slower flowing water as they increased in size (e.g. Ayllón et al. 2010) and (2) primarily feeding upon small benthic invertebrates before switching to larger invertebrates and later to fish prey (e.g. Nagy 1976; Sánchez-Hernández et al. 2011a; Poursaeid and Falahatkar 2012; Barca et al. 2019). Although we currently have a good comprehension of the nature, causes and consequences of ontogenetic dietary shifts in fish species (reviewed by Sánchez-Hernández et al. 2019a), the knowledge is normally biased towards common model organisms and local study systems, possibly limiting the recognition of general patterns applicable to a range of model organisms such as, for example, salmonids (Sánchez-Hernández et al. 2019b; Sánchez-Hernández 2020a). Thus, this section focusses on compiling relevant information about ontogenetic dietary shifts of both socio-economic and uncommon salmonid species in order to disentangle broad and common biogeographic patterns in feeding.

2.1 Driving Mechanisms of Ontogenetic Changes in Feeding

The driving mechanisms of ontogenetic dietary shifts of fish have been recently reviewed by Sánchez-Hernández et al. (2019a). These include a broad suit of factors such as predation risk, competition, prey availability, habitat use, morphological constraints, swimming ability, gut length, physiological mechanisms (metabolic rate, digestive enzymes and muscle enzymatic activity), and feeding behaviour and foraging modes (Fig. 2). There are good examples using salmonids as model organisms showing the driving mechanisms of ontogenetic changes in feeding (e.g. Mittelbach and Persson 1998; Sánchez-Hernández et al. 2011a; Hasegawa et al. 2012; Sánchez-Hernández and Cobo 2018). Sánchez-Hernández et al. (2011a) observed that niche breadth of newly emerged brown trout fry largely increases at the moment of complete yolk absorption, likely as a consequence of an improvement of swimming and handling ability of fry for capturing and ingesting prey both on the bottom and at the water surface. Thus, ontogenetic changes in feeding of salmonids may occur in association with improvements in vision and swimming

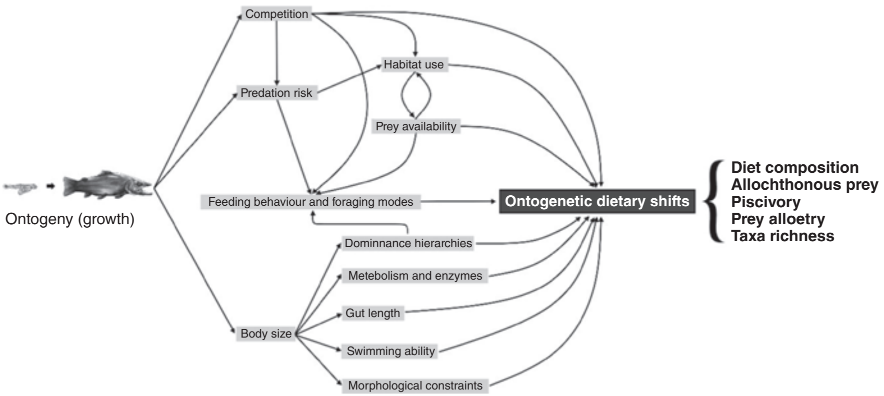

Fig. 2 Drivers of ontogenetic dietary shifts of stream-dwelling salmonids (modified from Sánchez-Hernández et al. 2019a)

performance and increases in gape size (e.g. Mittelbach and Persson 1998; Ojanguren and Braña 2003; Hasegawa et al. 2012; Sánchez-Hernández et al. 2013). Indeed, increased swimming ability over ontogeny of salmonids enables access to additional habitat types and/or new foraging opportunities (Hasegawa et al. 2012; Sánchez-Hernández and Cobo 2018). For example, Hasegawa et al. (2012) demonstrated that salmonids can exploit higher velocity and deeper water as they develop and grow. These changes in habitat use consequently drive changes in diet composition as many aquatic invertebrates show habitat-specific requirements (Tachet et al. 2002). In addition, because salmonids are commonly territorial and populations are regulated through density-dependent mechanisms (e.g. Elliott 1994; Nicola et al. 2016; Grossman and Simon 2020), dense fish populations can play a key role in driving ontogenetic changes in feeding to alleviate intra- and inter-specific competition for food (Sánchez-Hernández et al. 2019a).

2.2 *The Nature of Ontogenetic Changes in Feeding*

2.2.1 *Coregonus/Prosopium/Stenodus* (Whitefish)

Most examples of ontogenetic changes in whitefish species come from mountain whitefish (genus *Prosopium*) (Pontius and Parker 1973; Thompson and Davies 1976; DosSantos 1985; Whiteley 2007), whereas fewer examples are available for *Coregonus* spp. and *Stenodus* spp. (Poursaeid and Falahatkar 2012; Novoselov 2014). Specially, there is a notable gap in the knowledge of ontogenetic changes in taxa richness and prey size of riverine whitefish species (Table 2). Poursaeid and Falahatkar (2012) recognised that fingerlings of Inconnu feed on invertebrates and small individuals of other fish species, whereas adults are piscivorous. Novoselov

Table 2 Scientific evidence of ontogenetic and seasonal dietary shifts of salmonids based on the data sources used in this compilation, providing representative examples of studies from different species of what information is available versus lacking. Allochthonous prey and piscivory refer to the consumption of terrestrial invertebrates and fish prey, respectively. Evidence supporting (plus symbols), evidence refuting (minus symbols) and lack of studies addressing the research hypothesis (asterisks). Exceptions in the general patterns are specified with letters (a-e)

	Ontogenetic dietary shifts					Seasonal dietary shifts				
	Diet composition	Allochthonous prey	Piscivory/ Cannibalism	Prey size	Taxa richness	Diet composition	Allochthonous prey	Piscivory/ Cannibalism	Prey size	Taxa richness
Coregonus lavaretus	+	*	*	*	*	+	*	*	*	*
Coregonus clupeaformis	*	*	*	*	*	+	*	*	*	+
Prosopium williamsoni	+	+	*	+	+	–[b]/+[c]	*	*	+	*
Stenodus leucichthys	+	*	+	*	*	*	*	*	*	*
Hucho hucho	+	*	+	+	*	+	+	*	*	+
Oncorhynchus mykiss	+	+	*	+	+	+	–[d]/+	*	+	*
Oncorhynchus clarkii	+	+	*	*	*	*	*	*	*	*
Oncorhynchus tshawytscha	+	+	+	*	*	+	+	*	*	*
Oncorhynchus kisutch	*	*	*	*	*	+	+	*	*	*
Oncorhynchus masou	*	*	*	*	*	+	+	*	*	*
Salmo trutta	+	+	+	+	+	–[e]/+	+	*	*	*
Salmo salar	+	+	*	+	*	+	+	*	*	*

(continued)

Table 2 (continued)

	Ontogenetic dietary shifts					Seasonal dietary shifts				
	Diet composition	Allochthonous prey	Piscivory/ Cannibalism	Prey size	Taxa richness	Diet composition	Allochthonous prey	Piscivory/ Cannibalism	Prey size	Taxa richness
Salvelinus fontinalis	+	+	*	+	*	+	+	*	*	*
Salvelinus alpinus	+[a]	+	+	*	*	+	+	*	*	*
Salvelinus confluentus	+	*	+	*	*	+	*	+	*	*
Brachymystax lenok	+	*	*	*	*	+	*	*	*	*
Thymallus thymallus	+	+	*	+	*	+	+	*	*	*
Thymallus arcticus	+	*	*	*	*	*	*	*	*	*

[a] Sinnatamby et al. (2012) observed high dietary similarity among age-classes, but higher proportion of terrestrial invertebrates and cannibalism in older juveniles

[b] DosSantos (1985) found no clear seasonal patterns in small individuals with diets dominated by chironomids

[c] Pontius and Parker (1973) showed no consistent seasonal dietary shifts except for minor fluctuations in the proportions of aquatic chironomids, trichopterans and other dipterans

[d] Buria et al. (2009) noticed no seasonal shifts in terrestrial prey

[e] Minor seasonal dietary shifts were observed in several works (e.g. Kelly-Quinn and Bracken 1990; Horká et al. 2017; Cochran-Biederman and Vondracek 2017)

(2014) observed that whitefish (*Coregonus lavaretus pidschian*) in Russia undergoes different ontogenetic feeding trajectories depending on the river system (i.e. first order tributary, main course or river mouth). For example, an increase occurred in the consumption of molluscs and crustaceans with fish age in the Emtsa River (or first order tributary), whereas the proportion of molluscs, crustaceans and larval insects decreased with fish age in Sukhoe More Inlet (river mouth) (Novoselov 2014). These differences are likely related to site-specific differences in prey communities between river sections (Novoselov 2014). However, some *Coregonus* spp. inhabiting large northern rivers of Canada, such as Arctic cisco (*C. autumnalis*) and Lake whitefish (*C. clupeaformis*), also eat fish (M. Power, personal communication), which represents a particularly promising area for future research in order to demonstrate whether or not ontogenetic dietary trajectories in *Coregonus* spp. can be applicable at broad spatial scales (American and Eurasian populations).

Regarding mountain whitefish, larger individuals are more generalised feeders, in terms of both composition and prey size, compared to smaller fish (Pontius and Parker 1973). There is a general consensus on the fact that consumption of Chironomids decreases over ontogeny (Pontius and Parker 1973; DosSantos 1985; Whiteley 2007), whereas adults have a significant portion of terrestrial invertebrates in their stomach contents (Thompson and Davies 1976). Additionally, Pontius and Parker (1973) also observed that the consumption of other aquatic invertebrates (mostly cased trichopterans) increases with fish size. These changes in diet composition coincide with changes in prey size use, i.e. young-of-the-year consume smaller prey sizes compared to juveniles and adults (Thompson and Davies 1976). Whiteley (2007) provided evidence of this allometry in prey size as larger Ephemeroptera nymphs and Trichoptera larvae occurred in stomachs of larger mountain whitefish.

2.2.2 *Hucho*

The switch to piscivory seems to be a common feature of stream-dwelling huchens (Nagy 1976; Holčík 1990; Šubjak 2013). In the early stages of the life cycle, huchen prey upon benthic invertebrates (mainly Diptera, Ephemeroptera and Trichoptera), but the switch to fish prey can be observed early in development (Nagy 1976; Holčík 1990). More precisely, the size-related timing of the switch to piscivory is variable and occurs at a minimum body length of 89 mm (Nagy 1976) or even between 50 and 90 mm (Holčík 1990). In addition, minor ontogenetic dietary shifts have been described in huchen fry as the dietary contribution of larger and particularly motile prey (mayfly nymphs) gradually increases with increasing fry size, whereas prey richness decreases (Nikcevic et al. 1998). The study of the ontogenetic dietary shifts in species other than huchen, such as taimen and Japanese huchen, deserves more attention; in particular, in relation to the consumption of terrestrial invertebrates and taxa richness (Table 2).

2.2.3 *Oncorhynchus*

This genus includes species with very different life histories in respect to freshwater residency (anadromous and freshwater resident) which may impose inherent limitations to explore common ontogenetic patterns in feeding among species of the genus. Some species have very short freshwater periods, limiting expression of ontogenetic dietary shifts, whereas other species have longer periods in freshwater or only include freshwater resident stages. Still, aquatic invertebrates commonly dominate the diet of trouts (*Oncorhynchus* spp.), but terrestrial invertebrates are more frequently consumed by older individuals (Oscoz et al. 2005; Rundio and Lindley 2019, 2021). Oscoz et al. (2005) observed an increasing consumption of terrestrial invertebrates and Chironomidae pupae with age in rainbow trout (*Oncorhynchus mykiss*), but a decrease in the relative importance of Ephemeroptera nymphs and Diptera larvae with fish age in Spanish populations. Rundio and Lindley corroborated the decreasing contribution of aquatic prey and the increasing contribution of terrestrial prey in the diets along ontogeny of steelhead (anadromous *Oncorhynchus mykiss*) and rainbow trout in coastal basins of central California (Rundio and Lindley 2019, 2021). Thus, terrestrial invertebrates may largely contribute to cover the energy intake of large individuals in *Oncorhynchus mykiss* populations. For instance, Rundio and Lindley (2019) estimated that terrestrial invertebrates represented 60% of the energy consumed by fish larger than 160 mm, whereas the contribution was lower (15–20%) in smaller fish (60–100 mm). Furthermore, these same authors demonstrated that the energetic value of terrestrial invertebrates in the stomach contents during the summer is high (more than 40% at most sites and up to 75% at some locations) (Rundio and Lindley 2021). Bozek et al. (1994) observed that Chironomidae was the main prey category in young-of-the-year (71.2%), juvenile (75.2%) and adult (38.8%) cutthroat trout (*Oncorhynchus clarkii*), but terrestrial invertebrates increased over the ontogeny. Despite piscivory has been broadly documented in rainbow trout, increasing over ontogeny (e.g. Kusabs and Swales 1991; Oscoz et al. 2005; Arismendi et al. 2012), several studies have reported limited piscivory (Rundio and Lindley 2008, 2021; Yard et al. 2011). For example, Yard et al. (2011) observed that the incidence of piscivory in rainbow trout is low compared to brown trout, consuming on average 4 and 10 fish/year in the upstream and downstream reach of the Colorado River, respectively. Bozek et al. (1994) observed no evidence of piscivory in cutthroat trout. In addition to the above-mentioned changes in the diet composition over ontogeny, diet breadth, prey size and variation among individuals typically increase with fish size in *Oncorhynchus* spp. (Bozek et al. 1994; Rundio and Lindley 2019).

In anadromous salmon species of the genus *Oncorhynchus*, such as Chinook salmon (*Oncorhynchus tshawytscha*), the diet of juveniles change among age-classes, with age 1+ being piscivorous but age 0+ having a diet manly composed by terrestrial invertebrates (Ibarra et al. 2011). In the same direction, Barca et al. (2019) corroborated that the diet of Chinook salmon largely changes among several freshwater development stages (juveniles, smolts and immature adults). More precisely, the diet of juveniles (Ephemeroptera, Plecoptera and Diptera) and smolts (Plecoptera and Ephemeroptera) is mainly composed by aquatic prey, whereas immature adults (3+ and 4+) are piscivorous (Barca et al. 2019).

2.2.4 *Salmo*

Similar to the genus *Oncorhynchus*, the genus *Salmo* includes anadromous species (Atlantic salmon *Salmo salar*) and species with anadromous (sea trout) and resident (brown trout) forms, and thus different life histories may also impose a handicap to disentangle ontogenetic dietary shifts when they include short freshwater periods. However, the current literature indicates that there is empirical evidence that *Salmo* spp. undergo ontogenetic dietary shifts (Table 2). Ontogenetic dietary shifts arise very early in the development of *Salmo* spp. and involve different levels of changes, including prey composition, prey size and niche breadth (Keeley and Grant 1997; Sánchez-Hernández et al. 2011a). Keeley and Grant (1997) observed that newly emerged Atlantic salmon fed primarily on small chironomid larvae, whereas larger individuals consumed larger prey (primarily dipteran adults and pupae). Likewise, Sánchez-Hernández et al. (2011a) demonstrated in brown trout that niche breadth greatly increased with fry size, especially in relation to the moment of complete yolk absorption. Also, the presence of aerial imagoes in the stomachs was only observed in fry with no yolk, suggesting an improvement of swimming and handling ability of fry for prey capturing at the moment of yolk reabsorption (Sánchez-Hernández et al. 2011a). Perhaps the most common feeding change along ontogeny in riverine populations of *Salmo* spp. is related with the proportion of allochthonous resources (terrestrial invertebrates) as underlined in many studies (e.g. Allan 1941; Kelly-Quinn and Bracken 1990; Bridcut 2000; Sánchez-Hernández and Cobo 2018).

Feeding studies of Atlantic salmon parr have demonstrated that the proportion of prey caught at the surface (allochthonous resources and emerged aquatic insects) increases with age (Allan 1941; Erkinaro and Erkinaro 1998; Amundsen et al. 2001). Allan (1941) observed that the prey caught at the surface was mainly composed by terrestrial insects (with some Chironomid and ephemeropteran imagoes) in British salmon populations, whereas little evidence of allochthonous resources were observed in other studies in subarctic territories (Erkinaro and Erkinaro 1998; Amundsen et al. 2001). Erkinaro and Erkinaro (1998) observed that the diet of small parr during midsummer (late July to early August) was mainly composed by all stages of dipterans and *Baetis* nymphs, whereas large parr in addition to dipterans consumed trichopteran larvae and ephemeropteran adults and nymphs. Amundsen et al. (2001) showed that mayfly nymphs and simulid larvae and pupae decreased in importance with increasing parr age, whereas the opposite trend was found for Trichoptera larvae and emerged aquatic insects (mainly Trichoptera, Plecoptera and Chironomidae). Thus, there are seemingly contrasting considerations about the differences in the use of allochthonous resources among riverine systems, which can be resolved if environmental factors (climate, riparian vegetation and stream size) are taken into account as they largely change along spatial broad scales and enable the availability of terrestrial invertebrates to riverine systems (e.g. Kawaguchi and

Nakano 2001; Syrjänen et al. 2011; Ryan and Kelly-Quinn 2015). Overall, similar patterns in the consumption of terrestrial invertebrates should be expected among riverine systems with similar conditions (climate, riparian vegetation and stream size), but larger differences should occur among non-similar regions.

Works focused on brown trout as model species have been extensive (e.g. Sánchez-Hernández et al. 2013 and references therein). Overall, juveniles mainly consume aquatic invertebrates while terrestrial invertebrates and fish prey are more frequently consumed by older individuals (Kelly-Quinn and Bracken 1990; Montori et al. 2006; Fochetti et al. 2008; Sánchez-Hernández and Cobo 2012). We currently have a good knowledge about the minimum size at which these dietary shifts (piscivory and terrestrial invertebrates) occur (Keeley and Grant 2001; Sánchez-Hernández et al. 2013; Sánchez-Hernández and Cobo 2018). For example, the shift from autochthonous (aquatic) to allochthonous (terrestrial) prey has been established at a body length of 81 mm (range 36–127 mm) (Sánchez-Hernández and Cobo 2018). The minimum size at which piscivory occurs is usually observed in the interval 140–300 mm (Sánchez-Hernández et al. 2013, 2017), although it has also been observed in individuals of smaller sizes (85 mm) in riverine and high-competition systems (Sánchez-Hernández et al. 2011b). This underscores the trophic flexibility of brown trout in respect to the onset to piscivory. It should be noted that the linkage between minimum size and piscivory appears to be complex and different mechanisms such as fish community configurations can potentially strengthen the switch to piscivory (i.e. piscivory increasing with fish species richness) (Sánchez-Hernández 2020a). Ontogenetic dietary shifts in brown trout can also be described in relation to the utilisation of aquatic prey (Fochetti et al. 2008; Sánchez-Hernández and Cobo 2012). For example, Fochetti et al. (2008) observed that the abundance of plecopteran nymphs in the stomach contents increased over ontogeny, whereas the abundance of trichopteran larvae decreased in older individuals. Sánchez-Hernández and Cobo (2012) revealed that trichopteran larvae (*Allogamus* sp.) and ephemeropteran nymphs (*Ecdyonurus* spp.) increase with age. In addition, ontogenetic changes in feeding occur at prey size and niche breadth levels, with prey size and niche breadth increasing across ontogeny (e.g. Dineen et al. 2007; Sánchez-Hernández and Cobo 2012).

2.2.5 *Salvelinus*

There are good examples showing ontogenetic dietary shifts in species within the genus *Salvelinus* (Hubert and Rhodes 1989; Cucherousset et al. 2007; Sinnatamby et al. 2012; Lowery and Beauchamp 2015). Hubert and Rhodes (1989) studied differences in diet composition between two length classes (≤150 and >150 mm) in brook trout (*Salvelinus fontinalis*), showing that terrestrial invertebrates occur to a much greater extent in larger (2.9–36.2%) than in smaller fish (8–9.0%). The same authors also recognised changes at the prey-size level, where smaller fish tend to consume small prey (mainly Chironomidae) and larger fish tend to prey on larger prey (mainly Plecoptera, Trichoptera and terrestrial invertebrates) (Hubert and

Rhodes 1989). The ontogenetic dietary shifts in brook trout was supported by stable isotope analysis, with δ15N increasing with increasing fish length (Cucherousset et al. 2007). Despite the proportion of terrestrial invertebrates and cannibalism is higher in older juveniles of Arctic charr (*Salvelinus alpinus*), high dietary similarity among age-classes has been observed with chironomid larvae and pupae being the most important food resources (Sinnatamby et al. 2012). Sinnatamby et al. (2012) also observed that cannibalism occurred at a minimum size of 124 mm. In this regard, Furey et al. (2015) described extensive feeding on sockeye salmon (*Oncorhynchus nerka*) smolts by adults of bull trout (*Salvelinus confluentus*), showing dietary switches as transient resource pulses became available (i.e. initial outmigration of sockeye salmon smolts). Lowery and Beauchamp (2015) demonstrated that bull trout becomes piscivorous at approximately 100 mm, with small individuals (30–95 mm) feeding mostly on aquatic insects. As other salmonid species, this genus includes species with anadromous and resident forms, being less consistent the riverine ontogenetic shifts in the individuals inhabiting short freshwater periods.

2.2.6 *Brachymystax*

Despite the fact that diet of stream-dwelling lenok (*Brachymystax lenok*) populations is well documented (e.g. Nakano 1999; Chandra et al. 2005; Yoon et al. 2013), few attempts have been made to specifically disentangle possible ontogenetic dietary shifts in this species (Table 2). An exception is found in the work by Olson et al. (2016), who showed that the proportion of Ephemeroptera nymphs declined with size whereas the proportion of Trichoptera larvae increased. It is likely that lenok undergoes similar ontogenetic patterns, i.e., higher consumption of larger prey items, terrestrial invertebrates and fish prey over ontogeny, as well-known for other genera with similar life history, habitat requirements and geographic range. However, scientific understanding of trophic ontogeny of lenok is still deficient, representing a particularly promising area for future research.

2.2.7 *Thymallus*

Available information on grayling species has demonstrated consistent ontogenetic shifts in feeding, particularly in terms of prey size and relation between aquatic and terrestrial prey (Table 2). Ontogenetic dietary shifts in early development stages of grayling (*Thymallus thymallus*) are rarely evident (Scott 1985; Sempeski et al. 1995). Chironomid larvae remains as the dominant food category for all sizes in larval grayling, while the size of aquatic prey (chironomid pupae, ephemeropteran nymphs and simulid larvae) increases with increasing larval size (Scott 1985). A comparative study of the diet of larval (15–30 mm) and juvenile (30–70 mm) grayling also demonstrated no large differences in diet composition as these stages largely relied on chironomid larvae, although juveniles frequently consumed other prey categories (chironomid pupae, simulid larvae and mayfly nymphs) (Sempeski et al. 1995). However, studies covering a wider age-spectrum of the grayling populations uncovered that the contribution of Crustacea to the diet increased with age (from age-0 to age-4), whereas Diptera larvae and Plecoptera nymphs decreased with age (Hellawel 1971). A recent study using stable isotopes has revealed that aquatic resource use decreases with increases in grayling size (Frossard et al. 2021). Ontogenetic dietary shifts have also been found in Baikal grayling (*Thymallus arcticus baicalensis*), as Olson et al. (2016) demonstrated that the proportion of Ephemeroptera nymphs declined with fish size, whereas the proportion of Diptera larvae increased in the stomach contents of larger grayling. In addition, ontogenetic changes in feeding not only include changes in diet composition, but are also represented by increases in prey size (Hellawel 1971).

2.3 Common Ontogenetic Dietary Patterns Among Stream-Dwelling Salmonids

This chapter, based on a representative sample of salmonid species, shows global geographic patterns in trophic ontogeny of stream-dwelling salmonids. That is, higher consumption of larger prey items (allometry of prey preferences), terrestrial invertebrates (the switch to the surface-foraging) and fish prey (piscivory) over ontogeny. Still, some geographic differences within and among species and populations need to be recognised, suggesting that environmental (stream-size gradients and climate-related geographical variability) and biotic (life history and body size range of salmonid populations) factors strongly influence ontogenetic dietary patterns (Fig. 2). As already pointed out, the size at which riverine salmonids become predominantly piscivorous is flexible and seems to be dependent on high-competition systems and fish community configurations (Sánchez-Hernández 2020a). As shown in Fig. 3, early develop stages of riverine salmonids primarily feed upon small benthic invertebrates before switching to larger invertebrates (both benthic and terrestrial invertebrates), and later to fish prey over the ontogeny (e.g. Nagy 1976; Sánchez-Hernández et al. 2011a; Poursaeid and Falahatkar 2012; Barca et al. 2019). The shift to the ultimate piscivorous niche is clearly seen in species that grow large enough to avoid morphological constrains (mouth gape limitations) such as huchens, charrs and trouts (e.g. Nagy 1976; Lowery and Beauchamp 2015), but also depends on how habitat constrains maximum fish size and not just on species (Sánchez-Hernández et al. 2019a). For example, it should be expected that piscivory increases along stream-size gradients in large rivers and remain low in small streams where individuals attain a smaller size than in larger rivers (individuals reach larger maximum size). Additionally, there is no evidence supporting piscivorous behaviour in riverine grayling (*Thymallus* spp.) and most whitefish (*Prosopium williamsoni* and *Coregonus lavaretus*) populations despite frequently been shown in lacustrine populations (Pothoven and Madenjian 2013), whereas some *Coregonus* spp. inhabiting large northern rivers of Canada also eat fish (M. Power, personal communication).

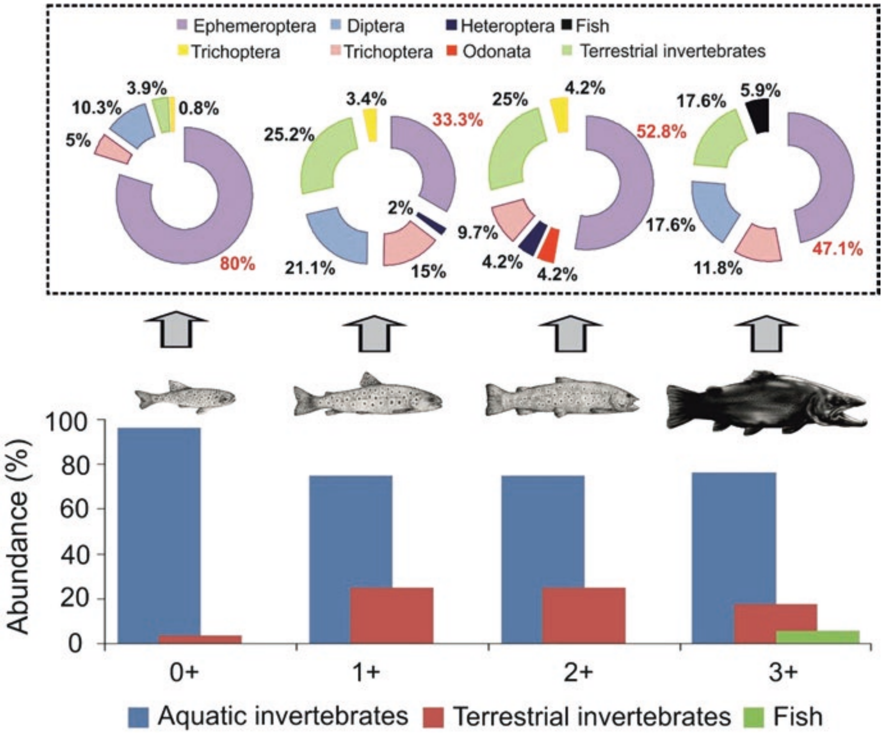

Fig. 3 Conceptual view of the ontogenetic dietary shifts in stream-dwelling salmonids based on feeding data of brown trout available in Sánchez-Hernández and Cobo (2012)

Mouth gape, mouth orientation (a more inferior mouth than other salmonid species) and the presence of a pointed snout in these species (e.g. Harrod et al. 2010; Persat et al. 2019) can act as a handicap for the switch to piscivory of grayling and whitefish populations. It is very unlikely that riverine grayling and whitefish populations display piscivory, in particular considering that handling ability is an important variable that determine food selection in salmonids (de Crespin de Billy and Usseglio-Polatera 2002; Sánchez-Hernández et al. 2011a), but facultative piscivory (i.e. using small fish prey as an alternative food source when availability of primary prey categories drastically decreases) similar to findings found in cyprinids (e.g. Vejřík et al. 2016). Thus, the switch to piscivory is currently unknown in riverine populations of grayling and some whitefish populations despite being commonly observed in most other salmonid species, which requires more attention in future studies. From another standing point of view, piscivory does not occur in some *Oncorhynchus* spp. (e.g. pink and chum salmon) that have short juvenile residence in riverine systems, which is related to life history and not morphological constrains.

Many stream-dwelling salmonids undergo ontogenetic dietary shifts from aquatic to terrestrial invertebrates as principal prey (e.g. Sánchez-Hernández and Cobo 2018; Rundio and Lindley 2019). However, the availability of pulsed terrestrial resources occurs primarily during summer, when the aquatic invertebrate biomass usually is low (Nakano and Murakami 2001). Thus, despite that this diet pattern can be widespread in salmonid species, it is reasonable to expect that the observation of ontogenetic shifts in allochthonous resources is primarily evident in summer and early autumn in temperate river systems. In contrast, phenology and development of terrestrial invertebrates are expected to differ among climate regions (i.e. geographical variation) or even within the same climate region along altitude environmental gradients (Scranton and Amarasekare 2017; Rebaudo and Rabhi 2018). Thus, seasonality and climate play a key importance for understanding possible spatial differences of ontogenetic patterns in the consumption of terrestrial invertebrates. Terrestrial food resources are more protracted across the year in populations located in Mediterranean climates compared to populations in northern and temperate biomes with patterns exacerbated during the summer (addressed in the Sect. 3). In addition, the terrestrial invertebrate input to the riverine systems greatly depends on riparian canopy cover (Edwards and Huryn 1996; Wipfli 1997; Kawaguchi and Nakano 2001; Ryan and Kelly-Quinn 2015), but also the importance of terrestrial invertebrates to salmonid diets can change across stream size—large individuals consume more terrestrial invertebrates in small river systems, whereas no patterns are observed in small individuals (Syrjänen et al. 2011). The fully understanding of ontogenetic patterns in terrestrial prey along broad geographical ranges appears to be complex as different mechanisms can potentially strengthen or alleviate the consumption of this food resource, but this chapter provides compelling evidence that stream-dwelling salmonids switch from aquatic to terrestrial prey over the ontogeny (Table 2). Consistent with the allometric scaling theory, prey size increases with salmonids size (e.g. Thompson and Davies 1976; Keeley and Grant 1997; Whiteley 2007; Sánchez-Hernández and Cobo 2012; Rundio and Lindley 2019). However, this common ontogenetic pattern could be biased among populations as body size range of salmonid populations is not similar among riverine systems, in particular because allometric changes in morphological traits (mouth gape and gill rakers) make new food resources available and consequently lead to ontogenetic shifts in feeding (Sánchez-Hernández et al. 2019a).

To sum up, some patterns can be recognised as general principles for stream-dwelling salmonids such as the allometry in prey size, switch to piscivory and a higher consumption of terrestrial invertebrates over ontogeny. Thus, this chapter provides novel macroecological insights into trophic ontogeny theory, providing evidence that such ontogenetic patterns (prey size, piscivory and consumption of terrestrial invertebrates) can be extended to broad spatial (geographic regions with similar climatic conditions) and taxonomic (among taxa within the family Salmonidae) scales. However, the recognised ontogenetic patterns are likely strongly influenced by habitat type (stream size), fish assemblage, life history (anadromous and resident individuals) and maximum attainable size of fish populations (Sánchez-Hernández et al. 2019a; Sánchez-Hernández 2020a). This has been recently highlighted on brown trout with respect to piscivory (Sánchez-Hernández 2020a), representing a particularly promising area for future research through studies beyond the model organism to corroborate or refute general conclusions. In particular, ecosystem size and the abundance and body sizes of fish prey assemblages have repeatedly emerged as an important determinant of piscivory (Eloranta et al. 2015; Jacobson et al. 2019). Thus, ontogenetic differences should be greatest in large systems where fish reach large sizes, but lesser in small systems where fish reach smaller size. Additional work will be needed to explore whether or not similar ontogenetic patterns can be generalised to other aquatic consumers and be applied to broad-scale geographic territories.

3 Seasonal Changes

The perception of seasonal variation, i.e. temporal variation of a variable (here prey resource availability and diet composition), can vary among studies as they differ in the sampling design: (1) monthly for the entire year, (2) across all four seasons (winter, spring, summer and autumn), (3) in some or several seasons (normally over the summer) and (4) over a specific time period of the year (e.g. months over ice-free season in subarctic river seasons). Despite these different study designs, trophic ecologists have largely demonstrated that stream-dwelling salmonids undergo seasonal changes in feeding (e.g. Kelly-Quinn and Bracken 1990; Sánchez-Hernández et al. 2016b; Kreiling et al. 2021). The studies disentangling seasonal dietary patterns have habitually focussed on single river systems or local territories, but we need to pay more attention to larger spatial scales in order to uncover global patterns in taxonomically related species in line with climate and prey seasonality. In this context, a recent study has highlighted the importance of climate seasonality for delineating biogeographic dietary patterns of salmonids (Sánchez-Hernández et al. 2019b). This study supports the view that climate-related geographical variability can be useful for understanding seasonal dietary patterns of salmonids because seasonal temperature is a crucial factor shaping life-history events of prey, and consequently the feeding of salmonids through bottom-up mechanisms (Sánchez-Hernández et al. 2019b). Factors other than temperature, such as precipitation, hydrological regimes, photoperiod and riparian vegetation also influence abundance and phenology of invertebrate communities which are important drivers of seasonal dietary changes (see Sect. 3.1.1).

3.1 Driving Mechanisms of Seasonal Changes in Feeding

To fully understand the driving mechanisms of seasonal changes in feeding of salmonids, we first need to recognise if prey communities change across seasons and the mechanism involved in such changes. In this regard, both aquatic and terrestrial food resources fuel fish, but the reliance of stream-dwelling salmonids on these food resources can largely vary among seasons in line with climate-related geographical variability, but also along altitude and latitude environmental gradients

(Sánchez-Hernández et al. 2019b). Ichthyologists have recognised that seasonal variations in both aquatic and terrestrial invertebrate communities (see Sect. 3.1.1 for factors responsible of seasonal shifts in prey communities) drive changes in salmonids' diet (e.g., Hellawel 1971; Fierro et al. 2016; Li et al. 2016; Kreiling et al. 2021). In this regard, the most feasible mechanism to understand global dietary changes of salmonids across seasons is linked to the effects of environmental factors on prey communities (either aquatic or terrestrial sources) which, in turn, directly affects the diets of salmonids (i.e. bottom-up mechanisms) (Fig. 4).

3.1.1 Factors Responsible of Seasonal Turnover in the Invertebrate Taxa

Aquatic and terrestrial invertebrate communities show seasonal turnover in terms of composition and size-structure (Fig. 4). Bridcut (2000) provided a good example demonstrating that the abundance of terrestrial invertebrates and aerial stages (imagoes) of aquatic invertebrates varies seasonally and is positively correlated with temperature in Scotland. Thus, seasonal water temperature is a crucial factor shaping life-history events in invertebrates (Bhowmik and Schäfer 2015; Glazaczow et al. 2016), with emergence of aquatic insects peaking around spring and early summer in temperate systems, which satiate predators seasonally (Sweeney and Vannote 1982; Nakano and Murakami 2001). However, emergence peaks of aquatic

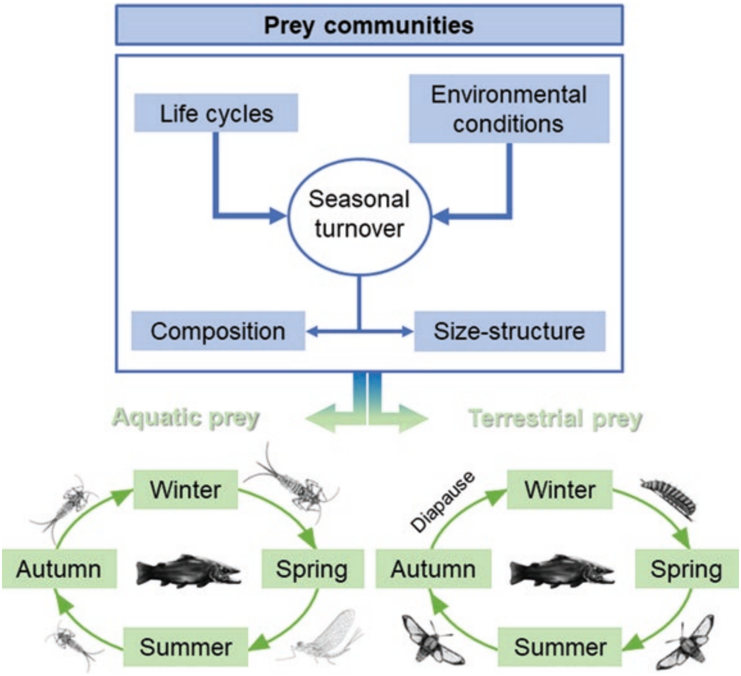

Fig. 4 Conceptual view of the seasonal dietary shifts in stream-dwelling salmonids

insects, in terms of phenology (timing throughout the year) and number (unimodal or bimodal), can substantially vary among territories with different climate but also within the same riverine system (i.e. year-to-year variation) (e.g. Huryn and Wallace 2000; Baxter et al. 2005; Wipfli and Baxter 2010). Overall, aquatic macroinvertebrate communities show high seasonal variation in abundance and taxonomic composition (Bêche et al. 2006; Johnson et al. 2012; Boehme et al. 2016; Kreiling et al. 2021). In Mediterranean-climate streams, interannual rainfall variability seems to govern seasonality of taxonomic composition and abundance (Bêche et al. 2006). Studies in other climate regions have provided evidence that the seasonal turnover in the macroinvertebrate community can be explained by the influence of taxa with seasonal life cycles and changes in environmental conditions (hydrological regimes and water physicochemical characteristics) (Álvarez-Cabria et al. 2011; Boehme et al. 2016; Wang et al. 2020). In addition, Verberk et al. (2005) found differences in the mechanisms responsible for the seasonal changes in the macroinvertebrate community, where water body characteristics like eutrophication and acidity are important factors early in the season (spring and summer) and microhabitat later in the season. The aquatic community not only changes in terms of the dominant groups, but also in body size and functional feeding groups (Li et al. 2016; Wang et al. 2020). Li et al. (2016) provided an excellent example showing that benthic prey was larger in spring than in summer or autumn.

Allochthonous food supplies (i.e. terrestrial insects) are another important food resource for stream-dwelling salmonids that suffer from seasonal changes depending mainly on temperature, photoperiod and riparian vegetation (Wipfli 1997; Wipfli and Baxter 2010; Hodgson et al. 2011; Rebaudo and Rabhi 2018). In fact, fluxes of terrestrial invertebrates can provide up to half the annual energy budget for stream-dwelling salmonids (Baxter et al. 2005 and references therein). Terrestrial invertebrates undergo diapause (i.e. the development delay in response to adverse environmental conditions) and geographical variation in phenology and development because of both plasticity to local environmental conditions and genetic diversity (Rebaudo and Rabhi 2018). In northern temperate latitudes, the availability of pulsed terrestrial resources occurs primarily during summer, when aquatic invertebrate biomass usually is low (Nakano and Murakami 2001). Additionally, the contribution of terrestrial insects to the drift may be very noteworthy in summer and autumn, being the largest drifting group in August (Johansen et al. 2000) or having a greater biomass than aquatic drifting in the autumn (Romaniszyn et al. 2007). However, the seasonal pattern may be different in other climate regions such as Mediterranean streams, in which river productivity peaking during the summer but terrestrial productivity starting to decline (Power and Dietrich 2002). This underscores the key importance of spatial and temporal variation in temperature to understanding phenology shifts in insects, with timing of emergence peaks occurring earlier in southern territories and warmer years (Hodgson et al. 2011). Thus, caution should be exercised regarding seasonal patterns in abundance of aquatic versus terrestrial prey as such patterns may not apply at large spatial scales with different climate.

3.1.2 Prey Communities Shape Diet Composition

Diet composition of salmonids can be explained by site-specific prey community structures via a bottom-up mechanism (Sánchez-Hernández et al. 2019b). A very illustrative example underscoring the importance of prey availability on feeding of salmonids was provided by Nakano et al. (1999a), who observed that stream-dwelling charrs are able to adapt their foraging mode according to the availability of drifting prey (i.e. the frequency of benthos foragers increases as the abundance of drifting prey declines and vice versa). Similarly, in the literature it is reported that, depending on the season and prey availability, either benthic or drifting invertebrates are the better descriptor of the diet of salmonids (e.g. Sagar and Glova 1995; Johansen et al. 2010; Nakano et al. 1999a). For example, Elliott (1973) observed that the diet of brown trout and rainbow trout in a Mountain stream (Pyrenees) is similar to the percentage of the drift but not the benthos. Sagar and Glova (1995) concluded that drifting invertebrates are more similar to stomach contents of juvenile brown trout than benthic invertebrates during summer in New Zealand streams. In contrast, Johansen et al. (2010) observed that stomach contents of juvenile Atlantic salmon were more similar to benthos than to drift samples in the subarctic River Alta (northern Norway) during the winter. Despite stream-dwelling salmonids are drift feeders that typically “sit-and-wait” to ambush prey from short distances in lotic habitats (Rader 1997; Tunney and Steingrímsson 2012), it is possible that (1) species-specific differences and (2) within-species variation in foraging mode and opportunistic feeding are responsible of the lack of consensus explaining whether benthic or drifting invertebrates are the best descriptor of the diet composition for stream-dwelling salmonids. Thus, adaptive flexibility in the feeding behaviour of riverine salmonids—switching their foraging mode (drift and benthic foraging) depending on prey availability (Nakano et al. 1999a)—is key to understand diet composition and thereby seasonal patterns in line with prey accessibility.

Many studies have demonstrated that most taxa are not proportionally preyed in line with their abundance in the environment, showing differences in prey composition between the stomach contents and the environment (e.g. Horká et al. 2017; Kreiling et al. 2021). For example, seasonal studies on feeding selectivity of salmonids have provided broad seasonal variation in feeding and that large-bodied benthic prey are selected over other more abundant benthic and drifting prey (Di Prinzio et al. 2015; Cochran-Biederman and Vondracek 2017). However, the process of prey-size selection can be controversial depending on the prey category (aquatic versus terrestrial). For example, Rincón and Lobón-Cerviá (1999) demonstrated that brown trout negative selects largest, and presumably most profitable, terrestrial (surface-drifting) prey but positive selects aquatic (water column or benthic) prey items. Thus, seasonal shifts of cross-habitat resource subsidies are key to understand diets of riverine fish species (Nakano et al. 1999b; Nakano and Murakami 2001; Baxter et al. 2005), which was largely provided in stream-dwelling salmonids regarding seasonal variation of allochthonous and autochthonous food supplies to stomach contents (examples in the following section such as, for example, Fochetti et al. 2003 and Falke et al. 2020). Thus, stomach contents may deviate from proportions of prey communities observed in the environment as above-mentioned, but it is reasonable to posit that temporal and spatial variations in site-specific prey communities likely shape foraging and diet composition of salmonid predators (Sánchez-Hernández et al. 2019b).

3.2 The Nature of Seasonal Changes in Feeding

3.2.1 *Coregonus/Prosopium/Stenodus* (Whitefish)

To date, current knowledge on seasonal changes in feeding of riverine whitefish species is limited to North American (Canada and USA) populations (Pontius and Parker 1973; Thompson and Davies 1976; Little et al. 1998), underscoring a lack solid evidence of whether seasonal feeding shifts between North American varies from Europe populations. Prey size consumed by mountain whitefish increases over the season (from May to October), but the species shows no consistent seasonal dietary shifts except for minor fluctuations in the proportions of aquatic chironomids, trichopterans and other dipterans (Pontius and Parker 1973). In the same direction, Thompson and Davies (1976) demonstrated that the diets of mountain whitefish are primarily composed by dipterans, ephemeropterans, trichopterans at all times of the year, but plecopterans are only abundant in stomach contents in autumn and dipterans are very noticeable in spring and early summer. Despite the consumption of three prey categories (Chironomidae, Ephemeroptera and Trichoptera) in mountain whitefish can represent the majority of the stomach contents across the year, it was observed a noticeable consumption of Gastropoda in late summer (August and September) by large individuals while small individuals show no clear seasonal patterns with diets dominated by chironomids (DosSantos 1985).

Developmental stages of Canadian lake whitefish (*Coregonus clupeaformis*) inhabiting lake tributaries, such as juveniles, show seasonal dietary shifts with the importance of ostracods to the diet decreasing from spring (dominant prey) to autumn (no presence in the stomach contents) (Little et al. 1998). In addition, Little et al. (1998) observed that summer is the season with the most diverse diet of lake whitefish juveniles inhabiting lake tributaries, with the diet being dominated by corixids, trichopteran larvae and gastropods. Findings on the feeding of whitefish in the lower reaches of the Northern Dvina River (Russia) have proved seasonal changes in feeding, with larval insects (September and October), molluscs (December), vegetation (January) and crustaceans (February and March) changing as the main prey category over the studied months (Novoselov 2014).

3.2.2 *Hucho*

Despite seasonal studies in diet variation of stream-dwelling salmonids are common, seasonal variation in dietary niches of *Hucho* spp. remains elusive because most studies are carried out in huchen populations of Central Europe (Witkowski et al. 1994; Nikcevic et al. 1998; Šubjak 2013) and no information is available on species with broader (taimen *Hucho taimen*) or narrower (Japanese huchen *Hucho perryi*) geographic distributions. The diet of age-0 huchen is mostly composed by Chironomidae larvae but the proportion of terrestrial invertebrates can vary substantially between spring (0%) and autumn (21%) (Witkowski et al. 1994). Another study focused on late spring and summer feeding of huchen fry has demonstrated that the main prey category (Baetidae nymphs) remains over the summer (June 10, June 27 and July 13) but its contribution to the diet can noticeably change over this time period (29.7%, 81.2% and 72.7%, respectively) (Nikcevic et al. 1998). In addition, Nikcevic et al. (1998) observed that the diet during late spring (June 10) was more diverse (13 prey categories) compared to June 27 and July 13 (five and three prey categories, respectively). The diet of huchen during winter mainly consists of fish (cyprinids and salmonids) (Šubjak 2013). However, we still lack basic knowledge of seasonal dietary shifts in piscivory and prey size of *Hucho* species (Table 2).

3.2.3 *Oncorhynchus*

Seasonal shifts in feeding are ubiquitous among *Oncorhynchus* species (e.g. Kitano et al. 1993; Kuzishchin et al. 2015; Falke et al. 2020). Kuzishchin et al. (2015) described seasonal changes in the feeding of juveniles of three *Oncorhynchus* species (coho salmon *Oncorhynchus kisutch*, masu salmon *O. masou* and chinook salmon *O. tshawytscha*) in western Kamchatka and concluded that the changes of the ratio of aquatic/terrestrial prey and consumption of salmon eggs in the diet are related to life-cycle seasonality (insect emergence and fish spawning, respectively). The diet of juvenile chinook salmon in New Zealand is mainly composed by chironomid larvae early in the summer, but diet breadth increases significantly as the summer progressed (Power 1992). Korean masu salmon undergoes seasonal changes in feeding with Trichoptera larvae and Ephemeroptera nymphs dominating the stomach contents in spring and summer, respectively, but shows similar contributions of Diptera larvae, Trichoptera larvae and terrestrial insects in autumn (Yoon et al. 2013). Similarly, Wipfli (1997) demonstrated that the quantity of terrestrial invertebrates to the diets of several *Oncorhynchus* species of south-eastern Alaska can remain relatively stable through the season (May–October).

Kitano et al. (1993) observed that Japanese populations of rainbow trout consume primarily aquatic and terrestrial invertebrates, but the contribution of eggs and fish increases over the spring. Buria et al. (2009) noticed a higher contribution of aquatic prey in the diet of Andean rainbow trout during spring, whereas no shifts occurred in terrestrial prey (terrestrial prey represented annually only 5 and 4% of total prey number and biomass, respectively). In contrast, Fierro et al. (2016)

observed that the consumption of terrestrial invertebrates by rainbow trout is higher in spring than the other seasons, but also the importance of Ephemeroptera nymphs to the diet is particularly important in summer and autumn. Li et al. (2016) demonstrated that the diet of steelhead, but also cutthroat trout, in temperate rivers of Oregon switches from a mixed diet (both aquatic and terrestrial invertebrates) in spring to a diet mainly composed by terrestrial prey in the summer, and then again to a mixed diet (in this case consuming dramatically less prey) in autumn. Another study carried out in the Oregon state has found seasonal changes in prey composition of cutthroat trout, particularly spring diets containing high proportions of terrestrial prey but high proportions of Diptera larvae and Ephemeroptera nymphs in summer and autumn diets (Falke et al. 2020). Rundio and Lindley (2019) have recently observed that terrestrial invertebrates (Isopoda and Hymenoptera) contribute to drive monthly and seasonal shifts in feeding of steelhead/rainbow trout in Mediterranean-climate streams, but the use of terrestrial pulses is lower compared to other salmonids of temperate systems (e.g. Kawaguchi and Nakano 2001; Utz and Hartman 2007). Also, Rundio and Lindley (2008, 2019) found that both inputs and use of terrestrial prey are less peaked in their study system than in some other studies but extended over more of the year, so annual inputs and use of terrestrial prey were similar to other studies. In this regard, climate and geographic location (latitude and elevation) emerge as important factors for understanding possible differences among territories in disentangling seasonal feeding patterns. In fact, Rundio and Lindley (2019) indicated that the most abundant prey category change across seasons; Ephemeroptera nymphs (Baetidae and Heptageniidae) dominating from late summer to winter, Simulidae larvae from late spring to late summer, Chironomidae larvae from autumn to spring, Isopoda (Armadillidiidae) from spring to early summer and Hymenoptera during the autumn.

Life history of *Oncorhynchus* species may influence seasonal patterns in feeding. For example, Rundio and Lindley (2019) demonstrated that fish size accounts for the majority of explained variation in consumption of terrestrial and total prey, while seasonal parameters account for most of the variation for aquatic prey. This underscores the high interaction between ontogenetic and seasonal patterns in attempting to delineate feeding patterns of riverine salmonids with the consumption of aquatic prey highly linked to seasonality and terrestrial prey to fish length (Rundio and Lindley 2019). Post-yearling (1+) steelhead shows a diet dominated by aquatic insect throughout all seasons (Hydropsychidae larvae, Chironomidae pupae, zooplankton and Baetidae nymphs) (Merz 2002). However, seasonal shifts in feeding may also change between two consecutive years; for example, aquatic dipterans (mostly chironomid pupae) were a dominant food source only during the autumn of 1 year but in all seasons of next year (Merz 2002). Godby et al. (2007) observed remarkable seasonal dietary patterns in age-0 steelhead between two neighbouring riverine systems of USA (Muskegon River and Bigelow Creek). In the Muskegon River, these authors observed that the diet composition is different in May (Hydropsychidae larvae as main prey with an abundance of 26.6%), August (Amphipoda as main prey with an abundance of 41.8%) and October (again Hydropsychidae larvae as main prey with an abundance of 58.2%) (Godby et al.

2007). In the Bigelow Creek, the most abundant prey was Hydropsychidae larvae (34.5%) and salmon eggs (93%) in May and October, respectively (Godby et al. 2007). Thus, seasonal patterns in feeding are common in riverine *Oncorhynchus* species but can vary among different spatial scales (both distant and neighbouring river systems) and between consecutive years in the same river system. In addition, Li et al. (2016) provided evidence of seasonal fluctuations in prey size use, including an increase in terrestrial prey size and a decrease in benthic prey size from spring to summer.

3.2.4 *Salmo*

Multiple studies have shown noticeable seasonal dietary shifts in *Salmo* species (e.g. Allan 1941; Amundsen et al. 2001; Gíslason and Steingrímsson 2004; Sánchez-Hernández et al. 2016a), whereas other studies support lower evidence of such seasonal shifts (e.g. Kelly-Quinn and Bracken 1990; Fochetti et al. 2003; Horká et al. 2017; Cochran-Biederman and Vondracek 2017). In this regard, studies showing noticeable seasonal dietary shifts focussed on subarctic territories (Amundsen et al. 2001; Gíslason and Steingrímsson 2004; Sánchez-Hernández et al. 2016a) or north of England (Allan 1941), whereas studies supporting lower evidence were carried out in locations at lower latitudes (Ireland, Italy, Czech mountain streams and south-eastern Minnesota). Thus, it is likely that climate–latitude environmental gradients could explain more noticeable patterns of seasonal feeding along northern populations, but increased and more detailed knowledge on these aspects is paramount to future research.

Studies supporting minor seasonal changes in feeding agree with the view that primary prey categories remain abundant in the stomach contents across the year despite secondary prey categories can be occasionally abundant to the diet during a specific season. For example, Kelly-Quinn and Bracken (1990) showed that age-0 brown trout primarily eat ephemeropteran nymphs and chironomid larvae across the year despite Gammaridae contributes noticeable to the diet during autumn and late winter. The same authors described similar seasonal patterns for older brown trout (age-1, age-2 and age-3) except for imagoes of aquatic insects and terrestrial invertebrates that largely contribute to the diet during July–September and March–May (Kelly-Quinn and Bracken 1990). Fochetti et al. (2003) observed that Plecoptera, Ephemeroptera, Trichoptera and Diptera were the most important and constant prey categories in the stomach contents regardless of the season, with Ephemeroptera dominating the spring and summer diets but Trichoptera the winter diets. Horká et al. (2017) demonstrated that, except in May and October (diets dominated by terrestrial insects), brown trout shows no consistent seasonal changes in feeding related to the proportions of aquatic and terrestrial prey during the summer (June–September) with Chironomidae larvae being the most abundant prey category in most cases. Similarly, Cochran-Biederman and Vondracek (2017) found that the composition of brown trout diets is similar across seasons with Chironomidae larvae being common in the stomach contents during all seasons. In contrast, Bridcut

(2000) found that terrestrial invertebrates and imagoes of aquatic insects constitute a large component of diet in older brown trout during the autumn.

Studies focussed on months within seasons may reveal small changes in diet composition during the study period, whereas patterns are usually more noticeable over broader temporal scales. In this regard, Gíslason and Steingrímsson (2004) observed that blackflies larvae are present in the diet of brown trout from late spring (1 June) to summer (31 August), being very dominant in the stomach contents in early June (59.8–97.8%) and late August (91.4–99.0%), but dropping drastically in July (4.9%) when Chironomidae larvae and the freshwater snails become more important. Studies on Atlantic salmon parr during the ice-free season in high-latitude populations have proved that Atlantic salmon parr undergoes noticeable seasonal changes in diet composition (Erkinaro and Erkinaro 1998; Gabler and Amundsen 1999; Amundsen et al. 2001; Sánchez-Hernández et al. 2016a). Erkinaro and Erkinaro (1998) found that Plecoptera nymphs predominate in the stomach contents in early spring, whereas simulid larvae and *Baetis* nymphs are the main components in early summer and the importance of trichopteran larvae increases towards the end of the summer. Gabler and Amundsen (1999) found that the Atlantic salmon parr diet is mainly composed by Plecoptera nymphs and Ephemeroptera nymphs in May, become more diverse in July and August (including larvae of Simuliidae, Chironomidae and Trichoptera) and is again dominated by Ephemeroptera nymphs in September and October. Amundsen et al. (2001) observed similar seasonal changes in the dominant Atlantic salmon parr prey categories, with mayfly and stonefly nymphs dominating in May, Simuliidae (larvae and pupae) and terrestrial insects in July and caddis larvae and mayfly nymphs in August and September. Sánchez-Hernández et al. (2016a) showed that the diet Atlantic salmon parr is dominated by Plecoptera nymphs in May and Trichoptera pupae in July, whereas the species predominantly feed on Ephemeroptera nymphs and Trichoptera larvae from August to September. The classical work by Allan in English populations evidenced that the consumption of terrestrial invertebrates by Atlantic salmon parr primarily occurs from August to October (Allan 1941). Another study focused on Irish populations showed that diets of age-0 and age-1 Atlantic salmon are dominated by Chironomidae larvae in summer with a shift towards Baetidae nymphs in autumn (Dineen et al. 2007). Other studies in Massachusetts (USA) corroborated the findings of European populations, describing that the diet composition of Atlantic salmon parr can vary considerably among months, with baetid mayflies (June, July and August), limnephilid caddisflies (October and November) and ephemerellid mayflies (February and April) dominating the stomach contents in specific months (Grade and Letcher 2006).

Flow regulations and life-history traits can cause changes in seasonal feeding patterns of *Salmo* species. In this regard, an interesting study focussed on different hydrological conditions (natural and artificial flow fluctuations located upstream and downstream of a hydropeaking station, respectively) revealed no clear seasonal dietary shifts in brown trout, consuming chiefly Baetidae nymphs and Chironomidae larvae in early summer and autumn under both natural and hydropeaking conditions (Lagarrigue et al. 2002). However, feeding activity (stomach fullness) is highest in summer (June) under both natural and regulated conditions, whereas it is lowest in autumn (October) coinciding with the low flow period under natural conditions and spring (April) coinciding with high peak flows in the regulated section (Lagarrigue et al. 2002). Brown trout, as well as several *Oncorhynchus* species, may also include polymorphic populations composed by resident and anadromous individuals that affects the variation in population length and degree of ontogenetic variation, which are likely to differ in their seasonal feeding patterns. As already mentioned, seasonal dietary shifts in resident individuals can be more pronounced in older compared to young individuals (Kelly-Quinn and Bracken 1990; Bridcut 2000).

3.2.5 *Salvelinus*

As for other salmonid taxa, the consumption of allochthonous resources captured at the surface water goes through conspicuous seasonal changes in charrs. For example, the contribution of terrestrial insects to the diet of brook trout changes over the summer, being the most abundant prey category in September (Hubert and Rhodes 1989; Webster and Hartman 2005). Webster and Hartman (2005) quantified the terrestrial proportion of the diet in terms of biomass, which changes between July (54%) and September (75%). Utz and Hartman (2007) emphasised that terrestrial prey (mainly terrestrial Coleoptera and Lepidoptera) is a key food resource for brook trout during warmer seasons, whereas large aquatic organisms such as vertebrates (fish and salamanders) and crayfish are important during winter. Another example in this model organism was presented by Horká et al. (2017), who concluded that the presence of brown trout force brook trout to consume higher proportion of terrestrial invertebrates to alleviate inter-specific competition. Thus, it seems likely that seasonal changes in feeding may be strengthened, at least for some salmonid species, by competitive interactions among sympatric stream-dwelling salmonids via water column segregation over seasons (e.g. Miyasaka et al. 2003; Mookerji et al. 2004; Sánchez-Hernández et al. 2016a). This also underscores the key relevance of gaining access to the best feeding patches through dominance hierarchies (i.e. with dominant and subordinate species) to fully understand seasonal dietary shifts in sympatric salmonid populations.

Stream-dwelling Arctic charr also shows seasonal changes in diet composition (Sánchez-Hernández et al. 2016a, b). The most abundant prey resource changes from Ephemeroptera nymphs and Diptera larvae in May and July to Trichoptera larvae, terrestrial insects in August and September and Ephemeroptera nymphs in October (Sánchez-Hernández et al. 2016a). After emergence, age-0 Arctic charr goes through consistent seasonal changes in feeding during their first ice-free season as the dietary contribution of terrestrial insects increases from July to September (from 1.9 to 62.8%). (Sánchez-Hernández et al. 2016b). More specifically, Sánchez-Hernández et al. (2016b) noticed that the diet of age-0 Arctic charr is mainly composed by Diptera in July, terrestrial insects in August and September, and Ephemeroptera and Chironomidae larvae in October. Kreiling et al. (2021) have recently corroborated that the diet composition of Arctic charr is mainly composed by Chironomidae larvae but can differ among months, as these authors revealed the highest dissimilarities in the diet composition between May and June and June and March. Overall, Ostracoda (March), terrestrial insects (June), predatory Diptera larvae (October), miscellaneous prey (October) can largely contribute to the diet of Arctic charr in addition to Chironomidae larvae (Kreiling et al. 2021).

Bull trout is considered as apex predators showing the highest piscivory during winter and spring (January–June) (Lowery and Beauchamp 2015). Small bull trout (96–300 mm) usually consumes salmon eggs in winter and juvenile coho salmon along with some aquatic insects during spring (Lowery and Beauchamp 2015). Despite the large contribution of fish prey across the whole year in large specimens of bull trout (301–450 mm), their main prey categories show seasonal shifts and precisely: salmon eggs during autumn, salmon fry during winter, immature aquatic insects and salmon fry in spring and resident fish during summer (Lowery and Beauchamp 2015). In contrast, the abundance of terrestrial invertebrate in the stomach contents of Dolly Varden (*Salvelinus malma*) can remain relatively stable through the season (May–October) (Wipfli 1997).

3.2.6 *Brachymystax*

Nakano (1999) showed the existence of trophic polymorphism in lenok, with the long-snouted form having a higher contribution of benthic invertebrates (Trichoptera larvae) in the stomach contents compared to the short-snouted that consumed terrestrial invertebrates as the main prey category and likely are better adapted for foraging on drifting prey. In this regard, it is reasonable to expect seasonal differences in feeding between these two trophic polymorphisms, but the lack of information prevents any predictions and thus constitutes a promising future research direction. An illustrative example of changes in diet composition of lenok across seasons can be found in Yoon et al. (2013), who observed that Ephemeroptera and Trichoptera dominate the diet in spring, terrestrial insects in summer and Trichoptera in autumn. Olson et al. (2016) have recently demonstrated that in presence of grayling with drift foraging feeding, the diet of lenok is primarily composed by benthic invertebrates. Although studies focussed on disentangling seasonal patterns in feeding of *Brachymystax* species are scarce (Table 2) and more attention should be paid, it is likely that seasonal dietary shifts of lenok could be flexible because of competitive interactions for food by dominant sympatric stream-dwelling salmonids as mentioned for other salmonid species.

3.2.7 *Thymallus*

European grayling mainly consumes benthic food resources (especially insect larvae, Crustacea and molluscs) and shows seasonal dietary variations likely related to variations in prey availability (Hellawel 1971). Thus, terrestrial insects are more frequently consumed during the summer, Gammaridae is the main food resource during the winter, and Diptera larvae declines steadily in importance from February onwards but is important again in December (Hellawel 1971). Zuev et al. (2017) observed that Trichoptera larvae remains dominant in the diet of European grayling during winter and spring, whereas amphipods represent the main prey category during the period from June to October. Smoliński and Glazaczow (2019) showed gradual dietary changes in European grayling from summer (Heteroptera and Diptera larvae) to autumn (terrestrial fauna, Trichoptera larvae, Ephemeroptera nymphs and Plecoptera nymphs). More attention needs to be paid to disentangle seasonal dietary shifts of *Thymallus* species in relation to prey size and taxa richness (Table 2).

3.3 Common Seasonal Dietary Patterns Among Stream-Dwelling Salmonids

The delineation of seasonal dietary patterns of stream-dwelling salmonids on global scales is difficult because such temporal shifts are driven by phenology of site-specific prey communities and can also be dependent on competitive interactions between sympatric stream-dwelling salmonids. Still, potential broad-scale patterns among riverine salmonids can be delineated in line with climate-related geographical similarity as climate and type of riparian revegetation are important drivers to understand the links between forest and stream ecosystems (Hjältén et al. 2016), which in turn influences on the subsidies of invertebrates between ecosystems and their phenological shifts. Thus, similar climatic domains along broad geographic zones (i.e. climate–latitude analogies among distant geographic zones) are probably responsible of large-scale patterns in feeding of stream-dwelling salmonids (Sánchez-Hernández et al. 2019b). This can be exemplified with model organisms inhabiting different climate regions (for example, temperate and Mediterranean streams), such as rainbow trout and brown trout, which largely consume terrestrial invertebrates during the summer regardless of geographic area (Table 2). On the other hand, it should be kept in mind that proximity, and thereby similarity in environmental conditions and aquatic invertebrate communities, is an important feature for the understanding of common dietary patterns of stream-dwelling salmonids (Sánchez-Hernández et al. 2019b). Thus, similar community composition and seasonal life-history traits (e.g. hatching, emergence, diapause, etc.) of prey taxa among neighbouring river systems seem fundamental to understand common seasonal dietary shifts of their salmonid consumers (Fig. 4). In this regard, some common patterns in temperate geographical areas can be recognised as the abundance of aquatic invertebrates with an aerial dispersal stage (e.g. Ephemeroptera, Trichoptera, Diptera and Plecoptera) drops after emergence (emergence peaking around spring and early summer; Sweeney and Vannote 1982; Nakano and Murakami 2001; Boehme et al. 2016), whereas strictly aquatic taxa (e.g. Oligochaeta, Mollusca and Crustacea) or first instars of aquatic insects become more important in the community after imagoes emergence. This implies seasonal changes in macroinvertebrate community structure in terms of abundance and size (Wang et al. 2020). However, different seasonal feeding patterns might be recognised in other climate types along altitudinal or latitudinal scales linked to differences in water temperature, such as Mediterranean-climate streams, where activity of terrestrial insects (e.g. butterflies) and emergence of aquatic insects (e.g. dragonflies and damselflies) occur significantly earlier in warmer riverine systems and will be magnified with climate warming (Deutsch et al. 2008; Anderson et al. 2019). In addition, seasonal dietary shifts in stream-dwelling salmonids have been commonly explored to disentangle changes in diet composition including seasonal switches in both aquatic and terrestrial invertebrates, whereas the exploration of seasonal patterns in piscivory, prey size and taxa richness remains almost unknown to date (Table 2).

One of the most outstanding seasonal dietary patterns among stream-dwelling salmonids is related to the high consumption of terrestrial invertebrates during the summer when they are accessible and vulnerable to salmonids (e.g. Kawaguchi and Nakano 2001; Utz and Hartman 2007; Syrjänen et al. 2011), a time period commonly characterised by low aquatic invertebrate biomass (Nakano and Murakami 2001). In return, terrestrial invertebrates provide important benefits to stream-dwelling salmonids during the summer such as a good energy subsidy, which largely contribute to the annual fish production and reduce food competition among sympatric salmonid species through food resource partitioning (e.g. Edwards and Huryn 1995; Utz and Hartman 2007; Sánchez-Hernández et al. 2016a). It should be also kept in mind that mouth morphology (i.e. sub-terminal mouth) of some salmonid species, such as whitefish and lenok, can constrain any seasonal dietary patterns in the use of terrestrial pulses, as diets become more homogeneous and dominated by aquatic invertebrates in those cases. Factors other than morphological differences, such as differences in feeding habitat use (i.e. surface, drift and benthic foraging) (e.g. Nakano and Masahide 1995; Nakano et al. 1999a; Sánchez-Hernández and Cobo 2018), may also be a keystone for undercovering consistent seasonal feeding patterns across studies. Because frequency of foraging attempts decreases as drift rate declines (Nakano et al. 1999a), it is reasonable to posit that surface-drift foraging of salmonids in northern temperate latitudes is a major determinant of summer feeding, whereas salmonid populations of other climate areas, such as Mediterranean-climate streams, are expected to consume terrestrial food resources over broader temporal scales. As a caveat, caution should be exercised regarding this conclusion because sympatric stream-dwelling salmonids may modify their foraging behaviour (i.e. species-specific differences in foraging mode) to reduce competition for food (e.g. Glova 1984; Nakano and Masahide 1995; Nakano et al. 1999a; Sánchez-Hernández et al. 2016a) and thus alter possible consistent patterns across salmonids.

In fact, this chapter shows that seasonal changes in feeding at species level could be masked by competitive interactions among sympatric stream-dwelling salmonids. There are many examples showing that water column segregation in resource use may alleviate competition for food between sympatric salmonids (Olson et al. 2016; Sánchez-Hernández et al. 2016a; Horká et al. 2017). For example, Horká et al. (2017) concluded that the presence of brown trout forces brook trout to consume a higher proportion of terrestrial invertebrates, which, in turn, alleviate inter-specific competition for food resources but also alter seasonal dietary patterns in comparison with allopatric populations. Olson et al. (2016) demonstrated that lenok can act as a benthic specialist, whereas Baikal grayling shows a more generalised and surface-oriented diet, preying upon both terrestrial and aquatic invertebrates. Thus, the delineation of seasonal patterns in feeding for a specific salmonid species may change under allopatric versus sympatric conditions. This highlights the importance of gaining access to the best feeding patches through dominance hierarchies (i.e. with dominant and subordinate species) in fish communities. In addition, population level studies may not be entirely accurate as seasonal patterns might be biased by specific-ontogenetic differences in feeding, as studies should include balanced datasets with size/age groups equally represented over the months. An illustrative example of this concern was provided by Amundsen et al. (2001), who showed that mayfly and stonefly nymphs are the dominant prey in May, but the contribution of mayfly nymphs decreases and stonefly nymphs increases with increasing fish age. Similarly, simulid larvae and pupae as well as prey caught at the surface (emerged aquatic insects) are the dominant prey in July, but the proportion of simulids decreases and emerged aquatic insects increases with increasing fish age (Amundsen et al. 2001). Thus, caution should be exercised in studies exploring interannual or seasonal dietary shifts at the population level as conclusions could be masked by uneven sampling effort of a specific age class or development stage (e.g. Sánchez-Hernández et al. 2022). In addition, the existence of trophic polymorphisms in stream-dwelling salmonids (e.g. Nakano 1999) makes it necessary to address the seasonal dietary shifts in each group independently to avoid confounding conclusions due to inherent feeding and foraging differences among groups.

4 Conclusions and Synthesis of Global Patterns in Feeding of Stream-Dwelling Salmonids

Despite ontogenetic and seasonal diet variation are ubiquitous among most stream-dwelling salmonids, the delineation of global feeding patterns remains unexplored. The current chapter shows that feeding patterns in stream-dwelling salmonids can be stablished over broad spatial and temporal scales. As already pointed out, these include ontogenetic (i.e. allometry in prey size, switch to piscivory and a higher consumption of terrestrial invertebrates over ontogeny) and seasonal (i.e. high consumption of terrestrial invertebrates during the summer in temperate rivers, but earlier or extended in Mediterranean systems) patterns. However, the recognition of global patterns appears to be complex because different factors (e.g. taxonomic relatedness of species, climate, stream size and life history) can potentially have a strong influence on the differences observed among territories and seasons:

(i) Feeding patterns should be easier to recognise in related species compared with species that are taxonomically more distant. For example, mouth orientation and gape can limit prey choice in salmonids, and thus patterns in feeding are more similar among species with terminal mouths (e.g. *Salmo*, *Salvelinus* and *Oncorhynchus*) compared with species with sub-terminal mouth (*Coregonus*, *Prosopium*, *Thymallus* and *Brachymystax*). The relatively sparse literature on this topic suggests that this would be a fruitful area for future research.

(ii) Climate and prey seasonality have a major importance for the understanding of global feeding patterns. Diet composition should be more similar among similar geographic areas (i.e. territories with similar climate characteristics), such as Mediterranean ecoregions located in different parts of the world, whereas larger differences should occur among non-similar regions (e.g. northern versus Mediterranean river systems).

(iii) One of the most outstanding ontogenetic and seasonal dietary patterns is related to the consumption of terrestrial invertebrates. However, phenology and development of terrestrial invertebrates differ among climate regions (i.e. geographical variation) or even within the same climate region along altitude environmental gradients. Thus, it is reasonable to posit that similar patterns, in relation to this prey category, should be observed among analogous climatic territories, whereas larger differences should occur among non-similar regions.

(iv) Stream size, a variable little reported in the literature sources (Table 1), can play a key role for the understanding of the contribution of some prey categories (fish prey and terrestrial invertebrates) to salmonid diets. That is, salmonids consume more terrestrial invertebrates in small river systems in line with the limitations imposed by the type of riparian vegetation and land-use types on terrestrial invertebrate inputs (e.g. biomass of terrestrial invertebrates entering pasture streams is significantly lower than forest and tussock grassland streams; Edwards and Huryn 1996). However, the pattern is reversed for fish prey, the likelihood of finding piscivorous behaviour increases with stream size. Thus, longitudinal changes in prey communities (i.e. River Continuum Concept-RCC; Vannote et al. 1980) impose a framework from which feeding patterns can be displayed (Sánchez-Hernández 2023). In particular, RCC predicts a continuous gradient in the structure of animal communities (both macroinvertebrates and fish) according to physical (stream discharge, stream width and riparian vegetation) and chemical (energy input and organic matter for production and stream metabolism or P/R) conditions (Vannote et al. 1980). Thus, attempts to integrate trophic ecology into RCC principles to disentangle longitudinal patterns in fish feeding (Sánchez-Hernández 2023), and its changes across ontogeny and seasons, represent a particularly promising area for future research.

(v) Drivers responsible of seasonal and ontogenetic feeding can interact with one another, expecting a high relevance for the understanding of common feeding patterns in riverine salmonids. For example, previous researchers have demonstrated that the consumption of aquatic prey is highly linked to seasonality and terrestrial prey to fish length in a Mediterranean system (Rundio and Lindley 2019), but this does not imply that this pattern should be applicable to broad spatial scales and climate domains. In addition, studies attempting to identify seasonal patterns might be biased by specific-ontogenetic differences in feeding because study designs may not include balanced datasets with size/age groups equally represented over the months/seasons. More attention needs to be paid in the future to understanding the connection between seasonal and ontogenetic patterns over broad spatial scales.

(vi) The delineation of global patterns in feeding of stream-dwelling salmonids can be difficult to disentangle when comparing populations with different life history (e.g. anadromy and maximum size). This chapter provides evidence that the shift to the ultimate piscivorous niche is clearly seen in species that grow large enough to avoid morphological constrains (mouth gape limitations) such as huchen, charr and trout species, but also depends on how habitat constrains maximum fish size and not just on species. For example, it should be expected that piscivory increases along stream-size gradients in large rivers and remains low in small streams where individuals attain a smaller size than in larger rivers (individuals reach larger maximum size) (Sánchez-Hernández 2023). Regarding polymorphic populations (populations composed by resident and anadromous individuals), this life-history trait affects the variation in population length among populations, and thus the degree of ontogenetic variation.

(vii) Further efforts should be oriented towards the study of ontogenetic and seasonal feeding of underrepresented species (e.g. taimen, Japanese huchen and lenok) and unexplored regions and climatic domains (see Fig. 1). Still, conclusions and implications of this chapter are relevant to fish ecologists providing broad-scale (in space and taxonomy) patterns in feeding of salmonids along ontogeny and season, being likely that similar responses can be extrapolated to related taxa (i.e. other fish groups) and may be a promising avenue for future research.

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Stream Salmonids on the Cormorant (*Phalacrocorax carbo*) Menu

Niels Jepsen and Gorm Rasmussen

Abstract Predation from endemic predators is a natural regulating factor for fish species in rivers and lakes, but recently there has been a great increase in the populations of some of these predators, and predation is now threatening particularly populations of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), North Sea houting (*Coregonus oxyrhynchus*), and grayling (*Thymallus thymallus*) throughout Europe. Especially the increased numbers of great cormorant (*Phalacrocorax carbo sinensis*) have resulted in a significant increase in predation pressure in Danish rivers, and a substantial decrease in numbers of salmonids and other river fish. The increased predation has led to intense conflicts between conservation of wild fish stocks and protection of predators, and given incentive to study the basis of the conflicts: Do cormorants significantly reduce fish populations? Despite decades of conflicts and political focus on the issue, only few scientific studies have focused on the results of these increased predation rates. In this chapter, we will describe the current situation and present some of the published and unpublished studies on predation from cormorants, and we will focus on the effects of cormorant predation on brown trout, Atlantic salmon, and grayling in Denmark.

Keywords Cormorant · Distribution · Abundance · Conflicts · Management · Atlantic salmon · Brown trout · Grayling

1 Introduction

Stream dwelling fish are on the prey list for quite a number of avian, mammal, piscine and even reptile predators. In European salmonid streams, the important fish predators include grey heron (*Ardea cinerea*), merganser/goosander (*Mergus*

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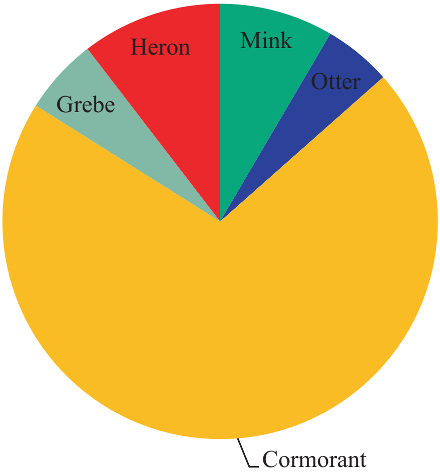

Fig. 1 Estimated fish-consumption from predators in Danish freshwater (total 12,595 tons). NB: Whereas the other predators get most of their food from freshwater, cormorants mainly find their food in coastal waters, Jepsen et al. (2014)

merganser), cormorant, otter (*Lutra lutra*), and invasive mink (*Neovison vison*) (Fig. 1).

2 Overall: The Cormorant Biology and Distribution

Two subspecies of cormorants occur in Denmark, the (*Phalacrocorax carbo sinensis*) breeds in Denmark, whereas the other subspecies (*Phalacrocorax carbo carbo*) only occurs in low numbers during migration and winter. Adult cormorants (*sinensis*) weigh 2.1–3.7 kg

3 Migration and Overwintering

From late summer to autumn, there is a shift in the distribution of cormorants away from the Danish fjords and freshwater areas and out to the more open coasts and remote small islands. The cormorants spread over relatively short distances and seek out lakes and coastal areas over most of the country as well as in northern Germany and southern Sweden. Toward September–October, they begin the autumn migration. Most Danish cormorants migrate down the Atlantic coast or through Germany, and the most important wintering areas are in the Netherlands, southern Germany, Switzerland, northern Italy, and France. Some Danish cormorants choose to stay in the Baltic Sea and Kattegat areas in winter, and do well in mild winters. The number of cormorants that overwinter in Denmark has increased as the winters have become milder because of increasing air temperature.

4 Current Distribution

The species was assumed extinct in Denmark since 1876, but during the last 30–40 years, it has become a very common breeding bird. Outside the breeding season, cormorants from our neighboring countries also occur in Denmark. These visiting individuals use Danish coastal areas, lakes, and streams briefly during their winter migration, while others stay over the winter. The total number of cormorants in Denmark has been estimated to be between 15,000 in winter and 250,000 in fall (Ministry of Environmental Protection 2022).

5 Development Across European Regions

In the first half of the twentieth century, the cormorant was close to extinction in Europe. In the early 1960s, the Northwest European population numbered only about 4000 breeding pairs. In the 1970s, the population began to grow in the Netherlands, Denmark, and Sweden, and the total number had increased to 13,500 pairs in 1981. The latest coordinated census of all cormorant colonies in Europe showed that between 406,000 and 421,000 pairs bred in 2012. Of this, the population of Great cormorants (*Phalacrocorax carbo carbo*) was 42,500 breeding pairs (Ministry of Environmental Protection 2022). The development in the breeding population of cormorants is influenced by a number of factors. These suggest that the future development in Denmark of the breeding population will primarily be determined by (a) the food supply; (b) the cormorants' opportunities to establish new colonies; (c) the extent of human intervention in the colonies; (d) the development in the population of the predatory sea eagle (*Haliaeetus albicilla*).

6 Abundance and Breeding Biology

Cormorants are flexible with regard to where they establish colonies. In Denmark, there are colonies where the cormorants build nests in trees, shrubs, and/or on the ground. They prefer small islands where they breed directly on the ground. However, if there are trees and shrubs on the island where they settle, they prefer building nests on them. When cormorants breed in lakes, the nests are built on trees right next to the lakeshore. The breeding season extends from March to July. The eggs are white to slightly blue. There are usually 3–4 eggs in the nest. The incubation period is almost 30 days. Breeding success depends primarily on food availability during the breeding season. After about 7 weeks after hatching, juveniles are ready to fly and typically leave the nests between late June and July.

7 Foraging and Diet

Cormorants feed almost exclusively on fish. The cormorant's individual food intake fluctuates throughout the season from 200 to 700 g/day. Food requirement is greatest in May–June, when the cormorants have juveniles. Cormorants prey on fish species most often in shallow water areas and rarely at water depths over 20 m. The cormorant usually seeks food alone, but it has been observed that several hundred cormorants may hunt together in fjords, lakes, rivers and at shallow marine areas. Cormorants are good at locating areas with many fish that are relatively easy to catch. Therefore, one can sometimes see flocks of cormorants foraging in a river mouth during brown trout and Atlantic salmon smolt downstream migration in spring or in a limited stretch of a river. In lakes and estuaries, true group-hunting is observed with several hundred birds involved. The cormorant feed upon most fish species and primarily those occurring in the largest numbers and are easiest to catch. In Denmark, food choices vary greatly depending on the geographical area and season. Studies of diet in coastal cormorant colonies show that they feed upon different marine fish species, but freshwater fish species (salmonids and cyprinids) plays a relatively important role in terms of biomass. Recently, cormorants, foraging in very small water bodies like garden-ponds, small streams of 1–2 m width and, even in underground concrete channels, have been documented by photos and video recorded by smart-phones by passersby. Thus, we now have proof that cormorants can utilize even the most unlikely habitats for foraging, indicating serious lack of food sources for the birds.

8 The Visiting Cormorants' Appearance in Denmark

The cormorants from abroad (15,000–65,000) arrive to Danish waters between July and November. They mainly come from Sweden, but also birds from Finland, northern Germany, and Norway may visit. The majority migrate to and through Denmark in September–November and wintering birds leave Denmark in March and April.

9 Interactions Between Cormorants and Fish in Denmark: The Conflict

The conflict between humans and cormorants primarily arise from competition for the same resources. The conflicts in Denmark started in the coastal pound-net fisheries, where much of the catch from cormorants was taken from the nets and larger fish were injured/damaged. The effects are amplified to some extent in areas where fish stocks are already under pressure from deteriorating habitats and exploitation. When the cormorants started to include forage in Danish rivers in 2010, the conflict changed character and now the anglers were impacted to a high degree, because cormorants left rivers with healthy, wild populations of salmonids almost barren after even short visits. The same type of conflicts (brown trout and grayling anglers) that has been reported for decades from the Central European rivers, became reality in Denmark overnight. The cormorant is an amazingly effective underwater hunter. Cormorants can survive on shrimps and tiny sand goby if other prey is absent, but can also eat rather large fish of up to about 2 kg. Cormorants have been observed walking around on salmonid spawning and rearing areas, picking out small YOY fish, and it can dive down to at least 30 m in search for fish. Studies have revealed what a superior all-round predator cormorants are, catching small and large fish of all species in rivers, streams, lakes, estuaries, and open marine coast. Conflicts involving cormorants have been studied in detail in EU through the INTERCAFE studies (http://cormorants.freehostia.com/; Behrens et al. 2008).

Interaction between cormorants and freshwater fish in Danish lowland rivers has been studied for a decade, and thus these results will be the central case here, acknowledging that many similar interactions between other predators and prey species may be important in other regions. When the term cormorant is used here, we refer to the subspecies *P. carbo sinensis*, not *P. carbo carbo*, as the last have a stable population and forage on open coasts, thus causing much fewer conflicts. It should be noted that conflicts based on high predation from cormorants have been intense in Central Europe for decades (Steffens 2010), where especially brown trout and grayling are threatened or have disappeared in several sub-alpine rivers.

A decrease in populations of river fish species in Denmark, specifically brown trout and grayling has been documented from several rivers, where the density of grayling abruptly decreased 5–10-fold (Iversen 2010; Jepsen et al. 2014). These results are very similar to what has been reported from a number of central European rivers in the period from 1992 to 2000, where grayling and brown trout populations were found to greatly decrease after cormorant visits (Steffens 2010).

Many studies have documented similar effects from cormorant predation, as well as tested management measures (Anon 2012; Klenke et al. 2012; Dorr et al. 2010, 2012). Unfortunately, most results from Europe are found in gray literature (e.g., Kainz 1994; Görner 2006, see also Ovegård et al. 2021).

Tagging studies (see later) have shown cormorant predation to be the main mortality factor in the few rivers where studies were conducted, but are there no alternative explanations for the general decline of river salmonids? Due to a very low sport fishing pressure in upper rivers in general in Denmark, and the fact that grayling has been protected (no take) since 2011, fishing mortality cannot be part of the explanation of the collapse of all grayling populations monitored. Generally, the surveyed rivers are in very good conditions with good water quality, high heterogeneity, and physical variation. The physical and ecological condition of most grayling and brown trout rivers have been greatly improved through 25 years of rather extensive and expensive river restoration and removal of most barriers. Thus, increased predation from cormorants is the most probable reason for the lack of local brown trout individuals >30 cm and grayling in Danish rivers.

The high cormorant predation in rivers is not only relevant for resident brown trout and grayling. Previous studies have documented significant loss of brown trout and Atlantic salmon smolts to cormorant predation in lower rivers and estuaries in Denmark (Dieperink et al. 2001, 2002; Koed et al. 2006, 2020; Jepsen et al. 1998, 2018a; Thomsen 2013; Schwinn et al. 2017; Källo et al. 2020). Estimated mortality (1997–2017; 23 studies) on brown trout and Atlantic salmon smolt caused by predation from cormorants, varied from 23 to 88% (mean 47%), and this variation likely reflects different geographical localities and density of cormorants (Källo et al. 2020). So far, this high level of smolt loss has been somewhat mitigated by habitat restorations, removal of barriers, and strict regulations on fishing (Koed et al. 2020).

The North Sea houting (*Coregonus oxyrhynchus*), endemic in the whole Wadden Sea area along the North Sea, has its last population in River Vidå, Denmark, and must be assumed to be highly endangered (Jepsen et al. 2012, 2017).

In 2020, Ovegård et al. published a meta-analysis in which they examined the impact of all cormorant species (*Phalacrocoracidae*) predation on fish. The combined effect of cormorant predation on fish was negative, but the overall effect was not significant at the 95% level. This analysis revealed a complex interaction between cormorants and fish, but overall, added to the consensus on the importance of considering cormorant predatory effects in research, conservation actions, ecosystem-based management, and environmental monitoring. This meta-study also highlighted that despite the amount of conflicts and political focus, only very little research have been done on quantifying the effect of cormorant predation on fish populations. An exception is the EU-funded REDCAFE/INTERCAFE project that sought to study these conflicts in detail, provide typical cases, and suggest solutions/mitigation measures (Anon 2012). Unfortunately the measures suggested have not been effective in solving the problems, mainly because they are based on an assumption that cormorant cannot seriously deplete natural, wild fish populations in high quality habitats. This assumption has proven wrong, and the only viable solution to protect threatened river fish is to decrease the number of cormorant visits in the rivers.

As an example to consider, a widely documented predation rate of 50% on sea trout- and Atlantic salmon smolt (Jepsen et al. 2018a) has the direct consequence, that the number of adult brown trout and Atlantic salmon entering the rivers for spawning is only half compared to the situation without cormorant predation. All else being equal, the number of subsequent recruits (fry) is halved, but because of density dependent population dynamics in the rearing areas for parr, i.e. increased growth rate and decreased natural mortality with smaller number of recruits, we do not know for sure the final effect from continued cormorant predation on brown trout and Atlantic salmon populations. The combined effect of docume greatly increased mortality on 1+ salmon and trout, 50% mortality on smolt and even a surprisingly high predation on sea trout kelt under 50 cm (Källo et al. 2023) is pushing many sea trout populations toward extinction despite greatly improved habitats.

When hunted by cormorant in rivers, brown trout and Atlantic salmon parr seek shelter in aquatic plants, under rocks, and along the banks, whereas grayling seek refuge in deep pools, where their hiding possibilities are low, compared to brown trout and Atlantic salmon. This difference in behavior between the species probably explains why grayling has largely disappeared in Danish rivers since cormorants started foraging in rivers in 2010.

The documented effects of predation in combination with frequent observations of foraging cormorants in the rivers, keep the conflicts and angler frustration intense. Thus, efforts are being made in four rivers to test the efficiency of angler-organized cormorant harassment and lethal regulation in reducing the predation from cormorants to an acceptable level. If successful in altering cormorant behavior and reducing predation, similar measures will be taken in many other river systems to safeguard vulnerable populations of freshwater fish. If not, the only way to protect the threatened river fish seems to be a general reduction of great cormorant numbers.

10 Documentation of Impact on Stream Salmonids

Studies have shown that the cormorant's foraging is of great importance for stocks of Atlantic salmon, brown trout, and grayling in Danish rivers. Salmonids in even the smaller streams are very prone to cormorant predation, and local stocks (especially grayling) are now much reduced and even endangered in several river basin (Table 1; Figs. 2 and 3). In Denmark, all grayling and most brown trout are of wild origin as grayling were never stocked, and most stocking of reared brown trout in streams was stopped long ago.

It is plausible that the vast majority of fish species in Danish watercourses are affected negatively by cormorant predation (Jepsen et al. 2014). This probably also applies to coastal and lake fish species, but this has been less studied. In the lakes, it is especially lake trout (*S. trutta*), perch (*Perca fluviatilis*), and pike (*Esox lucius*) that are exposed to high predation pressure (Skov et al. 2013). The direct impacts of predation on population level is often difficult to document, but in Denmark a sudden, general change of cormorant behavior made it possible to disentangle effects and focus on the predation. After more than 20 years with very high cormorant abundance, the birds were foraging on the open coast, in fjords and some larger lakes, but not in rivers. This changed dramatically after a cold winter 2009/2010, where the wintering cormorants found coast, fjords, and lakes to be covered in ice. Most cormorants sought new feeding grounds and now showed up in rivers, all over the country. This was immediately followed by alarming reports from anglers, who did not see or catch fish where there used to be good populations of brown trout and

Table 1 Catch of grayling by electrofishing a 2 km stretch of river Omme Å in 2009 and 2010. Same area, same equipment, same team (Iversen 2010)

No. grayling/km	2009	2010
YOY	147	0
1+	250	5
Older	15	1
Total	412	6

Fig. 2 Grayling that survived cormorant attack but in bad condition

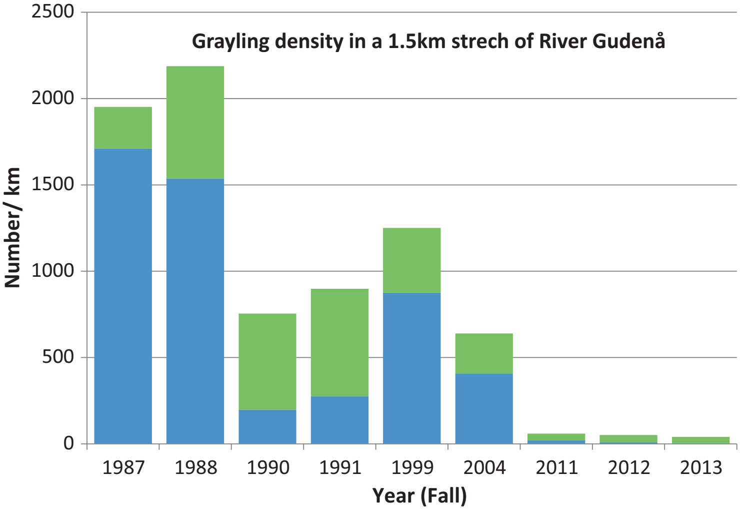

Fig. 3 Grayling numbers per km in a 1.5 km stretch of River Gudenå. Blue: YOY, green: older. Cormorants were first observed in the river in 2010

grayling. All the monitoring of fish in all rivers pointed in the same direction; after 2010, the number of larger fish was very low.

A survey program was then initiated to clarify the magnitude of the problems. A number of rivers (6) were carefully selected. These were amongst the very finest grayling and/or brown trout rivers in the country. These former prime fishing reaches were electro-fished, all 1+ and older grayling and all brown trout over 25 cm were tagged with 12 mm passive transponders (PIT). These 2–6 km reaches were surveyed every year from 2011 to 2014 to recapture tagged fish and tag new. Results showed that there were never a high/normal density of larger brown trout or grayling and that the (relative) survival for PIT-tagged trout was very low (0–10%) (Jepsen et al. 2018b). A southern river (Kongeå) used to hold very good grayling populations, but experienced the same trend after 2010, but the locals did not observe any cormorants, so they claimed that something else had caused the collapse in fish populations. This was interesting and a few adult grayling (60) were captured in October 2015. Of these 25 grayling were radio-tagged and the rest PIT-tagged and all were released back into the river. All fish species caught in the 6 km river-stretch were recorded and weighed to estimate fish biomass. The tagged grayling were tracked manually through the winter, and two data logger stations recorded potential fish leaving the area. Six game cameras were mounted along the river. In October, November, December, and most of January, the tagged grayling were moving around without very long excursions, but during a cold period in Jan/Feb, a few cormorants showed up on the cameras and during the next 10 days a number of cormorant observations were done, but never more than 7 birds. Most of the tagged grayling disappeared during this period and by the end of February, only two grayling were still alive and a number of radio-tags were found under a roosting site by the river. The conclusion of the study was that even few cormorants in a short period could remove 23 of 25 grayling and app. 80% of the fish biomass, without anybody noticing them in the river (Jepsen et al. 2018b).

A large amount of voluntary work is being done among anglers to improve conditions for fish stocks, including the establishment of spawning habitats, restoration of channelized river stretches, removal of migration barriers, fishing restrictions, and the release of Atlantic salmon (½-years). The anglers are now experiencing that the cormorants, after decreasing abundance of coastal fish species, have started to look for food in the smaller streams, where several healthy fish stocks of, e.g., grayling have almost disappeared. It seems that the cormorants now have "learned" to forage in running waters during winter. Now many anglers have formed volunteer "cormorant guard patrols" trying to scare or shoot cormorants away from grayling rivers.

11 In-River Predation on Trout and Salmon Juveniles

After the cormorants changed their behavior and started foraging in the rivers and even in small streams, they could have an impact, not only on the larger fish, but also on the YOY salmonids during winter. To study this, exclusion experiments were carried out in two Danish streams of only 3–6 m width through two winter seasons 2017/18 and 2018/19 (Fig. 4). Four sites of app 100 m length were selected and two game cameras were mounted at each site. All sites were measured for stream area and electro-fished twice by wading (thinning method) to give a solid estimate of salmon and trout density. Most fish (95%) were 0+ and 1+ salmonids, only very few other fish species or older salmonids were found. The following October the experiments were repeated, but now the two control sites were covered and the two covered sites were left as controls (Fig. 5). Thus, we got standardized results of fish density from 2 × 4 sites. The images from all cameras were analyzed and there were cormorants on all the control sites, but none in the covered sites. Both heron and otters were observed under the nets, so the potential difference in relative survival from October to March was only assigned to cormorant effect.

The results clearly demonstrated that relative survival of 0+ and 1+ salmonids in the covered areas was higher than in the control areas. The mean effect was a 49% survival in covered areas reduced to 18% in control areas (Fig. 6). In praxis, this means that three times more juveniles have the chance of surviving to smolt age in areas protected from cormorants. However, there are of course density dependent growth and survival in such salmonid rearing habitats, so the actual influence on smolt production is likely less than 1:3. On the other hand, many juveniles will be 2 years old before smoltification, thus having to experience two winters, doubling the negative effect of the high predation. This is also the case for river resident brown trout that are vulnerable for cormorant predation for at least 5 years before reaching size refuge (see below), making predation the most likely reason for a dramatic decrease in numbers of trout over 30 cm length in Danish rivers surveyed. The very simple method used here may not give "true survival," because we do not follow each individual and because immigration and emigration are possible in the open reaches. We do, however, use the results of double electrofishing as "relative survival," because it is well-known that ½+ and 1+ salmonids rarely move between spawning/rearing areas and the fact that the mounted nets could not be recognized (by fish) as "cover/shelter" due to the large mesh size.

12 Adult Sea Trout

Cormorants can catch and swallow quite large fish and recent studies have shown, that even adult sea trout are targeted by cormorants after spawning (Figs. 7 and 8). Thus, a total of 800 adult sea trout were tagged with PIT-tags in 2015 in river Villestrup Å, and subsequently 112 of these tags were recovered in one cormorant

Fig. 4 Upstream view of one of the covered sites in river Fjederholdt Å

Fig. 5 Image from a game camera overlooking a control stretch in river Von Å

roosting site, indicating that a significant proportion of sea trout <50 cm were eaten by cormorants (Källo et al. 2023). The fact that cormorant successfully can target and eat such large fish points to the fact that only very few river dwelling salmonids can reach a size refuge.

13 Conclusion

Predation from increasing populations of (protected) birds and mammals does have the potential to suppress wild stream salmonid populations in healthy, relatively unaffected rivers. This is the case in Danish rivers, where cormorants are now the main regulating factor for most river fish species.

This is also claimed as being the case in many other EU countries, where a combination of unregulated fish stocking, heavily modified streams, and lack of research has made documentation of this scattered, scarce, and most often found in gray literature. In today's Europe, management of stream salmonids must take into account the factor of "natural predation" at least at the same level as recreational fishing and habitat modification, because a number of fish predators have increased in population size and geographical range. Many more "exclusion" studies should be performed in Europe to shed more light on the basis of an increasing number of conflicts

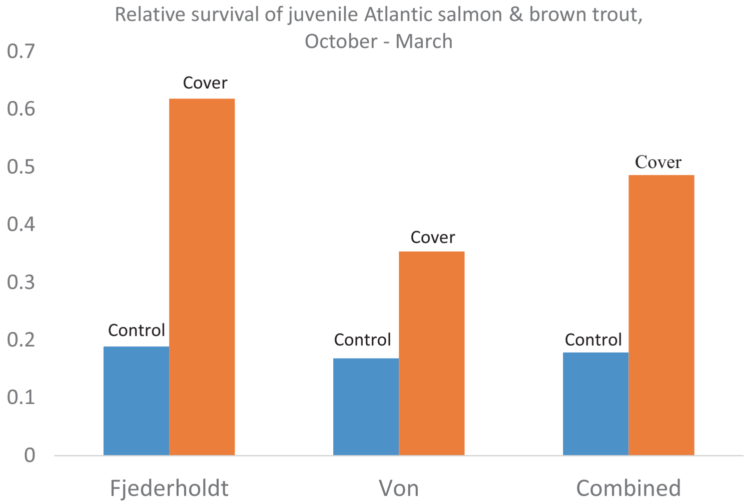

Fig. 6 Results from two rivers (river Fjederholt Å and river Von Å), divided into four stretches, two covered, two controls. Stretches were electro-fished in October and March. Second winter, the sites were switched so that former controls were covered and covered became controls. Thus, results from 4 sites from 2 years, total 8 sites were combined. Relative survival was the density of 0+ and 1+ Atlantic salmon and brown trout (number/100 m^2) found in March divided by the density in October

Fig. 7 Picture from a game camera overlooking a control stretch in river Binderup Å

involving especially cormorants throughout EU. Several NGO's including EIFAAC (European Inland Fisheries and Aquaculture Advisory Commission) and EAA (European Anglers Alliance) have pushed for an EU-wide cormorant management

Fig. 8 A cormorant found dead with a 59 cm (2.2 kg) brown trout, too big to swallow

plan, but often the lack of scientific documentation more than lack of political will have stopped the process.

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Partial Migration in Salmonids: Focusing on Asian Endemic Masu Salmon (*Oncorhynchus masou*) and White-Spotted Charr (*Salvelinus leucomaenis*)

Genki Sahashi and Kentaro Morita

Abstract Partial migration is perhaps one of the most striking features of life-history polymorphism, in which a population displays both migratory and resident behavior. Not surprisingly, both plasticity and genetics are involved in the life-history divergence between residents and migrants. The most plausible mechanism for the persistence and evolution of partial migration is a status-dependent conditional strategy, in which the adoption of alternative migratory tactics is influenced by the status (e.g., body size, condition) of individuals to maximize fitness. To uncover the factors affecting life-history divergence, approaches comparing traits (e.g., growth rate) between residents and migrants are common, but care must be taken in interpreting cause and effect as the onset of life-history divergence precedes the actual timing of outmigration. Individuals planning to migrate will change their behavior and growth rate for a period of 6 months or more to pre-adapt to life at sea, which is very different from life in a river. Early studies of partial migration often dichotomously divided the life histories of residents and migrants, but recent studies have shown there is remarkable diversity within migrants. It is important but challenging to study diverse migration life-history strategies. In this review, we focus on Asian endemic masu salmon and white-spotted charr, which to date have received little attention in studies of partial migration, to seek a comprehensive understanding of the partial migration phenomenon in these salmonids.

Keywords Alternative tactics · Anadromous fish · Conditional strategy · Fitness · Maturation · Threshold trait

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1 What Is Partial Migration?

Partial migration, in which a portion of the population migrates while the rest of the population remains as residents, is a common form of migration (Chapman et al. 2011; Pulido 2011). Partial migration is especially common in fishes (Chapman et al. 2012) and is particularly well studied in salmonids (Jonsson and Jonsson 1993; Dodson et al. 2013; Quinn 2021).

All salmonids breed in freshwater (Thorpe 1998). In populations in which partial migration is observed, there are two broadly different types of life histories can be distinguished—residency versus migration—with further life-history differences possible within each type: residents, which live in the freshwater river where they were born until they reproduce, and migrants, which descend to the sea (or a productive habitat such as a lake or the main stream of a large river) to feed prior to reproduction (Fig. 1; Box 1).

Although migrating to the sea provides increased access to food and space for salmonids, allowing them to grow bigger than their resident counterparts, it also brings a higher risk of mortality. By contrast, if they remain in the river, the risk of mortality is low, but the food quality is also lower than in the ocean, and they cannot grow as large. In other words, migration is high-risk and high-reward, whereas residency is low-risk and low-reward. In general, an individual is both physiologically and ecologically constrained from adopting both life histories and must become either a resident or a migrant, which represent alternative life-history tactics (Thorpe 1987) (but recent studies have clarified that migration patterns cannot simply be divided into two groups, but are complex and diverse; see Sect. 6).

Regardless of whether they are residents or migrants, males form a size-dependent competitive hierarchy during reproduction, with larger individuals being dominants and inferior individuals being subordinates or sneakers that steal spawning pairs at the moment of spawning (Koseki and Maekawa 2000; Maekawa et al. 2001; Watanabe et al. 2008; Sato et al. 2016). When resident and migrant males occur together, the migrant males often become dominants and the resident males become sneakers (Fleming 1996, 1998), but the life-history type does not necessarily correspond to the breeding tactics.

The partial migration of salmonids has long been a topic of interest in Japan, as it has in Europe and North America (Morita 2019). In Japan, masu salmon (*Oncorhynchus masou*) and white-spotted charr (*Salvelinus leucomaenis*) are representative species that exhibit partial migration. However, most of the older literature on these two species is written in Japanese, and little is known about them outside of the Japanese-speaking world. In this chapter, we will introduce the Japanese literature and review the partial migration of masu salmon and white-spotted charr.

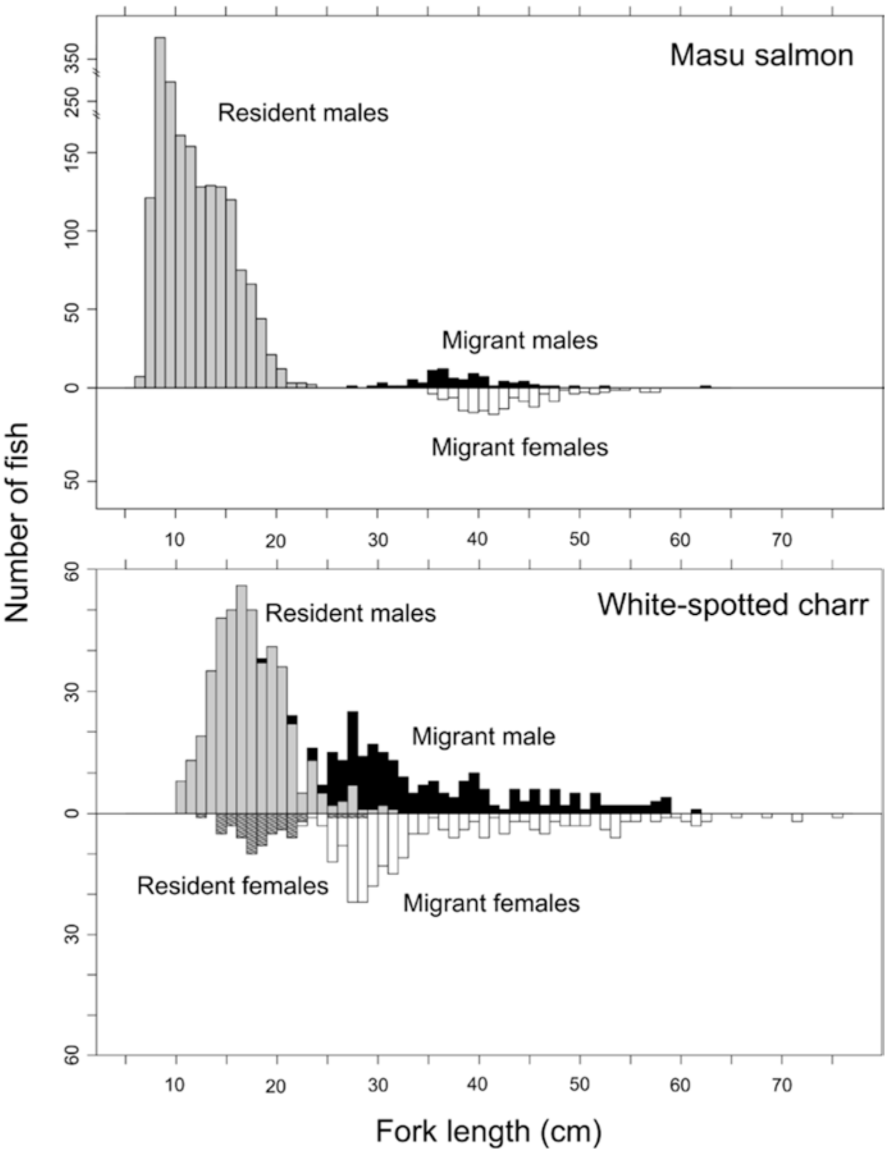

Fig. 1 Body size composition of reproductive individuals of masu salmon and white-spotted charr during the breeding season in Hokkaido, Japan. Resident females are more common in white-spotted charr than in masu salmon. Data sources: Morita (2018) and Morita et al. (2018) for masu salmon, and Morita et al. (2000) and Morita et al. (2013) for white-spotted charr

Box 1. Life Histories of Masu Salmon and White-Spotted Charr

In populations of both species where partial migration is observed (Fig. 2; Table 1), the majority of individuals descend to the sea after spending several years in the river (Kato 1991b; Morita et al. 2009a). The age at smolting is generally age 1+ to 2+ years for masu salmon (Ono 1933a, b; Sugiwaka 1991; Morita et al. 2014), and age 2+ to 4+ years for white-spotted charr (Yamamoto and Morita 2002). Time spent at sea per migration is 1 year for masu salmon (Morita and Sahashi 2018), and 1–8 months for white-spotted charr (Morita 2001). However, the individuals of both species with the fastest growth in early summer (July) become residents. The age at first maturity of residents varies among populations, but the earliest ages are age 0+ years for male and age 1+ years for female masu salmon (Morita et al. 2009b; Morita and Nagasawa 2010; Morita et al. 2014) and age 1+ years for male and age 2+ years for female white-spotted charr (Yamamoto et al. 1999a; Morita and Morita 2007). The residents of both species and migrants of charr are iteroparous (Ono 1933b; Morita 2001; Morita and Morita 2002; Morita et al. 2018). By contrast, migrants of masu salmon are semelparous (Ono 1933a, b). Similar to other semelparous salmonids, migrant female masu salmon guard their spawning beds for 2–8 days after spawning, until their swimming ability declines, and they are swept away (Kato 1991b). By contrast, migrant female charr and resident female masu salmon do not guard their nests after spawning. Most charr migrants that survive spawning return to the sea (Morita 2001; Morita et al. 2013).

There is also a latitudinal cline in the life-history types of mature individuals of both species (Sakai et al. 1992; Yamamoto et al. 1999a; Malyutina et al. 2009). In northern Japan, populations of both species contain both migrants and residents, whereas at the southern limit of distribution in Japan, populations of both species contain only residents; these southern populations showed little migratory behavior and are physically prevented from migrating to the sea by waterfalls, dams, or high-temperature thermal barriers (i.e., they are land-locked) (Kimura 1972, 1989; Yamamoto et al. 1999a). In additions, the pattern of latitudinal clines differs by sex. In northern Japan, all females and most males become migrants, and a portion of males become residents (Sakai et al. 1992; Yamamoto et al. 1999a). On the other hand, near the southern limit, it is almost exclusively females that become migrants (Sakai et al. 1992; Yamamoto et al. 1999a). In landlocked populations, during reproduction, resident males become fighters and large resident male become dominant, whereas small resident males become sneakers (Maekawa et al. 2001). Even in a partially migratory population, if there are no migrant males, the resident male will reproduce as a dominant, paired with a migrant female, instead of becoming a “sneaker” (Watanabe et al. 2008; Sato et al. 2016). As most males diverge into residents and only a few migrant males are found at southerly latitudes, migrant females more often spawn with resident males rather than migrant males (Sato et al. 2016).

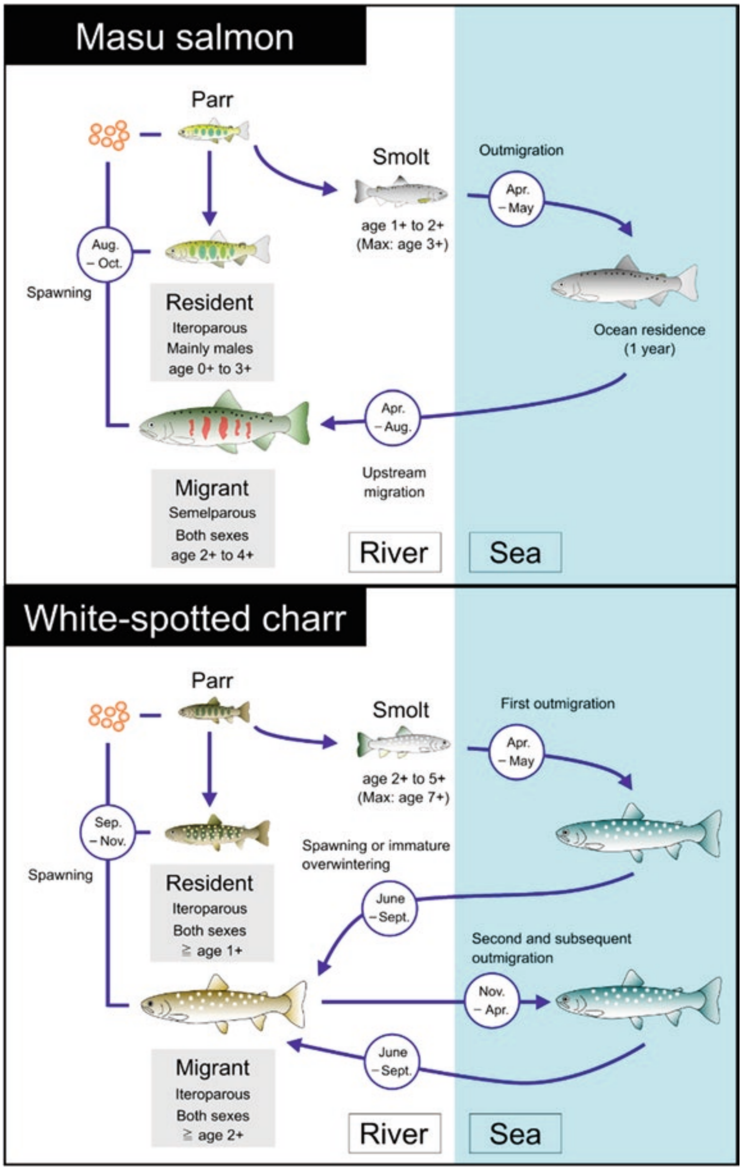

Fig. 2 Life histories of masu salmon and white-spotted charr in populations with partial migration

Table 1 Size at maturity, age at maturity, age at smolting, marine life period, and number of reproduction events of (**a**) masu salmon and (**b**) white-spotted charr

Life history	Size at maturity	Age at maturity	Age at smolting	Marine life period	Number of reproduction	References
(a) Masu salmon						
Migrant (♂♀)	35–65 cm Max: 78 cm	2+ to 4+ years	1+ to 2+ years Max: 3+ years	One year (rarely jack[a] appears)	Semelparous	Hayano et al. (2003); Ivankov et al. (2003); Machidori and Kato (1984); Malyutina et al. (2009); Morita (2018); Morita et al. (2014); Tamate (2015); Tsygir (1988); Tsiger et al. (1994)
Resident (♂)	7–28 cm Max: 36 cm	0+ to 4+ years Max: 6+ years			Iteroparous Max: 3–5 times	Kato (1991a); Morita (2018); Morita et al. (2018); Morita and Nagasawa (2010); Tsunagawa and Shirai (2018)
Resident (♀)[b]	10–28 cm Max: 36 cm	1+ to 4+ years Max: 4+ years			Iteroparous Max: 3 times	Kato (1989); Kiso and Kosaka (1994); Morita (2018); Morita and Nagasawa (2010); Morita et al. (2009b, 2018); Ono (1933a, b); Tsunagawa and Shirai (2018)
(b) White-spotted charr						
Migrant (♂♀)	25–60 cm Max: 108 cm	2+ to 5+ years Max: 17+ years	2+ to 5+ years Max: 7+ years	1–8 months; repeated over several years	Iteroparous 3 times is normal	Morita and Morita (2007); Morita et al. (2009a, 2018); Savvaitova et al. (2007); Shimoda et al. (2002); Yamamoto and Morita (2002)
Resident (♂)	10–30 cm[c] Max: 58 cm	1+ to 5+ years Max: 17+ years			Iteroparous 3 times is normal	Kimura (1970); Morita (2001); Morita and Morita (2002, 2007); Savvaitova et al. (2007); Shimoda et al. (2002); Yamamoto et al. (1999a)
Resident (♀)	15–30 cm[c] Max: 71 cm[d]	1+ to 5+ years Max: 17+ years[d]			Iteroparous 3 times is normal	Esin and Sorokin (2012); Morita (2001); Morita and Morita (2002, 2007); Morita et al. (2009a); Savvaitova et al. (2007); Shimoda et al. (2002); Yamamoto et al. (1996, 1999a)

(continued)

Table 1 (continued)

[a] Jacks are anadromous males and return to the river in their first ocean year (i.e., they spend only some months in the sea) (Tsiger et al. 1994)

[b] In Hokkaido, resident female salmon are collected very rarely (Morita and Nagasawa 2010), thus data for the resident female salmon are not covered in the Fig. 1 dataset

[c] Quite rare characteristics, but male charr can mature at age 0+ years and 8.3 cm, and female charr mature at age 1+ years and 9.9 cm (Kato 1992)

[d] A charr captured in the Chitose River was determined to be a female resident, based on trace element analysis of otoliths. Age assessment based on otoliths indicated it was over age 17+ years old, but additional annuli were indistinguishable (Morita and Honda, unpublished data)

2 The Involvement of Both Genetics and Plasticity

Genetics

Crossbreeding experiments conducted with masu salmon nearly a century ago suggested that female residents can produce migrant offspring and that female migrants can produce resident offspring (Soguri 1936). Thus, both migrants and residents belong to the same gene pool. In addition, when female migrant and male resident masu salmon are mated, eggs are fertilized and show normal development, with growth of the offspring tending to be improved when the males are residents as opposed to migrants (Hokkaido Salmon Conservation Society 1936; Hokkaido Salmon Hatchery 1937). However, in most salmonids, the offspring of residents are more likely to become residents, and the offspring of migrants are more likely to become migrants (Nordeng 1983; Ohkuma et al. 2016; but also see Thorpe and Morgan 1980; Yamamoto et al. 2021).

There is a long history of research to identify the genetic differentiation between residents and migrants at the molecular level. However, when residents and migrants are sampled from different locations or time periods, even in the same water system, it reveals differences between local populations and not between life-history types (Hindar et al. 1991; Adams et al. 2016; Fig. 3). For example, in a study of masu salmon, Yu et al. (2010) detected neutral genetic differences (significant Fst) between residents and migrants in the Shari River, eastern Hokkaido, Japan. However, although residents and migrants were collected from the same river system, they were collected from different tributaries, and the migrants were from a tributary where hatchery releases were conducted. Thus, the results may not indicate neutral genetic differences between salmon with different life histories, but differences between salmon from different tributaries (or hatchery versus wild). In many cases, life history is heritable but does not represent a neutral genetic differentiation between different life histories within a population, instead representing a single population belonging to the same gene pool. Note that the interpretation is different when the focus is on adaptive loci rather than neutral markers. If a single locus affects whether fish become migrant or resident, this locus might exhibit high Fst between different life histories within a population.

However, when migrants and residents are reproductively isolated but sympatric, there may be genetic divergence between the two life histories, resulting in distinct populations with overlapping ranges. This was seen with sockeye salmon and kokanee (*O. nerka*) (Wood and Foote 1996) and Atlantic salmon (*Salmo salar*) (Adams et al. 2016). In this case, it is possible to infer to some extent (though not perfectly) from the breeding population size structure whether residents and migrants are genetically distinct populations (Fig. 4).

In recent years, researchers have attempted to identify the genes involved in determining migration tactics in salmonid species. For example, in rainbow trout (*O. mykiss*), multiple genomic regions on several chromosomes have been implicated in life-history divergence (i.e., divergence of alternative migratory tactics) (e.g., Hecht et al. 2013; Rundio et al. 2021). Identification of candidate genes involved in migration is also underway in brown trout (*Salmo trutta*) (Lemopoulos et al. 2018) and sockeye salmon (Veale and Russello 2017). Unfortunately, however, similar studies have not yet been conducted on masu salmon or white-spotted charr, and the genes involved in the life-history divergence of these species are currently unknown.

Plasticity

In addition to genetics, plasticity is also involved in life-history divergence. In masu salmon and white-spotted charr, energy/resource availability, water temperature, river width, and population density are environmental factors that influence the plasticity of tactic expression.

For white-spotted charr, a transplant experiment using a common genetic origin of the fish demonstrated that the narrower the river and the higher the water temperature, the higher the proportion of residents at a given body size (i.e., the lower maturation threshold) (Morita et al. 2009d). Similarly, in masu salmon, higher water temperatures lead to a higher proportion of residents with a lower maturation threshold (Morita and Nagasawa 2010). The lower threshold size in narrower rivers is thought to be due to the relative increase in the number of hiding places for male residents to sneak around during breeding, thus increasing their reproductive success. By contrast, the smaller threshold size in warmer waters is related to the fact that higher temperatures drive plasticity in growth, making these fish more likely to be residents (see Sect. 3 for the relationship between growth and life-history divergence). In the Japanese archipelago, there is a latitudinal cline in water temperature, which is thought to explain the pattern of masu salmon in northern areas being more likely to become migrants and those in southern areas being more likely to become residents (Morita and Nagasawa 2010; Morita et al. 2014).

If female migrants, which have large body size and high fecundity (Morita and Takashima 1998; Morita et al. 2009c; Morita 2018), cannot return from the sea as rivers are blocked by dams, the density of juvenile fish in the river decreases (Morita et al. 2000; Morita and Nagasawa 2010). Such decreases in population density in the river result in better initial growth, which makes residency more likely (Morita et al. 2000; Morita and Nagasawa 2010). Similarly, in other salmonids, density-dependent food availability has been shown to have an effect on life-history divergence via growth conditions (Olsson et al. 2006).

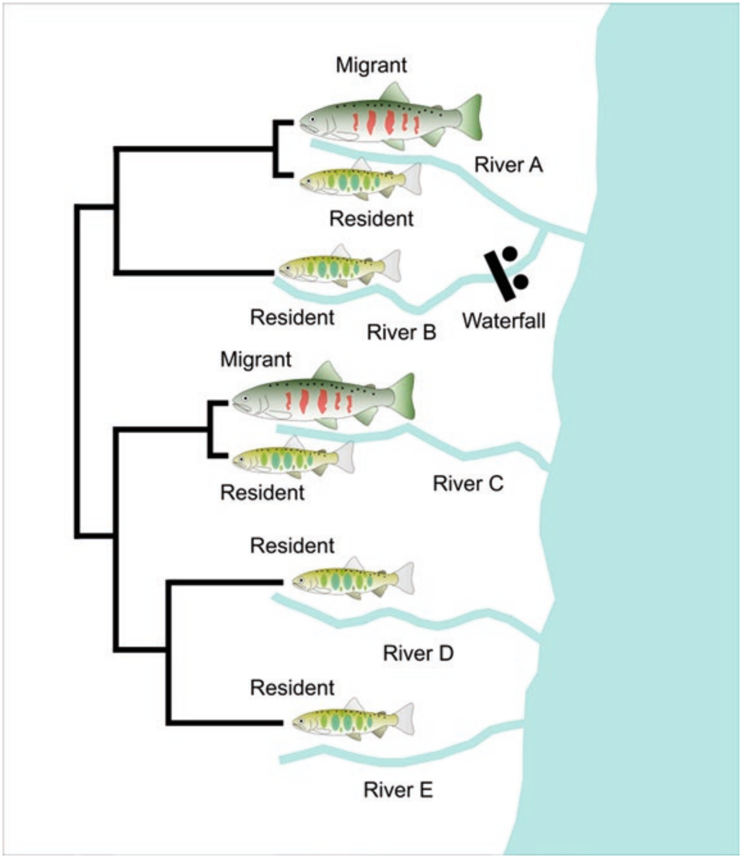

Fig. 3 Conceptual diagram of neutral genetic differentiation between residents and migrants. The length of the black line indicates the neutral genetic difference. Neutral genetic differences are greater between populations than between life-history types (modified from Morita et al. 2009b)

As such, multiple environmental factors are involved in life-history divergence. However, these environmental cues are often not independent of each other, nor are they mutually exclusive. Moreover, although water temperature and food, or a combination of both, affect migration tactics via growth, they do not necessarily have the same growth effects on the phenotypic divergence of migration tactics (Archer et al. 2020).

Genetics and Plasticity Explain Spatial Variation in Partial Migration

Both genetics and plasticity play roles in life-history divergence in masu salmon and white-spotted charr but to what extent do environmentally-induced versus genetically-based differences explain life-history divergence among individuals or populations?

In white-spotted charr, two studies have explored this question, and although the study catchments were in close proximity, conclusions differed. One study

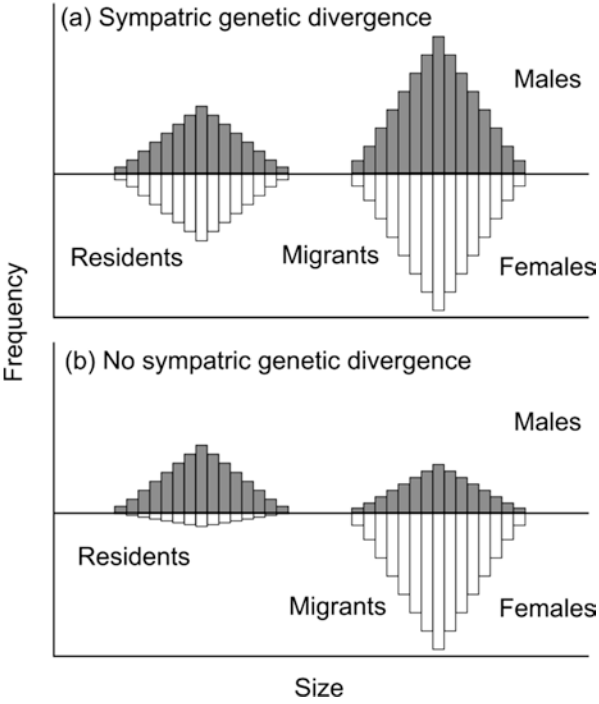

Fig. 4 Genetic relationships and population size structure between residents and migrants. (**a**) Type-assortative mating, with sympatric genetic differentiation between residents and migrants (e.g., sockeye salmon vs kokanee; Wood and Foote 1996); (**b**) no type-assortative mating, and no genetic differentiation between residents and migrants (e.g., masu salmon, white-spotted charr; Fig. 1). In the case of a conditional strategy based on phenotypic plasticity, the sex ratio of the migrants is frequently biased toward females, and that of the residents is biased toward males

suggested that plasticity based on water temperature and river width influences life-history divergence (Morita et al. 2009d). However, the other study suggested that genetic factors based on migration cost affect life-history divergence (Sahashi and Morita 2013). These results may have been influenced by differences between the studies in the range of the physical environmental conditions. For example, water temperatures where Morita et al. (2009d) conducted their study differed by a maximum of 3.4 °C among tributaries, whereas Sahashi and Morita (2013) found a maximum difference of only 0.9 °C among tributaries. By contrast, the migration distance, which is an index of migration cost, was considered to be almost equal among tributaries in Morita et al. (2009d), but differed by up to 82 km in Sahashi and Morita (2013). Although intense research has been conducted in recent years to clarify the relative importance of genetics and plasticity (e.g., Debes et al. 2020), interpretation of the results needs to take into account the research methods and range of physical environments in each study.

3 A Status-Dependent Conditional Strategy to Maximize Individual Fitness

It is important to explore under what conditions an individual migrates to the sea or remains a resident in the river. A number of studies have investigated the relationship between growth status and life-history divergence. The growth status is not limited to body size but also includes body mass index and nutritional status, and these indicators vary among studies (review: Hutchings 2011; Dodson et al. 2013; Sloat et al. 2014; Ferguson et al. 2019).

In principle, in male masu salmon, the fastest-growing individuals do not migrate to the sea but mature and become residents (Kubo 1974; Utoh 1976, 1977; Toda 1992). Female residents are rare and have not been well studied, but as with males, individuals with extremely rapid growth become residents (Morita and Nagasawa 2010). An almost exact pattern of growth and life-history divergence has been observed in white-spotted charr (Yamamoto et al. 1996).

When alternative phenotypes are interpreted using the status-dependent conditional strategy, the fitness of each phenotype is a function of individual status in which: (1) individuals adopt one phenotype to obtain higher fitness at a given status, (2) average fitness is unequal between alternative phenotypes, and (3) fitness of the alternative phenotypes is equal at the switchpoints (i.e., size threshold) (Gross 1996). A threshold for alternative phenotypes has been hypothesized to have additive genetic variation, and the threshold position would move with environmental change under the status-dependent conditional strategy (Gross 1991, Gross and Repka 1998). A number of studies have supported the idea that partial migration is a status-dependent conditional strategy that diverges into migrants or residents depending on growth conditions/status (Lundberg 1988; Jonsson and Jonsson 1993; Chapman et al. 2011; Hatase et al. 2013), however, empirical support for this ultimate mechanism is surprisingly limited. Morita et al. (2014) succeeded in explaining the ultimate mechanism by which rapid growth leads to salmon becoming residents by calculating the expected lifetime reproductive success for the migrant and resident tactics, respectively, as a function of body size at age 0+ years (i.e., early growth conditions) (Fig. 5).

In female masu salmon, the expected lifetime reproductive success of migrants always exceeds that of residents, within the range of realistic body size in the wild; in males, above a certain threshold size, however, the expected lifetime reproductive success of residents is higher than that of migrants (Fig. 5). This explains why in general the proportion of residents is small among females. In other words, this pattern is not driven by small females' physiological inability to mature, but rather by the higher fitness of migrant females compared to resident females. In fact, in landlocked populations, some small females mature at just over 10 cm in size (Table 1a). By contrast, males that are larger than a certain threshold size become residents and have higher reproductive success if they remain small and mature that year instead of migrating to the sea the following year. Therefore, for individuals whose body size is below a certain threshold, migrating to the sea is the best choice when growth status is poor.

The relationship between growth status and expected lifetime reproductive success can vary depending on conditions (Fig. 6). For example, as migration costs increase, the expected lifetime reproductive success of migrants will decrease (Fig. 6b). In this case, the threshold at which the expected lifetime reproductive success of the alternative phenotypes is equal would shift to the left, and it would be adaptive for fish to mature at a smaller size and become residents. In fact, Sahashi and Morita (2013) examined the threshold size of male salmon and white-spotted charr at the watershed scale and found that, in both species, the threshold sizes to become resident were smaller in tributaries located farther from the sea. This result supports the above prediction based on the increased cost of migration (Fig. 6b).

Under hatchery conditions in which selective breeding is used, the outcome is different. If residents are not used as parents in the hatchery, only the expected lifetime reproductive success of migrants would be increased, and it would be more adaptive to become migrants without maturing, no matter how well they grow (Fig. 6c). In this case, the threshold size is predicted to shift to the right, making it more likely that fish become migrants. Sahashi and Morita (2018) found support for this prediction by showing that, in hatchery masu salmon, the threshold size to become resident was larger than that of wild fish in the Shari River system in Hokkaido, Japan, where the hatchery had only used migrants as parent fish for approximately 80 years. Contrary to this case, some Japanese hatcheries of masu salmon use only residents as parent fish. For this style of hatchery management, Ohkuma et al. (2016) have confirmed that hatchery fish are less prone to smoltification and that many individuals become residents.

How long will partial migration be maintained in a population if conditions continue to favor one migration tactic over the other? In white-spotted charr, populations above dams where only residents have reproduced for five or six generations smolt at about one-tenth the frequency of those below dams with migrants, and only females smolt (Morita et al. 2000, 2009a). Moreover, in the Imsa River in Norway, some Arctic charr migrate to the sea even though migrants are unable to return upriver (Jonsson et al. 1989). By contrast, smolts do not appear in a brown trout population that was land-locked between 6000 and 7000 years ago (Jonsson 1982). Prof. Tatsuro Kubo, a leading expert on salmonid breeding in Japan, stated that he had bred and smoltified a variety of salmonids in Japan, including masu salmon, amago salmon (*O. masou ishikawae*), southern Asian Dolly Varden charr (*Salvelinus curilus*), nikko-iwana (*Salvelinus leucomaenis pluvius*), and Sakhalin taimen (*Parahucho perryi*). Kubo could not, however, smoltify the subspecies kirikuchi (*Salvelinus leucomaenis japonicas*), which is distributed at the southern limit of the charr range and is considered to have been land-locked for a relatively long period. In a modeling study using a species of bird, Eurasian blackcaps (*Sylvia atricapilla*), when a migratory-only population was subjected to directional selection favoring residents, it took six generations for the population to show partial migration, but 98 generations before the population became residents only (De Zoeten and Pulido 2020). These results suggest that partial migration may be maintained in a

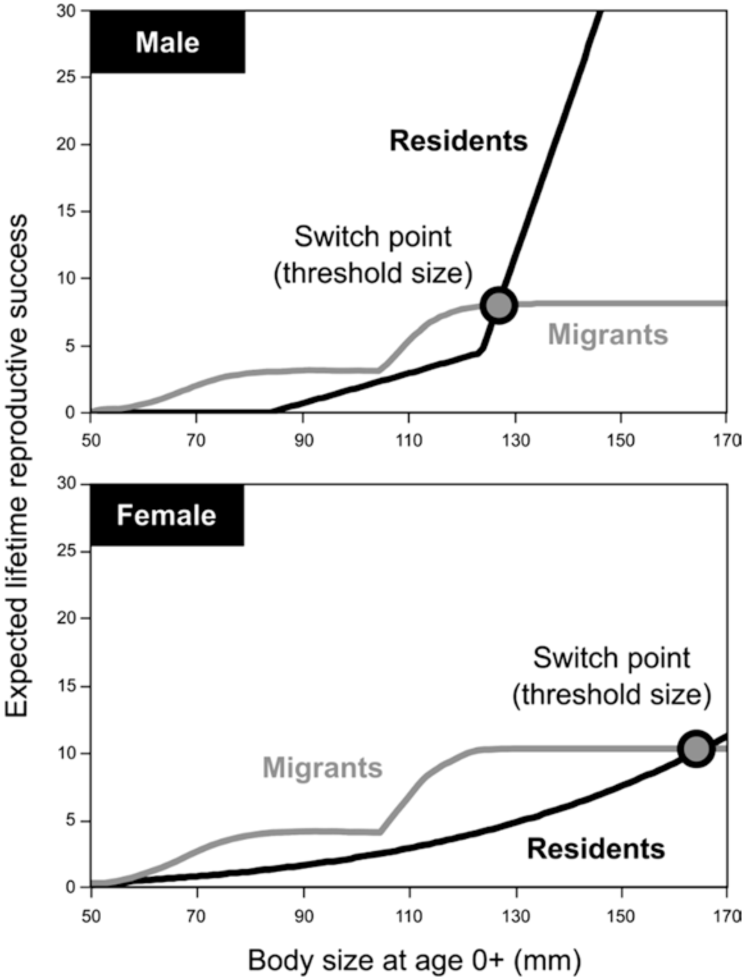

Fig. 5 Curves depicting the expected lifetime reproductive success for alternative migratory tactics in male and female masu salmon, as a function of body size during the breeding season at age 0+ years. The switchpoint is further to the right in females than males (modified from Morita et al. 2014)

population for a long time, over tens of generations, even if the situation continues to favor one migration tactic over the other.

As a general rule for masu salmon and white-spotted charr, the fastest-growing individuals of both sexes become residents (Yamamoto et al. 1996; Morita and Nagasawa 2010), but this does not mean that all other individuals will become migrants. In the case of male masu salmon, the group of fish with the third-fastest growth rate will also become residents (Fig. 7). In other words, individuals that belong to the second- or fourth fastest-growing groups become migrants. In fact, in rearing experiments using masu salmon, it has been shown that the fastest-growing

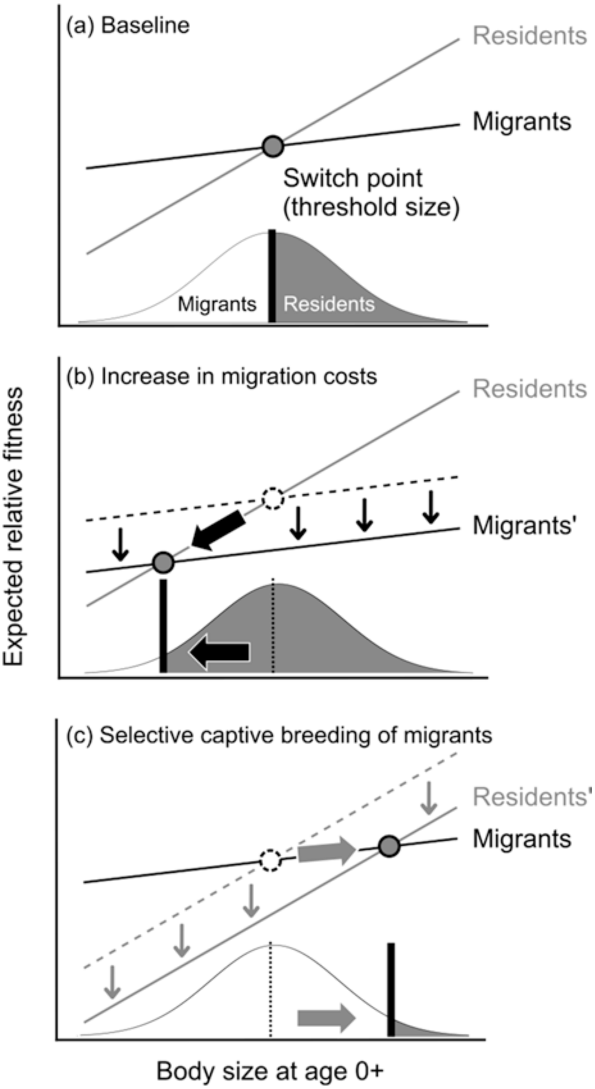

Fig. 6 Status-dependent fitness functions of alternative migratory tactics in three situations: (**a**) Baseline. When evolutionary factors influence migrants or residents, the switchpoint (i.e., size threshold) at which the fitness of each tactic is equal will shift right or left, and the proportion of the alternative migratory tactics will change with the size threshold; (**b**) Increase in migration costs. Higher migration costs reduce migrant fitness, and the size threshold will shift left and promote residency; (**c**) Selective captive breeding of migrants. Selective captive breeding of migrants reduces resident fitness, and the size threshold will shift right and promote migration (modified from Sahashi and Morita 2018)

group becomes the age 0+ years residents; the second-fastest-growing group becomes the age 1+ years smolts (migrants), and the third fastest-growing group becomes the age 1+ years residents (Tamate and Maekawa 2002).

However, the fastest-growing group may not always become residents, as average growth varies with geographic location. For example, as described above, at southerly latitudes, average growth is good because temperatures are high, so the fastest-growing group becomes residents, and the second-fastest-growing group becomes migrants. By contrast, at northerly latitudes, average growth is poor as temperatures are low, so the relationship between growth and life history discussed above is different. Namely, the fastest-growing group becomes migrants, and the second-fastest-growing group becomes residents (Gruzdeva et al. 2013). Therefore, even for the same species, it is important to recognize which life-history divergence of a target population you are focusing on, as the relationship between growth and life history varies by location. This raises the question as to why the relationship between growth and life history might flip, becoming opposites, in different populations.

4 Exploring Mechanisms of Life-History Divergence, with Careful Interpretation of Cause and Effect

There has been a great deal of interest in the factors underlying life-history divergence between residents and migrants. It goes without saying that body size is only one indicator, and that many more traits are involved in the life-history divergence. Many studies have compared traits between mature individuals in the river (mature parr, residents) and immature individuals (prospective migrants), or compared traits (e.g., growth, morphology, and behavior) between smolting individuals (migrants) and non-smolting individuals (prospective residents). However, since both smoltification and maturation are physiologically determined more than 6 months prior (Hunt et al. 1982; Ikuta et al. 1987; Yamamoto and Nakano 1996; Tamate and Yamamoto 2004), care should be taken in interpreting cause and effect. For example, in masu salmon, individuals smolting at age 1+ years have poor growth in the river before switching to smolts, but good growth after the switching. It is difficult to interpret cause and effect when considering whether individuals smolt because they are growing well and are active, or whether they begin to grow well and become active due to smolting.

As migrant masu salmon are more valuable to fisheries than residents, hatchery release projects have aimed to produce juveniles that do not become residents but smolt instead. Therefore, hatchery technicians are well aware of how to increase smoltification rates by producing certain growth conditions for specific periods of development (Akaishi 1992; Toda 1992; Matsumura et al. 1995). By suppressing growth with low water temperature until July when fish are age 0+ years, fork length can be kept at or below 7 cm and body weight at 10 g or less, which reduces the appearance of aged 0+ years residents in September (Fig. 7). By accelerating growth from July to November (when fish are aged 0+ years) to reach a fork length of 9 cm and a body weight of 10 g or more, then inhibiting growth again during the winter, smoltification rates are increased in the spring when fish are aged 1+ years (Fig. 7). This rearing method can produce a 85–90% age 1+ smoltification rate, even in unselected groups (Japan Fisheries Resource Conservation Association 2008). Thus, by controlling growth just before the onsets of maturation and smoltification, hatcheries have produced an artificially high percentage of migrants (i.e., age 1+

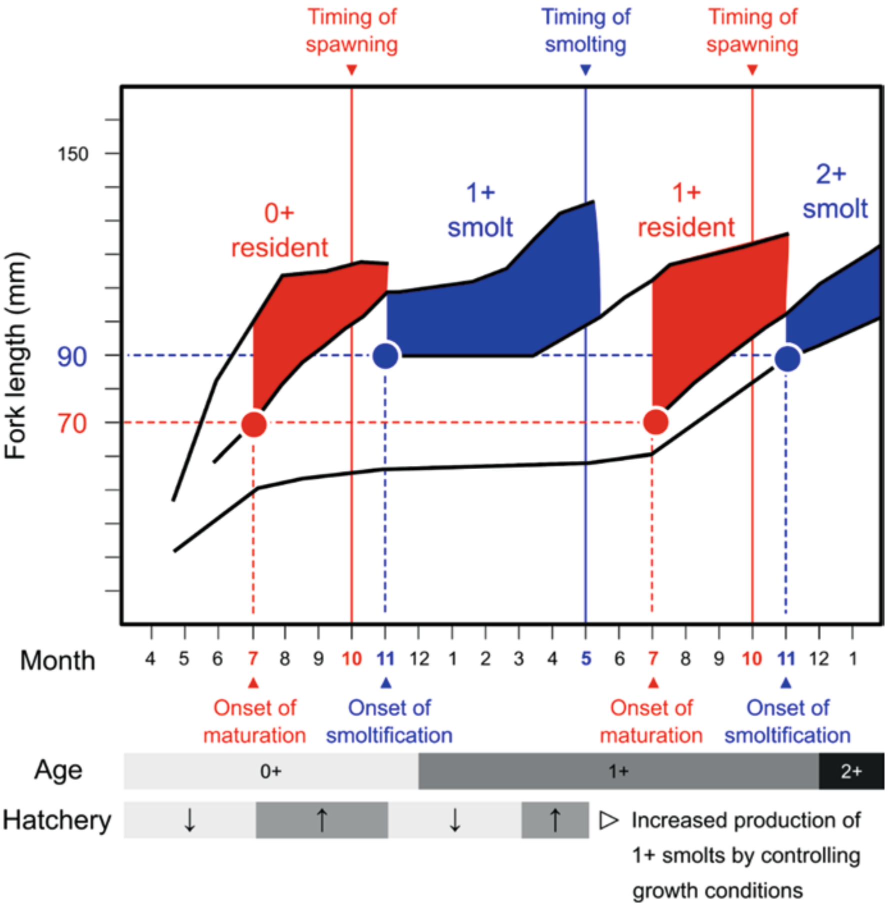

Fig. 7 Schematic diagram of the life-history divergence of male masu salmon in southern Hokkaido, Japan. In order of fastest growth, life histories diverge into 0+ residents, 1+ smolts, 1+ residents, and 2+ smolts, where numbers denote years of age. Dashed and solid lines indicate the approximate onset and timing of each life-history event. The resident life history is determined in early summer (July), whereas the migrant life history (smolts) is determined in autumn (roughly November). Individuals with a fork length of 70 mm or more in July become residents in October, and those with a fork length of 90 mm or more in November become smolts in following May. The bottom row (Hatchery) indicates a proposed rearing method to artificially increase the production of 1+ smolts (i.e., migrants) in the hatchery. Upward arrows indicate periods of accelerated growth, and downward arrows indicate periods of inhibited growth for this method (modified from Kubo 1974; Utoh 1981; Japan Fisheries Resource Conservation Association 2008)

smolts). It should be noted that there is a gap of about 3–6 months between the onset of maturation and spawning periods and between the onset of smoltification and the seaward migration/smolting periods.

5 Stream Life of Prospective Migrants (Prior Preparation)

Interesting ecological features of smolt-switching individuals (i.e., individuals on a migration trajectory) have been mainly studied in Atlantic salmon. Groups that will smolt the following spring (i.e., smolt-switching individuals) are known to have higher growth than other individuals in winter, resulting in a bimodal distribution of body size in the juvenile stage (Thorpe 1977; Metcalfe et al. 1988). Such "catch-up-growth"—increasing consumption and growth rates following a period of slowed development—is thought to be a precaution against size-dependent mortality in the ocean (Nicieza and Metcalfe 1997; Futamura et al. 2022b). This has also been confirmed in masu salmon and white-spotted charr, where after the decision to smolt but immediately prior to smolting, there is higher growth of prospective migrants compared to other individuals in rivers (Hirata et al. 1986, 1988; Takami et al. 1998; Yamamoto and Nakano 1996).

Studies suggest that changes in behavioral patterns of Atlantic salmon following smolt-switching can lead to increased growth. Normally, when water temperatures are low, metabolism and foraging efficiency decrease, and individuals shift to nocturnal behavior that reduces predation risk (Fraser et al. 1993). However, a higher proportion of prospective migrants are diurnal even when water temperatures decrease (Metcalfe et al. 1998). In masu salmon, prospective migrant individuals are also active during the daytime, even in winter when water temperatures are low (Kubo 1976). It has also been shown that smaller prospective migrants grow more and approach a certain threshold size by the time they descend to the sea (Futamura et al. 2022b).

Masu salmon and white-spotted charr migrating to the sea tend to have a similar body size across populations, although there is some interpopulation variation (Tanaka 1965; Yamamoto and Morita 2002), and there seems to be a threshold (Yamamoto et al. 1999b). A larger body size does not always increase the probability of survival in the ocean (Shimoda et al. 2003; Miyakoshi 2006). The expected probability of survival increases with body size up to a certain threshold size, but smolts larger than that of threshold benefit less. This may be because body size-dependent salinity tolerance and escape from predators become critical below a certain threshold (Misaka et al. 1998; Futamura et al. 2022a). This relationship is crucial in the above-mentioned calculation of the expected lifetime reproductive success for residents and migrants. If the survival rate in the ocean increases with smolt size, then individuals that have grown well in the river should descend to the sea and become migrants. No matter how large an individual's body size, there is no guarantee of survival in the ocean, and the effect of large body size has an upper limit; these factors are important for assessing lifetime reproductive success.

6 Beyond Dichotomous Life Histories

In the previous sections, we discussed life-history divergence as a dichotomous pattern, with residents and migrants. In recent years, however, it has become clear that migration patterns cannot simply be divided into two groups; they are complex and diverse. Migrants were thought to spend several years in the river (i.e., the parr stage) before becoming smolts in the spring and descending to the sea. Some individuals of Atlantic salmon and brown trout, however, do not smolt and instead migrate to the ocean as parr in the autumn (Birnie-Gauvin et al. 2019). In coho salmon (*O. kisutch*), some individuals enter estuaries as fry, where they survive and grow well (called "nomads"). However, instead of migrating to offshore waters, the nomads return upstream to freshwater to overwinter before migrating to the ocean as smolts (Koski 2009; Bennett et al. 2015). Nomad-like individuals have also been found in masu salmon and white-spotted charr (Arai and Morita 2005; Matsubayashi et al. 2017; Kuroki et al. 2020). In iteroparous Dolly Varden (*Salvelinus malma*), some migrants remain in the river, essentially becoming "retired" migrants (i.e., previously migratory fish that have returned to a resident life history following one or more migrations to the sea and back) (Bond et al. 2015). Since life-history diversity results in spreading of risk (den Boer 1968, 1981) and contributes to population persistence and fishery stability (Schindler et al. 2010), dividing life-history polymorphisms into a simple dichotomous pattern may overlook something essential. Thus, the study of the full diversity of migration tactics is likely to be a fruitful avenue for future research.

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The Role of the Soundscape in the Behavioral Ecology of Stream-Dwelling Salmonids

K. A. Murchy, R. A. Rountree, and F. Juanes

Abstract Stream salmonids inhabit areas impacted by aerial, terrestrial, and underwater sounds which make up the holo-soundscape. Components of the holo-soundscape include sounds from biological sources (biophony), natural sources (geophony), and human activities (anthropophony). Here we review and synthesize the limited research on freshwater soundscapes as they pertain to stream-dwelling salmonids and suggest that holo-soundscape characteristic differences among habitats and along stream-order gradients likely play a role in salmonid ecology. We suggest that the holo-soundscape interacts with other biotic and abiotic attributes of habitats and has the potential for both indirect and direct effects. Direct effects occur when sounds are perceived by, or have a physiological impact on a given species, while indirect effects impact a species by affecting other species, or other components of its habitat. The role of the holo-soundscape in the ecology of salmonids and the potential for direct and indirect impacts of anthropophony have rarely been considered and represent an area for future research. To do this, simultaneous aerial and underwater recording should be incorporated in research programs. Finally, there is a critical need for documentation of salmonid hearing ability and sound production at all ontogenetic stages.

Keywords Freshwater soundscapes · Sound production · Ambient sounds · Anthropogenic noise · Passive acoustics · Fish behavior · Fish ecology · Habitat selection

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1 Introduction

Salmonids are important members of both marine and freshwater ecosystems throughout the northern hemisphere with 223 recognized species with three subfamlies: Coregoninae (88 spp), Salmoninae (121 spp), and Thymallinae (14 spp) (Nelson 2016). Some species of salmonid spend their entire lives in fresh water (e.g., *Oncorhynchus clarkii*), while other species spend a portion of their lives in the marine environment (e.g., *Oncorhynchus tshawytscha*) and others exhibit a mix of these life strategies (e.g., *Oncorhynchus nerka*) (Pavlov and Savvaitova 2008). However, freshwater habitats represent spawning and rearing habitats for all salmonids, with the majority spawning in stream habitats. For example, in North America, 78% of salmonids have their primary spawning habitat listed as streams, with an additional 17% that can spawn in streams (Willson 1997). Even though salmonids have a strong reliance on stream habitats for spawning, the soundscape in stream habitats and the role it plays in the ecology of salmonids is not well understood. The soundscape of streams is a complex interaction among aerial, terrestial, and underwater soundscapes constituting a "holo-soundscape" for the habitat (Fig. 1; Rountree et al. 2020).

To begin understanding the role of the holo-soundscape to salmonids, first we must understand the components that make it up (Fig. 1). A soundscape is the ambient acoustic environment (intensity and frequency composition) an animal is exposed to in its specific habitat (terrestrial or underwater) in time and space which encompasses sounds produced by geological (geophony), biological (biophony), and anthropogenic (anthropophony) sources (Pijanowski et al. 2011; ISO 2017). The geophony is made up of many types of "natural" sounds that characterize a habitat or location, such as wind, rain, and surf. An often-overlooked component are sounds produced by the effects of moving water on objects such as pebbles, logs, and plant matter (Fig. 1). Similarly, the biophony is composed of natural sounds that characterize a habitat and that are produced by vertebrates such as fish, turtles, amphibians, birds, and mammals, but also includes sounds made by invertebrates such as insects. In contrast, the anthropophony is composed of sounds from human-made sources that are invasive to the habitat, such as, but not limited, to sounds from boats, traffic, trains, and construction (reviewed in Duarte et al. 2021), hereafter referred to as noise. Noise from the human voice, and human movements can be considered anthropophony or biophony depending on the specific circumstances, but like other human activities, can have an impact (Fig. 1).

The first recognition of the potential importance of the soundscape to salmonid fishes dates back to 1969 (Stober 1969), but unfortunately, the freshwater soundscape of stream-dwelling salmonids has yet to receive significant attention (Table 1). In fact, freshwater soundscapes in general have only recently received attention from the scientific community (see reviews in: Gammell and O'Brien 2013; Linke et al. 2018; Rountree et al. 2019, 2020; Decker et al. 2020; Desjonquères et al. 2020). Much of the focus to date has been on the effects of anthropogenic noise on specific species (Mickle and Higgs 2018), description of sound production by

Fig. 1 Illustration of some of the holo-soundscape components found within stream-dwelling salmonid habitats that contribute to direct or indirect effects: micro-habitat specific (turbulence and bubbles at riffles and falls, movement of falling logs and submerged vegetation, gas seeps); movement and vocalizations of predators (birds, bears, humans, and other mammals); movement and vocalization of conspecifics and other fishes (redd cutting, air-movement sounds, jumps and splashes, catfish barks); movement and vocalization of other aquatic organism (insects, crayfish, turtles, frog): invasive noises (traffic, planes, boats, fishing)

specific species (reviewed in Rountree et al. 2018), or quantification of ambient sound levels (see review in Rountree et al. 2020). Only a handful of studies have attempted to describe the overall soundscape composition of, or ecological importance to, freshwater habitats in temperate regions within the geographic range of salmonids (Table 1).

Here, we argue that the holo-soundscape is an important defining characteristic of aquatic habitats and the ecological niches of resident and transient biota. We start by outlining and synthesizing the current state of research on all freshwater soundscapes since there is limited information on each individual habitat. Due to the inconsistent naming of freshwater habitats in the literature, we have grouped habitats together into broad categories. We will be grouping lotic habitats (ponds and lakes) together and arbitrarily grouping lentic habitats into two categories: smaller habitats that are higher order (stream/creek/brook/run) and relatively large rivers (main stem rivers) that are lower order.

Table 1 Selected review of passive acoustic studies in temperate freshwater habitats found within the geographic distribution of salmonids

Lake	Pond	River	Stream	Other	*N*	Sample duration	Duty cycle	Ambient reported	Ambient method (freq range)	Anthropophony	Biophony	Citation
1					2	1–5 min	Continuous	106 ± 1 dB re 1 μPa	L_{Leq} (0.005–20 kHz)	Boat noise	No	Amoser et al. (2004)
3(3)	1(1)	1(3)	2(2)	3(3)	12	1–3 min	Continuous	100 dB re 1 μPa (stagnant); 110–135 dB re 1 μPa (fast moving)	L_{Leq} (0.005–20 kHz)	No	No	Amoser and Ladich (2005); Wysocki et al. (2007)
2(2)		1(2)	1(1)	2(2)	42	1–3 min	Continuous	77–138 dB re 1 μPa	L_{Leq} 60 s (0.005–20 kHz)	No	No	Amoser and Ladich (2010)
		1(6)			40+	7–12 h, 3–210 min	Continuous	no	None	Boat, traffic, train	21 types	Anderson et al. (2008)
1(6)					6	10 min	Continuous	No	None	Boat noise	No	Bolgan et al. (2016a, 2016c)
3(3)		1(1)			9	24 h	5 min/h	86–87 dB re 1 μPa (lake) 86–110 dB re 1 μPa (river)	Lsp (0.01–100 kHz)	Boat noise	Char and macroinvertebrate sounds	Bolgan et al. (2018)
2(39)					51	10 min, 24 h	Continuous	No	None	Boat noise	Not itemized	Bolgan et al. (2016b)
	3(12)				12	84 days	1 min/15 min	No	None	No	48 types	Desjonquéres et al. (2015)

Lake	Pond	River	Stream	Other	*N*	Sample duration	Duty cycle	Ambient reported	Ambient method (freq range)	Anthropophony	Biophony	Citation
		1(6)			6	15 days	1 min/h	No	None	No	128 type	Desjonquères et al. (2018)
			1(9)			1 min	Continuous	57–80 dB re 1 µPa/Hz[a]	Peaks from power spectrum level (0.0215–2 kHz)	Traffic	Shiner sound	Holt and Johnston (2015)
2 (5)					6	1 month	3 min/10 min	No	None	No	9 types, most attributed to lake trout	Johnson et al. (2018)
7(7)					7	24 h	15 min/h	No	None	1–2 kHz frequency band	3–8 kHz frequency band	Kuehne et al. (2013)
			1 (6)		593	10 sec	Continuous	58–100 dB re 1 µPa (cascade); 80–110 dB re 1 µPa (Waterfall base); 50–90 dB re 1 µPa (glide); 55–99 dB re 1 µPa (pool); 53–100 dB re 1 µPa (riffle); 60–80 dB re 1 µPa (Run)[a]	SPL_{rms} (0.1–10 kHz)	No	No	Kacem et al. (2020)

(continued)

Table 1 (continued)

Lake	Pond	River	Stream	Other	N	Sample duration	Duty cycle	Ambient reported	Ambient method (freq range)	Anthropophony	Biophony	Citation
1(24)					24	2–2.5 h	1 min averages	30–50 dB re 1 µPa/Hz[a]	Spectrum level by frequency (0.011–0.250 kHz)	No	No	Lomask and Saenger (1960)
			1(7)		7	1 min	Continuous	45–80 dB re 1 µPa/Hz (quiet); 65–102 dB re 1 µPa/Hz (noisy)[a]	Spectrum level by frequency (0.03–1 kHz)	No	No	Lugli and Fine (2003, 2007)
			2	3	177	1 min	Continuous	63–78 dB re 1 µPa/Hz (Vegetated Spring); 75–90 dB re 1 µPa/Hz (Stony Stream); 76–90 dB re 1 µPa/Hz (Brackish Lagoon); 86–98 dB re 1 µPa/Hz (Sandy Shore); 104–117 dB re 1 µPa/Hz (Rocky Shore)[a]	Spectrum level by frequency (0.05–1 kHz)	No	Goby	Lugli (2010)

Lake	Pond	River	Stream	Other	N	Sample duration	Duty cycle	Ambient reported	Ambient method (freq range)	Anthropophony	Biophony	Citation
1					1	80 days	Continuous	85–96 dB re 1 µPa	Median rms (0.01–8 kHz)	Ice road traffic, airplane, other	Burbot	Cott et al. (2012); Martin and Cott (2016)
		1(12)			12	24 h, 47–89 days	Continuous	79–82 dB re 1 µPa	rms (0.1–2.5 kHz)	Boat, traffic, airplane	Examples, not quantified	Martin and Popper (2016)
		1(1)			10	48 h	10 min/h and 1 min/15 min	No	None	No	25 sound types, 3 common	Morgan (2014)
15(15)					30	1 h	Continuous	58–74 dB re 1 µPa (summer), 50–65 dB re 1 µPa (winter)	rms (0.1–12 kHz)	Boat, ice auger	26 types	Putland and Mensinger (2019a)
		1(1)			1	Not reported	Continuous	No	None	Boat noise	No	Roh et al. (2008)
19(32)	17(18)	20(99)	20(24)		173	1–119 min	Continuous	99.4 ± 2.2 (SE) dB re 1 µPa (Brook), 101.1 ± 1.4 dB re 1 µPa (river), 98.7 ± 2.2 dB re 1 µPa (Pond)	rms (0.016–24 kHz)	9 categories of sound	8 categories of sound	Rountree et al. (2020)

(continued)

Table 1 (continued)

Lake	Pond	River	Stream	Other	*N*	Sample duration	Duty cycle	Ambient reported	Ambient method (freq range)	Anthropophony	Biophony	Citation
1(2)					2	Not reported	Continuous	No	None	Boat noise	No	Seppänen and Nieminen (2004)
1(3)			2(2)		Not reported	Not reported	Continuous	No	None	No	Cutthroat trout	Stober (1969)
		2(4)			16	2–60 min	Continuous	No	None	No	Sucker spawning	Straight et al. (2014)
		12(30)			30	5.5 min	Continuous	112 ± 9 dB re 1 µPa (pool); 114 ± 7 dB re 1 µPa (run); 126 ± 9 dB re 1 µPa (run sed); 142 ± 10 dB re 1µPa (riffle); 151 ± 7 dB re 1 µPa (step-pool)	Broadband mean (rms) (0.0315–16 kHz)	No	No	Tonolla et al. (2010)
		5(6)			6	5.5 min	Continuous	126–154 dB re 1 µPa	Broadband mean (rms) (0.0315–16 kHz)	No	No	Tonolla et al. (2011)
		3(3)			30	Several days	3–5 min/h	60–118 dB re 1 µPa/Hz[a]	Mean Spectrum level by frequency (0.0016–16 kHz)	No	No	Vračar and Mijić (2011)

L_{Leq}, equivalent continuous SPL averaged over 60 s; rsm, root mean squared SPL

[a] Values estimated from graphs

Next, we discuss the few studies on the hearing abilities and sound production in salmonids to understand the direct and indirect effects of a changing freshwater soundscape. To do this, we first briefly discuss sound and how it is detected by fishes. All sounds have two components: sound pressure and particle motion. Sound pressure is created by the compression and expansion of water (or other media such as air) and propagates as a pressure wave, while particle motion is the oscillation of individual particles due to the pressure wave and is a measure of particle displacement (ISO 2017). Although recently published reviews on fish hearing have highlighted the importance of particle motion (Popper and Hawkins 2018, 2019), most freshwater soundscape studies to date have relied on pressure measurements because of the difficulty of measuring particle motion in the field and lack of widely available and affordable detectors. While we recognize the importance of measuring particle motion in future freshwater soundscape studies, here we focus on the current state of the literature that has been sound pressure dominated.

Lastly, we address the potential role the holo-soundscape plays in the ecology of salmonids in streams. Like other attributes of habitats, sounds can have both direct and indirect effects on a given species. For example, a sound can adversely affect a study species that does not perceive the sound itself, by adversely affecting its prey. We suggest that a more holistic consideration of soundscapes is needed to understand their role in salmonid ecology. For this reason, we define "noise" as any sound that alters the natural soundscape regardless of how it may be perceived by a given study species.

2 Ambient Sound

One component of the soundscape of particular importance is the ambient sound. Ambient sound is defined as the background sound when no individually recognizable sounds are observed (Amoser and Ladich 2010). Ambient sound is typically measured as the sound pressure level (SPL) in decibels (dB) relative to a standard such as 1 μPa (underwater) and over a specified frequency range (see Hawkins and Popper 2014; Merchant et al. 2015 for a review of methodologies). In most cases, it should be understood SPL values are the received values, i.e., the level at the location of the hydrophone, and not the source level. However, only a handful of studies have made comparisons of ambient sound levels among different freshwater habitat types (Stober 1969; Amoser and Ladich 2010; Wysocki et al. 2007; Bolgan et al. 2018; Kacem et al. 2020; Rountree et al. 2020, Table 1).

Previous studies have reported ambient sound levels from lake (Bolgan et al. 2016b, c; Putland and Mensinger 2019a; Rountree et al. 2020), pond (Desjonquéres et al. 2015; Rountree et al. 2020), and river/stream (Tonolla et al. 2010, 2011; Vračar and Mijić 2011; Desjonquères et al. 2018; Kacem et al. 2020; Rountree et al. 2020) habitats. Studies conducted in small lakes and ponds indicated these habitats are relatively quiet with low SPL values (Desjonquéres et al. 2015; Putland and Mensinger 2019a). In Minnesota, small lakes (<7 km^2 surface area) were found to have broadband (100–12,000 Hz) sound pressure levels that ranged from 60 to 78 dB re 1 μPa in the summer then the SPL dropped to 51–65 dB re 1 μPa in the winter months (Putland and Mensinger 2019a). Another study examined sounds produced in temperate ponds in France (Desjonquéres et al. 2015), but no sound pressure metrics were reported. In comparison, river habitats tended to have higher SPL values compared to lakes and ponds (Amoser and Ladich 2010; Bolgan et al. 2018; Rountree et al. 2020). Rountree et al. (2020) compared three broad habitat types: stream/creek/brook, pond/lake, and river, and no significant differences among mean total SPL were detected, but a significant difference in sound level spectra was observed. Rivers demonstrated the highest SPL and ponds and lakes the lowest SPL, except at frequencies below 500 Hz where brooks, streams, and creeks demonstrated the highest SPL values (Fig. 2). Similarly, the Danube River exhibited sound pressure levels ($L_{\text{Leq, 60s}}$) between 80 and 138 dB re 1 μPa (0.005–20 kHz) depending on which section of the river the readings were taken from (Amoser and Ladich 2010). In a study conducted on large rivers in Europe, the highest mean spectral energy was at lower frequencies (20–40 Hz), then SPLs continually decreased up to the maximum frequency recorded (10 kHz: Vračar and Mijić 2011). Similarly, when examining the power spectral density plot for a lock chamber on the Mississippi River, ambient sound was higher for lower frequencies (10–1000 Hz) at 80–100 dB re 1 μPa^2/Hz compared to frequencies above 1000 Hz which were <80 dB re 1 μPa^2/Hz (Putland and Mensinger 2019b). In contrast, Bolgan et al. (2018) documented higher SPL values in a lake (110 ± 1.4 dB) compared to a river (87 ± 0.6 dB) but this difference was attributed to anthropogenic factors.

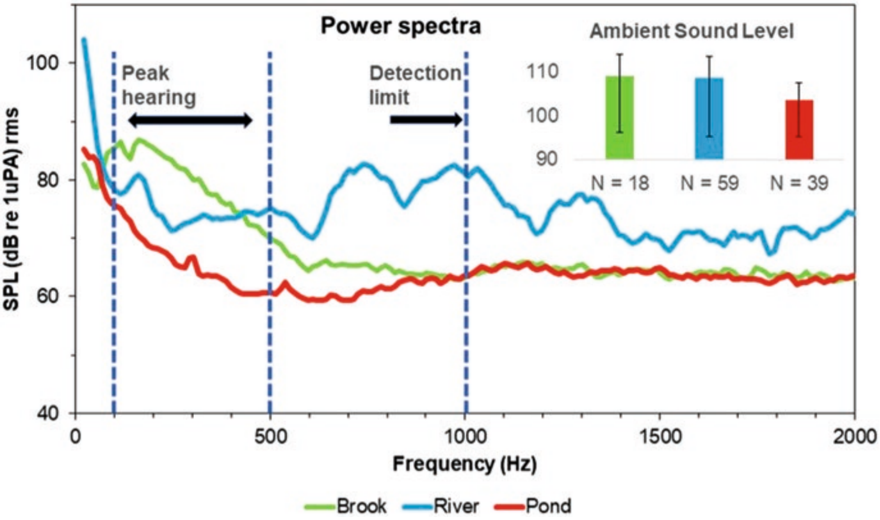

Fig. 2 Comparison of ambient sound spectra among three habitat types in relation to the known hearing ability of salmonid fishes. Inset is the mean (SE) total ambient sound levels (24 kHz bandwidth) by habitat. Adapted from Rountree et al. (2020)

Different river sections can also influence the SPL within a single river (Tonolla et al. 2011; Desjonquères et al. 2018; Kacem et al. 2020). Rivers are classified by river order, with smaller order values given to headwater tributaries and order values increasing as the river flows toward the lowlands (Zaimes and Emanuel 2014). Within one stream in Canada, six different habitat types were identified, and SPL generally rose with increasing river order, while water velocity, water depth, and habitat type were found to be the most important hydrological components to impact SPL values within the stream (Kacem et al. 2020). Additionally, Desjonquères et al. (2018) documented changes in acoustic communities that were significantly correlated to lateral connectivity on a flood plain on the River Rhone, but the mechanism could not be evaluated. In addition, during 5.5 min drift surveys of five river systems, Tonolla et al. (2011) found significant differences between median SPL values in all octave bands by river segment, indicating SPL trends are conserved across rivers. Another study compared ambient sound in locations in one river with changes in sound composition observed, but no SPL values were reported (Anderson et al. 2008).

Rivers are also separated by habitat type with increasing water movement: pools are areas of deeper waters with slow moving water, runs are areas with moderate current and constant depths, riffles are shallow areas of fast-moving water, and step pools are sections of steep drops followed by a pool. Although studies documenting the likely unique holo-soundscapes of these habitats are limited, a few have noted differences in ambient sound. Generally, river sections with stagnant waters (e.g., pools) have SPL values below 100 dB re 1 μPa compared to sections with fast-moving waters (e.g., rapids: Fig. 1) that are above 110 dB re 1 μPa (Wysocki et al. 2007), with some faster moving environments having SPL values 20–30 dB above low flow environments (Tonolla et al. 2010). Finally, step pools have the highest SPL of all river habitat types, with recorded SPL as high as 150 dB re 1 μPa (Tonolla et al. 2010).

Frequency composition of freshwater ambient sound also differed by water flow rates and river habitat type. Stagnant sections contained the highest energy in low frequencies (< 100 Hz) followed by a fast decline between 100 and 800 Hz, while fast-moving sections also had most energy in low frequencies (<100 Hz) but energy declined only to rise again after 500 Hz (Wysocki et al. 2007; Tonolla et al. 2011). Likewise, small streams have a similar acoustic profile to fast-moving sections of large rivers (Holt and Johnston 2015). Ambient sound was highest at 43 Hz (~80 dB re 1 μPa) then again at 581–1140 Hz (~66 dB re 1 μPa), creating a window between 170 and 450 Hz for biological sounds (Wysocki et al. 2007; Holt and Johnston 2015). The highest SPL occurred at low frequencies for all riverine habitats, but values increased with flows and habitat type by up to 20 dB (Tonolla et al. 2011). Even though flows increase sound pressure levels (up to 13 dB at 125 Hz), the mid frequency window of lower SPL remains, creating acoustic space for animals to communicate (Tonolla et al. 2011).

3 Geophony

Sounds produced by natural processes such as weather, water flow, mechanical movements of wood, rocks and vegetation, and gas seeps constitute the geophony (Fig. 1). Rain can increase ambient sound conditions by 10 dB depending on the rate and size of droplets (Bom 1969; Nystuen 1986) and has been indicated as a main factor influencing broadband sound levels in shallow waters of a freshwater lake (Bolgan et al. 2016b). Wind is another important factor, ranging from only influencing frequencies below 500 Hz to the entire spectrum from large gusts (Karaconstantis et al. 2020). For example, in Lough Na Fooey (Ireland), wind speed and direction were connected to broadband sound levels, with wind speed more important at deeper depths while both wind speed and direction were important for shallow environments (Bolgan et al. 2016b). Wind was also connected to the significant difference observed between seasons in a lake in Minnesota; lakes are ice covered in the winter, and wind no longer impacts the soundscape (Putland and Mensinger 2019a). Other studies in marine systems have documented wind increasing ambient sound levels. An increase in wind speed from 2.5 to 17.5 m/s can increase ambient sound by 17 dB at depths of 258 m (Ødegaard et al. 2019), and shallower depths are more impacted in lower frequencies (<400 Hz). Noise that is generated by wind is predictable in marine environments (Cauchy et al. 2018), and likely the same is true for freshwater systems.

Unfortunately, little attention has been paid to other types of sounds that contribute to the geophony but may play important roles in stream ecology (Fig. 1). Noise created from ice in freshwater habitats has only been minimally accounted for in the literature. Peak frequency for ice-cracking noise was between 400 and 600 Hz and increased hourly SPL_{rms} by around 6 dB (Martin and Cott 2016) in a lake in northern Canada and in an Arctic lake ice cracking produced SPL_{rms} values >130 dB re 1 μPa (0–22 kHz: Mann et al. 2009). While not describing ice noise, another study documented a drop in SPL values in the winter months due to ice covering lakes (Putland and Mensinger 2019a). Each micro-habitat within streams and rivers (still pools, rushing water, rapids, small and large waterfalls) likely have unique acoustic signatures just from the geophony. For example, areas with faster moving water will have movement of sediment (rocks, pebbles) that creates sounds, with the fast-moving current moving larger sediment and resulting in increased geophony sounds. Also, areas surrounded by forests will have lots of woody debris that will make noise in the current from water splashing and the logs creaking. Riffles and small waterfalls created by rocks and woody debris create turbulent noise from bubbles and falling water (Fig. 1). Areas with submerged and emergent vegetation create unique sound signatures from their movements brushing against each other and effects on water flow. In addition to unique ambient sound characteristics due to the geophony, habitat related differences in the biota likely produce different biophonic signatures contributing to habitat-specific holo-soundscape signatures.

4 Biophony

Biological sounds add to the soundscape as well and lead to variation among locations depending on species composition (Fig. 1). Sounds produced in different freshwater habitats vary by location and time of day (Desjonquéres et al. 2015, 2018; Karaconstantis et al. 2020; Rountree et al. 2020). Desjonquéres et al. (2015) documented that the sounds produced in ponds varied each day and different sounds were produced in different ponds. A similar trend was observed on a floodplain where the acoustic community at each site was highly variable and site specific, with sites only having 15% of the same sounds produced (Desjonquères et al. 2018). The acoustic differences were correlated with differences in the macroinvertebrate communities sampled at each site (Desjonquères et al. 2018). Likewise, spatial and temporal variation in river sounds was linked to diel patterns in fish and insect activity, with fish most active during the day and insects starting to call at dusk and increasing in activity until midnight in the Einasleigh River, Australia (Karaconstantis et al. 2020). However, the opposite was observed in a survey of multiple freshwater habitats in North America, where insect sounds (see an example in Fig. 3a)

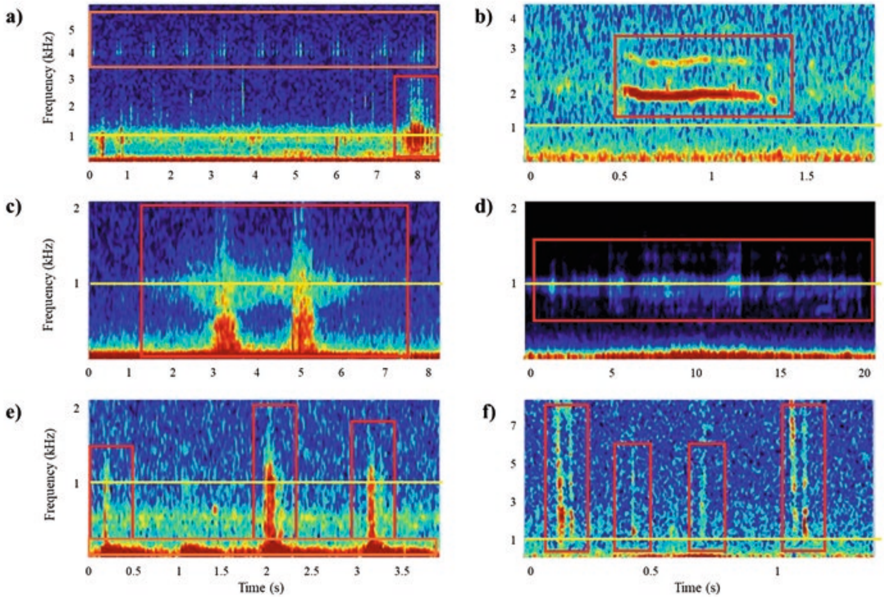

Fig. 3 Examples of biological and anthropogenic sounds recorded under water in freshwater habitats. (**a**) Catfish (red box) and insect sounds (orange box), (**b**) herring gull sound, (**c**) car crossing a bridge, (**d**) lawn mower, (**e**) human walking on shore with low frequency footfalls (orange box) and higher frequency noise when stepping on gravel (red boxes), (**f**) fishing fly-line hitting water. Yellow line denotes the upper limit of known hearing in salmonids

composed the majority of biological sounds produced during the day while fish sounds were the most dominant at night (Rountree et al. 2020). Air movement sounds (examples in Fig. 4) produced by various fish species dominated sounds produced at night and were most prevalent in deeper pond, lake, and river habitats; however, insect sounds dominated in shallower, fast-moving habitats (brook/creek: Rountree et al. 2020). In the Hudson River, a similar trend was observed, with biological sound produced mainly by fish increasing at dusk (Anderson et al. 2008). Biological sounds can have a significant impact on the soundscape, sometimes increasing the sound pressure level by over 10 dB when calls are present (Martin and Cott 2016).

Underwater soundscapes are not only influenced by sounds produced under water; aerial and terrestrial sounds can also be detected. Shallow systems, like smaller rivers and streams, are strongly influenced by aerial and terrestrial sounds because some sound energy penetrates to shallow depths or is transmitted through the sediment. Sounds made by terrestrial predators (bears, otters, humans, eagles, etc.: Fig. 1) can also sometimes be transmitted into the underwater soundscape and thus contribute to the holo-soundscape. For example, the sounds of a human walking along the shore can be detected under water (Fig. 3e). Additionally, Rountree et al. (2020) reported that bird sounds occurred in 5–15% of recordings depending on habitat type, with one example being herring gull (*Larus argentatus*) calls (Fig. 3b). Sounds of fish splashing or jumping, ducks landing and taking off, and sounds made by aquatic and terrestrial mammals can all contribute to the soundscape (Fig. 1) but are poorly studied.

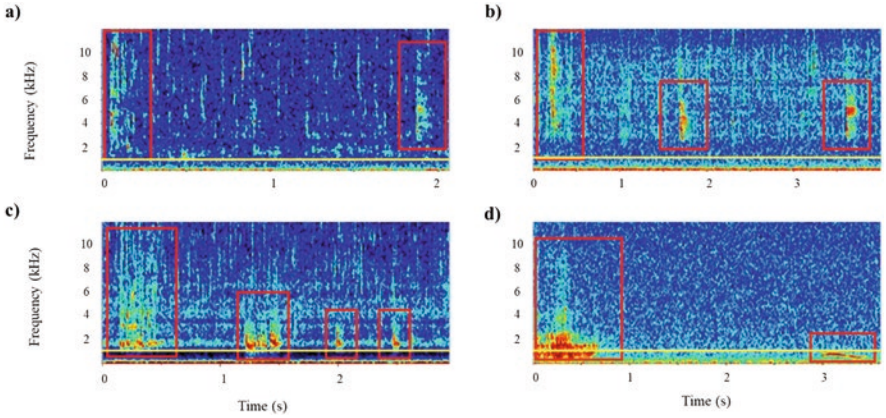

Fig. 4 Comparison of air movement related sounds produced by four species of salmonids. (**a**) Brook trout: quiet surface event followed by snitch sound, (**b**) Brown trout: quiet surface event followed by two vFRTs, (**c**) Rainbow trout: loud splash followed by a gurgle sound and two snitches, (**d**) Atlantic salmon: loud jump followed by a moan. Yellow line denotes upper limit of known hearing in salmonids

5 Anthropophony

Human generated noise has been documented as an important component of the soundscape in marine environments but has only recently been examined in freshwater habitats (Table 1). In various freshwater habitats, anthropogenic noise was the dominant noise source based on relative time (92% day, 88% night) but with different composition depending on time of day (Rountree et al. 2020). During the day, boating activities comprise the highest proportion of anthropogenic noise detected (Rountree et al. 2020) and can influence the SPL in freshwater habitats. In small lakes, boats have shown an increased power spectra density across all frequencies (100–12,000 Hz) by greater than 10 dB re 1 μPa (Putland and Mensinger 2019a). Similarly, outboard motors from boats increased noise levels in a lake by 10–40 dB re 1 μPa (0.005–20 kHz) and a powerboat race created significantly different noise levels compared to ambient conditions (Amoser et al. 2004). Large rivers can also be heavily impacted by boating, with recreational boats increasing the broadband SPL (200–5000 Hz) by a maximum of 35 dB and commercial vessels with a maximum of 40 dB during a single transit by a hydrophone (Putland and Mensinger 2019b). Additionally, boat wakes can increase ambient sound levels at 8 kHz in lakes as they break at the shoreline, and at 5–6 kHz for trailing waves (Stober 1969).

Aerial anthropogenic noise is also a problem for fish in freshwater habitats (Kuehne et al. 2013; Holt and Johnston 2015; Erbe et al. 2018) and contribute to the sound composition during both day and night (Rountree et al. 2020). Traffic noise can be detected underwater (Fig. 1, and an example in Fig. 3c) and have been documented to increase low frequencies (<475 Hz) above ambient sound pressure levels (Holt and Johnston 2015), while being the most numerous sound detected during both day and night recordings (Rountree et al. 2020). Additionally, airplanes passing overhead (Fig. 1) can be heard under water (e.g., Rountree et al. 2020), which can be problematic near airports where airplanes are frequently landing and taking off (Erbe et al. 2018). In the Canning River by the Perth Airport (Australia), planes landing were detected for 30–40 s and increased broadband noise below 3 kHz, with the highest increase below 300 Hz (Erbe et al. 2018). Other important types of anthropogenic noise including trains, shoreline construction, and shoreline activities such as lawn mowing (example Fig. 3d) have been documented (Rountree et al. 2020). The sound of humans walking along the shore or in the water (example Fig. 3e) and fishing activity (Fig. 3f) can also be detected (Marley et al. 2016; Rountree et al. 2020). Overall, aerial anthropogenic noise sources show strong correlation with elevated noise levels (0–8 kHz) under water and have been linked to the level of urbanization (Kuehne et al. 2013). As an accumulation of anthropophonic sounds, noise levels have been shown to have a strong impact on the biophony (Rountree et al. 2020).

While anthropogenic noise is present in most freshwater habitats, composition varies by habitat and river order (Rountree et al. 2020). In lower order locations like brooks and creeks, traffic sounds were detected most often, and this pattern was consistent during both day and night. In comparison, boat noise was not present in brooks or creeks but dominated all other habitats (Rountree et al. 2020). Additionally, regions of rivers that are closer to marine systems (tidal zones) had significantly more boat noise compared to nontidal zones, with boat noise occurring 31% of the time compared to 2% of the time (Rountree et al. 2020). Limited research has occurred on the differences in anthropogenic noise based on river habitat or order, but this is a key component that needs to be evaluated further.

6 Salmonid Hearing Abilities

Fishes hear through three otoliths located in semi-circular canals located inside their inner ear (Popper and Lu 2000). Otoliths are composed of calcium carbonate and move in response to the displacement (particle motion and pressure) created near a sound source, which moves the cilia of sensory hair cells and triggers an electrical impulse to be sent to the brain (Popper and Fay 1973). However, to be able to detect higher frequencies (>1000 Hz) or detect sound further from a source, additional specialized structures are required (Popper et al. 2003). These specialized structures increase sensitivity by connecting the swim bladder to the inner ear, which allows for pressure changes to be transferred. The two main ways this is achieved are through Weberian ossicles (Diogo 2009) or anterior extensions of the swim bladder (Fletcher and Crawford 2001). Additionally, fish are also able to detect low frequency sounds (<400 Hz) through the lateral line (Higgs and Radford 2013).

Hearing abilities in fishes are typically broken down into two categories, hearing generalists and hearing specialists (which have specialized structures to increase hearing range). Salmonids are hearing generalists with no specialized structures. The hearing ability of most salmonids has not been evaluated, but from the few that have (4 out of 223 species), we can estimate that the hearing abilities are similar across the family. Atlantic salmon (*Salmo salar*) had their hearing evaluated for both particle motion and sound pressure and were found to have a hearing range of 100–580 Hz, with highest sensitivity to 160 Hz (Hawkins and Johnstone 1978). Hawkins and Johnstone (1978) also found that Atlantic salmon are more sensitive to particle motion compared to sound pressure. When the speaker was moved outside of the exposure tank (low particle motion), the hearing abilities documented were dramatically different from the hearing abilities when the speaker was within the tank (high particle motion), suggesting that particle motion may be the dominant sound component in salmonid hearing. However, Atlantic salmon could still detect the sounds produced though the sound pressure component but required a higher decibel level to invoke a response. Similarly, broad whitefish (*Coregonus nasus*) had both components tested for their hearing abilities and had peak sensitivity at 200 Hz (106 dB) and were least sensitive at 800 Hz (133 dB), but sensitivity started to increase again at 1600 Hz (123 dB), the highest frequency evaluated (Mann et al. 2007). However, broad whitefish are again more sensitive to particle motion, even though pressure and particle motion could not be separated (Mann et al. 2007).

Other studies of salmonid hearing are primarily based on sound pressure rather than particle motion. Chinook salmon (*Oncorhynchus tshawytscha*) exhibit maximum sensitivity between 100 and 300 Hz at under 110 dB re 1 μPa and are able to detect sounds of up to 1000 Hz at a higher decibel level (130–150 dB re 1 μPa); however, hearing was not evaluated above 1000 Hz (Oxman et al. 2007). Similarly, European whitefish (*Coregonus lavaretus*) demonstrated peak sensitivity at 300 Hz with a maximum frequency of 800 Hz, while sensitivity above 800 Hz could not be identified (Amoser et al. 2004). Likely salmonids can only effectively detect lower frequencies (<300 Hz), but are sensitive to both the sound pressure level and the particle motion components of a sound source, with the latter being more important.

7 Salmonid Sound Production

Sound production has been documented in 15 species of salmonids (Table 2): European whitefish *Coregonus lavaretus* (Dubois and Dziedzic 1989), cutthroat trout *Oncorhynchus clarkii* (Stober 1969), pink salmon *O. gorbuscha* (Kuznetsov 2009), chum salmon *O. keta* (Kuznetsov 2009), coho salmon *O. kisutch* (Neproshin 1972), rainbow trout *O. mykiss* (Rountree et al. 2018), sockeye salmon *O. nerka* (Neproshin 1972), Chinook salmon (Neproshin 1972), Atlantic salmon (Rountree et al. 2018), brown trout *Salmo trutta* (Rountree et al. 2018), Arctic char *Salvelinus alpinus alpinus* (Bolgan et al. 2016a), brook trout *Salvelinus fontinalis* (Rountree et al. 2018), Dolly Varden *Salvelinus malma* (Neproshin 1972), lake trout *Salvelinus namaycush* (Johnson et al. 2018), and grayling *Thymallus thymallus* (Persat and Zakharia 1992). However, much of this is based on limited observations or is anecdotal information (Table 2). Air movement sounds (sometimes referred to as pneumatic sounds) are the most common sound type in salmonids (Rountree et al. 2018). Air movement sounds are highly variable, often species-specific, and are produced by internal air movement between the gas bladder and other anatomical structures, and sometimes by external air release through the anus, pneumatic duct, operculum, or mouth. Other common sound types include percussion (jaw snapping), sounds produced by splashing or jumping during air gulping (Stober 1969; Bolgan et al. 2016a; Rountree et al. 2018) which may also be species-specific (Rountree et al. 2018), and sounds produced during redd cutting (Stober 1969; Satou et al. 1994; Moore and Waring 1999).

Air movement sounds are produced in association with air gulping and occur in a sequence including the rise, air gulp, dive, and resumption of activity (Stober 1969; Rountree et al. 2018). Most sounds are produced after the fish has returned to pre-rise activity. Examples of air movement sounds produced by four species of salmonids include fast repetitive ticks (FRTs), very fast repetitive ticks (vFRTs), chirps, moans, whistles, and gurgles (Fig. 4). Some air movement sounds are from gas release out of the anus or gills but there are also sounds produced through internal movement into the pneumatic duct (Neproshin and Kulikova 1975), but all air movement sounds are associated with air gulping at the surface (see Fig. 12 in

Table 2 Description of known sounds produced by salmonid species

Common name	Species	Sound description	References
Cutthroat trout	*Oncorhynchus clarkii*	Air movement (squeaks, squawks), thumps, redd	Stober (1969)
Pink salmon	*Oncorhynchus gorbuscha*	Air movement and thumps	Kuznetsov (2009)
Chum salmon	*Oncorhynchus keta*	Air movement, thumps	Kuznetsov (2009)
Coho salmon	*Oncorhynchus kisutch*	Air movement (whistle), thumps, knocks	Neproshin (1972)
Rainbow trout	*Oncorhynchus mykiss*	Air movement (gurgle, vFRTs, FRTs)	Neproshin (1972); Phillips (1989); Rountree et al. (2018)
Sockeye salmon	*Oncorhynchus nerka*	Air movement (FRTs), vibrational cues	Neproshin (1972); Satou et al. (1987, 1991, 1994)
Chinook salmon	*Oncorhynchus tshawytscha*	Air movement (whistle, FRTs), knocks	Neproshin (1972)
Atlantic salmon	*Salmo salar*	Air movement (gurgle, snort, moan)	Rountree et al. (2018)
Brown trout	*Salmo trutta*	Air movement (FRTs, vFRTs)	Rountree et al. (2018)
Salmon	*Salmo, Salvelinus, and Oncorhynchus*	Air movement, hydrodynamic, drumming	Neproshin and Kulikova (1975)
Arctic char	*Salvelinus alpinus*	Air movement (FRTs, gulps, and snaps), clicks	Bolgan et al. (2016a)
Brook trout	*Salvelinus fontinalis*	Air movement (FRTs, vFRTs, snitch)	Rountree et al. (2018)
European whitefish	*Coregonus lavaretus*	Stridulation sounds	Dubois and Dziedzic (1989)
Dolly Varden	*Salvelinus malma*	Air movement, knocks	Neproshin (1972)
Lake trout	*Salvelinus namaycush*	Thumps, growls, snaps	Johnson et al. (2018)
Grayling	*Thymallus thymallus*	Excavating gravel sounds	Persat and Zakharia (1992)

Rountree et al. 2018). Chum and pink salmon produce air movement sounds and the resonance frequency of their sounds are associated with their swim bladder morphology (Kuznetsov 2009). Arctic char have been documented to produce air gulps (pulse trains of broadband sounds) and snaps (short high frequency sounds) associated with air gasping behaviors and bubble release, but also have sounds (FRTs) that could not be linked with air exchange behaviors (Bolgan et al. 2016a). Fast repetitive ticks (FRTs) produced by Arctic char were infrequent and consisted of repetitive, short (98–107 ms) ticks (690–760 Hz: Bolgan et al. 2016a). Other salmonids have been documented to produce a similar sound to FRTs, but have ticks occurring much closer together, known as a very fast repetitive tick (vFRT).

Multivariate analysis of air movement sounds among four species of salmonids demonstrated they are species-specific although there was strong overlap in characteristics of individual sound parameters (e.g., peak frequency and duration; Rountree et al. 2018). Each species produced multiple sound types. Brook (Fig. 4a), brown (Fig. 4b), and rainbow trout all produced vFRT sounds, while Atlantic salmon did not (Rountree et al. 2018). In addition, brook trout produce a snitch sound at a peak frequency of 4617 Hz, while brown trout produce a chirp like sound that had a peak frequency of 4760 Hz, and rainbow trout produce a “gurgle” sound that had a peak frequency of 2409 Hz (Fig. 4c). Atlantic salmon also produced a lower frequency gurgle sound (748 Hz) and a unique “moan” sound (943 Hz, Fig. 4d). Air gulping behavior and associated sounds also differed among the four species. Brook and brown trout tended to make little splash or noise when gulping air (Fig. 4a, b), while rainbow trout and Atlantic salmon tended to make loud splash or jumping sounds (Fig. 4c, d). Additionally, brown trout also occasionally produce bubble sounds at a lower peak frequency of 1031 Hz (Rountree et al. 2018).

Other potential air movement sounds have been documented in coho and Chinook salmon that sound like a whistle (up to 6000 Hz), while low frequency knocks (100–500 Hz) were observed in Dolly Varden, sockeye, coho, and Chinook salmon, but only sockeye salmon produced high frequency (100–1600 Hz) knocks (Neproshin 1972). However, peak frequency or behaviors associated with these sounds were not reported. Air movement sounds have also been documented to show a diel pattern in a variety of species with differences in the pattern depending on the species. Pink and chum salmon sound production increases at dawn and dusk (Kuznetsov 2009), but lake trout increase only at night (Johnson et al. 2018). Similarly, brown trout also demonstrated a diel pattern with peak sound production at dusk (Rountree et al. 2018).

Other common sounds include substrate thrashing (e.g., redd building: Stober 1969; Moore and Waring 1999; Satou et al. 1987, 1991, 1994), jaw snapping (Neproshin and Kulikova 1975; Bolgan et al. 2016a), and hydrodynamic sounds (Neproshin and Kulikova 1975). Sounds produced through redd building (example Fig. 5) are also thought to serve a behavioral purpose by potentially priming the

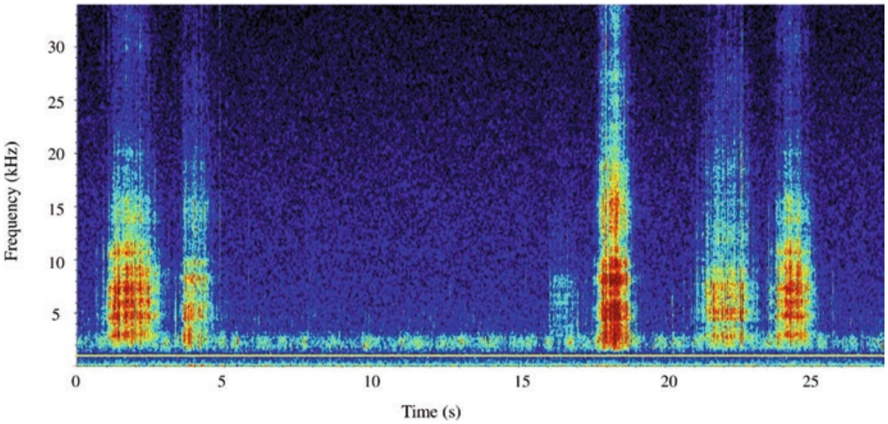

Fig. 5 Sounds produced by Atlantic salmon redd cutting in relation to their known hearing range (yellow line)

females for gamete release (Moore and Waring 1999) and could be vital for reproduction in salmonids. Cutthroat trout have been documented to produce sounds associated with behaviors like digging redds (Fig. 1) at frequencies between 700 and 2000 Hz (Stober 1969). Likewise, Arctic char produce sounds associated with gravel movement during courtship, with interactions like chasing and biting linked with sediment sounds (Bolgan et al. 2016a). Spawning grounds for grayling were also acoustically sampled, and spawning activity (gravel excavation) was detected at up to five meters away with a frequency range of up to 40 kHz (Persat and Zakharia 1992). Additionally, some other types of sounds have been documented to be associated with spawning. Lake trout produce “growls” (20–100 Hz) while spawning which do not occur at other times (Johnson et al. 2018).

Some species of salmon have been documented producing clicking or scraping sounds that are likely attributed to jaw movements (Neproshin and Kulikova 1975). Scraping sounds could be linked with movement of the tongue rubbing against the teeth, while clicking noises produced by snapping the jaw shut can be detected at 85–165 dB, with the upper end occurring infrequently (Neproshin and Kulikova 1975). Similarly, Johnson et al. (2018) found snaps (170 Hz) were produced with jaw movements and/or nudging in lake trout, and Bolgan et al. (2016a) documented clicks associated with mouth closing behaviors in Arctic char. European whitefish have been documented to produce stridulation noises (100–300 Hz) produced during contact between males and females during courtship (Dubois and Dziedzic 1989). Cutthroat trout produce thump sounds (150 Hz) associated with tail-flip behaviors (Stober 1969). Lastly, splashing and jumping sounds made by salmonids when gulping air prior to production of air movement sounds were found to be species-specific and ranged from barely detectable sounds in brook trout, loud splashes in rainbow trout, to noisy jumping in Atlantic salmon (Fig. 4: Rountree et al. 2018).

Due to their hearing abilities, salmonids might not be able to detect some of their own sounds, which makes researchers suspect the sounds may be incidental. However, some air movement sounds have sufficient energy in the low frequencies to be potentially detectable by salmonids (Fig. 4, Rountree et al. 2018). In addition, if the sounds are detectable with hydrophones, they may serve as markers for species identification in passive acoustics monitoring regardless of why or how they are produced (Rountree et al. 2018). Such sounds can also contribute to the holo-soundscape with the potential to be recognized by other species and predators. Studies of Atlantic (*Clupea harengus*) and Pacific herring (*Clupea pallasii*) suggest that air movement sounds may be socially mediated and function in schooling and/or predator avoidance behavior (Wilson et al. 2004). Similar behaviors have been hypothesized for salmonids (Neproshin and Kulikova 1975; Rountree et al. 2018). Even though few salmonids have been evaluated for sound production, it can be assumed that since they are all physostomous (connection between swim bladder and external environment) there is a potential for many other species to exhibit air movement sounds.

Sounds produced by other salmonids might not be the only acoustic signals to which salmonids may be paying attention, sounds produced by prey and predators might also be important. In various species of fish, sounds produced by prey have invoked a behavioral response in the predator. Holt and Johnston (2011) found cyprinid fishes are attracted to a speaker (UW-30, Lubell Labs) playing rock shuffling sounds over white noise. The response declined with repeated playback indicating the fish were maybe expecting a prey item near the sound, and when they did not find one, they stopped moving towards the sound (Holt and Johnston 2011). This study demonstrated that cyprinids are able to forage using acoustic signals from their prey, and that in low visibility areas they might rely on acoustic signals even more. Another study on piranhas (*Serrasalmus* spp.) documented a similar trend; piranhas were observed to attack prey that were moving and splashing at the surface more often than silent prey (Markl 1972). For salmonids, one main prey source in streams are insects, however, sounds produced by aquatic insects are well above the known hearing range (Fig. 3a), so it is not likely that salmonids can use these sounds to locate invertebrate prey. Similarly, it is not known if salmonids can detect sounds produced by insect movement and other activities.

Multiple species of salmonids have been documented to alter their behavior (e.g., startle response, dive deeper) when exposed to visual predators, aerial (Stober 1969; Gotceitas and Godin 1991; Miyamoto 2016) or under water (Gregory 1993), as well as when chemical cues of predation are present (Miyamoto 2016), so it is likely that hearing sounds from predators or conspecifics could elicit an antipredator response. Sounds produced by predators walking along shore (Fig. 3e) are within the known hearing range for salmonids and could serve as another cue that predators are present (Fig. 1). In cutthroat trout, tail-flips produce thump sounds (150 Hz) that were only observed when aerial predators were present and could be part of an antipredator response (Stober 1969). Stober (1969) also suggested only one individual made the thump noise but others responded suggesting they could be used sound as a warning for the entire school. Additionally, differences in surface behaviors associated with air movement sounds (splashing at surface vs being quiet) could be related to predator avoidance in areas with heavy terrestrial predators, where silently gulping air at the surface would be an advantage (Fig. 1).

Sounds produced by predators could also be important to salmonids (Figs. 1 and 3). Some are above the known hearing range of salmonids, like herring gull sounds (Fig. 3b) and other bird species (peak frequency: 2800 Hz Rountree et al. 2020), but there is more overlap with sounds produced by other fish species (average peak frequency: 700 Hz Rountree et al. 2020) and the peak hearing range in salmonids. For example, catfish sounds are well within the hearing range of salmonids (Fig. 3a). While it is unclear if salmonids can hear many of these sounds, future research should examine how these sounds might be important for salmonids and their antipredator and foraging behaviors in streams, based on indirect as well as direct effects.

Another interesting theory that has not been fully evaluated is the impact of different river soundscapes on navigation and homing in salmonids. This idea was first proposed by Stober (1969) but has taken a back seat to other signals important for homing (e.g., chemicals, magnetic). Salmon can potentially use these differences in SPL and frequency composition to identify locations for building redds or site-specific breeding, resting, and foraging locations (Kacem et al. 2020). Additionally, river order could be important and changes in the holo-soundscape could aid in deciding how far to move upriver before selecting a breeding location. Previous literature has also suggested that redd building sounds could be important for reproduction (Moore and Waring 1999); however, redd building sounds are generally above the known hearing range of salmonids (Fig. 5). The impact the acoustic environment plays in salmonid homing and reproduction remains unknown, but future research should evaluate this topic to fully understand its importance.

Ambient and biological sounds may not be the only sound sources influencing salmon behavior in freshwater systems. When the noise spectra from a powerboat race was compared to audiograms from fish species, significant overlap between peak sensitivity and highest noise levels was observed, and it was demonstrated that boat noise should be detectable by fish species in close range regardless of hearing ability (Amoser et al. 2004). Vessels that pass nesting sites for another hearing generalist (oyster toadfish, *Opsanus tau*) were detectable at a peak SPL of between 117 and 123 dB re 1 μPa when the vessel SPL was corrected for their hearing abilities (Sprague et al. 2016). Additionally, boat activities have been known to alter behavior (Jacobsen et al. 2014) and induce a stress response in fish of varying hearing abilities (Wysocki et al. 2006). European perch (*Perca fluviatilis*), which has a similar hearing range as salmonids (100–1000 Hz), demonstrated increased swimming speed when boat noise was present but did not change their spatial distribution in a lake (Jacobsen et al. 2014). Similarly, European perch displayed increased cortisol when exposed to playback of ship noise. The increase in cortisol was also observed in other freshwater species with elevated hearing abilities, demonstrating that the stress response observed was consistent regardless of the species hearing abilities (Wysocki et al. 2006). However, boat noise differs greatly depending on the boat type and activity (Rountree et al. 2020). While a running boat creates noise largely above the hearing range of salmonids (mean peak frequency 875 Hz, max peak frequency 4266 Hz), noise from a boat at idle strongly overlaps salmonid hearing (mean peak frequency 435 Hz, max peak frequency 1406 Hz; Rountree et al. 2020). Moreover, while running boat noise tends to be transitory (short duration), idling boat noise is more chronic (long duration; Rountree et al. 2020). To our knowledge, there has been no research on the impacts of boat noise on salmonids. In contrast, pile driving impacts have been observed in a marine system (Feist et al. 1992); juvenile pink and chum salmon demonstrated movement away from pile driving activities when sounds were 25 dB above ambient making them audible to the salmon (Feist et al. 1992). Similarly, pile driving can cause physiological effects. Chinook salmon exposed to pile driving sounds in a lab had significant tissue damage and sometimes experienced organ hemorrhage, depending on the sound exposure level (Halvorsen et al. 2012). Understanding the impacts of boat noise on salmonids is crucial and should be evaluated in future studies in both marine and freshwater systems.

Anthropogenic noise could also influence sound production in salmonids. Holt and Johnston (2015) found that traffic sounds resulted in significant masking of blacktail shiner (*Cyprinella venusta*) knocks (160–630 Hz) and growls (100–315 Hz) up to 12 km from a bridge at 108 Hz. Similarly, traffic noises from a bridge (Fig. 3c) show that most of the acoustical energy recorded is within the known hearing range for salmonids (peak frequency: 225 Hz: Rountree et al. 2020) and could have a similar masking effect in streams (Figs. 1 and 3c). Noise created by boats has also been documented to mask sound production in a variety of species in marine systems (Vasconcelos et al. 2007; Codarin et al. 2009; Luczkovich et al. 2016). Additionally, humans walking (Fig. 3e) along the shore strongly overlaps with documented peak frequency for salmonid hearing (100–300 Hz), and other human activities like mowing lawns (Fig. 3d) and fishing lines hitting the water (Fig. 3f) overlap with the upper range of their hearing abilities. These anthropogenic activities could be influencing behaviors and survival in streams, but no research has yet been conducted on this topic.

Increased noise levels can also change antipredator behaviors in fish and could vary depending on hearing abilities. Three-spined stickleback (*Gasterosteus aculeatus*) responded faster to a visual predator when noise levels were elevated, but European minnow (*Phoxinus phoxinus*) did not change their behavior with additional noise (Voellmy et al. 2014). Predator–prey interactions may also play a role in what type of response a species might exhibit to a noise disturbance. European roach (*Rutilus rutilus*), perch and pike (*Esox lucius*) were all exposed to boat noise, and each displayed varying reactions that could be linked to their antipredator behaviors (Jacobsen et al. 2014). European perch have also been shown to respond to predators by fleeing to the bottom and using structure as a refuge (Christensen and Persson 1993). When exposed to boat noise perch increased their swimming speed for a short period (1 h), which could indicate they were relocating to a deep refuge and then remaining still (Jacobsen et al. 2014). Increases in anthropogenic activities could also affect predator–prey interactions by allowing one species to exploit increased noise levels to forage more without increasing the risk of being preyed upon themselves, creating an acoustic refuge (Roca et al. 2020). Additionally, anthropogenic sounds have been documented to mask communication in other freshwater fishes (Holt and Johnston 2015), so there could be a similar impact on salmonids if their sounds are used to communicate. Some species (cutthroat trout: Stober 1969) have already been documented to produce sounds in association with predator avoidance and these sounds could serve as a warning to others, if these signals are masked it could result in increased predation risk and decreased survival.

Passive acoustic monitoring could provide another option for understanding population dynamics of salmonid species. Since most salmonids have consistent spawning grounds, an underwater hydrophone could be placed in close proximity and be used to monitor numbers and species that are returning to various habitats. Passive acoustics has been proposed as an option for monitoring invasive species in freshwater habitats (Rountree and Juanes 2017) and could be an option for many salmonid species of concern. However, before this can be possible more research into acoustics in freshwater environments and the sounds produced by salmonid species needs to be documented.

8 Synthesis: The Holo-Soundscape

The time salmonids spend in freshwater habitats could be influenced by the sounds produced in both underwater and terrestrial environments (holo-soundscape) which generate a unique environment (Fig. 1). However, little research has been dedicated to understanding the holo-soundscape and its role in ecological habitat identification and niche development for salmonids and freshwater fish in general. Within a river there are multiple microhabitats that likely have different acoustic signatures (Kacem et al. 2020), and stream order (Strahler 1957; Shreve 1966) is an important factor in creating these different signatures (Fig. 6). Habitat characteristics, environmental conditions, and predation risks form gradients along the stream order (e.g., Platts 1979; Barila et al. 1981; Rountree and Able 2007), as do holo-soundscape characteristics, yet the role of interactions between these phenomena on the ecology of stream-dwelling salmonids is not known. As an organism moves down a river from lower order streams (headwaters) to higher orders, elevation and substrate size decrease along with increased depth and volume of water moving through a section, and these factors are important for creating the acoustic environments in the different order streams (Fig. 6). For example, propagation of sound depends on the

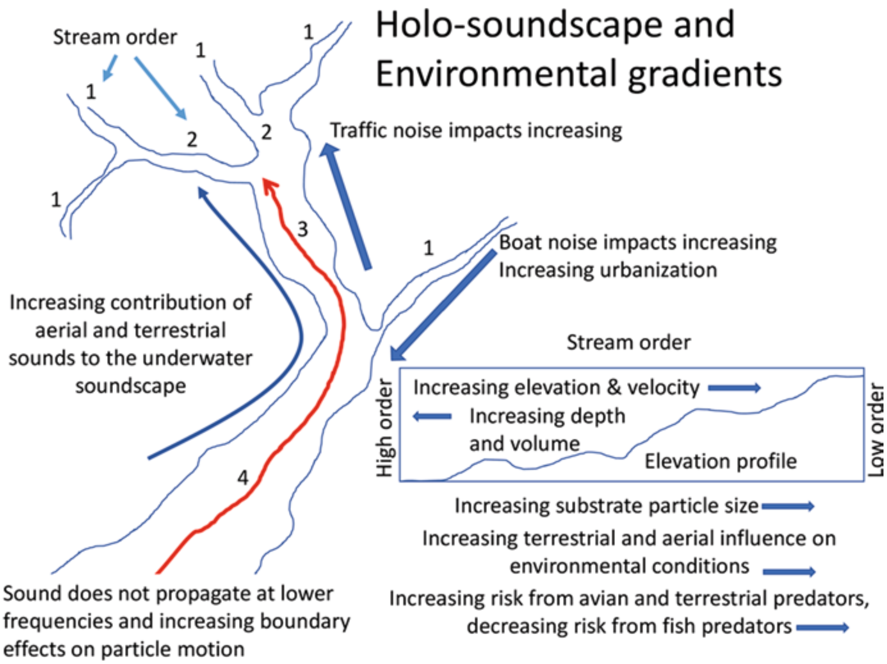

Fig. 6 Schematic of impact of stream order on the holo-soundscape and salmonid habitat and niche characteristics (numbers indicate stream order). Gradients are formed along the stream order in habitat characteristics, anthropogenic noise impacts, and sources of predation risk. Sound pressure and particle motion properties are also strongly influenced by these gradients

wavelength of the sound and depth of the water and therefore is affected by stream order. The cut-off depth is the depth at which sound of a given frequency (hence wavelength) will not transmit beyond the source (Au and Hastings 2008). Particle motion, on the other hand, could be increased in shallow habitats due to sound pressure being converted to particle motion at the surface since air is more elastic compared to the water (Popper and Hawkins 2018). Sediment type also affects the cut-off depth and particle motion. In marine systems, at a depth of 10 m, the lowest frequency that can be detected under ideal conditions ranges from 30 to 200 Hz from a rocky to soft bottom type, while at 1 m the range is 300–2000 Hz (Au and Hastings 2008). Additionally, particle motion is affected by different sediments in the river. Hard bottom substrate can reduce particle motion by stopping movement between individual particles (Hawkins et al. 2020) compared to soft bottoms where particle motion is expanded into sediment (Popper and Hawkins 2018). So, habitat characteristics could be very important for salmonids as their hearing is most sensitive at frequencies between 100 and 300 Hz, with particle motion the more crucial component, and suggests a mismatch between hearing sensitivity and habitat selection in salmonids since many stream-dwelling salmonids live in habitats too shallow for sounds of those frequencies to propagate.

These different habitat signatures could be aiding in homing, like Stober (1969) first suggested, as salmon need to be able to locate optimal locations within a river to mate, rest, or forage. Often these are different habitats with different holo-soundscape characteristics (e.g., noisy fast-flow spawning sites vs quiet deep-pool resting and foraging sites). One study examined a link between salmonid densities and acoustic properties (Kacem et al. 2020). They found more brook trout present when SPL (>100 dB) values were elevated within their best hearing range (100–300 Hz) in pools and riffles but not glide or cascade habitats in a stream in Canada (Kacem et al. 2020). The presence of more salmon in regions of elevated SPL could be indicating salmonids are choosing to be in a certain location based on the acoustic signature which could be serving as a proxy for habitat quality (e.g., increased food availability due to higher flows) as suggested by Kacem et al. 2020. However, if locations in the river are too noisy, foraging and finding a mate could be significantly hindered, so salmon could be using sound to find the best acoustical environment. Salmon could also be using these acoustic cues to detect areas of a lower predation risk in streams (Fig. 1). In shallower environments, there is a higher risk of predation from avian and terrestrial predators, but if salmon can locate a deeper pool within a section of a river, that habitat would provide a safe haven as well as shelter from the current (Fig. 6).

The holo-soundscape is not only important for salmonids but also could be important for predators of salmonids (Fig. 1). One specific sound that could be important is redd building sounds (Fig. 1). To build an effective redd, salmon need to move gravel around which produces sound (Fig. 5) well above their hearing range but is within the range for many predators. These sounds could cue in underwater predators to locations with salmon and eggs, which if disturbed would decrease fecundity. Furthermore, terrestrial predators like bears (Fig. 1) and otters could likewise use the sounds of salmon jumping and splashing (Fig. 4c, d) to know where good places are to hunt. As it remains unclear if predators are homing in on specific habitats based on the soundscape signature to locate prey, future research should examine this knowledge gap.

Depending on the importance of the acoustic environment to salmonids, anthropogenic activities could alter survival in streams. Anthropogenic activities have been documented to substantially impact various fish species, and salmon are running out of locations that are free of human disturbances. Depending on the location within a river there are different anthropogenic noise sources, with lower order streams and rivers having more traffic and other aerial sounds (e.g., airplanes: Fig. 1). Higher order rivers and tidal regions have more boating activities and their associated sounds as well as increased urbanization since many large cities are located on the water (Fig. 6). Since salmonids are already limited to few suitable acoustic environments in streams, noise could have significant impacts on their abilities to locate these "quieter" regions of the river that are optimal for reproduction and survival. The high impact of anthropogenic activities in streams and rivers suggests that reducing human impacts in these locations is a crucial conservation concern to protect salmonid populations.

In our review, we focused on the adult life stage for salmonids due to a lack of research on other ontogenetic stages. To our knowledge, no research has been published on hearing or sound production in juvenile salmonids. In other marine species, hearing ability has been documented in larval fish as small as 9 mm, and sensitivity to sounds increases with size (Wright et al. 2011). Sound has also been shown to be important for settlement in coral reef fishes (Radford et al. 2011), such that larval and juvenile stages of salmon could also be using sound cues from an early age, but more research into this topic is required.

9 Next Steps

Passive acoustic monitoring could provide another option for understanding population dynamics of salmonid species. Since most salmonids have consistent spawning grounds, an underwater hydrophone could be placed in close proximity and be used to monitor species returning to various habitats. However, before this is possible more research into acoustics in freshwater environments and the sounds produced by each species needs to be documented. Luckily, these are relatively simple to accomplish. Underwater hydrophones are inexpensive and can record autonomously in a diverse range of habitats to understand the acoustics (Rountree et al. 2006; Chapuis et al. 2021; Lamont et al. 2022). Hydrophones are also compact and easy to transport to remote locations away from the influences of human activities. Each hydrophone can be deployed for short or long periods to help understand the influences of geophony, biophony, and anthropophony. However, we contend that the holo-soundscape is of critical importance and research should attempt to record both underwater and aerial sounds whenever possible. Building a library of sounds produced by salmonids can also be incorporated into already existing research projects without having to add much more work. Many salmonids have at least some locations where they are reared in hatcheries or housed in local aquariums. These locations provide an opportunity to record species and see the different sounds produced, but also come with some issues. Hatcheries and other facilities that house fish in captivity are noisy, with an assortment of pumps and other equipment, so recording fish vocalizations in these environments can be quite challenging and results in low signal-to-noise ratios (Riera et al. 2018). Additionally, rearing under these high noise environments can significantly affect the hearing abilities of these fish (Caiger et al. 2012), which could impact sound production and survival. If recordings are made in these environments, care should be taken to reduce background noise as much as possible. Sound production can also be recorded in the river if the underwater hydrophone is paired with video or real-time observations on species near the hydrophone. The use of acoustic arrays in conjunction with video or human observations has recently been used to validate sound production in marine fishes (Mouy et al. 2018) and hold promise in freshwater systems.

In addition to collecting more data on the ambient sound pressure levels in freshwater habitats, the inclusion of the particle motion component of sound is required to truly understand the holo-soundscape in freshwater systems. Many fishes and invertebrates are more sensitive to particle motion compared to sound pressure, but to date no information has been collected on particle motion when describing freshwater soundscapes likely due to the complexity of shallow habitats. The best way to measure particle motion is through an accelerometer, but accelerometers are not only sensitive to particles moving from sounds but all movement, so they do not work in a flow field that has continuously moving water (Popper and Hawkins 2018). Accelerometers are also not as readily available in comparison to hydrophones used to collect sound pressure levels, making it challenging for researchers to collect necessary data. Currently, technology does not exist to effectively measure particle motion as it relates to the soundscape (Miksis-Olds et al. 2018) outside the lab or other controlled settings, but hopefully as new technology is developed, particle motion will become a standard component of holo-soundscape analysis.

Understanding the holo-soundscape represents a new frontier for researching the ecology of salmonids in freshwater habitats but will require substantial research to fully evaluate. Classification of holo-soundscape characteristics along stream order and unique freshwater habitats will allow for detailed descriptions of the acoustic environments of these habitats. Then these different acoustic environments can be used to understand if salmonids and their predators are using acoustic signatures for niche specialization. Research should also continue to evaluate sound production and hearing in salmonids, as linking the acoustic environment they are choosing to their hearing abilities and sounds they produce will aid in understanding salmonids behavior in freshwater habitats. Salmonids are important species around the world, and understanding the acoustic environments they are exposed to and their contribution to the holo-soundscape will add to our understanding of their behavior, ecology, and conservation in freshwater habitats.

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The Freshwater Pearl Mussel: A Costly Stowaway or an Important Habitat Engineer?

J. Höjesjö, N. Wengström, and M. Österling

Abstract The freshwater pearl mussel (FPM) (*Margaritifera margaritifera*) has a fascinating lifecycle that includes a parasitic life stage on host fish; the brown trout (*Salmo trutta*) and/or the Atlantic salmon (*Salmo salar*) (Geist et al., Aq Conser: Mar Freshw Ecosystems. 16:251–266, 2006) in order to successfully reproduce. Freshwater mussels, including the FPM, have large effects on ecosystem functions in streams and rivers. The FPM is thus an important habitat engineer and keystone species where healthy populations indicate a well-functioning ecosystem (Geist, Hydrobiol 644: 69–88, 2010). In this chapter, our aim is to provide a general overview of the present knowledge regarding the FPM and (1) the interaction with its host fish (2) its habitat requirements, (3) the threats to the mussel, and (4) successful restoration measures.

Keywords Freshwater pearl mussel · Brown trout · Host fish · Parasite-host interaction · Restoration

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1 Distribution and Life History of the Freshwater Pearl Mussel

The freshwater pearl mussel (FPM) (*Margaritifera margaritifera*) has a Holarctic distribution covering parts of North America on the Atlantic coast from Newfoundland, Canada, down to Delaware and Pennsylvania, USA (Walker 1910). In Europe, the species occur in Austria, Belgium, Czechia, Denmark, Estonia, Finland, France, Germany, Ireland, Latvia, Lithuania, Luxembourg, Norway, Poland, Portugal, Slovakia, Spain, Sweden, and the United Kingdom (Geist 2010; Moorkens et al. 2017). The species is decreasing throughout its distribution range (Quinlan et al. 2015), and it is believed to have gone extinct in Belarus, Denmark, Lithuania, and Poland (Lopes-Lima et al. 2017). It is on the IUCN red list of threatened species in the category endangered (EN) (Moorkens et al. 2017).

The FPM is a relatively large mussel that can grow to 160 mm with a thick and heavy shell that enables it to inhabit streams with high discharge (Dunca et al. 2011). They have separate sexes but can also switch to hermaphroditism (Bauer 1987; Grande et al. 2001). The age of maturity is reached at an age of 10–15 years, and they reproduce until they die (Bauer 1987). The size of the glochidia (larval stage of the FPM) is between 45 and 70 μm and a female can produce 2–4 million larvae every reproductive season. The FPM are known for their long longevity (>80 years) and the oldest documented individual was dated 280 years (Dunca et al. 2011; Lopes-Lima et al. 2017).

Life history traits like body size, glochidia size, lifespan, brooding period, gill brooding area, host infection strategy, and host use, are only known for some of the >800 species of freshwater mussels (Graf and Cummings 2007). The life cycle and life history of the freshwater pearl mussel are relatively well-known and described in Fig. 1.

The reproductive period of the FPM takes place annually between June and October. Females carry the glochidia in special pouches on the gills (both gill pairs) called marsupia. The FPM are short-term breeders meaning that the females only carry the glochidia for 5–7 weeks before releasing them into the water. The release of glochidia into the water column is a synchronized temperature-driven event; Hastie and Young (2003) reported that within Scottish rivers generally at least 300-degree days were needed before glochidia release. The glochidia then must attach to a host fish, exclusively brown trout (*Salmo trutta*) and/or Atlantic salmon (*Salmo salar*) in Europe and possibly brook charr (*Salvelinus fontinalis*) (Ziuganov et al. 1994) in North America for approximately 10–12 months from late summer until early summer the next year (Taeubert et al. 2013; Taeubert and Geist 2017). During the parasitic stage where they develop and metamorphose from a glochidia into a juvenile mussel, the larvae grow 6–10 times in size before they excyst off the fish (Hastie and Young 2003; Young and Williams 1984). Temperature is also important here and Marwaha et al. (2017) predicted that the number of excysted individuals increased from 5.63 at 11 °C to 35.65 at 18 °C. After excystment, the juvenile mussels bury themselves in the substrate for approximately 5 years (Young and

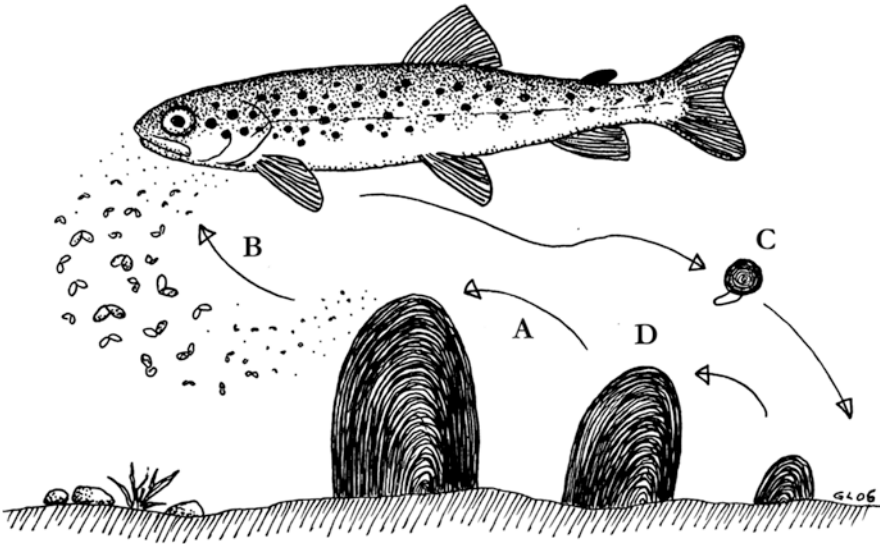

Fig. 1 The life cycle of the freshwater pearl mussel. (**a**) Males release sperm that females inhale, and the eggs get fertilized. (**b**) Females release mature glochidia that get encysted on the gills of the host fish. (**c**) Juvenile mussels excyst from the host. (**d**) Juvenile mussels grow into adult sexually mature mussels. Drawing by Gunnar Lagerkvist

Williams 1984; Bauer 1992, 1998) before they emerge to the gravel bed and mature at a size of 65 mm (Hastie et al. (2000).

2 Preferences

2.1 Habitat Preference

The FPM lives in running water, in northern Europe generally at sites located downstream of lakes, which secure the mussels from droughts (Degerman and Tamario 2017). The FPM are distributed both in small shallow streams at a depth of a few cm but also in large rivers with a depth over 10 meters. Streams with healthy FPM populations, which include mussels of all age classes, are clear with low turbidity and well-oxygenated hyporheic zones, and poor in phosphorous and nitrogen (Boon et al. 2019, Geist and Auerswald 2007; Österling et al. 2008 and 2010). Mussels can be found in a variety of substrate types, from fine substrates such as silt and sand to mixtures of sand and larger substrates such as pebbles, cobbles, and boulders. The general within-stream distribution of the FPM is patchy. Interactions with the host fish (Haag and Warren 1998; Hastie and Young 2001; Hastie and Young 2003) and with physical factors such as substrate structure and water flow (Hastie et al. 2000; Brown and Banks 2001; Box et al. 2002), sedimentation (Box and Mossa 1999), and water chemistry (Bauer 1988; Buddensiek et al. 1993) are believed to contribute to the distribution of the FPM. Some studies suggest a positive relationship between host and mussel densities (Arvidsson et al. 2012) but only until a certain threshold is reached (Geist et al. 2006). This suggests that beyond this threshold, further eutrophication may only be beneficial for the host, but not for the juvenile pearl mussels when buried within the stream bed facing an increasing risk of embeddedness and depletion of oxygen (Geist and Auerswald 2007). Hastie et al. (2000) computed habitat suitability curves and reported that water depths of 0.3–0.4 m and current velocities of 0.25–0.75 m/s at intermediate water levels were optimal but also that riverbed characteristics were the most important physical parameter for predicting FPM distribution. Hence, stability of sediments during flooding and low shear stress are important factors that are probably associated with FPM assemblages (Lehner et al. 2006; Strayer 1999; Hastie et al. 2001). In streams where high turbidity and sedimentation load results in the large cover of fine material, unfavorable conditions such as low oxygen levels and a high degree of embeddedness can be detrimental for juvenile mussels, hence why only adult mussels exist here (Geist and Auerswald 2007; Österling et al. 2008).

2.2 Host Preference

The glochidia infection is associated with a cost for the host fish, and the glochidia larvae can thus act as a selective force resulting in a potential mussel–salmonid host coevolution (Douda et al. 2017; Chowdhury et al. 2021). Whether the FPM can live as a parasite on one or both fish species when they co-occur is complex and not fully understood. According to Salonen et al. (2017), the occurrence of glochidia infestation is highest on Atlantic salmon in large main channels where salmon is the dominant host. In small tributaries without presence of Atlantic salmon, brown trout is a functional host. Thus, FPM glochidia can be adapted to either Atlantic salmon *or* brown trout in some rivers, even though both species live in sympatry (Larsen et al. 2000a, 2000b; Larsen 2012; Dunca and Larsen 2012). Salonen et al. (2017) reported that the FPM generally prefers *S. salar* rather than *S. trutta* as a host, even if both can be suitable hosts. Moreover, Geist et al. (2018) detected two main conservation units of pearl mussel in Ireland: one mostly salmon-dependent Western cluster and one trout-dependent central–eastern cluster. Other studies have shown that FPM can also parasitize only *S. trutta* during sympatric conditions with *S. salar* (Hastie and Young 2001, 2003; Österling and Wengström 2015).

The host suitability also differs among host fish strains, and although no clear pattern of local adaptation to the host fish has been shown in some studies (Karlsson et al. 2014; Wacker et al. 2019; Österling and Larsen 2013), Taskinen and Salonen (2022) recently validated the hypothesis that glochidia can show local adaptation by being more successful when attached to local fish strains which are of crucial importance for management. Wacker et al. (2019) could also show that when both salmon and trout were exposed to larvae originating from "salmon- and trout-mussel," respectively, salmon-mussel larvae almost never infected brown trout and vice versa suggesting that host specificity can explain variation in natural infection among FPM populations. In addition, Taubert et al found evidence of local co-adaptation between pearl mussel and brown trout with different rates of metamorphosis success on different strains of FPM where the brown trout strain originating from the natural pearl mussel distribution range was identified as the most suitable host. Lastly, in a comparison between tributary-resident and sea-migrating *S. trutta* as hosts for the FPM, the sea migrating strain was the most suitable host (Österling and Söderberg 2015), which adds to the complex interactions between the FPM and its host fish species. Thus, to be able to manage mussel populations, careful selection and management of appropriate host fish strains is mandatory for sustainable conservation and more research on adaptation and suitability between different mussel and host fish strains and species are needed.

3 Threats

Freshwater mussels are among the most threatened aquatic species on the planet (Lydeard et al. 2004; Goodrich et al. 2022). Factors affecting the species and leading to impoverishment of populations are habitat destruction and degradation, loss of host fish, commercial exploitation, and biological invasions (Bogan 2008). Since the 1960s enigmatic mass mortality events have occurred in North America and recently these mass mortality events have also happened in parts of Europe (Haag et al. 2019; Wengström et al. 2019). Erosion and high loads of fine sediments have been correlated with low or no juvenile recruitment success (Österling et al. 2010; Geist and Auerswald 2007; Denic and Geist 2015; Hoess and Geist 2020). Climate change with drought, floods, and increased sediment depositions have also been shown to affect mussel populations with catastrophic results (Hastie et al. 2001; Sousa et al. 2018; Baldan et al. 2020, 2021). A lack of host fish is another major threat to the freshwater pearl mussel and there is a low probability of finding juvenile mussels in streams with densities of host fish below 5 fish/100 m^2 (Degerman et al. 2013). In contrast, a high density of host fish and a large fish species richness can be indicative of non-functional streams for the FPM (Geist et al. 2006). Mass mortality events in FPM populations have often been described as enigmatic without any obvious causes but with a new focus on mussel health assessments knowledge about pathogens associated with mass mortality events has been gained (Waller and Cope 2019; Haag 2019; Richard et al. 2020, 2021).

Free-living FPM glochidia have a high natural mortality since they lack swimming ability, drift with the current, and have to find a host fish. If they attach to a non-functional host fish, they will be fended off from the fish and die (Jansen et al. 2001). During the drift, there are also several predators such as fish, copepods, and flatworms that consume glochidia (Jansen et al. 2001). Glochidia and juveniles are vulnerable to acidification and their survival decreases with decreasing pH, below pH 4.5 they will not survive for more than 24 hours (Taskinen et al. 2011).

Wengström and Höjesjö (2020) found no juvenile recruitment in streams with pH < 6.0.

Habitat alterations like channelizing and man-made barriers are common threats to the FPM in headwaters and tributaries. For example, small hydropower plants have been shown to have a negative impact on freshwater pearl mussels (Sousa et al. 2020). Hydropower plants have a negative effect through modified downstream flows, channel morphology, water temperature, sediment transport and deposition, and as fish barriers (Couto and Olden 2018).

Historically, adult freshwater pearl mussels have been caught and killed to collect pearls, and this eradicated populations from many streams (Bauer 1988; Makhrov et al. 2014). In Sweden in the late seventeenth century more than two million freshwater pearl mussels were killed every year to support the king's demand for pearls (Awebro 1995).

In Europe, invasive species like the signal crayfish (*Pacifastacus leniusculus*) and brook trout (*Salvelinus fontinalis*) have been shown to be a threat to the FPM (Sousa et al. 2019; Salonen et al. 2016). Laboratory experiments suggest that especially younger mussels were more vulnerable to predation by signal crayfish (Sousa et al. 2019). In Europe, brook trout can be infected by FPM glochidia but in most cases the larvae will fall off before metamorphosis is complete (Salonen et al. 2016). Both signal crayfish and brook trout have negative effects on the population size of brown trout which can ultimately reduce the number of suitable hosts for the freshwater pearl mussel (Peay et al. 2009; Lovén Wallerius et al. 2017; Lovén Wallerius et al. 2022).

4 Interaction with Salmonids

The definition of a parasite is usually simplified into “an organism that lives on or in an organism of another species, known as the host, from the body of which it obtains nutrients” or “an organism that lives and feeds on or in an organism of a different species and causes harm to its host” (Crofton 1971). Generally, parasites affect their hosts negatively, which in many cases may lead to reduced fitness of the host (Lehmann 1993; Moore 2002). It has been argued that the relationship between the FPM and their host fishes can be considered as either parasitic, mutualistic, or commensal (Ziuganov et al. 1994; Skinner et al. 2003; Geist 2010; Barnhart et al. 2008). The presence of adult mussels might for example reduce the content of particulate matter and nutrients in the water column by their filtering activity and by the creation of microhabitats for juvenile fishes (Ziuganov et al. 1994; Skinner et al. 2003). However, the FPM clearly fulfills the criteria for a parasitic relationship where the glochidia larvae thrive as encysted parasites on the gills of juvenile salmonids for almost a year from which they obtain energy that allows them to grow and metamorphose into a juvenile free-living mussel. The infection load on the gills of salmonids in nature can be very high, reaching up to the 1000s of glochidia at least during the initial phase of infection (Österling et al. 2008; Hastie and Young

2003). However, the glochidia load generally decreases within a couple of months and there are also reports on differences in infection rate both between year classes where young of the year salmonids generally have a higher degree of infection and between strains of fish suggesting an active and evolving immune response in the fish (Hastie and Young 2001). A lower infection load has also been found after a second infection in the laboratory. Clearly, brown trout can eliminate FPM glochidia by both tissue and humoral reaction so that repeated exposures strengthen the immunologic responses indicating an acquired immunity against FPM (e.g., Bauer 1987; Zotin and Zyuganon 1994; Hastie and Young 2001; Bauer and Vogel 1987; Chowdhury et al. 2018; Marwaha et al. 2019). Hence, for efficient conservation of the FPM it is important to emphasize the availability of young of the year fish that are immunologically more naive than older cohorts.

Clearly, the number of glochidia established on the fish and the growth of glochidia might be expected to adversely impact host fish directly or indirectly, but the understanding of how glochidia of FPM affect brown trout both in terms of direct costs (e.g., growth and survival) and indirectly (altered behavior and competitive interactions) is very limited. Below we aim to summarize the current knowledge on the effects that the glochidia infection might have on juvenile salmonid fish host.

4.1 Direct Effects

Mortality of infected salmonids in nature and/ or at low infestation rates are not well examined but Taeubert and Geist (2013) detected host fish mortality at an infection rate of ~350 glochidia/g fish weight and a mortality of 60% at the highest infection rates (~900 glochidia/g fish weight). For the surviving host fishes, a high infection load decreased swimming performance, with infection intensity of ~900 glochidia/g fish reducing the critical swimming speed of the host by ~20% compared to infection with 6 glochidia/g fish weight. In contrast, Chowdhury et al. (2021) used a much lower degree of infestation (~140 glochidia/g fish) and could not see any difference in mortality in brown trout due to infection of FPM. Recent studies have also shown that glochidia encystment increases respiration where trout encysted with glochidia took almost 6 h. longer to reach basal levels compared with trout without glochidia (Thomas et al. 2013) and standard metabolic rate (SMR) in infected host fish were on average 26% higher than non-infected fish (Filipsson et al. 2017). There are to our knowledge only two studies that have examined the effects on growth rate in host fish being infected with glochidia from FPM; Treasurer et al. (2006) could not detect any effect of FPM infection on the growth of Atlantic salmon at an early stage but a negative effect after 15 weeks which again disappeared by the end of the first year. In contrast, Chowdhury et al. (2021) reported how non-infected trout gained 11% more weight than infected trout no matter season and/ or density of food. In agreement Terui et al. 2017, using a similar host–parasite system (larval parasites of the freshwater mussel *Margaritifera laevis* and its salmonid fish host *Oncorhynchus masou masou*) showed reduced growth in smaller host fish. These studies suggest that at least for highly infected fish the FPM will act as a parasite with a resulting increased mortality, impaired swimming capability, reduced metabolic rate, and most likely a reduced growth rate.

4.2 Indirect Effects

Foraging behavior and competitive interactions in salmonids have been thoroughly investigated (Lima and Dill 1990, Keenleyside and Yamamoto 1962,) and there is a number of papers describing how drift-feeding salmonids forage at a focal point where their net energy intake (NEI) will be maximized (Bachman 1984; Fausch 1984; Hughes et al. 2003; Piccolo et al. 2014) and how the relative dominance rank will influence foraging and habitat utilization where the dominant fish usually is winning the position with the greatest NEI potential (Hughes 1992), thus achieving the greatest potential fitness (Nilsson et al. 2004; Höjesjö et al. 2002, 2004). This theoretical framework has been used to predict behavior (Hughes 1992), distribution (Hughes and Dill 1990), growth (Hayes et al. 2000), and production (Hayes et al. 2007) of stream salmonids (Piccolo et al. 2014). However, parasitic infections of the FPM will most likely affect both inter- and intraspecific interactions among the juvenile salmonids such as dominance behavior and competition for food and territories (Barber et al. 2000; Österling et al. 2014). Österling et al. (2014), for example found that uninfected juvenile brown trout had higher drift foraging rates than infected fish and were able to capture more prey items further away from a focal point. Furthermore, Filipsson et al. 2016 studied the pairwise interaction between an infected and a non-infected brown trout and showed how high encystment rates decreased prey items caught, activity, and the number of initiated interactions relative the non-infected individual. Low glochidia loads, however, did not seem to affect feeding or competitive interactions suggesting a threshold in glochidia load before any negative effect on host fish performance can be detected. There is to our knowledge, only one study on the performance of infected host fish in the field; Wengström (2022) showed that infected fish covered a larger range in the field compared with non-infected and utilized habitats with different bottom substrates and velocities in the autumn. Similarly, using chub (*Squalius cephalus*) as a model species, Horký et al. (2014), have shown that chub infected by the larval stage of the freshwater bivalve; the duck mussel (*Anodonta anatina*) dispersed less far upstream and maintained position further from the riverbank.

5 The FPM as Habitat Engineers

Freshwater mussels are described as umbrella species and keystone species because of their effect on the ecosystem in streams and rivers (Collier et al. 2016; Geist 2010; Dudgeon et al. 2006; Strayer et al. 2004) and the FPM is the first species for which a standardized monitoring approach has been developed (Boon et al. 2019). Their filter feeding transfers the energy of phytoplankton, bacteria, and organic particles from the free-flowing water to the benthos. The mussels release nutrients such as phosphorous and nitrogen, some of which can be assimilated by algae and macrophytes, thereby positively affecting their growth (Howard and Cuffey 2006; Strayer et al. 1994; Vaughn 2010, 2018; Vaughn and Hakenkamp 2001). Hence, the mussels can strongly affect the number of suspended particles in the open water (Lummer et al. 2016), some of the filtered materials are converted and biodeposited as feces and pseudofeces providing food for the secondary production of benthic fauna (Aldridge et al. 2007; Limm and Power 2011; Vaughn et al. 2008). When insect larvae, which are a dominant part of this increased faunal production, hatch and become flying adults, many of them ultimately end up in the terrestrial ecosystem, providing food for terrestrial predators (Vaughn 2018). However, the effects of mussels on macroinvertebrates may be less strong in agriculturally impacted catchments (Richter et al. 2016). It has also been proposed that the increased abundance of benthic fauna can provide food for fish, thereby increasing fish densities (Ziuganov et al. 1994; DuBose et al. 2020). Mussel beds can constitute a dominant part of the benthic biomass, and the physical structure provides a habitat for other benthic fauna and fish (Spooner et al. 2013). Finally, mussels can stabilize the sediment, and when they move vertically and horizontally in the sediment, they cause bioturbation leading to increased oxygen concentrations in the sediment (Vaughn and Hakenkamp 2001; Gutiérrez et al. 2003; Strayer 2008, Boeker et al. 2016).

6 Reintroducing the FPM, Successful Examples on Habitat Restoration and Artificial Infection

Several actions have been taken to secure the future of the FPM in Austria, Czech Republic, England, Finland, France, Germany, Ireland, Luxembourg, Norway, Scotland, Spain, Sweden, and Wales (Moorkens 2011; Gum et al. 2011; Wengström 2012). There are different methods to apply when trying to revive FPM populations (McMurray and Roe 2017).

Controlled propagation—Includes the collection of gravid females or wild glochidia, inoculation of host fish, recovery and care of juveniles, captive grow-out, and captive breeding, usually within a controlled environment.

Controlled propagation/captive breeding is a method that is widely used in several European countries (Gum et al. 2011). It is often applied in EU-funded LIFE projects and the method is quite costly (Moorkens 2018), but since it is performed in a controlled environment, data can be quantified and the chance of enhancing the results is greater than with other methods. Using this methodology, Hruška (2001) produced several thousands of FPM over a period of 3 years. Here, maintained infected fish were hosted under controlled conditions from which excysted juveniles were collected daily and transferred to boxes in the stream.

Augmentation—The addition of individuals of a species within the geographic boundaries of an existing local population.

Augmentation involves the methods of moving adult/juvenile mussels between sites in the same basin, and the release of infected fish hosts using glochidia and fish hosts from the same basin. These methods are used to support already existing populations with recruitment problems. These actions should only be performed when all reasons for the species decline are understood, and the cause of the problems are managed (McMurray and Roe 2017). In the river Lutter, Germany, the release of artificially infected fish hosts has been a success with a self-sustaining FPM population after 10 years (Altmüller and Dettmer 2006). The river had previous severe problems with high sedimentation loads from ditches but the sedimentation have been reduced over a period of 10 years using sediment traps. Today the population of FPM contains more than 80% juvenile FPM. Another good example of the method comes from the Southwest of Sweden where the Swedish Anglers Association (SAA) has released infected brown trout into a small creek since 2011. This creek had in 2011 no known individuals of FPM. In the same year, the SAA also performed a site-specific restoration at five sites in this creek, adding boulders and gravel to enhance the environment for the brown trout. After 10 years, the first juvenile FPM were found at two of the restored sites.

Reintroduction—The release of a species at a location where it is not currently present and that is outside the geographic boundaries of existing local populations or metapopulations, but where there is evidence for the former presence of the species in historical times.

There are few studies describing different strategies to enhance the chance of a successful reintroduction of FPM (Bolland et al. 2010; Geist 2010; Moorkens 2018), but all of them emphasize the importance of habitat quality regarding the requirements of the FPM, and they do not recommend any actions before the requirements are fulfilled. Unfortunately, there are to our knowledge no scientific papers describing the results from any of the recommended actions where the habitat has been restored prior to the release of juvenile or adult FPM. This is something that needs to be investigated in the future. Such measures are, however, associated with the risk of spreading diseases and parasites, which must be taken into consideration when reintroduction programs are being planned (Brian et al. 2021).

7 The Future

There are numerous studies on the ecology of salmonids and on the ecology of freshwater pearl mussels, but surprisingly few on the interaction between these species and the effects of the infection. In this chapter, we have tried to summarize what we know and highlight the current knowledge gaps. One part that clearly is missing and where more knowledge is needed is the effects on the long-term fitness and life history tactics on fish that have been infected with larvae. Here, more field-based studies are needed to validate the movement and habitat choice of host fish on a finer scale, perhaps by using detailed habitat mapping, pit-tagged fish and a combination of stationary and portable antennae. In such a setup, it would also be possible to investigate to what extent the FPM are spread to different regions using the salmonid host as a vector.

To understand what determines a successful reintroduction it is also important to increase our knowledge on parasite-host coevolution. More infection experiments, using different strains of fish and stages may inform managers if the parasitic stage and combination of host is functioning properly and to what extent it can be improved especially in the long term. Such experiments may have applications in breeding programs for mussels.

It is also of uttermost importance to predict how this system will be affected by climate change, i.e., an increasing temperature. At present, it is clearly the juvenile fish (under yearlings, 0 + fish) with their poorer immune responses that are the better target for the larvae. However, salmonid fry might emerge earlier with a prolonged growth rate as an effect of an increasing temperature. If this imposes a shift in habitat from shallow riffle habitats to deeper habitats earlier in the season (Kaspersson and Höjesjö 2009; Höjesjö et al. 2016) there is a risk of a potential mismatch between the availability of suitable host and glochidia larvae at the given time frame.

Invasive species is also of major concern and we need to learn more. Brook trout has not been reported to act as a functional host of FPM in Europe. Instead, the larvae generally are repelled from the brook trout after a few weeks. This could be problematic in regions of a relatively high density of brook trout where the number of successful infections will be reduced due to the decreased likelihood of finding a suitable host.

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Habitat Selection and Segregation Among Stream Salmonids: The Case of Juvenile Coho Salmon (*Oncorhynchus kisutch*) and Steelhead Trout (*Oncorhynchus mykiss irideus*)

John J. Piccolo, Mason D. Bryant, and Johan Watz

Abstract We use the case study of coho salmon and steelhead trout to discuss the coexistence of two similar stream salmonid species. The question of coexistence between these two species dates back to the early 1960s, making it a good example of the application of ecological theory to explain patterns observed in nature. Explanations for habitat selection and segregation between coho salmon and steelhead trout have included the mechanisms proposed by Nilsson (The biological basis of freshwater fish production. John Wiley and Sons, New York, 1967), interactive segregation and selective segregation. Through examples of laboratory and field studies of coho salmon and steelhead trout in Southeast Alaska, we suggest that habitat selection appears to be largely selective, but interactive segregation may become important during times of resource limitation. Despite a half-century of scientific inquiry into the coho-steelhead coexistence question, there is still much to be learned about habitat selection of these species; given the precarious status of many populations of coho salmon and steelhead trout within their native range, efforts to understand their ecological requirements are warranted.

Keywords Coexistence · Competition · Energetics · Foraging · Sympatry · Water velocity

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1 Introduction

The objective of this chapter is to reflect upon how two similar sympatric salmonid species may manage to coexist in the same streams. We use the case study of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss irideus*) in streams in Southeast Alaska, USA. Juvenile coho and steelhead were among the earliest subjects for studies on how salmonid species coexist—the question was first asked by Gordon Hartman (1965), harking back the N.A. Nilsson's (1967) pioneering studies on niche segregation and competition in salmonids. Hartman (1965) postulated that state- and habitat-dependent differences between coho and steelhead allowed them to partition habitat seasonally in artificial streams in British Columbia; in summer trout were more aggressive in riffles and coho were more aggressive in pools. In winter, when energetic demands were low, defense behavior was reduced. During the past half-century of research on competition and habitat segregation among sympatric salmonids much has been learned (see, e.g., Fausch 1988), but much remains unknown. As salmonid populations continue to decline in many places, understanding the mechanisms that govern coexistence becomes ever more relevant—predicting the effects of invasive salmonids, for example, relies on knowledge of competitive interactions with native species (e.g., Hasegawa and Maekawa 2006).

Coho and steelhead are distributed around the Pacific Rim from Central California to Southeast Alaska and into parts of Asia (Behnke 1992; Groot and Margolis 1991). Coho salmon are semelparous fall spawners, and steelhead trout are iteroparous spring spawners (Behnke 1992; Groot and Margolis 1991). Juveniles of both species rear in freshwater for one or more summers before migrating to ocean environments, and they are often found in sympatry where their distributions overlap (Hartman 1965; Allee 1974; Bugert et al. 1991). Coho salmon fry emerges earlier in the year than steelhead trout, and coho salmon fry is typically larger than steelhead during their first summer in streams (i.e., at age 0+) (Hartman 1965). Steelhead trout grow more quickly than coho salmon, however, and by the end of the first growing season, individuals of both species are often of the same size (Hartman 1965; Fraser 1969). In the southern portions of their respective ranges (e.g., California and Oregon), most coho salmon emigrate as age 1+ smolts, thus avoiding size overlap and potential competition with steelhead trout during their second summer (Hartman 1965; Allee 1974). In these systems steelhead typically smolt the following year as age II+. In Southeast Alaska, both species usually spend an extra summer in streams, and size overlap occurs among age 1+ coho salmon and steelhead trout before the coho salmon emigrate the following year as age 2+ (Lohr and Bryant 1999; Halupka et al. 2000).

Although they often occur within the same stream reach, coho salmon and steelhead trout have been documented to segregate spatially and use different microhabitats, with coho salmon using slower, deeper pools and steelhead trout using faster, shallower riffles (Hartman 1965; Allee 1974; Bisson et al. 1988; Bugert et al. 1991). A similar pattern of pool/riffle segregation has also been reported for other sympatric stream fish, both salmonid (see Hearn 1987), and non-salmonid (Gorman and Karr 1978), and it has been hypothesized that habitat complexity influences species richness of stream fishes (Gorman and Karr 1978; Young 2001).

Explanations for habitat segregation in coho salmon and steelhead trout have included two proposed mechanisms (Nilsson 1967) for species segregation: (1) interactive segregation, whereby one species displaces the other from a preferred habitat (Hartman 1965; Young 2004), and (2) selective segregation, whereby the species select their respective habitats based on differential foraging abilities (Fraser 1969; Allee 1974; Bugert and Bjornn 1991). Hartman (1965) documented the distribution of age 0+ coho salmon and steelhead trout in the Salmon River, British Columbia, and conducted laboratory experiments to identify the mechanism for segregation. He found that in summer, coho salmon were more aggressive in pools, and steelhead trout in riffles, and he proposed that these behavioral differences facilitated segregation. Allee (1974) observed that in natural streams, however, interspecific interactions between coho salmon and steelhead trout were relatively rare, and he concluded that segregation was largely selective and size based. In other laboratory studies, Fraser (1969) and Bugert and Bjornn (1991) have also favored the selective hypothesis, whereas Young (2004) has documented a size-based competitive advantage for coho. Observational intensive field studies of coho salmon and steelhead trout in sympatry are lacking, however, so the relative importance of interactive vs. selective segregation is unknown in natural systems.

2 Water Velocity- and Depth-Specific Foraging Abilities as Mediators of Microhabitat Segregation

Ecological theory suggests that the niches of two sympatric species cannot entirely overlap (Zaret and Rand 1971; Schoener 1974; Abrams 1983), and habitat segregation in sympatric stream salmonids is hypothetically related, in part, to species-specific differences in foraging abilities (Allee 1981; Bisson et al. 1988; Bremset and Berg 1999; Young 2001). Bisson et al. (1988) proposed that the more laterally compressed body and taller median fins of coho salmon allow them to forage better in slower water, whereas the more cylindrical body and shorter median fins of steelhead trout facilitate foraging in faster water. They suggested that coho salmon are better at rapid acceleration and turning, which facilitates foraging on patchy prey in slower water, whereas steelhead trout are better at foraging in faster water because of reduced hydrodynamic drag. Although morphology-based differences in foraging efficiency have been demonstrated to facilitate habitat segregation by pond-dwelling sunfish (Werner and Hall 1979), Piccolo et al. (2008a) demonstrated in a series of stream laboratory experiments that water velocity was not likely the main determinant of habitat segregation between coho salmon and steelhead trout.

Coho salmon have been shown to forage near the surface, and steelhead trout commonly feed near the substrate (Fraser 1969; Allee 1981). Both species have also been shown to segregate along the water depth niche axis with other species of salmonids (Bravender and Shirvell 1990; Dolloff and Reeves 1990) or intraspecifically by size (Nielsen 1992; Harvey and Nakamoto 1997). Water depth is an important niche axis for segregation in other species of stream fish as well, including both salmonid (Gibson and Power 1975; Bagliniere and Arribe-Moutounet 1985; Heggenes et al. 1999), and non-salmonid (Greenberg 1991; Reyjol et al. 2001; Jowett 2002; Hesthagen et al. 2004). Depth is a commonly measured stream habitat feature (Bovee 1978). There has been virtually no research on the underlying reasons why fish select certain depths or why depth-based segregation is common in stream fish. Habitat selection in coho salmon and steelhead, however, is likely not influenced strongly by depth (Piccolo et al. 2007).

Animals are thought to select feeding habitats based in part on the relative costs and benefits of foraging there (MacArthur and Pianka 1966; Stephens and Krebs 1986). For drift-feeding salmonids, the metabolic cost of sit-and-wait foraging by holding position against a current is balanced against the benefit of more prey encounters in faster water (Everest and Chapman 1972; Wankowski 1981). The velocity at which a fish can maximize net energy intake rate is determined by the relative magnitude of costs vs. benefits; it follows that two coevolved sympatric species such as coho salmon and steelhead trout might reduce niche overlap by maximizing net energy intake at different water velocities. Piccolo et al. (2008b) modeled the optimum foraging velocities for coho and steelhead, and found very little difference based on the respective foraging abilities of the two species.

3 Other Explanations for Microhabitat Segregation

Juvenile coho salmon and steelhead trout possess a surprising degree of similarity in foraging capacity (Piccolo et al. 2007, 2008a; Fig. 1), and net energy intake models predict that there is little difference in optimal foraging velocities between the species (Piccolo et al. 2008b), even assuming large increases in prey capture costs for coho salmon (Fig. 2). Thus, habitat segregation between coho salmon and steelhead trout is likely not based on different foraging abilities, at least not under average conditions. Habitat segregation between coho salmon and steelhead trout may instead be largely selective, or based on other condition-specific traits than foraging ability, for example, predator avoidance (Fig. 3).

Differences in size during their first growing season, and differences in growth trajectories during their period of size overlap are two other possible explanations for segregation between coho salmon and steelhead trout juveniles. In theory, for juveniles of similar species such as coho salmon and steelhead trout to coexist, their niches cannot completely overlap (Zaret and Rand 1971; Schoener 1974; Abrams 1983). During their first summer of growth, coho salmon maintain a size advantage, and this alone may be enough to allow them to segregate spatially (Everest and Chapman 1972). Because the species appear to have similar foraging abilities, this segregation may be based more on long-term concerns such as growth trajectories, rather than on short-term energetic concerns.

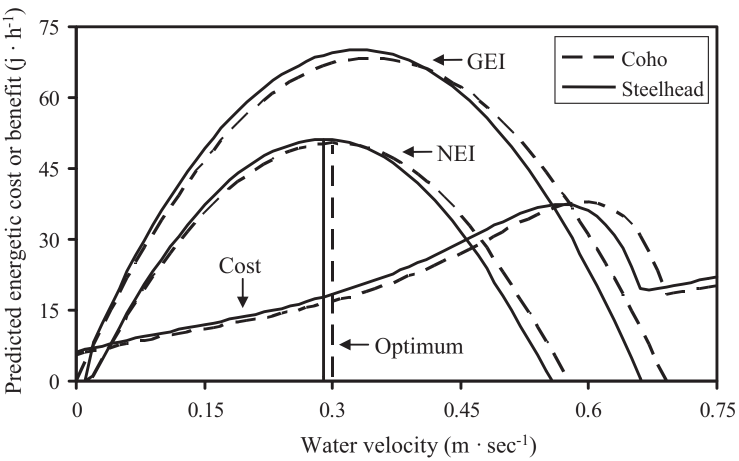

Fig. 1 Estimated gross energy intake (GEI), net energy intake (NEI), and costs vs. water velocity for coho salmon (solid lines) and steelhead trout (dashed lines). Vertical lines indicate optimum foraging velocity for coho salmon (solid) and steelhead trout (dashed). The steep declines in the cost curves at high velocities occur because as capture rates fall to zero, costs are only those of holding station at the focal point

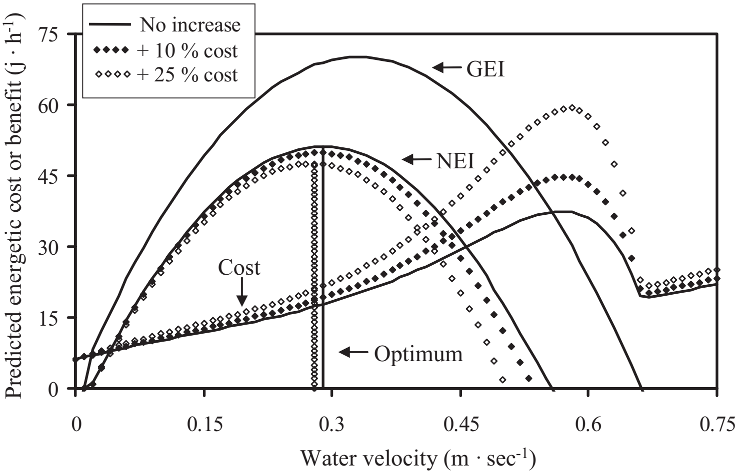

Fig. 2 Estimated gross energy intake (GEI), net energy intake (NEI) and costs vs. water velocity for coho salmon under three different cost scenarios relative to steelhead trout costs: (1) equal to steelhead trout (no increase, solid lines), (2) + 10% cost, solid diamonds, and (3) + 25% cost, open diamonds. Vertical lines indicate optimum foraging velocities (no increase and + 10% costs are superimposed). The steep declines in the cost curves at high velocities occur because as capture rates fall to zero, costs are only those of holding station at the focal point

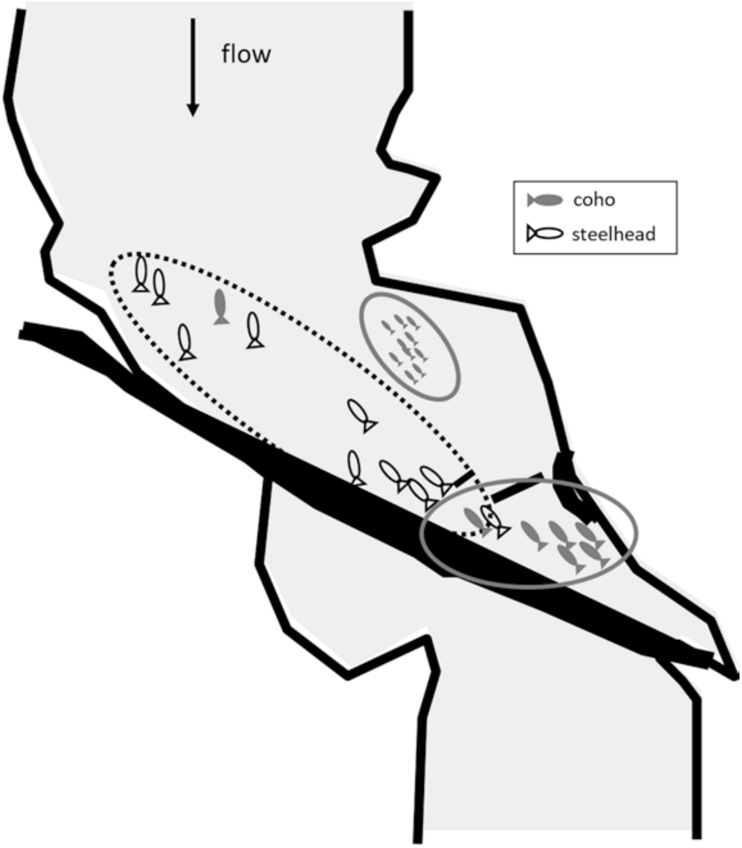

Fig. 3 Surveyed map of actual coho salmon and steelhead trout use positions during a daytime field survey, Peterson Creek, Alaska, July 2002. Note that there are two sizes of coho salmon (0+ and 1+, small and large, respectively) and one size of steelhead trout (1+). During this survey age 1+ steelhead trout were observed foraging during the daytime in the energetically favorable habitat along the edge of the thalweg near the shelter of the large woody debris. During the day, all age 1+ coho salmon except one were found in the pool habitat at the downstream end of the reach and little active foraging was observed. Conversely, age 0+ coho salmon were found on the shallow edge of the profitable thalweg, and these made periodic excursions as a group into the faster water to exploit drifting prey resources, returning to the shallow slow-flowing water presumably to minimize costs

4 Phylogeny and Coevolution

Most researchers believe that the Pacific trout and salmon groups diverged from a common ancestor by around 5–6 million years ago (Walpes et al. 2008). Fossil and molecular evidence points to the Pacific salmon group as having branched off the rainbow trout group (*Oncorhynchus mykiss* spp.), and this must have occurred before the subsequent separation and radiation of the semelparous Pacific salmon

(Behnke 1992; Stearley and Smith 1993). *O. mykiss* and *O. kisutch* or their progenitors, therefore, have potentially a long history of coevolution in fluvial environments. During this period, the species would be expected to evolve differences that allow them to coexist, such as timing of life history events or differences in habitat preferences. Because both coho salmon and steelhead trout usually spend at least a year in sympatry in streams, some of these differences are likely to involve this life phase.

It is tempting to speculate that steelhead, having evolved from the ancestral lineage, colonized fluvial habitats before coho salmon. If so, they might have adapted to the most favorable habitats, such as fast-flowing water where energy, in the form of drifting invertebrates, was most available. When coho salmon subsequently invaded, they were relegated to marginal habitats such as pools and backwaters, and they evolved strategies to cope with these, such as scrambling for prey, use of small streams, and large surplus reproduction; population sizes of coho salmon are often an order of magnitude greater than those of steelhead (Fraser 1969; Allee 1974). The fact that steelhead trout grow faster than coho salmon (Hartman 1965; Fraser 1969) and that coho salmon grow faster in fast water (Puckett and Dill 1985; Nielsen 1992), supports this hypothesis; however, the extensive history of local extinction and recolonization by Pacific salmon due to glaciation precludes such a simple model for habitat differentiation between the two species. Long-term adaptations to fluvial environments remained when the two species recolonized the Pacific Rim, and subsequently local populations later evolved specific strategies based on local environmental demands (e.g., spawning time and age of smolting).

Having evolved in such a highly variable environment, both species, and salmonids in general, appear to have maintained considerable plasticity in their genomes (Hendry and Stearns 2004). This clearly extends to foraging abilities, because both coho salmon and steelhead trout are able to forage in lacustrine as well as fluvial habitats. There may be subtle differences in the species' relative abilities to forage on different prey types or sizes, or under different environmental conditions such as light intensity, that allow them to segregate habitat temporally or spatially or during times of limited resources. The latter has been shown for two sympatric species of charr (Nakano et al. 1999). Further experiments on the effects of prey size and type on coho salmon and steelhead trout foraging are warranted, as are further observations of diurnal and seasonal patterns of habitat use.

Although most of the research on competition and coexistence of stream salmonids has been carried out from the individual fish fitness perspective, alternative interpretations of coevolution and coexistence of similar species have been promoted by the well-known behavioral scientist Kinji Imanishi (De Waal 2003). Imaishi began his studies with niche segregation of mayflies in Japanese torrents (Matsuzawa and McGrew 2008), and he developed views which disagreed with the neo-Darwinian environmental explanations for species divergence and coexistence. He opted instead for a more holistic vision of complex interactions among social, biological, and physical factors among individuals and collectives, to explain species' distributions (Imanishi and Asquith 2002). Imanishi suggested that biotic communities are shaped by cooperation, as well as competition (Darwin (1859) in fact, emphasized the importance of biotic relationships over environmental factors). When Imanishi later shifted focus to primatology, his ideas concerning primate behavior (and neo-Darwinian animal behavior in general) were quite innovative (De Waal 2003). A fresh look at cooperation among hierarchies of stream-dwelling salmonids is warranted, and would likely lead to novel reinterpretations of coexistence of sympatric species.

5 Conclusions

Competition is broadly accepted as a mechanism influencing habitat segregation in stream salmonids (Hearn 1987), but direct experimental evidence is often lacking (Fausch 1998; Watz et al. 2019). During periods of high population densities or low prey availability, coho salmon and steelhead trout may directly compete for resources, but much evidence exists for selective segregation. Hartman's (1965) landmark laboratory study of coho salmon and steelhead trout remains the most detailed behavioral research on interactions among the two species. The conclusion that habitat-specific differences in aggression facilitate segregation is one possible explanation for how the species coexist during periods of resource limitation. The present study demonstrates that the species have remarkably similar physical abilities, so it seems likely that social factors are at least as important as physical environmental factors. Further studies are necessary to identify potential mechanisms responsible for habitat selection and segregation by coho salmon and steelhead trout, and how they vary in space and time. Such experiments will need to add behavioral interactions between the species in addition to physical habitat measurements, particularly in natural streams where research has been limited. More than 55 years after Hartman (1965) first posed the question of how these two similar stream salmonids coexist, ecologists still have much to learn about habitat selection and segregation by juvenile coho salmon and steelhead trout and sympatric salmonids in general.

The extremely high levels of biodiversity of salmonids, fostered by local adaptation resulting from homing instinct, have been reduced much more quickly than science has been able to account for these unique values (Behnke 1992; Piccolo 2011, 2017; Gustafson et al. 2007). Studies of the behavioral ecology of stream salmonids, i.e., their eco-evolutionary relationships, are insightful tools for protecting their biodiversity and abundance (Healey and Prince 1995; Piccolo and Watz 2018). Indeed, understanding species' habitat requirements is essential to their protection and restoration (Healey and Prince 1995). Few temperate watersheds on Earth remain in the relatively pristine condition as those in Southeast Alaska, where these studies were conducted. Millions of hectares of old-growth forest provide a stream habitat of the highest quality (Bryant 2009), yet these forests are still being clear-cut for short-term economic gain. Permanent protection of these areas from anthropogenic extractive activities is critical to the persistence of functioning salmonid communities that may one day serve as models for the ecological restoration of degraded rivers.

Acknowledgments The coho-steelhead case study was conceived by the late Nicholas F. Hughes, whose insights into stream salmonid ecology remain a legacy (see Piccolo et al. 2014). Many people helped with the fieldwork and video data collection for the case studies, special thanks to Robert M. Fagen for behavioral analyses and inspiration. "Play" is also a four-letter word.

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Trout Under Drought: A Long-Term Study of Annual Growth and Condition of Stream-Living Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*)

Ivan Arismendi, Brooke E. Penaluna, and Stanley V. Gregory

Abstract Quantifying the dynamics of natural populations is a central issue in ecology. In the Pacific Northwest of North America, climate extremes are becoming more frequent and severe with projections of increasing winter floods and prolonged droughts during summer. Using a 13-year dataset of adult (Age 1+) Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*), we evaluated the effects of three droughts on annual growth and condition in two stream reaches of Mack Creek, H.J. Andrews Experimental Forest, Oregon, USA. In the three drought years, the onset of seasonal low flow consistently started earlier than reference water years and extended longer, from mid June until the end of September. We found consistent evidence of slower individual growth rates across sizes in drought years relative to reference years, with an apparent greater effect in larger trout. The median annual responses of trout were highly synchronous between stream reaches. There was evidence of slower growth and reduced condition associated with higher trout abundances in the two reaches. In addition, we found that growth rate and condition were associated with timing (annual maxima) and frequency (days >14 °C) of warm events, and habitat size (pool depth). Faster growth rates, higher abundance, and improved condition occurred in the second-growth forest reach compared to the old-growth forest reach. These results illustrated that a combination of density-dependent and density-independent processes can explain observed patterns in growth and condition over time. Each drought year had different climatic characteristics compared to reference years, including differences in the timing of precipitation, timing and magnitude of winter peak flows, and stream temperatures (especially in winter). Collectively, our findings suggest that growth and condition of adult trout

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are influenced by a complex interplay between density-dependence and density-independent factors. Thus, predictions about the effects of droughts on growth and condition in stream salmonids are difficult to generalize across regions. Our study highlights the value of long-term datasets because we can weigh the importance of processes that occur over both the short- and long-term.

Keywords Population regulation · Density-dependent · Density independent · Cascade Range · Environmental extremes · Refuges · Ecohydrology · Climate change

1 Introduction

The main mechanisms regulating growth in stream salmonids have been extensively discussed (reviews by Elliott 1994; Grossman and Simon 2020). Growth is predominantly regulated by density-dependent factors, even at low population densities (Grant and Imre 2005; Lobón-Cerviá 2007; Jenkins et al. 1999; Utz and Hartman 2009; Grossman and Simon 2020) owing to competition for food and space (Chapman 1966). Density-dependence can decrease resource availability per capita resulting in reduced individual fitness (e.g., growth). However, understanding the role of density independence in the regulation of population of stream salmonids is of great relevance given that droughts are expected to increase in frequency, magnitude, and duration (Huntington 2006; Vörösmarty et al. 2010; Trenberth 2011).

Drought affects species and their environments including habitats, water quality (e.g., temperature, fine sediments), food abundance, and predation (Lake 2003; Magoulick and Kobza 2003; Walters 2016; Lennox et al. 2019). All of these are central components influencing the growth regimes of fishes (Armstrong et al. 2021). Drought, defined as "significant low-flow periods" (Humphries and Baldwin 2003; Garner et al. 2015), reduces the size and diversity of riverine habitats and decreases pool connectivity (Lake 2003; Hakala and Hartman 2004; Kaylor et al. 2019; Lennox et al. 2019). Extreme high temperatures and low dissolved oxygen concentrations can also occur more frequently during drought (Lake 2003; Magoulick and Kobza 2003). In addition, site-specific changes in invertebrate densities (Cowx et al. 1984; Lake 2003; Bogan et al. 2015; Piniewski et al. 2017) and drift (Harvey et al. 2006; Wooster et al. 2016; González et al. 2018) have been observed during extreme low-flow periods. Some habitats can operate as temporal drought refuges (Keppel et al. 2012), concentrating resources and likely increasing species interactions (Dunham and Vinyard 1997; Humphries and Baldwin 2003; Lake 2003; Magoulick and Kobza 2003; Lennox et al. 2019). However, drought and its effects are often idiosyncratic owing to differing frequency, magnitude, and duration (Garner et al. 2015), as well as the condition of the ecosystems (Lake 2003; Magoulick and Kobza 2003; Walters 2016; Lennox et al. 2019). The recognition of this idiosyncrasy can help improve the assessment and forecasting of the vulnerability of species and ecosystems (Walters 2016). To date, studies about the responses of stream salmonids to drought are scarce and often short term, <5 years (Walters 2016; Piniewski et al. 2017; Lennox et al. 2019; Kaylor et al. 2019).

Fishes that are adapted to regular seasonal low flow seem to recover rapidly after drought (Humphries and Baldwin 2003; Piniewski et al. 2017; Kaylor et al. 2019). Stream salmonids in areas with connected habitats can move (Milner et al. 1978; Mann et al. 1989; Gowan et al. 1994; Gresswell and Hendricks 2007) and likely seek out temporal drought refuges (Klemetsen et al. 2003; Magoulick and Kobza 2003; Sotiropoulos et al. 2006). Population responses of stream salmonids to drought seem relatively consistent, including a short-term reduction in abundance (Elliott 1984; Hakala and Hartman 2004; Kaylor et al. 2019), biomass (Sotiropoulos et al. 2006; James et al. 2010; Kaylor et al. 2019), or recruitment (Cowx et al. 1984; Titus and Mosegaard 1992; Lobón-Cerviá 2009; Elliott 2015; Blum et al. 2018). Less is known about the growth and condition of stream salmonids in response to drought. Growth seems to be reduced on both seasonal (Harvey et al. 2006; Nuhfer et al. 2017) and annual (Elliott 1984; Weatherley et al. 1991) bases during drought. Interestingly, potential compensatory growth responses (Ali et al. 2003) can emerge after consecutive summer droughts (Elliott 2015). Body condition of stream salmonids appears to be less consistent in whether there is a response to drought. For example, in one case, a significant reduction in condition was observed, suggesting limited food resources (Hakala and Hartman 2004). In other cases, no apparent changes in condition occurred during drought compared to reference years (Weatherley et al. 1991; James et al. 2010; Kaylor et al. 2019). Important questions remain about the relationship of individual growth variability by size or age as well as long-term patterns of growth between droughts and regular seasonal low-flow periods. Understanding these relationships between trout and flow is relevant to establish a baseline for species and ecosystems under climate change.

Here, we use 13 years of data (2008–2019), including three drought years, to characterize patterns of growth in adult Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) near the headwaters of Mack Creek, Oregon. Drought disproportionately affects headwater locations relative to downstream areas (Lake 2003; Nuhfer et al. 2017; Olson and Burton 2019) and large rivers appear to be more drought tolerant than small rivers (Lennox et al. 2019). Consequently, small, headwater streams are the ideal study system to understand the effects of drought. We assess the influence of drought on individual annual growth rate and condition of trout collected at the end of the low-flow period each year. We use concurrent information to describe density-dependent (trout abundance) and density-independent (temperature, flow, and habitat size) factors influencing the observed growth and condition of trout over time.

Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) populations are widely distributed from Alaska to California (Behnke 1992; Penaluna et al. 2016a). They are a tertiary consumer that numerically dominates headwater streams in the Pacific Northwest of North America (Hawkins et al. 1983). For stream-living trout, their lifespan is often 4–5 years, but can be up to 7–8 years. Individuals mature at age 2 and their home range is generally restricted to within 200 m of their birthplace (Trotter 1989).

Seasonal low flow is associated with lower survival of Coastal Cutthroat Trout (Berger and Gresswell 2009; Sheldon and Richardson 2021), and the ability of this species to move in headwaters is more restricted than in downstream areas (Trotter 1989; Gresswell and Hendricks 2007). Most behaviors of Coastal Cutthroat Trout are responses to cope with the perceived threat of predation (Harvey and Nakamoto 2013; Penaluna et al. 2016b; Penaluna et al. 2021), such as grouping, habitat shifting, and lack of feeding (Penaluna et al. 2021), which would be more energetically costly during drought. Energy expenditure is exacerbated as warmer temperatures increase trout metabolism (Dwyer and Kramer 1975) and drought refuges will likely support higher trout densities, leading to more intraspecific competition (Dunham and Vinyard 1997; Penaluna et al. 2021) and slower growth rates. Eventually, these extreme circumstances could lead to mortality or migration to other habitats, resulting in lower densities at the end of the drought. We hypothesize that slower growth and reduced condition of adult trout will occur during drought relative to reference years because of increased energy expenditure and competition for food resources. Collectively, our findings show that long-term studies provide foundational information for answering complex questions that emerge from climate change and support the conservation of stream salmonids.

2 Methods

2.1 Study Sites and Historical Context

The study sites (Fig. 1) were two stream reaches in Mack Creek (old-growth and second-growth; 580 ha), which is part of the H.J. Andrews Experimental Forest in the Willamette National Forest and is protected for research purposes (Swanson et al. 1982). The old-growth stream reach flows through a dense old-growth conifer forest dominated by ancient Douglas-fir (*Pseudotsuga menziesii*) up to 700 years old (Gregory et al. 1991). The second-growth stream reach was clearcut in 1964 (46 years before the start of our study in 2008; Gregory et al. 1991). Physical legacy effects of forest harvest are expected to be minimal after 20 years (Jones and Post 2004; Mellina and Hinch 2009; Moore and Wondzell 2005; Penaluna et al. 2015).

2.2 Animal Collection and Tagging

Each captured trout was measured to fork length (FL; 1.0 mm) and mass (1.0 g). In each stream reach, we sampled trout from the same three contiguous 50-m sections (150 m total) during the first week of September every year. We used a standard

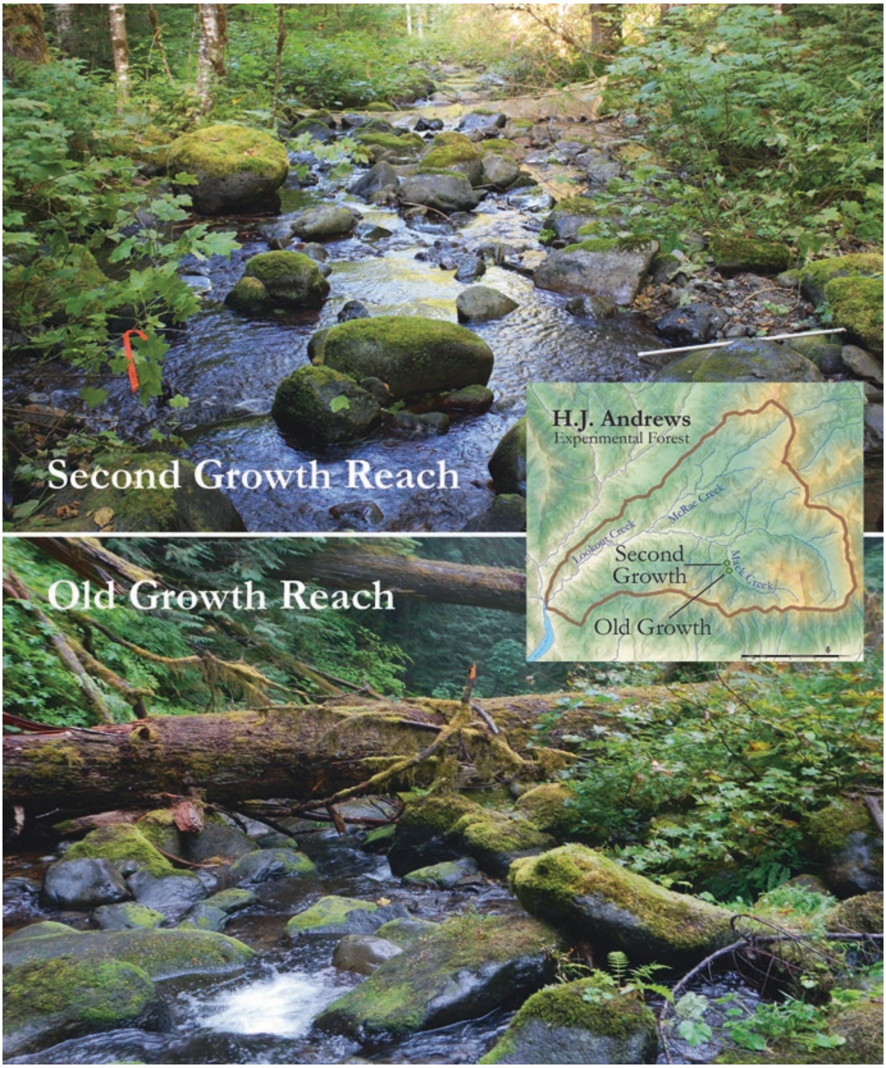

Fig. 1 Our study sites, including second- and old-growth reaches in Mack Creek, H.J. Andrews Experimental Forest, Oregon

electrofishing procedure with block nets for each 50-m section. Abundance was estimated using the two-pass depletion method (Seber and Le Cren 1967); sampling was limited to two passes to minimize negative impacts on fish. Probability of capture exceeded 0.7 in all reaches; two-pass depletion is considered unbiased if probability of capture exceeds 0.2 (Stewart et al. 2019). All trout FL ≥ 60 mm were implanted with a 12-mm full-duplex passive integrated transponder (PIT tag;

Oregon RFID, Portland, Oregon) in the ventral body cavity using a syringe sterilized in 90% ethanol.

In our analysis, we focused on recaptured adult trout (Age 1+; FL > 70 mm). We estimated the relative annual growth rate (RGR, Ricker 1975) from the previous year to the time of capture as $RGR = [(L_i - L_{i-1})/L_{i-1}] \times 100$ where L_i is the length at the time of capture and L_{i-1} is the length from the previous year. In addition, we calculated Fulton's condition factor (Ricker 1975) as a measure of the well-being of fishes (Blackwell et al. 2000; Froese 2006). Fulton's condition factor was calculated as $K = (M_i/L_i^3) \times 100{,}000$ where M_i and L_i were the observed individual mass (g) and length (mm) at the time of recapture.

We tagged 3695 trout in the two reaches (54% at the second-growth reach; 46% at the old-growth reach) between 2008 and 2019. The percent of recaptured trout per year relative to the number of tagged trout in the previous year was comparable between reaches (second-growth: median = 26%, range = 21–32%; old-growth: median = 28%, range = 22–41%). The median number of recaptured trout across years was 41 in the two-stream reaches and fluctuated between 36 (2010) and 55 (2015) in the second-growth reach, and between 31 (2013) and 57 (2012) in the old-growth reach. There was no association in the number of recaptured trout between reaches over time (Pearson Product Moment Correlation $r = 0.48$, $P = 0.213$).

2.3 Environmental Datasets

We extracted daily hydrometeorological information from existing datasets available at the H.J. Andrews Experimental Forest. These data were air temperature and precipitation (Daly et al. 2019), daily streamflow (Johnson et al. 2020), stream temperature (Gregory and Johnson 2019), and geometry of pool habitats (Gregory and Arismendi 2020). Specifically, we selected three sentinel pools representing essential trout habitat during seasonal low flow in each stream reach. We used the same three pools per reach each year. We used maximum pool depth and calculated the pool area (A) as an ellipse (i.e., $A = \pi \times a \times b$, where a is the max length and b is the max width of the respective pool).

We defined drought as a "significant low-flow period" (Humphries and Baldwin 2003) within the water year (WY; from October 1 to September 30). The low-flow period in our study system extended from June 15 to September 30, we classified Water Years 2015, 2018, and 2019 as drought years as they had both lowest and longer low-flow periods in our study. In addition, 2015 and 2018 were classified regionally as drought years (https://www.drought.gov/states/oregon/county/lane).

2.4 Statistical Analyses

Because limits on annual growth rates related to size can be affected by multiple limiting factors (e.g., age, food, temperature, and metabolism), we adopted a quantile regression approach (Cade and Noon 2003) to model growth rate in drought versus reference years. We fitted multiple quantile regression models between individual size and annual growth rate of recaptured trout ($n = 849$) using the "quantreg" package (Koenker et al. 2018) in *R* (Version 3.6.0).

We tested difference in median growth rate of trout among years (2009–2019) using a Kruskal-Wallis ANOVA on ranks. We adopted this test because our somatic data were not normally distributed. In addition, we used Dunn's method as pairwise multiple comparisons to identify years that differed from the others. We conducted a similar procedure to test differences in condition (K), and size of recaptured trout over the years. We tested for potential differences in trout abundance between the two stream reaches during our study period using Student's t-test.

We performed simple Pearson product moment correlation analyses to explore potential coherence between reaches in the association of annual metrics of trout (i.e., growth and condition) and relevant covariates representing density-dependent (adult trout abundance) and density-independent environmental factors (streamflow, stream temperature, and habitat size). We used several metrics of flow and temperature to account for seasonality of the stream environments (magnitude, variability, and timing) and their relevance for stream salmonids in this region (Arismendi et al. 2013; Olden and Poff 2003). For streamflow, we included annual minimum, maximum, as well as mean, and standard deviation during relevant periods (winter: Jan–Feb; spring: Mar–May, summer: Jul–Aug). For stream temperature, we included annual minimum and maximum, mean and standard deviation of relevant period (winter, spring, and summer), timing of the annual max, and frequency of days >14°C and < 16°C (peak growth of *O. clarkii* is 13.6°C and 16°C based on a fitted curve and measured empirically based on Bear et al. 2007, respectively). For habitat size, we included the mean maximum depth and area of sentinel pools. Lastly, we used simple Pearson product moment correlation analyses to test the synchrony of median annual metrics of trout (growth, condition, size, and abundance) between stream reaches. All statistical analyses were performed using the software R ver. 3.6.0.

3 Results

3.1 Growth and Condition of Adult Trout Between Drought and Regular Seasonal Low Flow

Individual annual relative growth rates of adult trout (mm/year) varied across size, ranging from 1.5 to 43% with higher variability in smaller compared to larger trout (Fig. 2). This pattern was consistent between the two stream reaches over the study

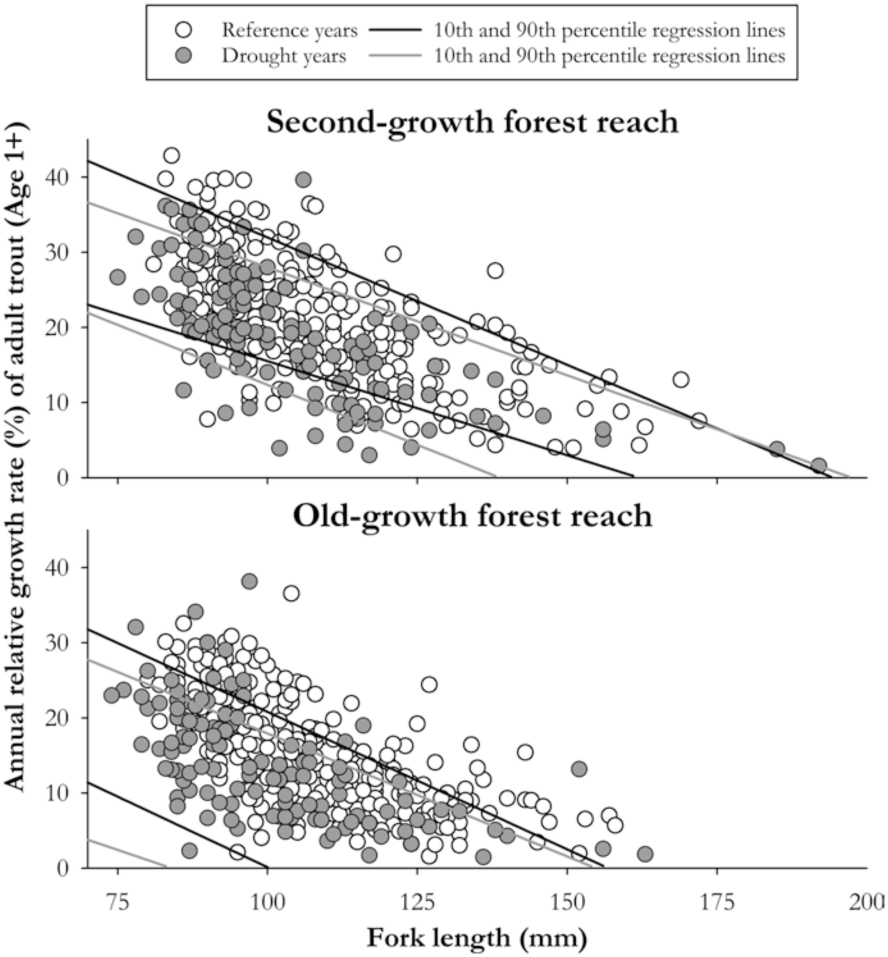

Fig. 2 Annual relative growth rate of individual adult trout (%) by size (mm) during reference (open circles; 2009–2014, and 2016–2017) and drought (gray circles; 2015, 2018–2019) years in the two reaches of Mack Creek in H.J. Andrews Experimental Forest, Oregon. Lines represent 10th and 90th quantile regressions curves for each second-growth (gray lines) and old-growth (black lines) reaches

period. Upper quantile regression lines (90th percentile) representing the maximum scope of growth of adult trout by size illustrated overall slower growth rates during water years of droughts compared to reference water years (hereafter referred to as drought years and reference years). The slope of the regressions across all quantiles (Tau in Fig. 3) appeared to be relatively similar between reaches during reference years. However, negative slopes tended to be more pronounced during drought in larger trout (upper quantiles), illustrating a potentially limited scope of growth for this size group. Consistently, there were statistically significant differences ($P < 0.001$) in the median growth rate of trout between drought and reference years

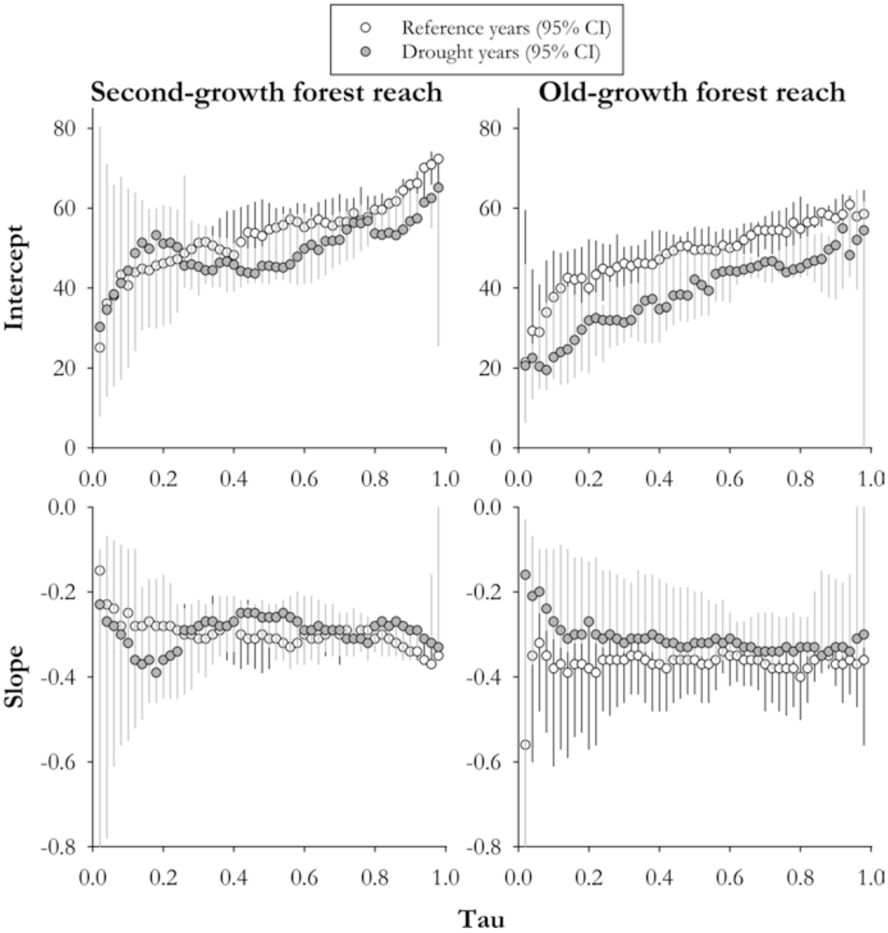

Fig. 3 Slopes and intercepts of multiple quantile (Tau) regression curves representing the scope of growth of adult trout across sizes during reference (2009–2014 and 2016–2017) and drought (2015 and 2018–2019) years in two stream reaches in Mack Creek, Oregon. Larger trout are represented by upper quantiles whereas smaller trout are represented by lower quantiles

in the two reaches (Fig. 4); adult trout had slower growth rates in drought years compared to reference years.

Median annual relative growth rates (%) of adult trout also fluctuated over time (Fig. 4), but they were highly synchronous between reaches ($r = 0.79$; $P = 0.003$). The slowest relative growth rates occurred during two of the three drought years (2015 and 2019), but also during some reference years (2012 in the old-growth

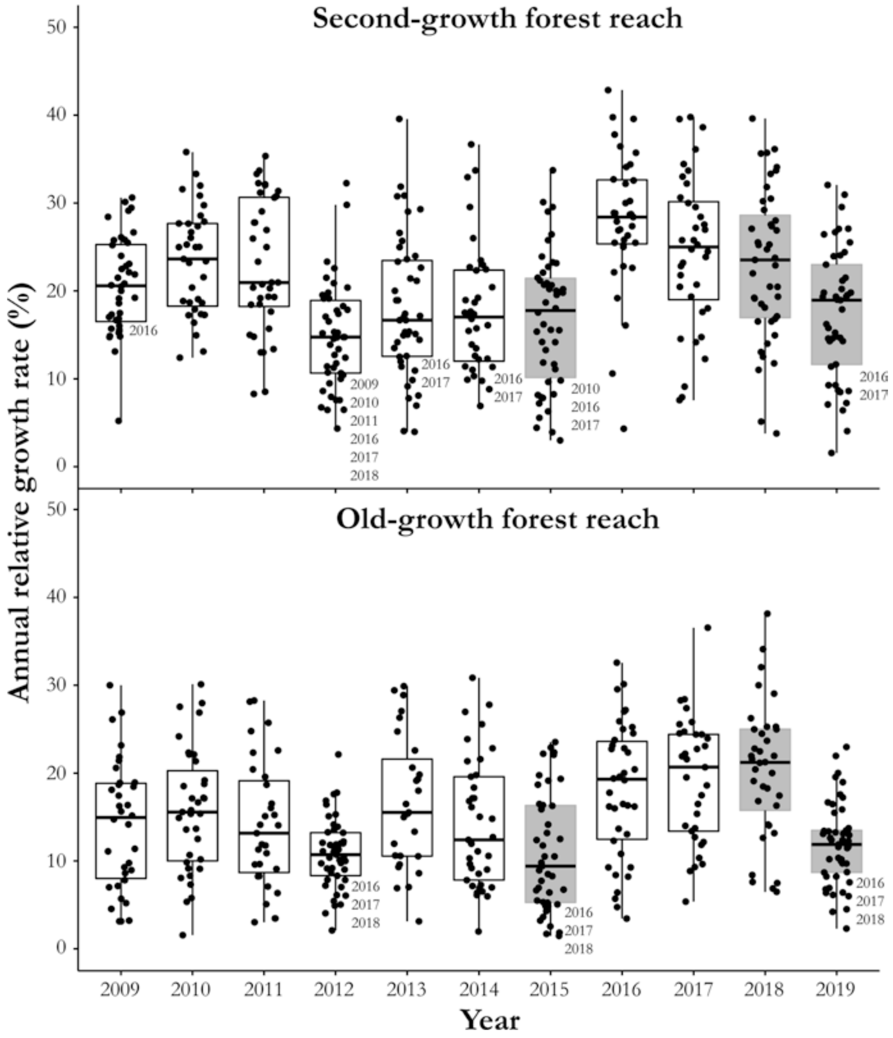

Fig. 4 Annual relative growth rate (%) of recaptured trout in two reaches of Mack Creek, Oregon. Gray boxes indicate drought years. Kruskal-Wallis one-way ANOVA on ranks showed significant differences among years (second-growth reach: H = 92.96, df = 10, $P < 0.001$; old-growth reach: H = 70.070, df = 10, $P < 0.001$). Numbers adjacent to boxes identify years with significant differences from pairwise comparisons (Dunn's Method $P < 0.05$)

reach, and 2012–2014 in the second-growth reach). Overall, relative growth rates were greater in the second-growth reach (median of 20.6%) compared to the old-growth reach (median of 14.9%). However, most abrupt differences among years were observed in the second-growth reach as illustrated by markedly low growth during 2012–2015.

Median condition of recaptured adult trout was relatively high (Fulton's condition >1.3) across years with notable annual fluctuations (Fig. 5), and relatively high synchrony between reaches ($r = 0.79$; $P = 0.004$). The median condition of trout across years was higher in the second-growth reach (median of 1.71) compared to the old-growth reach (median of 1.56). Yet, the largest differences in condition were observed in the second-growth reach as seen during 2012–2015. Interestingly, the two lowest condition values of trout did not occur during a drought year (2012 or 2014) in the second-growth reach. In the old-growth reach, the highest condition score occurred during a drought year (2018), whereas the lowest median condition score occurred in the drought year 2015 and the second lowest score in the reference year 2012. Median annual Fulton's condition and median annual growth rate of adult trout were strongly associated in both reaches (second-growth reach: $r = 0.96$, $P < 0.001$; old-growth reach: $r = 0.90$, $P < 0.001$).

Given growth rates were inversely related to trout size (Figs. 1 and 2), changes in size over time could influence year-to-year growth rate estimates. Median size (FL) of recaptured adult trout (Fig. 6) was synchronous between reaches ($r = 0.58$; $P = 0.047$). In the second-growth reach, recaptured trout had a median size of 102.5 mm, ranging between 96 (2016, 2019) and 115 mm (2012). In the old-growth reach, the median size of recaptured trout was comparable to the second-growth reach (104 mm, ranging between 91 in 2018 and 113 mm in 2013). Recaptured trout in the old-growth reach were smaller ($P < 0.05$) in 2018 and 2019 compared to reference years. In the second-growth reach, recaptured trout were larger in 2012 compared to 2015–2016 and 2018–2019.

3.2 Density-Dependence Affecting Growth and Condition of Adult Trout

There were two distinct periods of relatively high (2009–2014) and low (2015–2019) adult trout abundances (Fig. 7) with a high synchrony between the two reaches ($r = 0.82$; $P = 0.002$). Overall, the mean (± SD) abundance of adult trout was slightly higher in the second-growth reach (70 ± 12 ind./50 linear m) compared to the old-growth reach (60 ± 7 ind./50 linear m). In the second-growth reach, highest abundance occurred in 2010, 2012, and 2014, whereas the lowest occurred in 2016. In the old-growth reach, the highest and lowest trout abundance occurred in 2014 and 2016, respectively. Moreover, there was a consistent negative association between annual trout abundance and growth rate in both reaches, especially in the second-growth reach (Table 1). Similarly, there was a negative association between annual

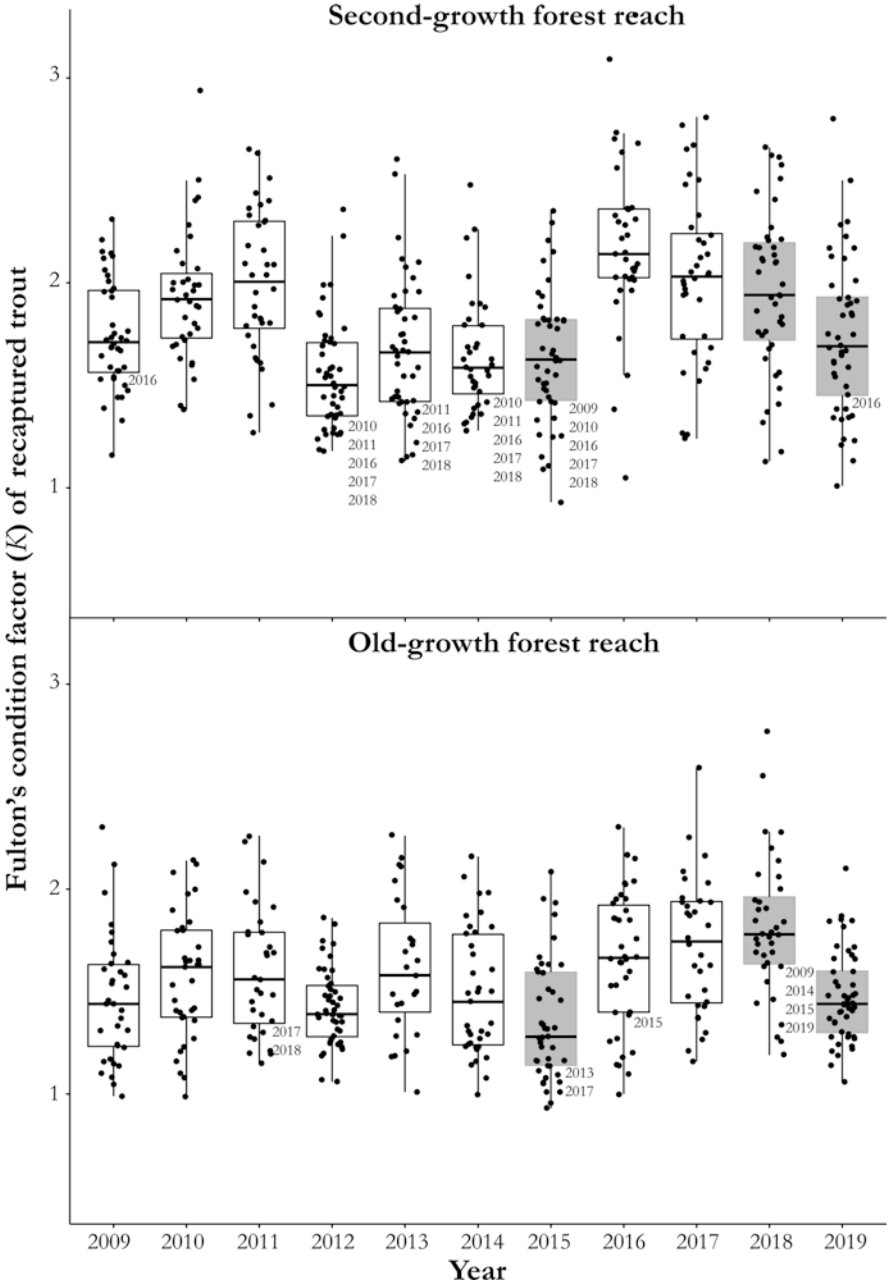

Fig. 5 Fulton's condition factor (K) of recaptured trout in the two reaches of Mack Creek, Oregon. Gray boxes indicate drought years. Kruskal-Wallis one-way ANOVA on ranks showed significant differences among years (Second-growth reach: $H = 106.58$, df = 10, $P < 0.001$; Old-growth reach: H = 64.30, df = 10, $P < 0.001$). Numbers next to the boxes identify years with significant differences from pairwise comparisons (Dunn's Method $P < 0.05$)

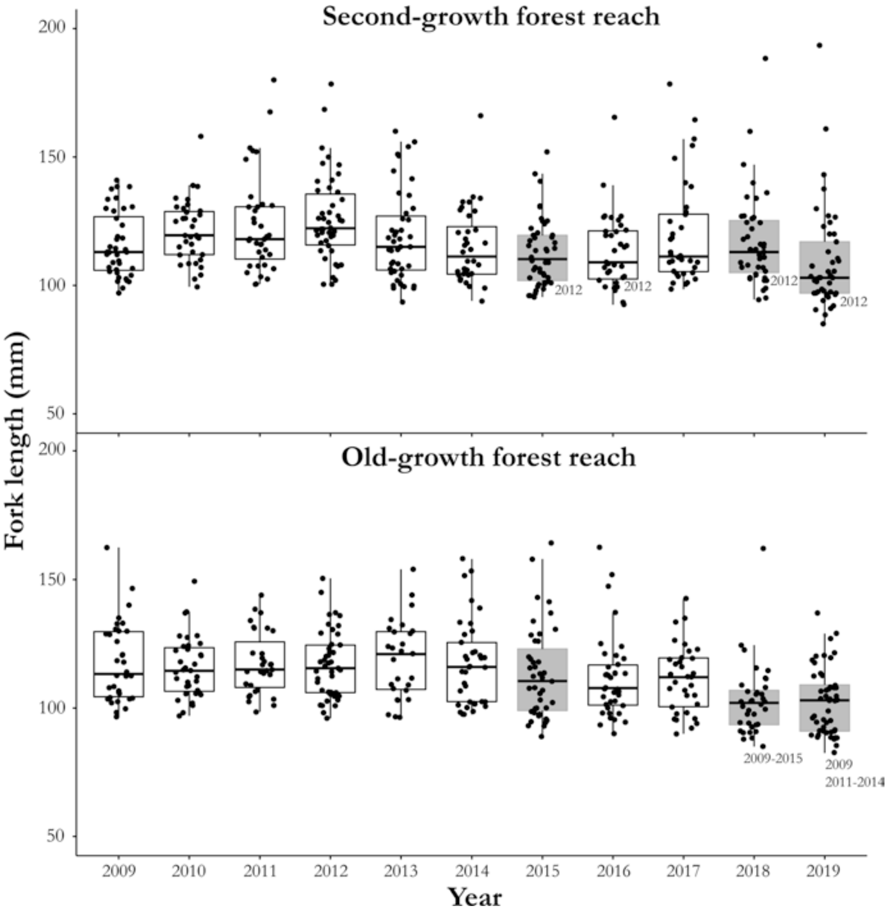

Fig. 6 Recaptured trout sizes in two reaches from Mack Creek, Oregon. Gray boxes indicate drought years. Kruskal-Wallis one-way ANOVA on ranks showed significant differences among years (Second-growth reach: H = 40.97, df = 10, $P < 0.001$; Old-growth reach: H = 60.87, df = 10, $P < 0.001$). Numbers next to the boxes identify years with significant differences from pairwise comparisons (Dunn's Method $P < 0.05$)

trout abundance and condition in both reaches that was marginally significant in the second-growth reach ($r = -0.53$; $P = 0.092$).

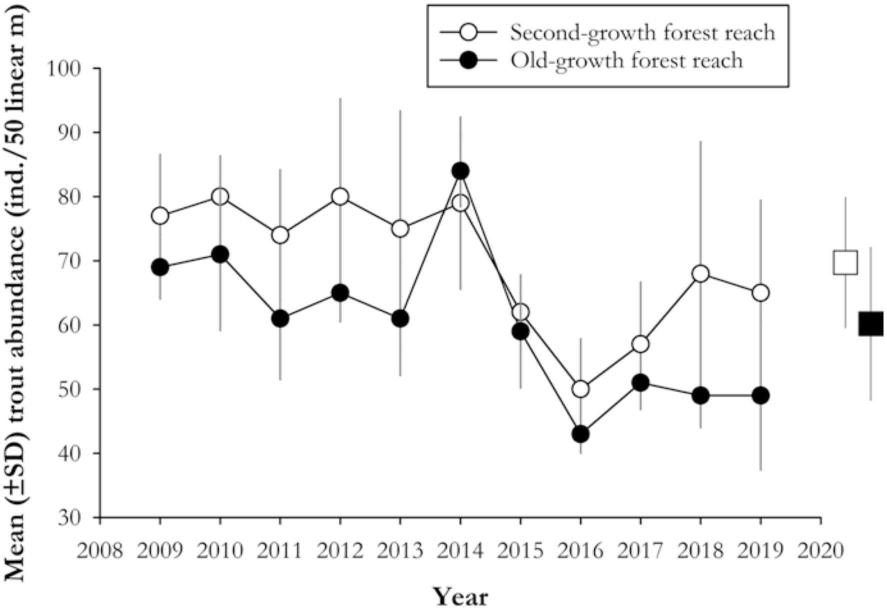

Fig. 7 Adult trout (Age 1+) abundance (mean ± SD) between 2009 and 2019 in two reaches in Mack Creek, Oregon. Square symbols at the right side of the graph show mean ± SD trout abundance for the entire study period. The difference in the mean trout abundance between the two stream reaches was marginally significant (Student's *t*-test $t = 2.023$, df = 20, $P = 0.057$)

3.3 Density-Independence Affecting Growth and Condition of Adult Trout

As is expected for a typical Mediterranean-climate region (hot-dry summers and cool-wet winters), the hydroclimate for the Mack Creek basin was influenced by a strong seasonality in precipitation, streamflow, and air/stream temperature (Figs. 8 and 9). Drought years (2015, 2018, and 2019) received approximately 21% less annual precipitation in summer and early autumn compared to reference years (2009–2014 and 2016–2017). Differences in hydroclimate were notable among drought years, with 2015 as the most extreme. In 2015 and 2018, a greater proportion of the precipitation (71% and 74%, respectively) occurred before the end of February compared to 2019 (61%) or the reference years (average of 59%; Fig. 8). Winter peak flows in 2015 and 2018 were also lower than during reference years. In 2019, there was an unusually high-flow event in April. In all drought years, the onset of the low-flow period started earlier, around mid June, and extended later until the end of September compared to reference years.

There was a consistent negative association between annual daily maximum streamflow and growth rate in both reaches ($r > |0.42|$; Table 1), but this relationship was not statistically significant. Relatively similar findings occurred for condition of trout in both reaches ($r > |0.36|$). Other metrics accounting for the magnitude and

Table 1 Pearson product moment correlation analyses between median annual responses of trout (growth rate and condition) and density-dependent and density-independent factors during 2009–2019 in two reaches (second-growth, and old-growth) of Mack Creek, H.J. Andrews Experimental Forest, Oregon. Significant values ($P < 0.05$) in bold and marginally significant ($P < 0.1$) in italics

	Annual relative growth rate (%)				Condition (Fulton's K)			
	Second-growth		Old-growth		Second-growth		Old-growth	
Metric	*r*	*P*-value	*r*	*P*-value	*r*	*P*-value	*r*	*P*-value
Density-dependent factors								
Mean adult trout abundance (ind./50 linear m)	−0.63	**0.039**	−0.49	0.131	−0.53	*0.092*	−0.40	0.219
Density-independent factors								
Streamflow								
Annual daily maximum streamflow (m^3/s)	−0.42	0.202	−0.49	0.125	−0.36	0.278	−0.51	0.108
Mean winter streamflow (Jan–Feb; m^3/s)	−0.10	0.779	−0.06	0.860	−0.12	0.717	−0.12	0.732
SD of winter streamflow (Jan–Feb; m^3/s)	−0.24	0.484	−0.27	0.425	−0.13	0.700	−0.23	0.497
Mean spring streamflow (Mar–May; m^3/s)	0.00	0.994	0.18	0.604	0.09	0.801	0.22	0.519
SD of spring streamflow (Mar–May; m^3/s)	−0.15	0.664	−0.10	0.770	−0.16	0.633	−0.08	0.805
Annual daily minimum streamflow (m^3/s)	−0.23	0.494	−0.13	0.694	−0.06	0.854	−0.08	0.820
Mean summer streamflow (Jul–Aug; m^3/s)	−0.19	0.574	−0.24	0.469	0.01	0.973	−0.02	0.955
SD of summer streamflow (Jul–Aug; m^3/s)	−0.22	0.513	−0.27	0.421	−0.01	0.966	−0.06	0.866
Stream temperature								
Annual daily minimum stream temperature (°C)	−0.18	0.610	−0.30	0.401	−0.19	0.601	−0.33	0.357
Mean winter stream temperature (Jan–Feb; °C)	0.17	0.638	−0.21	0.554	0.10	0.778	−0.24	0.514
SD of winter stream temperature (Jan–Feb; °C)	0.09	0.798	0.01	0.972	0.04	0.906	0.05	0.887
Mean spring stream temperature (Mar–May; °C)	0.12	0.747	−0.07	0.851	0.10	0.789	−0.13	0.729
SD of spring stream temperature (Mar–May; °C)	−0.02	0.949	0.13	0.727	−0.03	0.938	0.05	0.891
Annual daily maximum stream temperature (°C)	−0.26	0.439	−0.21	0.536	−0.44	0.175	−0.40	0.224
Timing of annual temperature max (ODWY)	0.26	0.478	0.41	0.239	0.43	0.211	0.58	*0.077*
Mean summer stream temperature (Jul-Aug; °C)	−0.32	0.344	−0.03	0.928	−0.34	0.303	−0.17	0.626

(continued)

Table 1 (continued)

	Annual relative growth rate (%)				Condition (Fulton's K)			
	Second-growth		Old-growth		Second-growth		Old-growth	
SD of summer stream temperature (Jul-Aug; °C)	0.09	0.798	0.01	0.972	−0.03	0.922	−0.07	0.834
Number of days >14 °C	−0.21	0.565	−0.39	0.265	−0.34	0.341	−0.56	*0.095*
Habitat size								
Mean maximum depth of sentinel pools (m)	0.17	0.613	−0.54	*0.084*	0.24	0.473	−0.55	*0.079*
Mean area of sentinel pools (m^2)	−0.44	0.180	0.37	0.270	−0.30	0.365	0.32	0.334

variability of seasonal streamflow did not show clear associations with either growth or condition of adult trout.

Thermal regimes in the Mack Creek basin differed among drought years (Fig. 9). The winter (January–February) of 2015 was 4.0°C warmer than the average of winters in reference years, but only 1.2°C warmer in 2018–2019. Similarly, the summer (July–August) of 2015 was 1.65°C warmer than the average of summers in reference years, but only 0.68°C warmer in 2018–2019. Water temperature conditions (7-day moving average) of Mack Creek were relatively cold, ranging between 0.9°C and 13.6°C. Summer stream temperatures in drought years were not the warmest in our study period, except for an early peak in late June of 2015. During this drought year, the average winter stream temperature was 1.9°C warmer than the average in reference-year winters.

There was a consistent positive association between timing of annual daily maximum temperature and growth rate in both reaches ($r > 0.26$, Table 1), but this association was not statistically significant. A similar finding occurred for condition of adult trout ($r > 0.43$; it was marginally significant in the old-growth reach). Later timing of maximum temperature was associated with faster growth and greater condition of trout. These associations were marginally significant in the old-growth reach ($r > 0.57$). In addition, there was a consistent negative association between the number of days exceeding 14°C and growth rate in both reaches ($r > |0.26|$) with similar patterns occurring for condition ($r > |0.43|$). The association was marginally significant in the old-growth reach for condition ($r = -0.58$). Similarly, there was a consistent negative association between annual daily maximum temperature and both growth and condition ($r > |0.21|$ and $r > |0.4|$, respectively, Table 1), but these associations were not statistically significant. Other metrics (Table 1) accounting for the magnitude and variability of seasonal stream temperature did not show clear associations with either growth or condition of trout.

Pool geometry from late summer (early September) was used as a proxy of trout habitat conditions during seasonal low flow for each water year. Sentinel pools showed relatively similar geometry during our study period (Fig. 10). Mean maximum pool depth across years was similar between reaches (0.56 m), whereas the pool area was 8% smaller in the second-growth compared to the old-growth reach. Mean annual maximum pool depth was deeper in both second-growth (21%) and

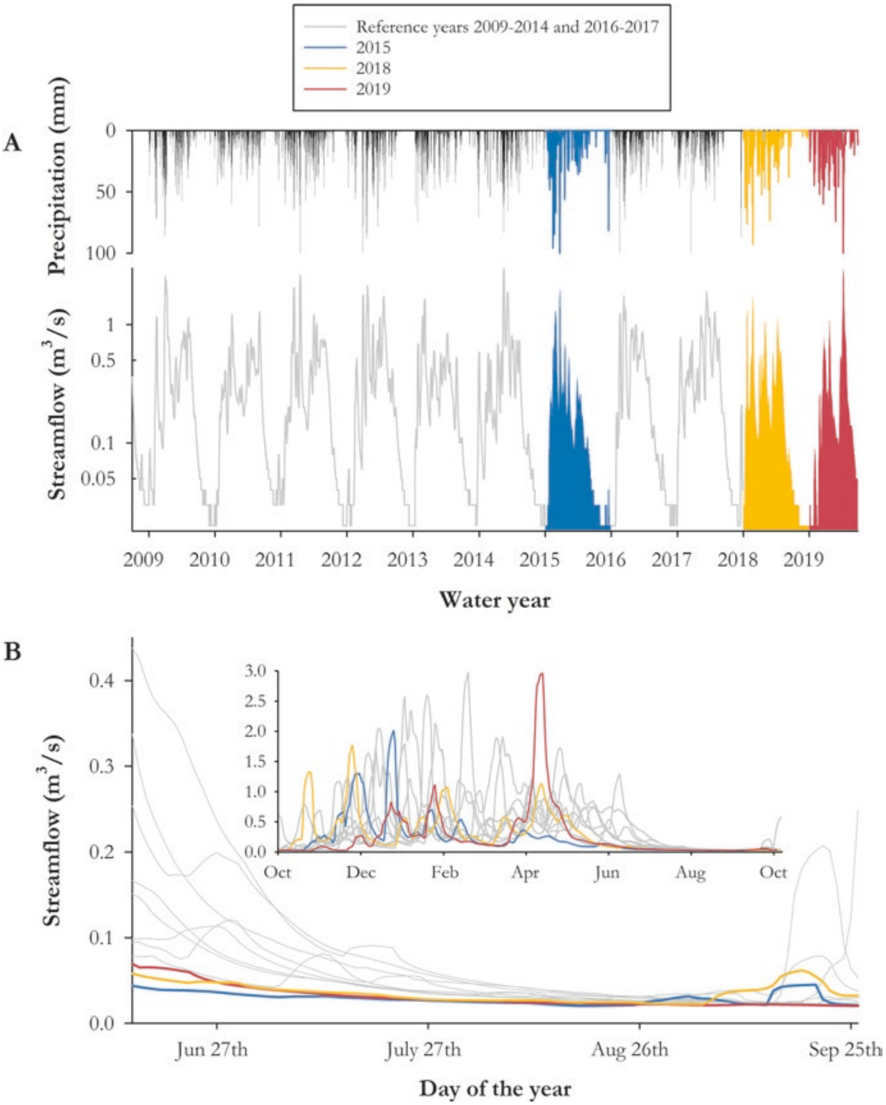

Fig. 8 (**a**) Time series (WY 2009–2019) of precipitation (mm) and streamflow (m^3/s) in Mack Creek, Oregon. Water years were classified as reference (2009–2014 and 2016–2017) or drought years (2015, 2018, and 2019). Total daily precipitation data (available up to March 18, 2019) were extracted from the UPLMET station (Daly et al. 2019) and presented as daily values. Daily mean streamflow data were extracted from the GSWSMC gauge station (Johnson et al. 2020) and presented as 7-day moving average values. (**b**) Zoom-in to the seasonal low-flow period and annual streamflow (inset) across years

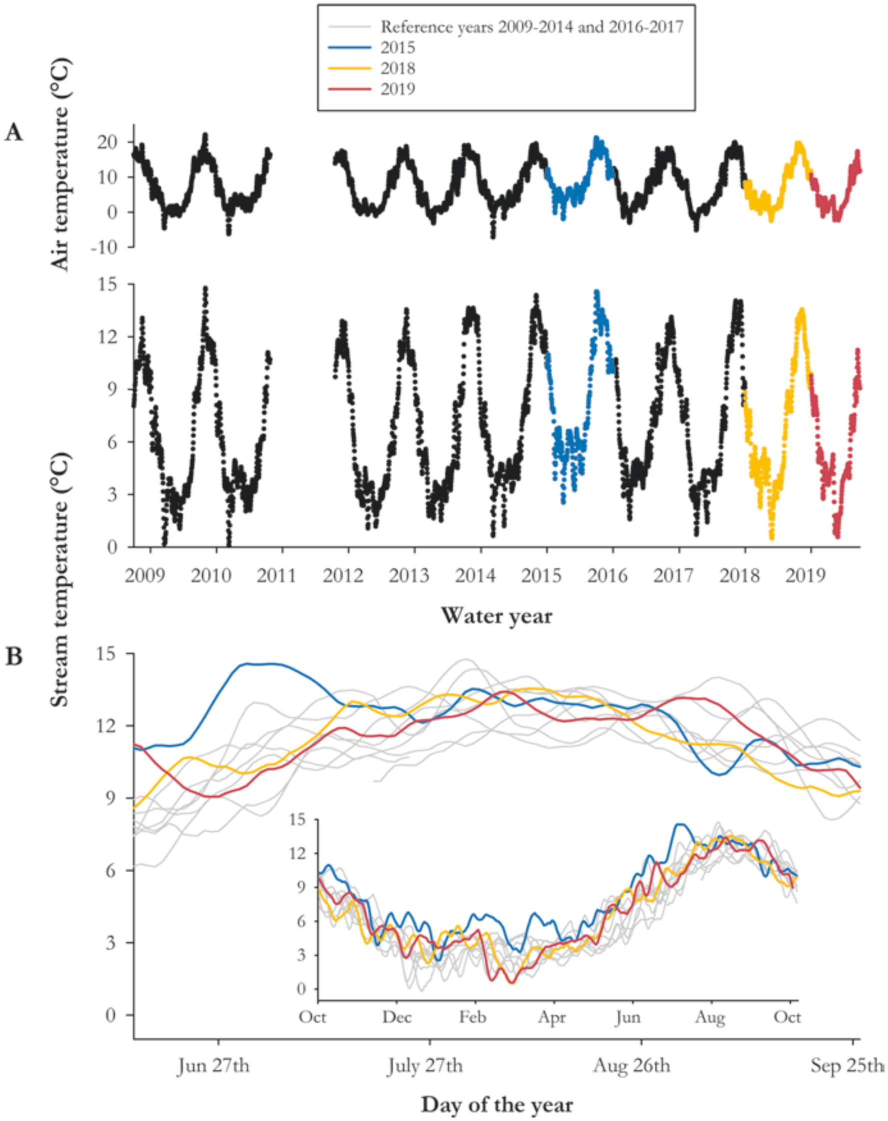

Fig. 9 (**a**) Time series (WY 2009–2019) of air and stream temperature (°C) for Mack Creek, Oregon. Water years were classified as reference (2009–2014 and 2016–2017) and drought years (2015, 2018, and 2019). Mean daily stream and air temperature data were extracted from the GSMACK and TSMACK stations (Gregory and Johnson 2019) and presented as 7-day moving average values. Small gaps (<30 days) in air temperature data were filled using a simple linear regression between GSMACK vs TSMACK ($y = 1.024x–0.29$; $R^2 = 0.95$). Small gaps (<30 days) in stream temperature data were filled using a simple linear regression between GSMACK vs TSMACK ($y = 1.01x–0.79$; $R^2 = 0.95$). (**b**) Zoom-in to seasonal low-flow period and annual temperature regime (inset) across water years

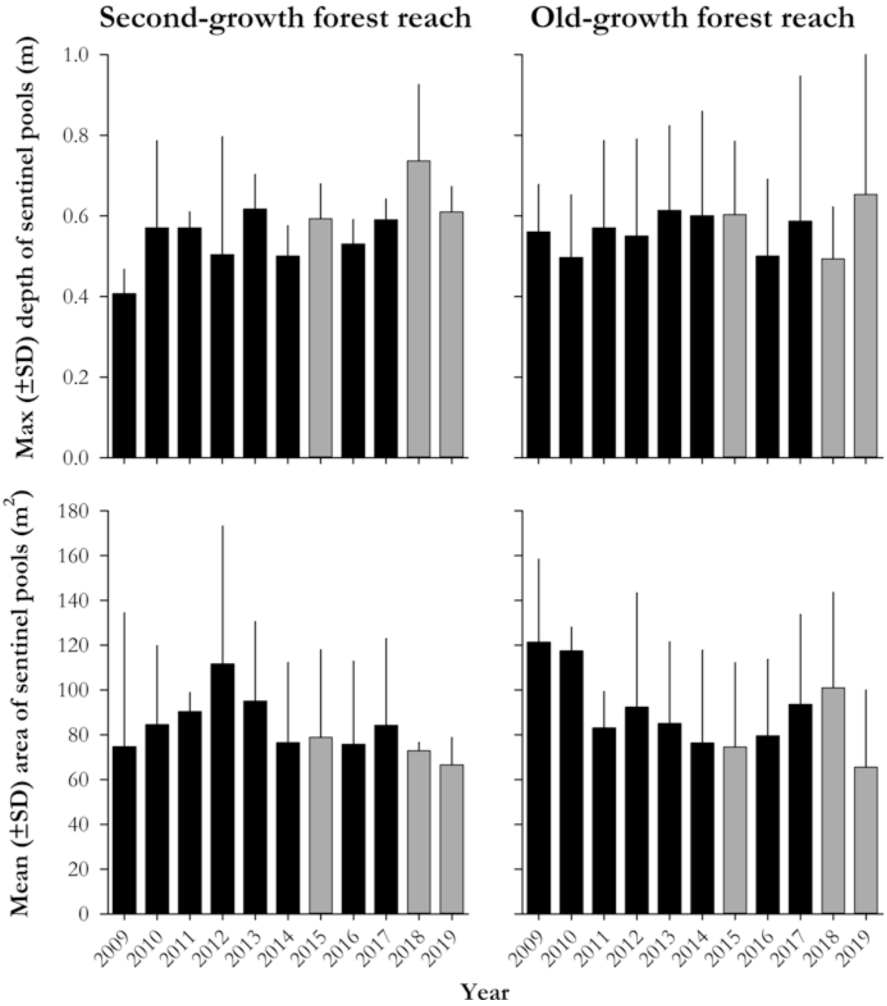

Fig. 10 Time series (WY 2009–2019) of the geometry of sentinel pools ($n = 3$) surveyed at the end of the summer in the two reaches from Mack Creek, Oregon. Gray bars indicate drought years

old-growth (4%) reaches during drought compared to reference years. However, mean annual pool area was consistently smaller in both the second- (26%) and old-growth (24%) reaches during drought relative to reference years. In particular, the drought in 2019 had the lowest pool area of all years at the two reaches.

There was a negative and marginally significant association between maximum pool depth and growth rate and condition of adult trout only in the old-growth reach ($r > |0.54|$, Table 1). This association was positive in the second-growth forest. Pool area did not show clear associations with either growth or condition of trout.

4 Discussion

Revealing the complex interplay between density-dependent and density-independent as regulators of growth in stream salmonids is essential for the conservation of species and ecosystems, especially given climate change. We demonstrated that there is low annual growth of individual adult trout (Age 1+) across size in drought years compared to reference years. The negative associations between growth or condition and abundance over time suggest density-dependence is a factor regulating the demography of trout populations in our study system. However, observed lower growth rates and reduced condition associated with years with higher annual peak flows, earlier timing of annual maximum stream temperature, and higher frequency of warmer days (>14°C) also are indications of density-independent effects. Collectively, our findings support both density-dependent and density-independent factors modulating growth and condition of adult trout, which has also been suggested in other studies (e.g., Elliott 2015; Uthe et al. 2019; Huntsman et al. 2021).

Density-dependent effects on growth seem to prevail under regular seasonal low flow, whereas density-independent factors become more relevant during droughts, similar to Power et al. (2008). Both annual growth rate and condition are negatively associated with abundance in our stream reaches across years. Yet, the logistic regression analysis revealed that (1) the variability of individual growth rates is greater in small compared to large individuals, suggesting that factors other than size can limit growth (see other examples in Cade and Noon 2003), and most importantly (2) the maximum scope of growth across sizes is reduced during drought compared to regular seasonal low-flow periods. A possible explanation for these findings is habitat segregation as a response to intraspecific competition during regular seasonal low flow (Chapman 1966; Elliott 1994; Lobón-Cerviá 2007; Jenkins et al. 1999). In the first case, dominant larger size-at-age individuals select and use best-quality habitats, whereas smaller size-at-age subordinate individuals occupy less-suitable habitats (Chapman 1966; Penaluna et al. 2021). As individual growth rates are likely a function of habitat quality (e.g., Wilzbach et al. 1986), the observed variability in individual growth rates during regular seasonal low flow would be indicative of the diversity and quality of available habitats between our stream reaches. In the second case, the slower growth rates of larger compared to smaller individuals can be explained by the higher metabolic requirements of larger individuals during summer (Dwyer and Kramer 1975; Hughes and Grand 2000), for example, increased allocation of energy to gamete production as trout grow. However, intraspecific competition and metabolic costs likely increase in importance owing to harsher environments during drought compared to regular seasonal low-flow periods. Specifically, streamflow and space are more constrained and a greater number of animals are likely to occupy drought refuges resulting in higher interference competition (e.g., Dunham and Vinyard 1997). Smaller and less diverse habitats available during drought (Lake 2003; Hakala and Hartman 2004; Kaylor et al. 2019; Lennox et al. 2019) would then result in the observed lower variability of individual growth rates. In addition, trout behavior, such as movement and interactions between individuals (Penaluna et al. 2021) are likely energetically more costly and could limit the maximum scope of growth, as seen in our logistic regression analysis. We show some evidence of growth limitation affecting larger trout more than smaller trout, as suggested in other systems during drought (Walters 2016). We suspect that density-dependent and density-independent processes likely lead to differential responses and explain the impacts of droughts in other stream settings.

The high synchrony of trout responses in our stream reaches suggests an overarching effect of climate on the regulation of growth and condition of trout and yet, local conditions of each stream reach can temper the effects of drought (e.g., Matthews 1998; Magoulick and Kobza 2003; Walters 2016). We found that growth and condition are negatively associated with deeper pools in the old-growth reach, but this relationship is positive in the second-growth reach. The longitudinal profile of the old-growth reach is dominated by large wood supporting steps up to 2.5 m high that create low-gradient upstream channel segments with finer streambed sediments, whereas the longitudinal profile of the second-growth reach is dominated by boulder steps and larger streambed sediments (Faustini and Jones 2003). Water depth during the low-flow period is similar between the two reaches, but deeper pools (>0.5 m) are more common in the old-growth than the second-growth reach (Faustini and Jones 2003). Because food availability can limit trout growth during seasonal low flow (Boss and Richardson 2002), differences in the quality of foraging habitats might affect our findings. For example, pool habitats differing in overhead shading can affect invertebrate drift densities and foraging efficiencies, resulting in slower trout growth rates (Wilzbach et al. 1986). In addition, terrestrial prey becomes more important in the diet of stream salmonids during seasonal low flow (Romero et al. 2005; Sweka and Hartman 2008) and differences in terrestrial food resources between stream reaches from riparian habitats (Naiman and Décamps 1997) might also influence our findings.

Our study had several limitations, especially considering the myriad of factors and processes affecting riparian ecosystems (Gregory et al. 1991) including climate stochasticity. For example, there is a lack of spatial and temporal replication of our stream settings and drought events that limits the use of more robust statistical analyses (e.g., generalized linear mixed models). However, most research evaluating the effects of drought in rivers are short-term opportunistic studies that, by nature, are unable to consider environmental stochasticity (Lake 2003; Magoulick and Kobza 2003; Walters 2016; Piniewski et al. 2017; Lennox et al. 2019). Our study considers two adjacent stream reaches during a 13-year period that included three droughts, with two of them as consecutive events. Droughts and their effects seem to be idiosyncratic (Lake 2003; Humphries and Baldwin 2003; Magoulick and Kobza 2003; Walters 2016; Lennox et al. 2019) and thus, the transferability of our findings across species and ecosystems is limited. We did not consider factors related to trout emigration (Penaluna et al. 2021) or the seasonality of growth regimes (Armstrong et al. 2021), but these may not be important influences on trout in Mack Creek (Trotter 1989; Gresswell and Hendricks 2007). We had relatively high annual recaptures

(21–41%). The timing of our sampling at the end of the seasonal low flow each year allowed us to acquire a reliable record of growth and condition of trout during a stressful and critical period for Coastal Cutthroat Trout (Berger and Gresswell 2009; Sheldon and Richardson 2021). In addition, we were not able to evaluate the availability of food sources and the quality of both foraging habitats and drought refugia (e.g., Millidene et al. 2006). The dynamics of drift (Naman et al. 2016) as well as prey subsidies from terrestrial systems (Baxter et al. 2005) are complex processes and additional research is needed to better understand the role of local conditions on the creation of foraging habitats that can potentially buffer effects of droughts and thus, affect the growth and condition of stream salmonids.

Idiosyncratic aspects of the hydroclimate during each drought coupled with the effects of trout abundance illustrate the complex link between density-dependent and density-independent processes that affect the growth and condition of trout. Although the seasonal low-flow period has consistently lower flows and is of longer duration in drought years, responses of trout are not always the same. Differences in timing of precipitation, magnitude of winter peak flows, seasonal temperatures, and size of habitats during drought years can affect abundance as well as growth and condition of trout. The drought in 2015 represented the most extreme low-flow season of our study period, including the warmest winter and summer. Trout abundance was lower than in the previous years, but growth rate and condition were among the lowest in our study period. However, the year following the 2015 drought had the lowest trout abundance, suggesting a delayed response. This could be affected by potential poor recruitment (Age 0) in 2015 that resulted in lower densities of adult (Age 1+) trout in 2016. At the same time, 2016 also had the fastest annual growth rate and highest condition score, suggesting a compensatory response of growth (Elliott 2015). The drought of 2018 seemed to have different influences on abundance, growth rates, and conditions than the drought of 2015. In 2018, there were no apparent effects on trout abundance the following year. Also, growth and condition of trout in 2018 were among the highest in our study, but they were reduced the following year. The drought of 2019 was the second consecutive drought in our study period, supporting one of the lowest growth rates and condition scores. Collectively, differential legacy effects of drought can influence population trajectories over time as is shown here and in other nearby streams (Kaylor et al. 2019). Many questions remain about the role of extensive and consecutive droughts versus single extreme droughts in population dynamics (Bell et al. 2000). Long-term ecological research is critical to answering these questions (Lobón-Cerviá 2009; Elliott 2015), as it has demonstrated in documenting rare events, legacy effects from previous events, and the resulting biotic responses (e.g., Dodds et al. 2012).

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Winter Ecology of Salmonids in Boreal Streams Under Climate Change

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Abstract Winter represents a challenging season for animals in boreal streams and is a period with low temperatures, extremely low levels of primary production, low metabolic rates of ectotherms, and little light. Yet, stabile ice cover provides shelter for salmonids residing in rivers. Despite low light levels in winter, stream salmonids are mainly nocturnal, which protects them from diurnally active predators. Climate change adds unpredictability, increases frequency of winter floods, and can reduce the time that salmonid embryos need to develop until hatching and emergence. These changes can increase natural winter mortality and cause recruitment failures in populations that already are under severe pressure from environmental changes and fishing. We identify a need to better monitor egg and fry survival to predict the effects of changing temperature and environmental stressors such as loading of organic material or flow regulation. Availability of microhabitats for sheltering during winter is crucial and should be considered in restoration efforts focused on recovering threatened salmonid populations. The importance of habitat quality will increase in an unpredictable environment, and both management attention and

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research on the early life-history phases of salmonids are needed to understand how climate change-induced environmental changes affect fish through winter processes.

Keywords Brown trout · Egg survival · Environmental change · Hydropower · Ice · Parr · Winter

1 Introduction

Winter in temperate and boreal regions is a challenging season for many animals. Some animals go to great lengths to avoid winter conditions completely, for example, by seasonal migration or by entering an inactive mode such as torpor or hibernation. Many aquatic animals, like salmonid fishes, do however remain active throughout winter but exhibit adaptive behavioral and physiological acclimatization, such as decreased foraging activity and metabolism (Storey and Storey 1989; Bull et al. 1996; Huusko et al. 2007; Marchand 2014). Yet, our knowledge of aquatic ecosystems in winter remains very limited compared to terrestrial ecosystems or to aquatic ecosystems in other seasons. Logistical constrains explain some of the scarcity of studies in salmonid winter ecology: streams and rivers are challenging to access and work in during winter. Winter has been considered a survival bottleneck for stream salmonids (i.e., both species that live their entire life in streams and certain life stages of migratory salmonids that live in streams), even though relatively little is known about the winter ecology of these species (Cunjak 1996; Reynolds 1997; Huusko et al. 2007; Carlson et al. 2008; Brown et al. 2011; Watz et al. 2015). Winter survival in riverine conditions is crucial, not only for resident populations but also for migratory salmonids; both for the juvenile life stages and for spawned adults that stay in running waters before returning to feeding areas the coming spring. The life cycles of autumn-spawning salmonids such as Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and Arctic charr (*Salvelinus alpinus*) also require that eggs survive and develop within the streambed substrate throughout winter. Winter conditions can thus be crucial for the recruitment of these species.

In this chapter, we will review the winter ecology of stream salmonids. We explore the conditions salmonids experience during winter and synthesize research on how they cope with the winter environment. This chapter also discusses how ongoing global warming changes winter conditions, and how this may affect salmonid populations. Finally, we will present some field examples of the winter ecology of brown trout in one of the northernmost countries in Europe, Finland. In these examples, we will report results from field surveys on the survival of brown trout eggs and juveniles throughout winter.

2 The Winter Environment

2.1 How Do We Define Winter?

Although the concept of winter may appear obvious, a definition may prove useful when we discuss winter from an ecological perspective. For most of us, winter in temperate and boreal regions is the season with freezing or near-freezing temperatures, accompanied by snow, ice, and short days. One could also argue that winter describes such seasonal conditions that induce consistent adaptive responses by animals and plants. In-stream salmonid ecology, there is a definition of winter that is partially linked to life history: winter is the period that starts from egg deposition by autumn-spawning salmonids and ends at ice break. Within this life-history context, spring starts from the commencement of smolt migration, or reproduction of spring-spawning riverine fishes (Cunjak 1996; Cunjak et al. 1998). These definitions encompass an extensive period of the year in boreal environments.

Although defining winter from spawning to ice break gives us a temporal definition of winter, it still is important to bear in mind that winter conditions vary considerably geographically. For example, many salmonids occur in northern and southern Europe, and in northern and southern (North) America. Winter conditions differ considerably within these regions and presumably so do fish populations that inhabit different latitudes. For example, in a study conducted in Norway, loss of energy stores during winter was measured in 13 Atlantic salmon populations along a latitudinal gradient (Finstad et al. 2010). Surprisingly, this study showed that energy depletion was lower in the northern than in the southern populations. Salmon from the northern populations also exhibited higher foraging activity when energy reserves decreased compared to salmon from the southern populations. Similarly, winter energy loss was positively correlated to latitude of population origin when no surface ice was present (Finstad and Forseth 2006). Hence, salmonid populations appear to show some counter-gradient variation, but adaptive differences along environmental gradients are yet generally poorly studied in salmonids. Similarly to counter-gradient variation, Jordan's rule (McDowall 2008) describes a direct eco-geographical relationship between latitude and intraspecific meristic characteristics, such as the number of fin rays, vertebrae, or scales. Whether this rule holds for salmonids remains to be studied. An array of local and latitudinal factors is likely to affect adaptive differences, which makes it challenging to determine the source of intraspecific variation without controlled experiments (McDowall 2008; Jonsson and Jonsson 2011; Morris et al. 2017).

2.2 Winter Conditions and Ice Formation

Short days, subfreezing temperatures, snow, and ice cover characterize winter (Hurst 2007; Huusko et al. 2007; McNamara and Houston 2008; Marchand 2014). In the northern hemisphere, 60% of all river systems develop ice, which affects discharge, water levels, hydraulics, habitat complexity, and light availability (Stickler et al. 2010; Brown et al. 2011). Ice conditions can affect salmonids both positively and negatively. For example, surface ice cover has positive effects on fish growth and survival (Prowse 2001; Finstad et al. 2004b; Huusko et al. 2007; Linnansaari et al. 2008; Brown et al. 2011; Hedger et al. 2013; Watz et al. 2015), presumably as ice cover provides protection against aerial and terrestrial predators, something we will explore in detail later in this chapter.

In late autumn, decreased air temperatures and reduced solar radiation induce cooling of water and ice formation begins. Surface ice first forms in slow-moving stream sections where thermal stratification of water layers may occur, for example close to streambanks (Fig. 1). Bridging of ice starts at the streambanks and on surface stones, and eventually the entire surface is covered by ice (Huusko et al. 2007; Hicks 2009; Marchand 2014). Ice-free pockets in an otherwise ice covered stream develop in areas where the water temperature does not reach freezing or the water velocity does not allow formation of surface ice. Ice cover may, therefore, not form in areas with groundwater input, substantial ground heat, or in areas with turbulence such as rapids that produce friction heat (Power et al. 1999). Large slow-flowing rivers often experience stable ice cover throughout winter, whereas small high gradient streams often have unstable ice formation where ice tends to form and break up throughout winter. In spring, the surface ice melts as solar radiation and temperatures increase, and spring floods mechanically break the remaining ice.

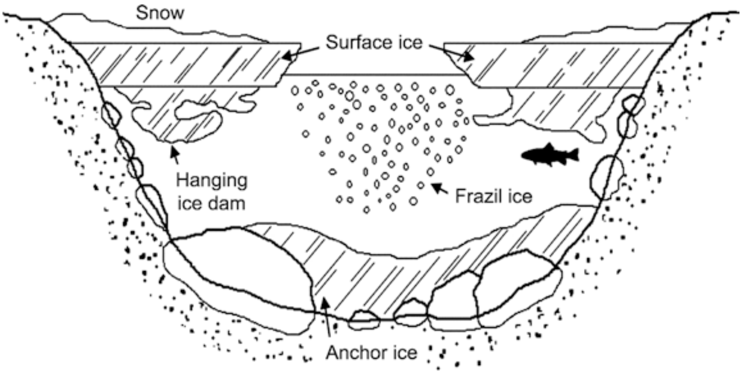


Fig. 1 Conceptual cross-section of a stream in winter. Surface ice forms in low-velocity areas close to the streambanks, and may eventually grow to cover the entire stream width. At high velocities and in turbulent water, temperatures may be <0°C, leading to formation of frazil ice platelets in the water. Frazil ice may attach to the streambed or to instream structures and form anchor ice. When frazil ice adheres to surface ice, the same process forms hanging ice dams

In streams with high flow and turbulence, stratification of water layers is inhibited and sub-zero temperatures can occur without freezing. Under these conditions, small disk-shaped platelets of ice, called frazil ice, are formed (Figure 1). Energy released during the formation of frazil ice, as water goes from a liquid to a solid state, inhibits further cooling, and the water temperature remains at approximately 0 °C. Frazil ice aggregates at instream structures such as rocks, stream wood, or surface ice, where it accretes and forms ice masses called anchor ice. Anchor ice may fully cover instream structures and in some cases even the entire streambed, which has major impact on the physical appearance of the instream environment. Aggregation of frazil ice not only occurs on structures located on the streambed, but it can also accrete to surface ice and form hanging ice sheets in slow-flowing areas. If frazil ice accumulates close to the water surface, ice cover can form and continue upstream as more ice aggregates (Hicks 2009; Marchand 2014). Anchor ice and hanging ice dams thus change the physical structure of fluvial ecosystems in winter, and also affect hydraulic properties such as depth and flow (Prowse and Gridley 1993; Brown et al. 2000; Kerr et al. 2002; Huusko et al. 2007). In addition to surface ice, anchor ice also has a substantial impact on the winter ecology of stream salmonids. How anchor ice affects salmonids will be explored in the forthcoming section on habitat choice in this chapter.

3 Salmonid Winter Ecology

3.1 Metabolism, Growth, and Survival

Salmonids experience the same challenges of low temperatures, predation, and diminished habitat availability during winter as most other animals. Compared to terrestrial winter-active animals such as mammals and birds, however, fish are poikilotherms. Poikilothermy means that animals cannot regulate their body temperature, except behaviorally. Hence, the body temperature of salmonids follows the ambient environment, which leads to reduced metabolic scope in winter. Physiological performance of poikilotherms is often constrained at low temperatures, with repercussions on behavioral activity, growth, and survival (Elliott 1994; Graham et al.1996; Johnston and Temple 2002; Guderley 2004; Jonsson and Jonsson 2011; Watz and Piccolo 2011; Watz et al. 2012; Huusko et al. 2013). Growth of stream salmonids is usually low in winter (Cunjak and Power 1986; Bradford et al. 2001; Härkönen et al. 2021), and there are even reports that juvenile salmonids can shrink (also in length) under harsh winter conditions due to catabolism of their own tissues (Huusko et al. 2011).

Despite river invertebrate abundance and biomass being highest during winter (Hynes 1970; Lillehammer et al. 1989; Haapala and Muotka 1998; Chi et al. 2017), energy depletion can be a major cause of winter mortality (Finstad et al. 2004a; Hurst 2007). This means that if fish stay inactive and save energy during winter, their chances of survival may increase (Cunjak 1988; Berg and Bremset 1998; Simpkins et al. 2003; Biro et al. 2004; Finstad et al. 2004a; Finstad et al. 2010; Hansen and Rahel 2015). As for fish in general (Garvey et al. 2004), body size plays a major role in overwinter survival of salmonids. Small fish experience higher rates of winter mortality, particularly predation, than large fish. This pattern has been reported for several salmonids including Atlantic salmon, brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchys mykiss*), and coho salmon (*O. kisutch*) (Quinn and Peterson 1996; Meyer and Griffith 1997a, b; Johnston et al. 2005). Nevertheless, there are also studies that have not found a relationship between fish size and overwinter survival (Bradford et al. 2001; Lund et al. 2003; Johnston et al. 2005). This could be related to inter-annual growth differences, if mortality is non-linear with respect to size. If fish attain a critical threshold size, mortality is reduced disproportionally (Lund et al. 2003; Huusko et al. 2007). However, even inverse relationships between salmonid size and winter survival have been reported (Carlson and Letcher 2003; Hedger et al. 2013). In a study of Atlantic salmon parr, it was not body size, but the size of energy stores that determined overwinter survival (Finstad et al. 2004a). This suggests conditions experienced during the previous summer could indirectly affect overwinter survival by regulating the energy reserves accumulated over the summer. However, limited food intake during fall did not impact overwinter survival in the study of Näslund et al. (2017). In either case, depleted energy reserves result in behavioral changes, such as increased foraging and reduced activity, and energetic status during winter determines the foraging intensity that is necessary for fish to survive (Bull et al. 1996). Hence, salmonid overwinter survival is determined by a combination of body size, energy reserves, and environmental challenges that occur both prior to winter and during winter.

While many have regarded winter as a period of high mortality for stream fishes, other studies have not found seasonal differences in mortality rates. For example, Scandinavian data on brown trout populations suggest that mortality during winter may not actually exceed mortality in other seasons (Carlson et al. 2008). This inconsistency among studies may be due to a high inter-annual variation in winter survival: when overwinter survival has been examined over several consecutive years, great inter-annual variation has been observed (Huusko et al. 2007). In fact, stable winter conditions in terms of ice cover and constant water flow seem to correspond to periods of low salmonid mortality (Huusko et al. 2007; Linnansaari and Cunjak 2010; Hedger et al. 2013; French et al. 2017). This in turn suggests that climate change-driven instability in winter conditions might increase winter mortality of salmonids. The direct mechanism explaining why stable surface ice cover may reduce overwinter mortality will be discussed in the forthcoming section on predator–prey interactions.

3.2 Habitat Choice

As for many other animals, a heterogeneous environment benefits growth and survival of stream salmonids (Mitro and Zale 2002). It creates opportunities both to find food and avoid predators. Surface ice, undercut banks, crevices within the substrate, stream wood, vegetation, beaver dams, or deeper stream sections such as pools are used as shelter by salmonids in winter (Heggenes et al. 1993; Mitro and Zale 2002; Johnson and Douglass 2009). To spend a considerable amount of time sheltering among instream structures appears to affect winter survival positively (Valdimarsson and Metcalfe 1998; Armstrong and Griffiths 2001; Mitro and Zale 2002; Coulombe-Pontbriand and Lapointe 2004; Finstad et al. 2007), as this both minimizes metabolic costs and results in reduced predation risk (Heggenes et al. 1993; Cunjak 1996; Huusko et al. 2007). In addition, if fish have access to different stream microhabitats in winter this seems to increase their chances of survival (Elso and Greenberg 2001). For example, Koljonen et al. (2012) found that brown trout that overwintered in channelized streams had smaller body mass and exhibited more competitive behavior than trout in streams with sheltering opportunities. In addition, Watz (2017) showed that stress levels of brown trout in winter were lower when fish had the opportunity to shelter among instream wood. Hence, one way for stream salmonids to increase overwinter survival is to use different microhabitats for finding food and avoiding predators. A heterogeneous instream environment thus provides these possibilities in winter.

Instream ice can shape the habitat available for fish in winter and alter flow regimes (Whalen et al. 1999). Formation of anchor ice can homogenize the streambed and reduce sheltering opportunities for fish, resulting in increased mortality (Maciolek and Needham 1952; Jakober et al. 1998; Linnansaari et al. 2008). Anchor ice formation can also lead to large fish aggregations as fish get stuck in between ice formations. Sometimes these aggregations consist of several different species (Jakober et al. 1998; Simpkins et al. 2003; Lindstrom and Hubert 2004). Anchor ice often exhibits a diel formation pattern, especially in northern regions, where ice formation occurs at night. The risk of fish becoming trapped in anchor ice could therefore be greater at night (Heggenes et al. 1993; Whalen et al. 1999). There are reports of fish trying to disperse in an attempt to avoid anchor ice (Brown and Mackay 1995; Jakober et al. 1998; Brown 1999). Patchy anchor ice has, however, been reported to provide a structurally complex habitat and may sometimes function as shelter for salmonids (Roussel et al. 2004; Linnansaari et al. 2008; Stickler et al. 2008). The impact of anchor ice on stream salmonid habitat choice and overwinter survival thus seems to vary considerably, depending on how anchor ice formation alters the instream environment.

In addition to the formation of ice, salmonids also react to ice breakup, which occurs both during mid-winter, e.g., when rain induces rapid snowmelt, or at the onset of spring (Lawford et al. 1995). Ice breakup has a major impact on the river winter environment and may remold river channels and affect substrate transport and riparian vegetation (Gatto 1994; Hicks 1994; Power et al. 1999). Stream fishes, both salmonids and other species, can move long distances when the river environment changes during ice breakup (Brown et al. 2001). A study of Atlantic salmon parr in Norway did, however, show that fish moved the least during ice breakup and significantly more during other ice-related events, such as the formation of anchor ice (Stickler et al. 2007). Cunjak et al. (1998) found that mid-winter ice breakup in Canada resulted in reduced survival of several early life stages of Atlantic salmon, especially the eggs. Some fishes seem to avoid ice breakup altogether, especially when it causes ice scouring, which has been proposed as the reason why rainbow trout overwinter in deeper river sections underneath rocks and rubble (Swales et al. 1986). Ice breakup can also lead to unfavorable conditions when flow regimes change. In extreme cases, both water storage caused by ice jams, and drawdowns when jams break, can lead to fish becoming stranded in dewatered reaches and side channels (Needham and Jones 1959).

Although heterogeneous environments provide sheltering opportunities for salmonids, interspecific competition still occurs. For example, brown trout and Atlantic salmon may compete for shelter in winter (Harwood et al. 2001, 2002), and the competition between these species is often size dependent. Dominance by larger individuals becomes more evident when size differences among fish increase, and at large size differences, dominance is usually established without physical interaction. High growth rate during previous seasons is therefore likely to have positive effects on overwinter survival, as large size helps fish defend resources through increased dominance (Orpwood et al. 2003).

3.3 Diel Activity and Foraging

Diel variation in prey availability, foraging efficiency, and predator exposure influence the behavior of stream salmonids, in general, but perhaps most so during winter (Metcalfe and Thorpe 1992; Bull et al. 1996; Metcalfe et al. 1999; Watz and Piccolo 2011). Stream fishes generally shift from day-active behavior to nocturnal activity at low temperatures (Rimmer and Paim 1990; Heggenes et al. 1993; Fraser et al. 1995; Bremset 2000; Watz et al. 2016). This can be exemplified by the changes that have been reported in diel behavior at the onset of winter in several salmonids, including brown trout (Griffith and Smith 1993; Heggenes et al. 1993; Filipsson et al. 2019), Atlantic salmon (Fraser et al. 1993, 1995), and European grayling (*Thymallus thymallus*) (Nykänen et al. 2004). Similar behavioral changes have also been observed in other stream fishes such as European minnow (*Phoxinus phoxinus*) (Metcalfe and Steele 2001) and galaxiids (David and Closs 2003). In general, during winter, stream fishes stop being active in daylight and instead are active in darkness, whether it be during nighttime or under ice at low temperatures (Heggenes et al. 1993; Fraser et al. 1995; Bremset 2000; Watz et al. 2016). Interestingly, low temperatures can relax intraspecific competition. Alanärä et al. (2001) studied competition between dominant and subordinate brown trout during different seasons and times of day. They showed that trout were temporally segregated when they foraged during summer, with dominant trout foraging at dusk and early night and subordinates in daylight. In winter, this pattern disappeared and all trout foraged during low light conditions regardless of their social status. Thus, the strength of intraspecific competition is reduced at low temperatures, likely as a result of slower metabolism and the reduced need to feed during winter.

At northern latitudes, salmonids experience winter temperatures that are suboptimal for physiological performance. Low temperatures impair locomotion, foraging efficiency, and reaction capabilities in encounters with competitors or predators (Webb 1978; Rimmer et al. 1984; Graham et al. 1996; Alanärä et al. 2001; Jonsson and Jonsson 2011; Watz and Piccolo, 2011; Watz et al. 2012). Performance in relation to predators may be weakened, especially against cold stenothermic (such as burbot, *Lota lota*) and endothermic (such as mustelids) predators. The drift-feeding rate of juvenile salmonids is positively correlated with water temperature in winter as observed empirically in brown trout, Atlantic salmon, and European grayling (Watz et al. 2014a, b). The reduced drift feeding at low temperatures results from reduced energy needs and impaired swimming and prey detection capabilities (Watz and Piccolo 2011). Prey density also seems to play a role in the drift-feeding behavior of juvenile salmonids, as reduced foraging times in cold water are most pronounced, likely due to satiation, when densities of drifting invertebrates are high (Watz et al. 2014a).

Brown trout, Atlantic salmon, and European grayling exhibit higher drift-feeding success in daylight than in darkness (Watz et al. 2014b). Therefore, it is surprising that these species are predominantly nocturnal in winter, when their foraging efficacy would be especially low due to both limited light and low temperature (Watz and Piccolo 2011; Watz et al. 2012; Watz et al. 2014a, b). However, stream fishes usually avoid being active in daylight if their energetic needs can be fulfilled at night, regardless of temperature (Orpwood et al. 2006). This pattern is often explained by the reduced risk of being preyed upon in darkness compared to in daylight. These and other aspects of predator avoidance will be discussed in the next section of this chapter.

3.4 Predator Avoidance

Predators directly impact prey populations by consumption, but also by inducing indirect physiological and behavioral responses that typically vary among individuals (Rehnberg and Schreck 1987; Lima and Dill 1990; Hawkins et al. 2004; McCauley et al. 2011; Vainikka et al. 2021). Predator intimidation affects habitat choice and explains lower foraging activity than expected based on bioenergetic considerations only (Greenberg et al. 1997; Vehanen and Hamari, 2004; Preisser et al. 2005; Orrock et al. 2013; Enefalk et al. 2017; Filipsson et al. 2019). Stream salmonids spend a substantial proportion of time sheltering to avoid predators in winter (Valdimarsson and Metcalfe 1998; Jonsson and Jonsson 2011; Enefalk et al. 2017; Filipsson et al. 2019), and diel activity patterns seem to result from behavioral trade-offs between food intake and predator exposure (Metcalfe et al. 1999). Many semi-aquatic mammals, such as otters (Lutridae) and mink (*Neovison vison*) (Gerell, 1967; Wise et al. 1981; Heggenes and Borgstrøm 1988), or birds, like herons, kingfishers, mergansers, and even certain owls may prey on stream salmonids in winter (Harvey and Nakamoto 2013). Fish are preferred winter prey by some terrestrial generalist predators because of the impaired predator detection and escape capabilities of fish at low temperatures. In addition, terrestrial prey such as reptiles, amphibians, and insects are generally unavailable in winter, which makes fish and river invertebrates the most abundant prey for many winter-active animals (Alexander 1979; Harvey and Nakamoto 2013; Marchand 2014).

Surface ice plays an important role in predator–prey dynamics in winter-time stream ecosystems, as it reduces predation risk, particularly from aerial predators (Huusko et al. 2007; Watz et al. 2013, 2015). Some semi-aquatic mammal predators, such as otters and mink, can forage under the ice. Nevertheless, otters usually exhibit a strong association with ice-free river sections or steeply banked shorelines where they can find access to the water underneath the ice (Melquist and Hornocker 1983; Marchand 2014). Salmonid activity during the day in winter can be positively correlated with surface ice thickness (Linnansaari and Cunjak 2013) and ice cover increases overwinter survival compared to ice-free conditions (Hedger et al. 2013). Exemplifying this, a population of rainbow trout occurring downstream of a dam decreased in size when reservoir water was released, preventing surface ice formation (Simpkins et al. 2000). In a field experiment, Watz et al. (2016) simulated ice cover by covering stream stretches with plastic sheets. Brown trout in uncovered stream stretches stayed closer to the streambanks during the day, often underneath undercut banks. Trout in covered stretches were, on the other hand, observed over the entire stream width. In addition, trout that spent the winter in plastic-covered stream stretches had higher growth rates than trout in areas without plastic sheeting.

Brown trout, Atlantic salmon, and Arctic charr show reduced metabolic rates under simulated ice cover (Finstad et al. 2004b; Helland et al. 2011). Several other studies also suggest that ice cover reduces stress levels, as indicated by body coloration (Watz et al. 2015), opercular beat rate (Millidine et al. 2008; Watz et al. 2013, 2015; Watz 2017), and cortisol levels (Watz 2017). In fact, high levels of stress hormones may directly influence overwinter survival, and artificially elevated cortisol levels correlate positively with winter mortality in brown trout (Midwood et al. 2015), which also exhibits a high expression of cortisol-related genes at low temperatures (Filipsson et al. 2020). In addition, studies have shown that bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarkii*) reduce the time they spend sheltering among instream structures when surface ice is present (Jakober et al. 1998) and that ice cover induces increased swimming activity, foraging intensity, and territoriality in juvenile salmonids (Watz et al. 2013, 2015). As most winter-active terrestrial piscivores such as otters, mink, and birds are visual predators, it is reasonable to assume that stream salmonids exhibit reduced vigilance and stress levels when ice cover is present, as it reduces the predation risk from these animals. Surface ice thus plays a major role in the winter ecology of stream salmonids (Finstad et al. 2007; Huusko et al. 2007; Watz et al. 2016), with bearing on several aspects of their ecology such as diel patterns, activity, habitat choice, and foraging behavior. Reduced surface ice cover, both temporally and spatially, is likely to become more evident in the near future as a result of warming winters. This change to the winter environment is thus likely to have negative effects on the overwinter survival of stream salmonids.

Stream salmonids are not only subjected to aerial and terrestrial predators in winter. There are other threats in the instream environment as well, from which surface ice provides little protection. Piscivorous fish also prey on stream salmonids in winter, and examples of piscivorous fishes in boreal regions include burbot (Tolonen et al. 1999; Kahilainen and Lehtonen 2003), northern pike (*Esox lucius*) (Hyvärinen and Vehanen 2004; Vehanen and Hamari 2004), and various salmonids (Hawkins et al. 2004). In an aquarium experiment, Enefalk et al. (2017) studied the shelter use of juvenile brown trout in winter at different times during the day and in the presence and absence of burbot. More brown trout sheltered among stream wood and within the streambed in daylight than in darkness. Trout sheltered less in the streambed, especially in daylight, when stream wood was available. Trout also avoided sheltering in the streambed in the presence of burbot. Likewise, Filipsson et al. (2019) showed that trout sheltered more under overhead cover in the presence of burbot when the amount of light increased, presumably to avoid terrestrial predators. At night and dawn, trout sheltered less than in daylight, but then instead spatially avoided the burbot. Hence, predator threat from piscivorous fish during winter may be most pronounced in darkness, when neither juvenile salmonids nor piscivorous fish are under strong predation pressure from mammals or birds.

4 Egg Survival and Embryonic Development

Not only do juvenile and adult salmonids inhabit streams in winter but these fishes also have overwintering eggs. Winter-time egg development is a crucial life stage for many salmonids and egg survival can form a significant population regulation bottleneck. Species like Atlantic salmon and brown trout spawn during the fall, deposit their eggs in the stream substrate, and their eggs hatch during late winter or in spring, depending on spawning time and river temperature from fertilization to late winter (Figure 2). The emergence of fry from the substrate occurs in spring or early summer. Many species of Pacific salmonids (such as coho, Chinook *Oncorhynchys tshawytscha*, sockeye *O. nerka,* chum, *O. keta*, and pink *O. gorbuscha* salmon) and chars (such as Arctic char and brook trout) also spawn in running waters during summer or fall and have eggs that hatch during the winter or early spring. Winter conditions can thus have a major impact on salmonid egg development, survival, and the time of emergence (Johnston 2006; Lavery and Cunjak 2019). Lavery and Cunjak (2019) found that several abiotic factors, such as water temperature, water level, dissolved oxygen, ice conditions, and substrate characteristics predicted the egg survival of Atlantic salmon. For instance, in gravel beds with low hyporheic quality and therefore low concentration of dissolved oxygen, Atlantic

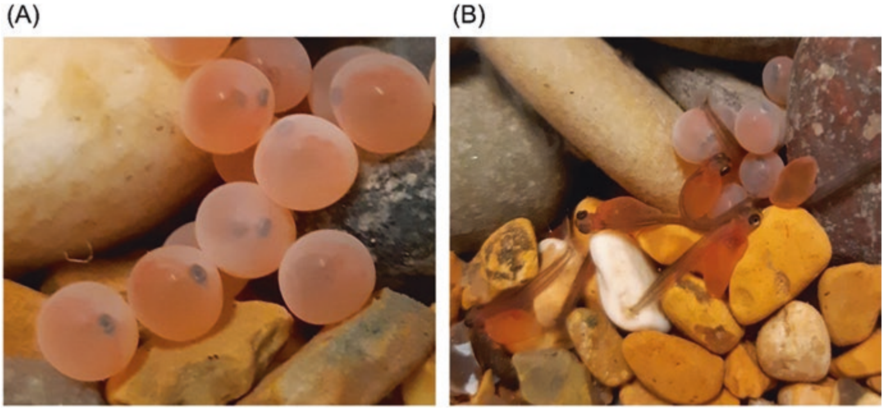


Fig. 2 Brown trout eggs at the eyed stage (A), and newly hatched yolk-sac fry (B) reared in captivity in artificial redds. Trout in the photos originate from the River Klarälven, Sweden, where developing eggs usually reach the eyed stage around the turn of the year and hatch in March–April. Photos: Karl Filipsson

salmon eggs suffer reduced egg survival (Malcolm et al. 2003, 2004, 2005). Lavery and Cunjak (2019) also found that interactions between different environmental factors likely play a major role in egg development, a conclusion drawn from other studies as well. For example, hatching success of Chinook salmon was reduced under hypoxic conditions, but even more so when in combination with warm water (Del Rio et al. 2019). Reduced oxygen concentration in hyporheic water often results from the upwelling of groundwater, causing egg mortality (Malcolm et al. 2004; Youngson et al. 2004; Bowerman et al. 2014), but it is unclear how groundwater–surface water interactions change if winter flow increases in rivers by repeated snow smelting. In ditched forests and peatlands, winter thaws may increase runoff of organic material, which in turn accumulates in bottom substrates, consumes oxygen when decomposing, and hinders water flow through interstitial spaces among gravel particles (Laine et al. 2001).

Temperature has the most important influence on salmonid embryogenesis (Hamor and Garside 1976; Tang et al. 1987; Elliott and Hurley 1998; Ojanguren and Braña 2003; Cingi et al. 2010; Janhunen et al. 2010), which is the case for ectothermic animals in general. Embryonic survival and development are highest at population-specific thermal optima and therefore reduced both at higher and lower temperatures (Ojanguren and Braña 2003; Réalis-Doyelle et al. 2016). Within the species-specific natural thermal range, time to hatching is shorter at higher temperatures. Lower temperatures throughout incubation seem to result in fewer deformities and reduced mortality (Ojanguren and Braña, 2003; Jeuthe et al. 2016; Lee et al. 2016). Temperatures approximately 5–10 °C above natural winter temperatures may result in suppressed development and increased mortality. Strengths of these effects and what thermal range a given species tolerates do, however, vary between species and populations (Janhunen et al. 2010; Lahnsteiner 2012; Réalis-Doyelle et al. 2016). Similarly, temperatures 5–10 °C above natural temperatures at the time of spawning have negative effects on gamete quality and gametogenesis of brown trout, e.g., sperm motility and enzymatic activity, thus affecting survival prior to the commencement of embryogenesis (Lahnsteiner 2012; Lahnsteiner and Mansour 2012). It is thus likely that warming winters can negatively impact the recruitment of autumn-spawning salmonids.

Embryonic temperature has been shown to affect gene expression associated with immunity and stress in brown trout (Meier et al. 2014). Gene expression responses influenced by thermal conditions during embryogenesis have also been found in Atlantic salmon, where salmon embryos subjected to heat shocks exhibited vertebral deformities in subsequent developmental stages. These deformities were related to the reduced expression of two genes that are involved in the proliferation and specification of skeletal cells (Wargelius et al. 2005). In contrast, incubation of lake whitefish (*Coregonus clupeaformis*) eggs at different temperatures exhibited deleterious responses at constant elevated temperatures but not during heat shocks (Lee et al. 2016).

Many animals prey on salmonid eggs, which results in extensive egg mortality during fall and winter. Several fishes and aquatic invertebrates such as cyprinids, cottids, and crayfishes consume salmonid eggs (Ellrott et al. 2007; Johnson et al. 2009; Palm et al. 2009; Findlay et al. 2015). In addition, salmonid eggs can be an important food source for both juvenile and adult salmonids (Johnson and Ringler 1979; Cunjak et al. 1986; Cunjak and Therrien 1998; Gende et al. 2002; Ruff et al. 2011), with reports of salmonid eggs constituting over 90% of the diet of juvenile salmonids during fall (Johnson and Ringler 1979). Hence, predation on salmonid eggs can be considerable and is likely to have major impacts on recruitment dynamics. Atlantic salmon parr feed readily on salmonid eggs in winter, and as eggs are of high caloric content this could possibly increase the likelihood of winter survival if lipid reserves of fish are low (Cunjak and Therrien 1998; Cunjak et al. 1998). As mentioned earlier, predators induce multiple sublethal anti-predator responses (Stoks et al. 2006; McCauley et al. 2011). Conditioning to predator cues during embryogenesis can affect fish after hatching. Rainbow trout juveniles conditioned to northern pike odors during embryogenesis, in combination with conspecific or heterospecific alarm cues, exhibited anti-predator behaviors in the presence of pike (Horn et al. 2019), whereas juvenile rainbow trout not subjected to predator cues as embryos did not react to the presence of pike. Direct embryonic responses to predator presence such as elevated heart rate have also been observed in a few teleost species (Oulton et al. 2013; Atherton and McCormick 2015), but have not been reported for salmonids.

Interestingly, factors affecting egg survival and embryogenesis may not only affect fish during the egg phase, but also various traits later on in ontogeny (Jonsson and Jonsson 2014, 2019), as in the above-mentioned example on predator-conditioned rainbow trout. Not only perceived predation risk during embryogenesis, but also abiotic conditions may impact fish later in life. For example, brown trout reared under hypoxic conditions as eggs exhibited delayed emergence from the streambed when compared to trout from eggs reared under normal oxygen conditions. Hypoxia-reared trout also had reduced swimming activity in encounters with predators and suffered from higher predation mortality as a result (Roussel 2007). Thermal effects during embryogenesis also play a major role in the development of salmonid life-history traits. In Atlantic salmon, higher temperatures during embryogenesis resulted in accelerated growth, and earlier smoltification and sea migration (Jonsson et al. 2005; Finstad and Jonsson 2012; Burgerhout et al. 2017). Differences in growth were still evident in adult salmon, in which they also resulted in larger eggs and higher gonadal mass (Jonsson et al. 2014). Jonsson and Jonsson (2018) studied how embryonic temperature influenced migration behavior of Atlantic salmon. They found that salmon subjected to 3 °C warmer water as eggs returned to the Norwegian coast about 2 weeks later on average during their spawning migration compared to salmon from eggs incubated at natural winter temperatures. In brown trout, juveniles incubated at elevated temperatures as eggs had a lower metabolism than trout from eggs incubated at natural winter temperatures (Durtsche et al. 2021). For sockeye salmon, the swimming performance of the fry is reduced when they are reared at elevated temperatures as eggs (Burt et al. 2011). Temperature during the egg phase may thus have a major impact on the physiology, behavior, and life-history traits of salmonids post-hatching. Warmer winters and their impact on salmonid eggs, juveniles, and adults are likely to become even more evident in the near future as a result of ongoing climate change (IPCC 2021). In fact, the air temperature increase caused by climate change is especially pronounced during winter and at boreal latitudes, a topic we will revisit toward the end of this chapter.

4.1 Embryonic Development and Survival of Brown Trout: Case Studies from Finland

In this section, we present examples where development and survival of brown trout eggs have been quantified in the field in Finland. These examples cover the ecological aspects of egg development and overwinter survival, and some additional methodological and technical considerations.

The area of Finland (337,030 km^2) is representative of northern latitudes, as the country is situated between latitudes 60° and 70° N. Winter (here defined as when the mean air temperature remains below 0 °C) lasts for about 100 days in southern Finland and about 200 days in the north (Finnish Meteorological Institute 2021). Typically, winter begins in mid-October in northern Finland and during November in the rest of the country. Seasonally permanent snow cover is typically found two weeks after the start of the thermic winter, and snow cover is the deepest around mid-March, with an average of 60–90 cm of snow in eastern and northern Finland and 20–30 cm in southwestern Finland (Finnish Meteorological Institute 2021). The lakes and rivers typically freeze over in late November and early December. The coldest temperatures in winter are from −45 °C to −50 °C in Lapland and from −35 °C to −45 °C elsewhere in inland Finland (Finnish Meteorological Institute 2021).

In Finland, the timing of brown trout spawning depends on latitude (Seppovaara 1962; Saraniemi et al. 2008; Niva et al. 2013). The spawning period begins when water temperature is 8−12°C and ends when temperature is 0−2°C (Syrjänen, unpublished). The eggs incubate in well oxygenated gravel, and the alevins typically hatch in March–May in southern Finland and in May–June to the north, depending on the water temperatures (Fig. 3) (Louhi et al. 2008; Syrjänen et al. 2017; Louhi et al. 2010). Alevins emerge from gravel mainly in May in the south and in June in the north. Favorable conditions (i.e., good water quality and suitable water temperatures) in winter and during snowmelt freshets are essential for the development and survival of eggs, and also for parr in the river. Generally, the early life stages, i.e., the eggs, emerging alevins, fry, and young juveniles, experience the highest mortalities (Huusko et al. 2007). However, true estimates of survival in the field are difficult to obtain due to the difficulty of counting eggs without harming them and the harsh winter conditions with ice cover preventing access to spawning sites. In fact, most estimates of survival are based on apparent survival rates (Huusko

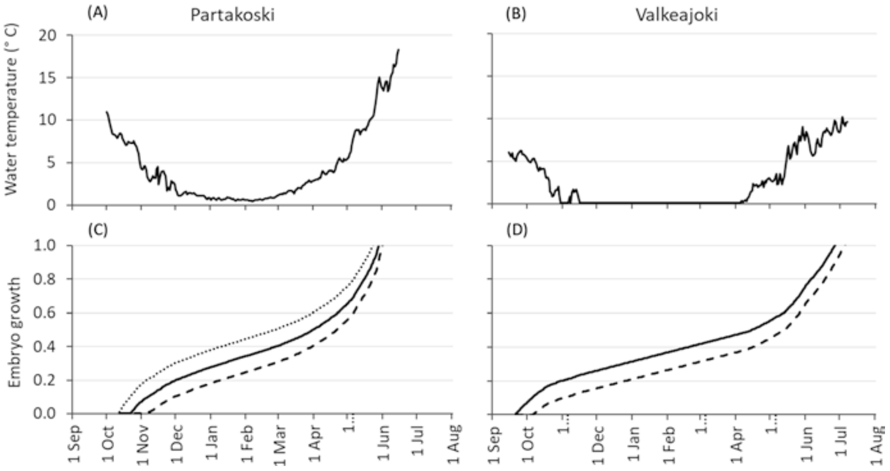


Fig. 3 River water temperature (**a**, **b**) and the progress of wild brown trout embryos (**c**, **d**) from fertilization to emergence in the Partakoski Rapids (61° 16.3’ N, 27° 42.0’ E) in southern Finland in 2017–2018, and the River Valkeajoki (67° 32.6’ N, 23° 54.5’ E) in northern Finland in 2019–2020. The fertilization period, that is the spawning period, was estimated with repeated redd counting in the study reaches and marking of new redds. The development of embryos was followed during the counting rounds when the earliest redds (dotted line), the highest number of redds (solid line), and the latest redds (dashed line), were found. The emergence day for alevins was estimated using the equation of Elliott and Hurley (1998), which reflects the consumption of yolk, or the growth of embryo, from fertilization to emergence. The average estimate (E_{50}, see Elliott and Hurley, 1998) was used, which reflects the day when half of the alevins from redds of each counting round had emerged. On the day of spawning and fertilization, the E_{50} was set to 0. Then, the daily development was calculated with the daily temperature value and added to the E_{50} of the day before. The yolk is absorbed, and emergence occurs the day when the cumulative sum reaches 1

et al. 2007), and few studies have actually compared survival rates of juveniles between winter and other seasons (Carlson and Letcher 2003; Carlson et al. 2008). Another difficulty in obtaining representative mortality estimates relates to the fact that most salmonids in southern Finland are of hatchery origin and known to display much reduced survival in the wild compared to native, wild populations (Syrjänen et al. 2017).

Mortality of embryos from fertilization to near hatching or to near emergence has often been studied in incubation chambers using hatchery-produced eggs deposited in natural streams (Syrjänen et al. 2017; Arola et al. 2019). The experimental design most often has included several plastic net cylinders filled with gravel, and 50 eggs in each cylinder. Cylinders have been placed in net baskets on the channel bottom of riffles in similar microenvironments where natural trout redds are situated. The survival of embryos has varied strongly between the studies and sites. Survival has been 85–98% in oligotrophic unregulated lake outlet rivers with stable channel substratum (Syrjänen et al. 2017), and 30–50% in forest streams that have ditched catchments and acidic water (Arola et al. 2019). The lowest documented survival levels, 0–10%, have been observed in streams with unstable substratum, i.e., sand that moves on the stream bottom and fills spaces between gravel particles and the eggs in the incubation cylinders (Arola et al. 2019), or streams situated downstream from peat mining sites (Laine et al. 2001).

Estimates of in situ growth of embryos have been performed in artificial incubation chambers by inspecting and lifting the chambers regularly throughout winter and spring (Syrjänen et al. 2008). Embryo development begins in autumn immediately after fertilization if water temperature is several degrees but slows gradually following a decrease in water temperature. In mid-winter, i.e., from December to February, development is very slow, as the water temperature is mainly 0–1 °C. In the spring, development accelerates again following a gradually rising temperature. The embryos mainly hatch from March to May, depending on degree days, latitude and distance to an upstream lake. In southern Finland, alevins in experiments have been estimated to emerge in late May and early June, but this may vary between years (Syrjänen et al. 2017).

A method to observe wild embryos in redds has been developed in recent years (Syrjänen, unpublished). In this method, the researcher systematically wades through the study riffles and inspects each redd encountered. This is done in November or December. The redds are verified by careful digging and visual confirmation of 2–3 eggs. The detected redds are marked on digital maps as well as with white-painted and numbered marker stones, in the field. The stone is placed precisely at the point where the eggs were found. The redds are visited again in April, May, or June, depending on the latitude and timing of freshets. Again, the redd is opened carefully, beginning from the marker stone so that 4–10 embryos are identified either in the gravel or are captured in a hand net positioned just downstream from the marker stone. If most or all of the exposed embryos are dead, the redd can be opened more to observe a larger number of embryos. Thus, the sample size per redd is often small, and only embryos situated nearest to the gravel surface are observed. There might be some differences in survival with redd depth, but this has not been studied. However, survival estimates with this method, as based on direct counting of live and dead eggs in spring, have been similar to egg incubation experiments conducted in natural rivers, as described earlier.

In most unregulated clearwater rivers and rapids, the average percentage of live embryos per redd (n = 5–30 in each case), hatched or unhatched, has been 85–100% of all observed embryos. In contrast, the proportion of live embryos has varied between 30 and 90% in riffle sections downstream of a hydroelectric power station. Observations have been made in two highly regulated Finnish rivers, in Ämmäkoski (in the city of Varkaus), Leppävirta watercourse and in Laurinvirta (in the city of Kontiolahti), Pielisjoki, both situated in the Vuoksi watershed, eastern Finland as well as in a regulated river with stable flow, i.e., Gullspångsälven, a tributary of Lake Vänern, Sweden. There may, of course, be other factors than fluctuating discharge affecting egg mortality in these regulated rapids, like the size of particles used in artificial gravel beds created when restoring the rapids or the amount of fine organic matter.

The development rate of wild embryos can be high already in autumn, which has been seen in redds during November or December, as eyes of embryos can often be observed through the eggshell when the embryos are 10–15 mm long. In some extreme cases in southern Finland, some alevins have been observed already in December. These may represent offspring from fish that spawned very early in the season at water temperatures of 10–12 °C. It is also common that the embryos are not visible in autumn, and these eggs may represent fish spawning later in the season at water temperatures of 0–2 °C. Some observations in 2017–2019 have shown that the spawning period may occur later, based on observations made in the twentieth century (Syrjänen, unpublished).

There are some unpublished survival estimates of wild brown trout from fertilization to parr (first autumn values) from southern Finland (Figure 4). Egg density in the study areas was calculated by counting the number of trout redds and measuring the tail lengths of the observed redds and estimating the lengths of female spawners (Crisp and Carling 1989; Elliott 1995; Syrjänen et al. 2014). The density of 0-year-old parr was estimated by electrofishing in the standard sampling areas located inside the redd counting areas, and the density estimates were corrected and calculated with catchability values estimated in the same rivers. The range in survival from egg to parr was large, i.e., 0–21% between years in three riffle sections in the River Rutajoki (n_{years} = 17–21), two sections in the River Arvaja (n_{years} = 11–12), and two sections in the River Saajoki (n_{years} = 4), all small rivers discharging to Lake Päijänne (Figure 4). The average density of 0-year-old trout parr was 1–23 ind./100 m^2 between the study reaches in the rivers, estimated by catchability, indicating incomplete parr production compared to the potential of riffles as parr habitats. One main reason for this is the lack of lake migrating females because of high fishing mortality in lakes (Syrjänen and Valkeajärvi 2010). Unfortunately, no estimate of winter survival of wild embryos exists for these rivers, but in incubation experiments, survival of hatchery eggs from fertilization to May was high (Syrjänen et al. 2008). Mortality is probably high during emergence and the period immediately after (Cattanéo et al. 2002; Lobón-Cerviá 2004). Possible factors affecting

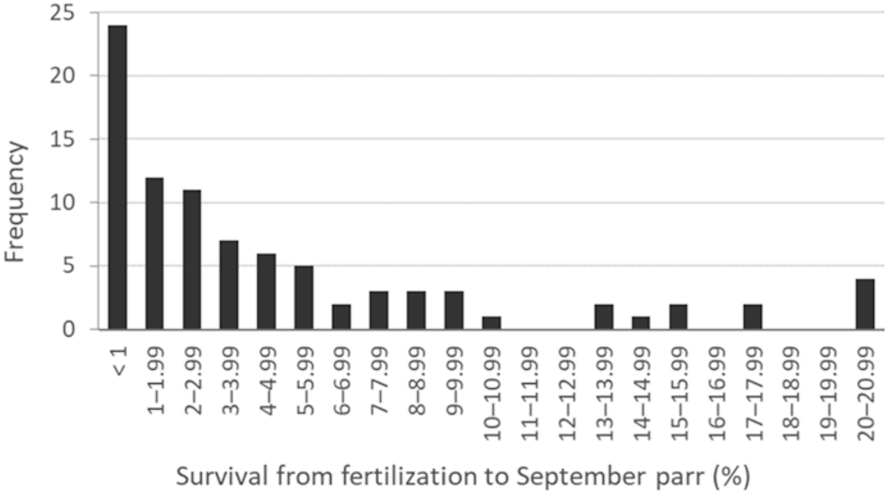


Fig. 4 Apparent survival estimates of brown trout from fertilization to parr (the following autumn) from Rivers Rutajoki (three riffle sections, 17–21 years in each section), Arvaja (two riffle sections, 11–12 years), and Saajoki (two riffle sections, 4 years) in southern Finland. Total number of observation years = 88

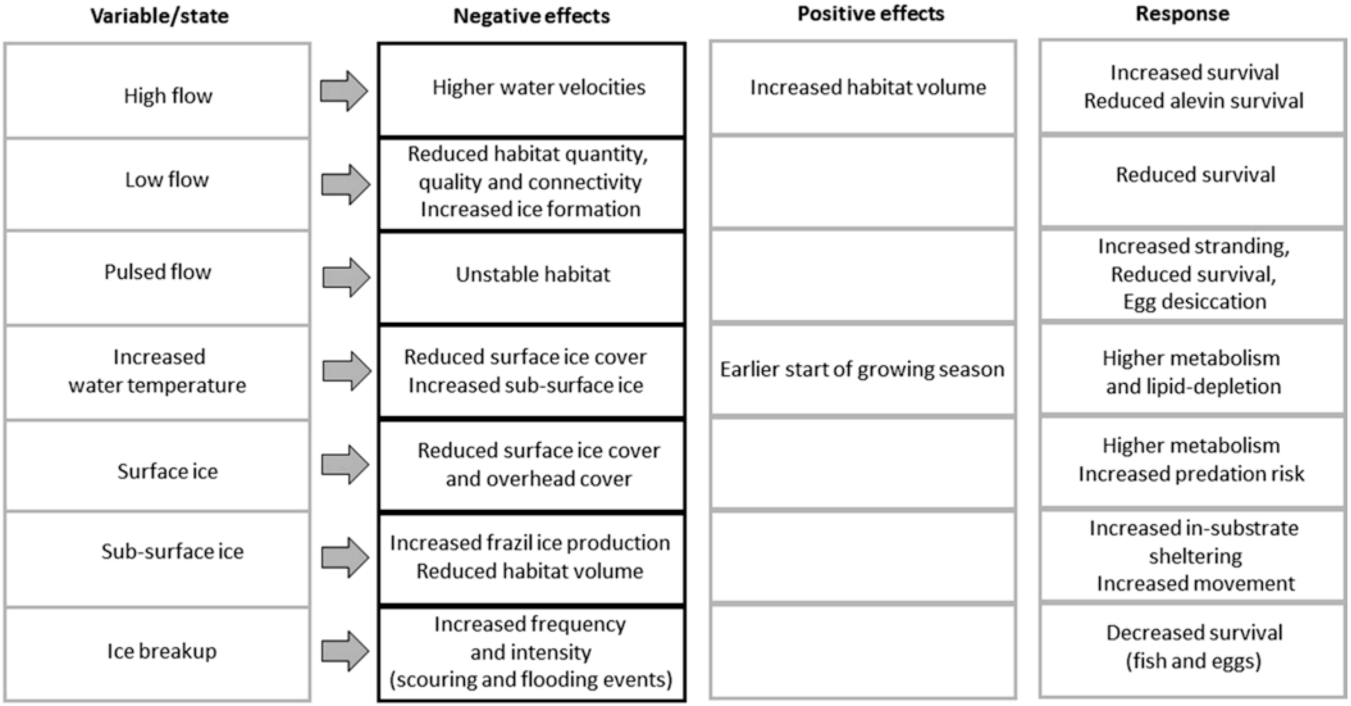
annual variation in egg-to-parr survival could be water temperature, river discharge, and fish predation during the emergence period. Unfortunately, during and just after emergence, survival estimates from nature are rare. Young parr are small and difficult to observe, so the density is difficult to estimate reliably at that point of the life cycle.

5 Regulated Rivers in Winter

Hydropower is a renewable energy source with substantial societal benefits, but it also has severe impacts on the riverine biota, particularly migratory fish (Soininen et al. 2019). The question that historically has attracted the most attention is the impact hydropower stations and dams have on fish migration and how to minimize this impact (Banks 1969). Dams and hydropower stations change the habitat and block movement to and from the natural spawning and feeding grounds for both upstream and downstream migrating fish, and therefore both technical and nature-like bypasses have been developed to facilitate migration of fish at hydropower stations (Clay 1995; Larinier and Marmulla 2004). Environmental impacts are likely to be complex in systems extensively regulated for hydropower, altering biodiversity and even life histories of the impacted species (Gillespie et al. 2015; Poff and Zimmerman 2010; White et al. 2017). The regulation system and operational strategy are the main drivers behind hydrological changes. Regulation systems can typically be divided into (1) high-head systems and (2) low-head or run-of-the river systems (Heggenes et al. 2018). High-head systems have high-elevation reservoirs and long transfer tunnels to the power station with bypass reaches receiving reduced residual or stable environmental flows. Empirical knowledge on the effects of short- and long-term regulation of flow and changes in water temperature on salmonid performance, survival, and production is relatively limited (Heggenes et al. 2018, 2021).

Winter river ice formation in naturally flowing rivers can be divided into (1) the dynamic period "freeze-up" in early winter with sub-surface ice, (2) more stable "mid-winter" with surface ice, and (3) the ecologically challenging "ice breakup" in late winter with potential mechanical ice runs and scouring (Turcotte and Morse 2013). The duration of these periods varies depending on prevailing climate. Flow regulation in hydropower production modifies these conditions, particularly in reaches downstream of power station outlets. This is caused by increased flow, higher water temperatures, reduced surface ice formation and increased sub-surface ice formation, and in bypass reaches by decreased flow and enhanced freezing. The stable mid-winter ice periods may be replaced by repeated unstable transition periods (i.e., repeated freeze-ups and breakups) or ice may become completely absent (Stickler and Alfredsen 2009; Gebre et al. 2013; Prowse et al. 2011; Weber et al. 2013). To this end, the environment downstream of hydropower stations in winter looks much like the changes forecasted by climate warming (Heino et al. 2016). In high-head hydropower regulation with large storage capacity and thermal stratification in the reservoirs, downstream effects from the power stations are stronger than in low-head systems. The latter may have small or no major impacts on downstream ice conditions and water temperature due to usually limited water storage capacity (Olden and Naiman 2010; Dickson et al. 2012). Systems with hydropeaking (pulsed flow regimes) are characterized by rapidly changing high and low flows, depending on down-ramping rate, ramping amplitude, and timing of pulses, creating unstable habitat conditions. In rivers with hydropeaking, flow changes typically match the demands in electricity consumption with high flows during day and low flows during night. Hydropeaking can have negative effects on salmonid populations, for example, by reducing overwinter survival, and has many ecologically harmful effects on river ecosystems (Puffer et al. 2015; Smokorowski 2022; Batalla et al. 2021).

Fish may suffer or benefit from winter flow regimes modified by hydropower, as regulation directly modifies stream habitat and thereby fish behavior, survival, and production, thus resulting in a variety of biological responses (Heggenes et al. 2018, 2021). In winter, the impacts are mainly related to higher downstream water temperatures and flows, or reduced water flow in bypass reaches, and associated changes in ice (Fig. 5). Flow and ice directly affect spatial habitat conditions for fish, and thereby fish behavior and activity, but temperature also directly affects fish metabolism (Shuter et al. 2012; Heggenes et al. 2018, 2021). Higher flows in winter may increase rearing and/or resting habitat, which may potentially benefit fish survival (Forseth and Harby 2014). Low flows may increase ice formation, reduce and fragment available habitat, and may reduce egg and fish survival. Sudden drawdowns of flow during daytime may result in fish stranding as the fish are less inclined to move



Variable/state	Negative effects	Positive effects	Response
High flow	Higher water velocities	Increased habitat volume	Increased survival Reduced alevin survival
Low flow	Reduced habitat quantity, quality and connectivity Increased ice formation		Reduced survival
Pulsed flow	Unstable habitat		Increased stranding, Reduced survival, Egg desiccation
Increased water temperature	Reduced surface ice cover Increased sub-surface ice	Earlier start of growing season	Higher metabolism and lipid-depletion
Surface ice	Reduced surface ice cover and overhead cover		Higher metabolism Increased predation risk
Sub-surface ice	Increased frazil ice production Reduced habitat volume		Increased in-substrate sheltering Increased movement
Ice breakup	Increased frequency and intensity (scouring and flooding events)		Decreased survival (fish and eggs)

Fig. 5 Impacts of winter flow regulation for hydropower on river habitat and potential salmonid responses (adapted from Heggenes et al. 2018)

and seek shelter during the day (Saltveit et al. 2001; Halleraker et al. 2003). To this end, Halleraker et al. (2003) recommended dewatering in darkness at all times of year to reduce stranding of salmonids, and to use slow ramping rates <10 cm h^{-1} (i.e., the rate of change of water level). If flow during the spawning season is higher than the minimum maintained flow during winter, dewatering and mortality of eggs are often unavoidable (see the section "Embryonic development and survival of brown trout—case studies from Finland" in this chapter). Forseth and Harby (2014) summarized that a reduction of over 30 cm in water level from the spawning period average to the lowest weekly average during winter potentially causes a moderate to severe bottleneck for egg survival, although this is dependent on the occurrence and distribution of spawning areas. Casas-Mulet et al. (2015) reported about 20% lower survival of Atlantic salmon eggs in the top layers of gravel beds in the dewatered areas. However, deeper in the gravel beds, due to surface water and groundwater interactions, egg survival was comparable to permanently wet areas. Embryo development is linked to water temperature, with warmer temperatures shortening incubation time and advancing alevin emergence, which leads to a potential mismatch in the emergence time and food availability for the fry (Shuter et al. 2012; Myers et al. 2017). The impact of altered case-specific temperature regimes on embryo development and the timing of initial feeding ("swim-up") can be estimated using, e.g., the model of Crisp (1988) or Elliott and Hurley (1998).

6 Winter Ecology and Climate Change

6.1 Warming Winters

Global climate change is likely the most widespread anthropogenic threat to the environment and to biodiversity. During the last century, the global mean temperature has increased by ~1 °C, with the most accelerated temperature increase after 1970 (Hansen et al. 2010; IPCC 2021). Importantly, the temperature increase varies geographically, where mean air temperatures at northern latitudes are increasing more than twice as fast as the mean global temperature increase. In the last decades, an air temperature increase of 2–3 °C has been reported in the Arctic and boreal regions, with the largest increases in winter and spring (Brown 2000; Marchand 2014; IPCC 2021). This has resulted in warmer winters with more precipitation, whether it be snow or rain, or extremely variable, both spatially and temporally (Magnuson et al. 2000; Smol et al. 2005; Jonsson and Jonsson 2009; Callaghan et al. 2011; Walsh et al. 2011; Kang et al. 2016).

Warming of the climate leads to the loss of snow and ice cover, especially at the southernmost limits where snow covered winters occur. A lack of snow cover results in reduced albedo and causes a feedback loop that accelerates warming. Albedo is a measure of how much solar radiation that is reflected from a given surface. Dark surfaces such as water and soil have low albedo and thus absorb a high proportion of solar radiation. White surfaces such as snow and ice reflect solar radiation and instead have high albedo. Thus, snow and ice, with their high albedo, have the potential to suppress air temperatures by as much as 4–8 °C. The lack of snow and ice therefore results in higher winter temperatures (Leathers and Robinson 1993; Choi et al. 2010; Marchand 2014). Climate change can thus accelerate thawing of permafrost in the Arctic. This subsequently releases methane from soil and water, which accelerates the greenhouse effect through a positive feedback loop (Christensen et al. 2004; Kort et al. 2012). Loss of albedo results in spatial and temporal asymmetries of climate change and will likely lead to even warmer winters during the coming decades. For example, snow cover duration in Scandinavia is projected to decrease by 30–40% by 2050 (Callaghan et al. 2011).

Stream hydrology is also predicted to change when winters get warmer. Fluctuations both in winter temperatures and discharge may lead to repeated ice formation and breakup throughout winter (Magnuson et al. 2000; Döll and Zhang 2010; Pörtner and Peck 2010; Tisseuil et al. 2012; Schneider et al. 2013; van Vliet et al. 2013a, b). In the northern hemisphere, later freezing and earlier breakup dates for stream and lake ice have been recorded throughout the twentieth century (Magnuson et al. 2000). As mentioned previously in this chapter, loss of surface ice cover can negatively affect the growth and survival of overwintering stream salmonids (Härkönen et al. 2021). Conditions can be further exacerbated in regulated rivers due to fluctuations in discharge and water temperature, resulting in longer periods without ice cover or repeated ice formation and breakup throughout winter (Simpkins et al. 2000; Ugedal et al. 2008; Gebre et al. 2013; Nafziger et al. 2017; Heggenes et al. 2018, 2021).

6.2 Winter Ecology of Salmonids Under Climate Change

In the last decades, climate change effects on salmonids have received considerable attention. With this in mind, we will only present research that has examined how climate change directly affects the winter ecology of stream salmonids. Therefore, subjects such as phenological mismatches that often are discussed in relation to the ecology of anadromous salmonids during other seasons (Pörtner and Peck 2010; Donnelly et al. 2011; Bell et al. 2017; Myers et al. 2017) will not be our focus.

Climate change is projected to alter the structure and dynamics of fish communities (Buisson et al. 2008; Williams et al. 2009; Linnansaari and Cunjak 2012; Shuter et al. 2012; Wobus et al. 2015), which leads to major changes in freshwater ecosystems (Smol et al. 2005; Woodward et al. 2010; Shuter et al. 2012, Heino et al. 2016). This includes thermal effects on aspects of fish ecology during the entire life cycle, including reproduction, embryonic development, migration, invasive species resistance, species distributions, and trophic dynamics (Stenseth et al. 2002; Jonsson and Jonsson 2009; Wedekind and Küng 2010; Brodersen et al. 2011; Cahill et al. 2012; Bhat et al. 2014; Morita et al. 2014; Chown et al. 2015; Trigal and Degerman 2015, Heggenes et al. 2021). Taking embryonic development as an example, the development and survival of salmonid embryos depend heavily on abiotic conditions throughout winter. Higher winter temperatures expedite embryogenesis, with the possible effects on embryo condition and development as mentioned in the section about egg survival and embryonic development in this chapter. Warmer winters also mean less snow and with that, more rain (IPCC 2021). Cunjak et al. (1998) found that high egg mortality of Atlantic salmon was caused by rain on snow, as it resulted in ice scouring of the streambed, including the salmon spawning redds. Highest mortality occurred during a mid-winter thaw and breakup, when high discharge was confined to the river channel, constrained by frozen ice and snow banks. Hence, mortality of salmonids eggs and fry is likely to be higher as winter temperatures increase in northern rivers. Warming winters may also affect spawners and may in many cases lead to later spawning. This seems especially likely considering that these reproductive traits are under strong selection pressure (Hendry and Day 2005; Carlson and Seamons 2008). Energy consumption is likely to increase in spawners when temperatures rise, and there are studies on salmonids that show how spawning survival is reduced when energetic costs are high (Jonsson et al. 1997).

Thermal effects on biotic interactions are also likely to be a consequence of the changing climate and may in many cases have more pronounced ecological repercussions than the direct impact of elevated temperatures. One example would be the aforementioned consequences of reduced surface ice coverage on salmonid mortality during winter, where less ice makes fish vulnerable to aerial and terrestrial predators. Indirect effects on biotic interactions not only include predator–prey interactions, but also interspecific competition. Arctic char exhibits both greater foraging efficiency and growth in winter compared to sympatric brown trout (Helland et al. 2011). In a study of 190 Norwegian lakes, ice cover duration correlated negatively with brown trout biomass, but only in lakes where trout occurred in sympatry with char. Ice cover duration did not affect brown trout biomass in lakes without other fishes. Similarly, a high abundance of Arctic char was associated with low trout population growth only when ice cover was present. This suggests that elevated temperatures and loss of surface ice cover will benefit brown trout at the cost of Arctic char (Helland et al. 2011; Ulvan et al. 2012). In fact, some anadromous Arctic char populations that live in sympatry with Atlantic salmon in northern Norway have decreased in size, possibly as salmon are enjoying a competitive benefit over char by their better resistance to climate warming in this region. Interestingly, a positive correlation between growth and summer temperatures was found for both salmon and char, but salmon had higher growth rates (Svenning et al. 2016).

Different species also have different thermal optima for physiological processes (e.g., locomotion and reproduction). These interspecific differences may lead to thermal asymmetries in biotic interactions, such as those between predator and prey. In studies of predator–prey interactions between northern pike and brown trout, water temperature has been a major predictor of the outcome of the interaction. Öhlund et al. (2015) found a threshold temperature of 11 °C, under which the attack success of pike was significantly reduced compared to the ability of brown trout to avoid the pike. Above 11 °C, the performance of pike and brown trout was approximately equal and other factors were likely to influence the outcome of the predator–prey interaction. Interestingly, the results of this experimental study are consistent with field observations from small lakes in northern Scandinavia, where pike and brown trout occur in sympatry in cold water lakes but not in warm water ones (Hein et al. 2013).

In addition to the direct effects of warmer winters, warmer summers may also affect overwintering salmonids. Periods with extremely high summer water temperatures result in reduced availability of preferred thermal habitats or absence of suitable riverine habitats altogether, with consequences for the balance between anabolism and catabolism, foraging opportunities and growth. This could consequently result in reduced growth and fecundity, and decreased accumulation of fat reserves. As size and energy stores can be crucial for the survival of juvenile salmonids in winter (Finstad et al. 2004a), this could negatively affect salmonid populations as the climate gets warmer. High summer stream temperatures may also affect spawning (Mantua et al. 2010; Warren et al. 2012). A study on brook trout in eastern North America showed that high summer temperatures delayed spawning and also correlated with a lower number of spawning redds. This particular population of lake-spawning brook trout spawns in areas with discharging groundwater that has relatively constant winter temperatures, which results in consistent times for egg incubation. Hence, delayed spawning could cause delayed fry emergence and possible mismatches with the occurrence of suitable food for salmonid fry (Warren et al. 2012). This highlights how the temperatures that salmonids experience during summer could influence both recruitment success and overwintering survival at mobile life stages.

7 Brown Trout and Warming Winters: Examples from Finland

Here, we present case studies of brown trout survival during winter from Finland. We compare apparent survival of brown trout during winter to other seasons, and use data on egg and fry survival to model the impact of climate change on the survival of brown trout.

Brown trout is native to Finland, with a distribution covering all of Eastern Fennoscandia (Kaukoranta et al. 1998). Throughout Finland, brown trout forms resident, mainly riverine populations, and migratory populations that feed in the sea (anadromous brown trout), large lakes (adfluvial brown trout), or larger riverine sections (potamodromous brown trout) (Huusko et al. 2018; Syrjänen et al. 2017; Rasmussen et al. 2019). Both resident and migratory individuals are found in sympatry in many systems. To compare apparent survival during winter with other seasons, we monitored the densities of brown trout juveniles for nine years (1999–2007) in six small forest streams (second-to-third order streams) with stable ice cover, situated in northeastern Finland (Figure 6). In a representative reach (~100 m long), containing several riffle-pool sequences, fish densities in each rapid were monitored

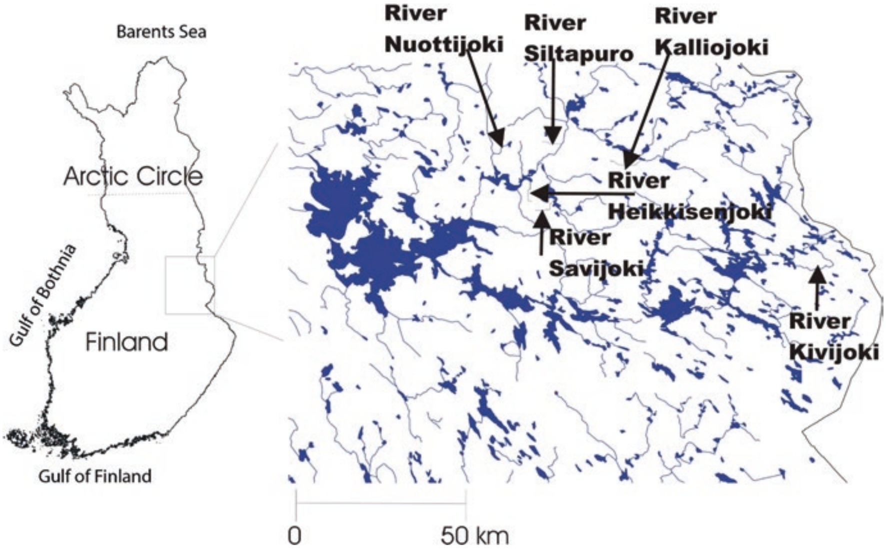


Fig. 6 Location of the six study streams

three times a year (June, August, October) using quantitative electrofishing (Vehanen et al. 2010; Louhi et al. 2016). The weight, length, and age (scale samples) of all fish caught were measured and fish densities were estimated by age group (Zippin 1956). Instantaneous daily loss rate (M_i, per day) was calculated for each period as $[\ln(N_{\text{initial}}) - \ln(N_{\text{final}})] \times (D_{\text{final}} - D_{\text{initial}})^{-1}$, where N is the density of parr observed, and D is the day of year. As the populations of brown trout in the study streams were very sparse in the beginning of the study, each study section was stocked with age-0 migratory brown trout (adipose fin clipped) at equal density (0.35 fish m^{-2}) every September, starting from 1998. The maximum summer water temperatures in the study rivers typically remained below 20 °C in July–August, and winter water temperatures were close to 0 °C.

Densities of stocked age-0+ brown trout declined substantially within one month following their release in September, indicating a high post-release natural mortality (Figure 7). The highest instant loss rates for hatchery trout were observed during this period (Figure 7). During October to June, i.e., the first winter, the densities declined noticeably, but instant daily loss rates were lower than in the fall. June to August had the highest survival for age-1+ and 2+ fish, but during August to October the loss rates increased again, with levels higher than winter (Figure 7).

In general, the densities of the age-0+ wild brown trout were low, and lower than the stocked fish of similar age (Figure 7). We assumed that the declines in densities of wild trout had already occurred before our first sampling in June, presumably during post-hatch stages in spring. The early life stages generally experience the highest mortalities (Huusko et al. 2007; Hayes et al. 2019). Thus, the instant loss rates for natural fish in our study were relatively low, and especially low during winter and summer (Figure 7). During autumn the loss rates, as

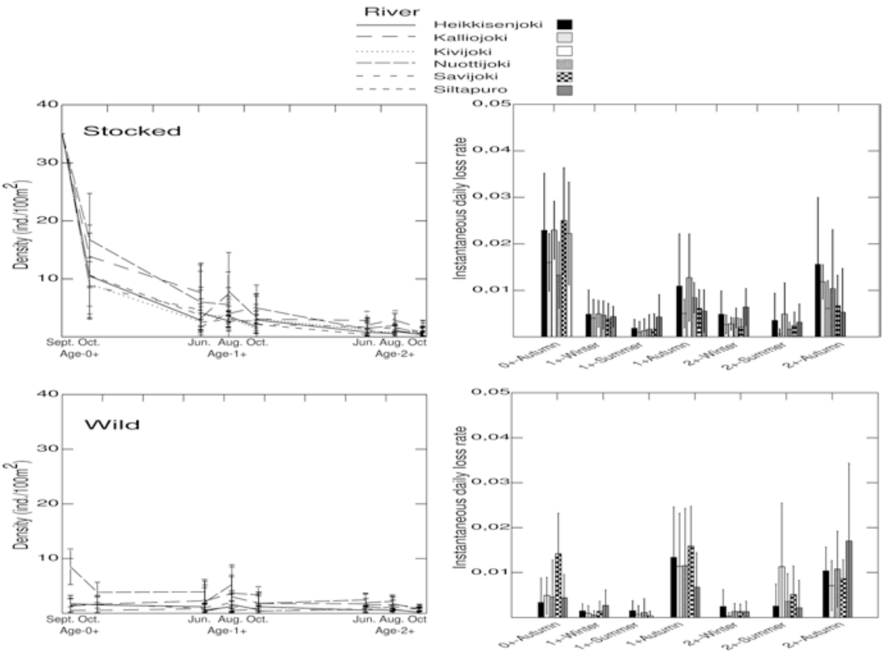


Fig. 7 Mean densities (mean ± SD, left panel) and instantaneous daily loss rates (mean ± SD, right panel) of brown trout in study streams. The upper panel shows the stocked fish (initial stocking density 35 ind./100 m^2), and the lower the wild brown trout

observed for stocked fish, increased. To conclude, our results from stocked and wild brown trout suggested that winter was not a period of especially high mortality in small streams under stable ice cover, when the duration of the period was considered.

We correlated the amount of precipitation (mm, sum) during September–October with the densities of 0+ natural wild fish (pooled from all rivers and over August and October samplings). There was a significant correlation between the September−October precipitation and the mean brown trout density of 0+-fish from the following year for the period 1999−2007 ($r = 0.74$, $p = 0.023$, $N = 9$) (Fig. 8). During a year with an exceptional drought, the brown trout year classes were at their lowest during the period monitored (Vehanen et al. 2010). Increased autumn stream flow due to precipitation increases potential spawning areas and can also support migrating spawning adults to reach these small streams (e.g., Kanno et al. 2014). We expect that this relationship between year class strength and autumn precipitation persisted, because winter water temperatures (Vehanen et al. 2010), and obviously also discharge conditions, remained constant under ice and snow cover. Winter conditions, such as water temperature, water level, and ice conditions, can have a large impact on salmonid egg survival (Kanno et al. 2016; Lavery and Cunjak 2019). Climate change is expected to shorten the

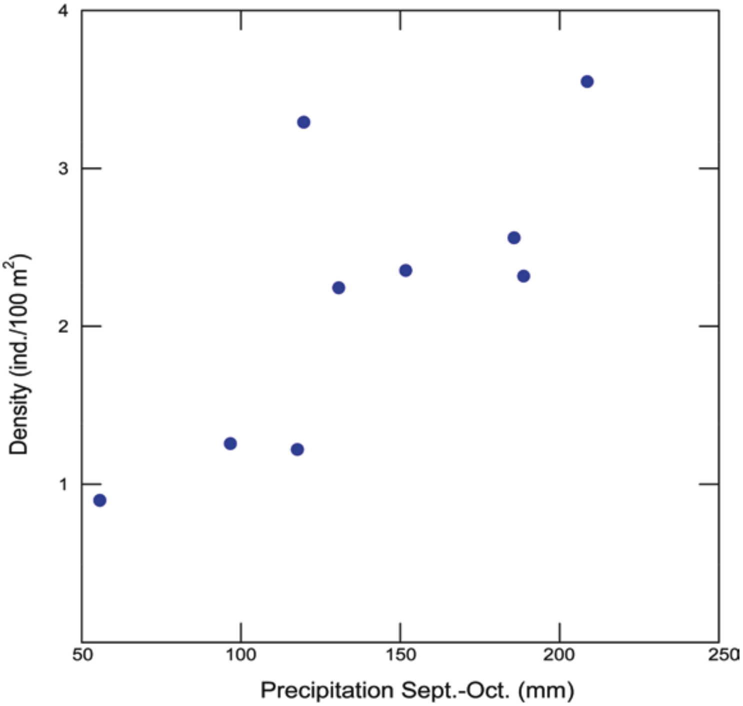


Fig. 8 Correlation between autumn precipitation (September-October, mm) and the mean density of natural wild brown trout populations in six study streams in Finland during study years 1999–2007

period of ice cover and increase winter rains, which can have a negative effect on egg survival in the future.

7.1 Modelling the Impacts of Climate Change

Factors such as increasingly frequent winter floods with potentially increased scouring (i.e., physical destruction of the eggs close to the gravel surface due to the erosion of the surface material), lack of surface ice cover and increasing runoff of fine sediments and organic material from terrestrial systems, caused by climate change, are all expected to decrease the survival of eggs, fry, and small parr (Montgomery et al. 1996; Cocchiglia et al. 2012; Gauthey et al. 2017; Junker et al. 2015). This may well be emphasized in dredged or poorly restored narrow river channels, and in dredged catchments. In some cold water locations, climate change might improve summer-time growth conditions for brown trout (optimum growth temperatures 15.4°C–19.1°C) (Forseth et al. 2009), but other effects, occurring via changes in egg and fry survival, might override the growth-related population-level effects. Thus, to quantify the population-level consequences of potential changes in winter-time survival of the developing eggs, we simulated an age-structured brown trout population model, parameterized for the Finnish–Russian River Oulanka system (see Syrjänen et al. 2017 for the model description) over a range of survival proportions from egg- to 1-year-old parr. Assuming constant mortality during other seasons, this parameter reflects changes in the winter-time survival of the developing eggs.

Through simulations with first-year survival varying from 1 to 30%, we showed that small changes in winter-time survival of eggs can have major population-level consequences (Figure 9a–c). In natural conditions, the critical egg-to-fry survival rate appears to be between 1 and 5%, while compensatory recruitment processes through Beverton-Holt type recruitment dampen potential effects at higher survival rates when the stock is close to the carrying capacity and the finite reproduction areas limit the total production of recruits (Figure 9a–c).

Simulations show that fishing at an annual instantaneous rate of 0.5 y^{-1} (i.e., 39% annual mortality) and a minimum size limit of 600 mm, gives a rapid increase in the population when the egg survival increases from 5% to approximately 10% (Figure 10a–c, see also Syrjänen et al. 2017). A fishing mortality rate of 0.5 y^{-1} but with a minimum size limit of 500 mm would require first-year survival of ~10% to sustain production (Figure 10d–f). In a scenario with historical brown trout fisheries management in Finland, i.e., with a fishing mortality rate of 1.0 y^{-1} (63%) and minimum size limit of 350 mm, the Oulanka brown trout population would likely become extinct even at first-year survival proportions up to 30% (Figure 10g–i). This result highlights the potential importance of ensuring low fishing pressure on populations under environmental stress during the first year of life. Thus, historical fishing regimes, rather than climate change, explain the poor historical trends of brown trout stocks in Finland.

The steep, nonlinear dependence of population metrics on first-year survival suggests that rather small environmentally driven changes in the survival of the early life stages of brown trout can have abrupt and detrimental effects at the population level if the winter time survival of eggs, alevins, and fry decreases due to environmental changes beyond the tipping point. Thus, this simple modelling exercise calls for better monitoring of egg and fry survival in natural waters under climate change. As we used rather conservative estimates of parr and smolt survival rates in the model (see Syrjänen et al. 2017 for the full parameter table), the absolute estimate of the critical 10% survival might be too pessimistic. Available data, for example, from the brooks of Gotland and rivers of the Pyrenean piedmont, suggest that this criterion is easily met in good quality spawning environments with egg-to-fry survival rates over 50% (Rubin and Glimsäter 1996; Dumas et al. 2007). Yet, the Finnish examples described in this chapter suggest that poor habitat quality may prevent recovery of many southern brown trout populations (see the previous section on embryonic development and survival of brown trout in this chapter).

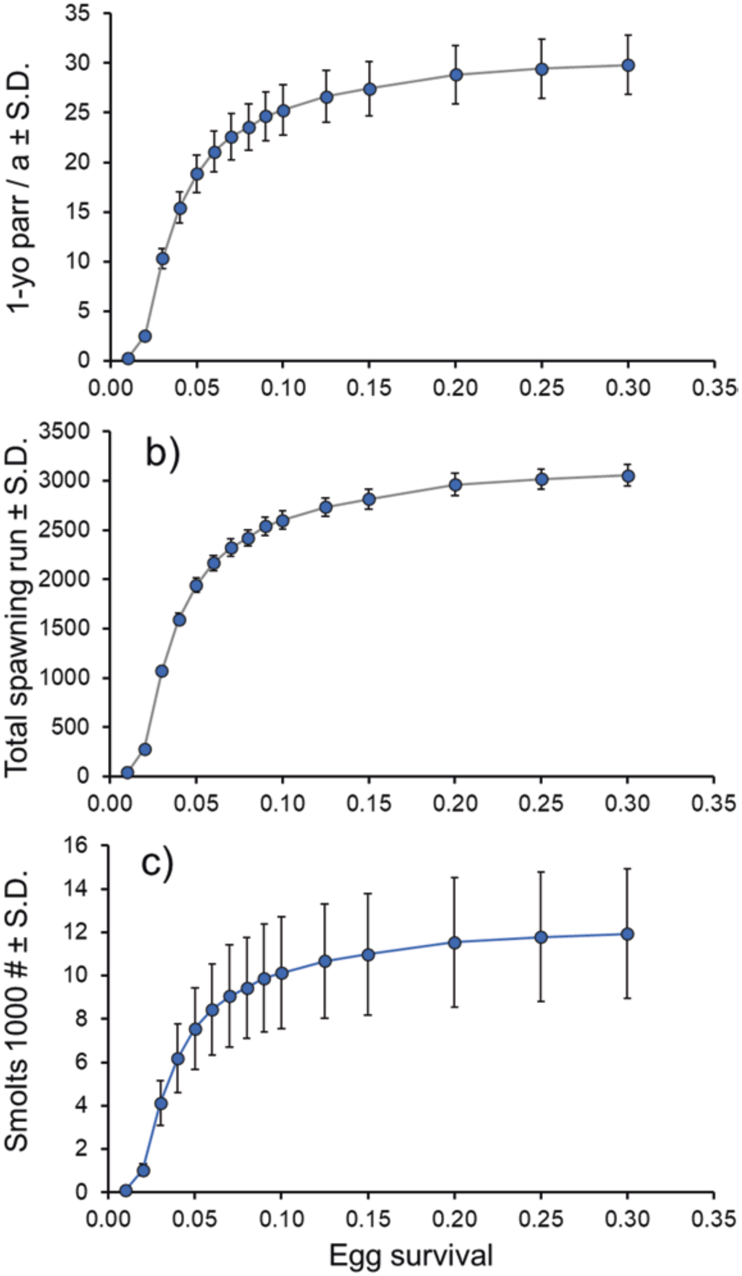


Fig. 9 The effect of varying egg survival on River Oulanka brown trout stocks as derived from the age-structured population models of Syrjänen et al. (2017). The standard deviation represents an average S.D. over ten model simulations

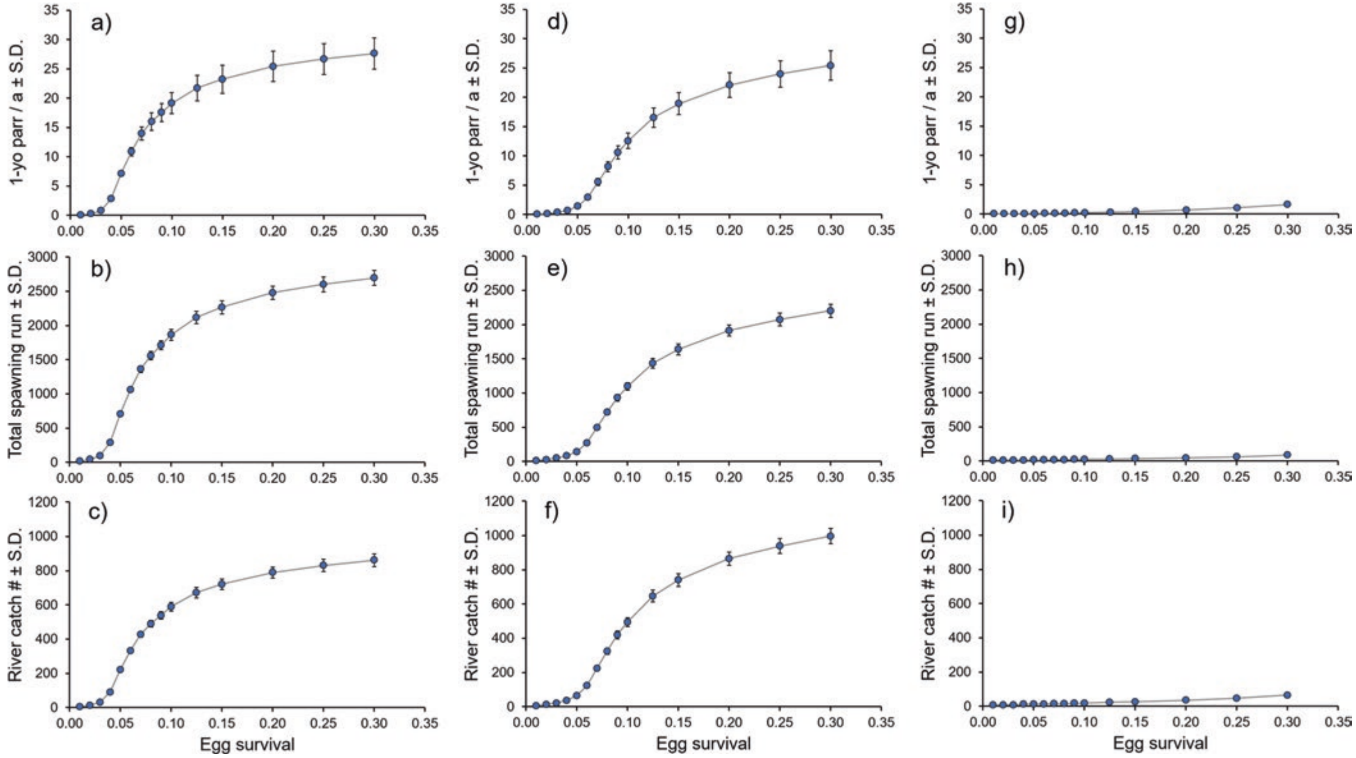


Fig. 10 The effect of varying egg survival on River Oulanka brown trout stocks under three different fishing scenarios (**a–c**): instantaneous fishing mortality rate *F* = 0.5/year, minimum size limit = 600 mm; (**d–f**): *F* = 0.5/year, minimum size limit = 500 mm; (**g–i**): *F* = 1.0/year, minimum size limit = 350 mm) as derived from the age-structured population model of Syrjänen et al. (2017). The standard deviation represents an average S.D. over ten model simulations

8 Concluding Remarks

In this chapter, we have reviewed the existing knowledge on the winter ecology of stream salmonids. We have presented the abiotic conditions that characterize winter in temperate and boreal regions and how salmonids are adapted to cope with them. The importance of abiotic conditions such as temperature, light, and ice (both surface ice and ice formations underwater) has been discussed in relation to survival, growth, and habitat choice. Not only juvenile and adult salmonids overwinter in running waters, but also the eggs. We have therefore also covered egg survival and embryonic development of salmonids and the impact of both abiotic and biotic conditions such as temperature and predation. Here, we also highlighted many of the issues we have discussed using examples from Finland. These examples demonstrate the contemporary importance of studies on egg survival and embryonic development of brown trout, and we have included both biological aspects and methodological considerations when surveying salmonid eggs in the field.

In addition to the natural stressors that shape the winter ecology of salmonids there are several human-induced threats that affect the survival and recruitment of salmonids. One such threat is the regulation of rivers for hydropower, which affects flow regimes, water temperature, and ice formation. The perhaps most evident threat to stream salmonids during winter, however, is the ongoing warming of the climate, which is especially pronounced at northern latitudes and during winter. Warmer winters are likely to directly affect metabolism and activity of overwintering fishes, as well as the timing of spawning and hatching of eggs. Warmer winters also result in several alterations to the physical winter environment, with the perhaps most obvious being the loss of surface ice, which makes stream salmonids susceptible to predation from mammals and birds. Changes in water temperature also lead to thermal asymmetries between species in biotic interactions, be it between predator and prey or competitors. Finally, this chapter presented an example from Finland, on how to estimate overwinter survival of brown trout. This example also included an exercise as how to model the potential impacts of climate change at the local scale.

Winter has long been the understudied season in salmonid ecology. It has often been considered as harsh and challenging and thus a contributor to fish mortality, although relatively few studies have explored whether this is actually the case. What we can conclude however is that winter conditions play a major role in the ecology of stream salmonids, with effects on adults, juveniles, and eggs. It, therefore, is of great importance that we understand how winter conditions affect these animals, and how changes in temperature, light, and ice impact their ecology. This knowledge is likely to be very important in light of ongoing climate change. We already observe major changes to the winter environment caused by climate warming, and these changes may have profound impacts on the ecology and recruitment of salmonids.

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Components of Brown Trout Age-Class Density Dynamics

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Abstract Brown trout population dynamics are driven by endogenous and exogenous factors acting together or interacting. Endogenous mechanisms include stock–recruitment relationship and cohort effects, whereas the main external driver is often stream discharge. However, detailed consequences at the cohort and population level of the effects of endogenous and exogenous drivers on age-class density dynamics remain less documented. Here we address the following issues: How do brown trout age-classes quantitatively respond to endogenous and exogenous factors and their interactions? How is this response affected by site-specific habitat characteristics and by stocking and flow regulation? What is the relative importance of these drivers on inter-annual age-class density fluctuations? How does the age-class density fluctuation transfer through the cohort lifetime? To address these issues, we explored a large-scale data sets across a diversity of stream habitats encompassing 82 sampling sites over the years 2002–2018, by fitting a non-additive

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linear regression model to a set of age-class detrended and standardized density series including flow-regulated/non-regulated and stocked/non-stocked sites. The response variables were 0+, 1+, and 2++ age-class densities at year $t + 1$. Predictors include seasonal discharge, as an exogenous driver, and 2++, 0+, and 1+ density at the previous year t, respectively, as endogenous drivers. Our findings include: (1) external drivers (i.e., seasonal discharge: high winter and extreme spring discharge) affect early stages more intensely than endogenous factors (i.e., recruitment rate), whereas cohort effects (survival rates) affect older stages more strongly than external drivers. (2) No evidence of negative relationships between densities of two successive age-classes of a cohort, or between spawners stock and the subsequent recruitment, but a positive feedback loop that makes the population density exhibit a sort of inertia over time and, (3) these endogenous effects interact with site-specific habitat characteristics that shift the response of age-class density. Finally, we offer compelling evidence that stocking and flow regulation smoothen the driver's effects on the age-class density dynamics.

Keywords Population ecology · Drivers · Endogenous · Exogenous · Discharge · Recruitment · Survival · Stocking · Flow regulation · Stream salmonids

1 Introduction

The large amount of monitoring programs on brown trout (*Salmo trutta*) populations has fueled the identification of the underlying factors and mechanisms of their density dynamics. Yet, there is still some controversy on the relative importance of the major drivers. Population density largely varies across scales of space and time, showing fluctuating patterns of inter-annual dynamics at the geographical scale of stream sites. Understanding this inter-annual variation is at the core of many fisheries management programs, and of paramount importance for species conservation.

Endogenous factors include stock-recruitment (SR) relationships determining 0+ age-class density, and among cohort effects (CEs) acting on the inter-annual density of 1+ and older (2++) age-classes. These mechanisms can be assessed by measuring the slope of linear and non-linear relationships between density, N, of an age-class at a given year $t + 1$: N^{0+}_{t+1}, N^{1+}_{t+1}, and N^{2++}_{t+1}, and the density of an age-class the year before, t: N^{2++}_{t}, N^{0+}_{t}, N^{1++}_{t}, respectively. These relationships are biologically meaningful: fry in a given year are dependent upon how many adults laid eggs the year before, and juveniles/adults that year are dependent upon how many of those fry/juveniles survived to the next age-class.

Exogenous drivers concern environmental components that exhibit inter-annual variability such as flow regimes. There is overwhelming evidence of the discharge effect on the abundance dynamics of these populations. Its influence on recruitment is highest in the pre-emergence stage, due to redd scouring caused by winter floods (Montgomery et al. 1996), and soon after post-emergence periods, due to habitat limitation caused by extreme spring discharges. Thus, the relation of 0+ density is often linearly negative to winter discharge (Bergerot and Cattanéo 2017; Bergerot et al. 2019; Gillson et al. 2020), and quadratic negative for spring discharge (Lobón-Cerviá et al. 2017). This implies that higher winter discharge reduces the subsequent 0+ density, whereas moderate spring discharge maximizes recruitment. Older age-class densities have also been shown to be affected by the flow regime, since it determines the combined distribution of depth and water velocity that, in turn, affects the net rate of energy intake (Hayes et al. 2007).

Moreover, the response of population density to stream discharge fluctuation is, in turn, mediated by site-specific habitat characteristics, such as depth, water current, substrate composition, and refuge availability (Heggenes 1996). The variation of these factors is synthesized in a combination of latitude and the epirithral (uppermost stream trout region, steep, and narrow reaches) to metarithral (lowermost stream trout region, flatter, and wider reaches) gradients, underpinning the production dynamics of the populations.

Unfortunately, native populations in fully natural conditions are not so common. As a consequence, to provide insight into their natural dynamics, it is imperative to control the noise induced by human-induced alterations. Such alterations, like stocking and flow regulation, might be excluded from the dataset. Nevertheless, the widespread distribution of stocking and flow regulation reduces the number of observations dramatically. We consider the influence of these management conditions as potential explanatory variables. And, therefore, we tested whether the among site differences in inter-annual density could be, at least partially, explained by differences in stocking and flow regulation, as well as by site-specific habitat characteristics.

Overall flow regulation for irrigation causes an inversion of the annual hydrograph downstream the weir, reducing the winter maxima and increasing the summer minima, with subsidiary changes in spring and autumn discharges. In the context of a strong control of population dynamics by the annual flow regime, irrigation may induce changes in the inter-annual variation of the populations (García de Jalón et al. 1992; Muhlfeld et al. 2012).

In this study, we addressed the following issues: (1) How does a given age-class quantitatively respond to an endogenous factor and to an exogenous driver (i.e., flow fluctuation) and their interactions? (2) How is this response affected by site-specific habitat characteristics and by stocking and flow regulation? (3) Which is the relative importance of these drivers on inter-annual age-class density? (4) How does the age-class density fluctuation transfer over the lifetime? (5) How does this fluctuation affect the whole population density?

Population regulatory effects have already been studied by means of long-term quantitative time series (50 years) for other stream salmonids such as brook trout (*Salvelinus fontinalis*) (Grossman et al. 2012). The latter study did not detect significant stock–recruitment relationships, but a widespread density dependence among populations for per capita rate of increase and individual growth. In the case of brown trout *Salmo trutta* populations, it has been recently shown that population regulation via negative density-dependent feedback loops is triggered by recruitment, and operates on growth, mortality, life span, and maximum size, which are inter-related and recruitment dependent (Lobón-Cerviá 2022). Instead, we analyzed how age-class density responds to drivers of inter-annual variation, whether endogenous (e.g., high to low density of a given age-class), exogenous (e.g., discharge conditions), or their interactions, and how this response has consequences over time affecting the cohort density and, ultimately, population size.

2 Study Area, Material and Methods

2.1 Study Area

Our study area includes all the streams permanently inhabited by brown trout in Navarra and La Rioja, Northern Spain (Fig. 1). This is a continuous territory including streams flowing over the Atlantic and Mediterranean slopes of the Bay of Biscay-Western Pyrenees and the Central-Eastern reaches of the Ebro River basin (41.00° – 43.31°N, and 3.12° – 0.72°W latitude and longitude range, respectively). These include three of the seven currently identified *S. trutta* evolutionary lineages (i.e., Atlantic, Mediterranean, and Adriatic) which is also the origin of the two genetically well-differentiated groups of Atlantic brown trout based on alleles at the LDH-C locus (*100) (Sanz 2017).

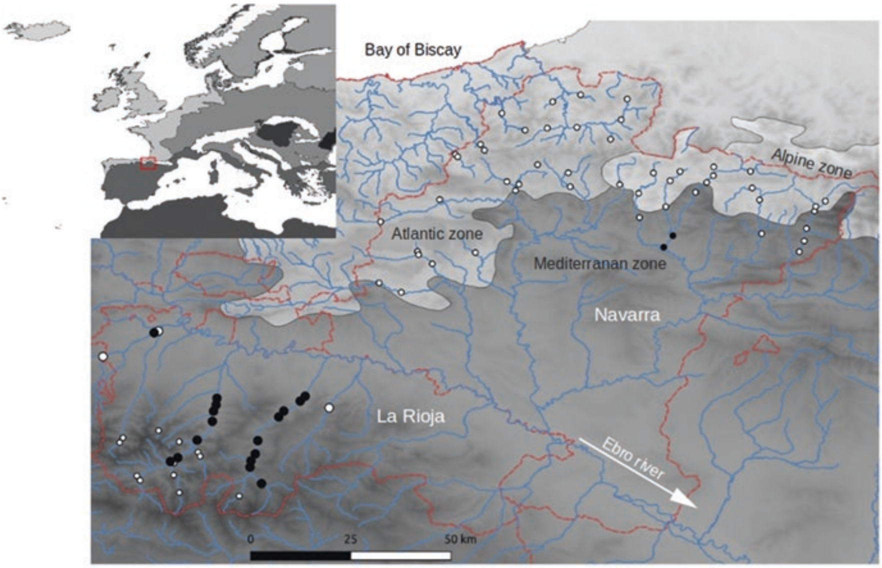

Fig. 1 Study area: Navarra and La Rioja autonomous communities. The selected sampling site network spans across three European biogeographical regions indicated as Atlantic (light gray), Mediterranean (dark gray), and Alpine (white) (Council of Europe (CoE), Directorate-General for Environment (DG ENV)). Management conditions of sites are represented by their size (large: stocked) and color (black: flow regulated)

Abundant and rather homogeneous rainfall over the northern slope of the Basque mountain range (mean annual rainfall 1500 mm, and monthly means between 90 and 175 mm), and a Föhn effect yield a cline toward Mediterranean conditions from the north to the southeast of the study area (peaked seasonality, with minimum rainfall being coincident to maximum temperatures, mean annual rainfall of 700 mm, monthly means between 40 and 80 mm).

3 Data Collections

3.1 Trout Monitoring Procedure

Monitoring procedures include long-term population density (1993–2018) estimates at 58 and 73 sampling sites in Navarra and La Rioja, respectively. Sites lengths ranged from 40 to 170 m (average: 105 m) with just a single site of 35 m, and width from 2 to 18 m (average: 8 m). Densities were determined by applying the two (Zippin 1958) and three pass removal methods (Carle and Strub 1978) with electrofishing (Lobón-Cerviá 1991). Fork lengths (to the nearest mm) were measured for all captured individual, indicating the number of removals, the sampled area, and the number of individuals in each removal. Sampling was conducted in July–September by the Gestión Ambiental de Navarra-Nafarroako Ingurumen Kudeaketa (GAN-NIK), Gobierno de Navarra, and Gobierno de La Rioja.

Age was determined according to the length frequency distributions estimated by the Bhattacharya method (Bhattacharya 1967). The limits of each age-class were determined independently of each site and year. Three age-classes were considered, fry (age-class 0+), juveniles (age-class 1+), and adults (>1+, indicated as 2++) otherwise stated.

For among sites comparisons, the density of each age-class was standardized by age-class and site. Thus, all standardized densities of each age-class have a mean value equal to zero and a standard deviation equal to one in the whole time series for every single site.

Prior to the standardization procedure, temporal trends of all age-class densities were corrected in order to not confound estimates of the population responses to inter-annual variation of the potential drivers (Yen et al. 2021). For this purpose, a linear model, $N(t) \sim a \cdot t + b$, was fitted to every single time series, and the residuals of the model were used in all the subsequent analyses as detrended densities. Thus, we kept the inter-annual signals while removing potential sources of correlation originating in long-term signals other than the inter-annual covariation of drivers and response variables.

3.2 Discharge

Mean daily stream discharges were obtained from the Spanish Official Gauging Network (ROEA). A gauging station was assigned to every sampling site according to the following nested criteria:

1. Gauging stations with the same flow regime as the fish sampling site, without tributaries or water abstraction between both sites.
2. Among two gauging stations that met the first criterion and when both covered the whole period of sampled years, the geographically nearest gauging station was selected.

When none of the gauging stations met these criteria (24 out of 82 sites), a station of a nearby watercourse was assigned only if the hydrological regimes could be assumed to be identical according to the geographical proximity and physiographical similarity. Prior exploration of the data set showed that the patterns of inter-annual variation were rather similar for nearby sites, as long as they were located in the same biogeographical region, had similar catchment size and altitude, and had the same bedrock materials. All other instances were excluded from the analyses.

Mean seasonal (winter: January to March, spring: April to June, autumn: October to December) discharge values were calculated from their corresponding mean daily values. As the annual sampling campaigns were conducted between July and September, the average discharges of these months were not used in the analyses. The seasonal mean discharges were subjected to the same detrending and standardization procedures as density.

3.3 Site Characteristics

Habitat variables were assessed through a Digital Elevation Model (DEM) with a mesh size of 200 m, obtained from the National Geographic Information Center (CNIG). This DEM200 was built by interpolating digital elevation of 5 m mesh pitches from the National Aerial Ortho-photography Plan (PNOA). From DEM200, hydrological GIS tools were used to define the fluvial network. A visual check of the correct location of the points, after this adjustment, was made once the position of the points was adjusted. Each sampling site was characterized by series of site-specific physiographic and habitat variables as follows:

Slope	Mean slope of the sampling site measured in the 1-km stretch of river whose center is the station. Calculated by digital elevation model.
Average width	Average width of the sampling site. Data provided by the Regional Government of Navarra and La Rioja.
Longitude	X UTM coordinate.
Latitude	Y UTM coordinate.

Altitude	Altitude of the site.
Mean February discharge	Average value of mean monthly discharges in February, calculated as the average value of all February daily discharges.
Mean august discharge	Average value of mean monthly discharges in august, calculated as the average value of all august daily discharges.
Mean January air temperature	Average value of mean monthly air temperature in January, calculated as the average value of all daily January mean temperatures.
Mean July air temperature	Average value of mean monthly air temperature in July, calculated as the average value of all daily July mean temperatures.

February and August were the months with the highest and lowest discharges, respectively. Their average values for the studied years (2002–2018) described the maximum and minimum discharge conditions of the hydrological regime. Similarly, January and July mean air temperatures are described as the coldest and warmest temperatures of the annual thermal regime. A meteorological station was assigned to the nearest sampling site. All habitat variables were standardized to allow comparisons of the estimates in the fitted model.

In order to account for the largest variation of the site-specific variables, a principal component analysis (PCA) was run based on the standardized values of all habitat descriptors, and stocked/non-stocked and flow-regulated/non-regulated conditions for all sites pooled. For all analyses, we selected all components accounting for 75% of the variance as potential site-specific predictors.

The discharge regime at every single site was classified as regulated or non-regulated, according to the assessment of the functional integrity of flows (Confederación Hidrográfica del Ebro 2010). Thus, river reaches were classified into six classes depending on the discharge regime alteration, as follows:

Class 1: Natural dynamics with no human interference.
Class 2: Slight changes in discharge.
Class 3: Variations in discharge, but the seasonal flow regime remains well characterized.
Class 4: Variations in the amount of discharge but no marked changes.
Class 5: Marked alterations in the circulating flow regime, at least in some periods, which entails reversions in the seasonal flow regime.
Class 6: Very important flow alterations so that the natural seasonal regime is reversed.

Sites located in stream reaches assigned to Classes 1–3 were considered "non-regulated." The remaining sites (Classes 4–6) were considered "regulated." Since hydropower or domestic water supply does not significantly change the annual flow regime, sites in Classes 4 and 5 with only these types of regulation, and no irrigation schemes, were included as non-regulated.

Flow regulation reduces the month-to-month amplitude of variation (Fig. 2), adding a secondary maximum in August, and rising the summer mean discharge. Autumn and winter mean discharges are, in turn, noticeably reduced.

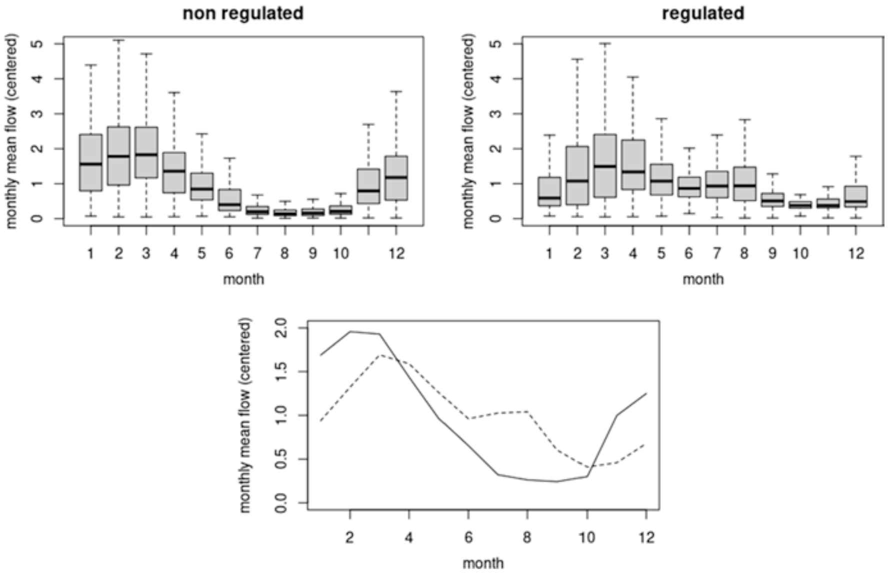

Fig. 2 Comparison of centered flow regimes (monthly mean discharge / mean annual discharge) in regulated (dashed) vs non-regulated (continuous) sites over the months

Stocking was a widespread management practice in Navarra and La Rioja until early 1990s, when Navarra stopped this practice. Since 1997, almost the entire river network of La Rioja has been stocked with farmed individuals from local fish farms. This lasted until 2002–2003 when stocking in headwaters stopped but not in the rest of the river network. Currently, stocking is carried out using native breeders kept in the Brieva de Cameros fish farms, and is based on the population structure observed on the monitoring programs. In approximately 300 km of river network, stocking is carried out annually with the following individuals:

Summer fry (0+), fish weighing ≈ 1 g: 1500–2000 ind./ha in summer.

Autumn fry (0+), fish weighing ≈ 7 g: 1500–2000 ind./ha in autumn (when the intense flow regulation is over).

Yearlings (1+), fish of ≈ 50–100 g: 300–400 ind./ha in autumn.

Adults (2++), 200–2000 g: 50–100 ind./ha in March. In sections with strong fishing pressure, adults are stocked in low densities, since they are released days before the commencement of the fishing season.

Embryonated eggs: about 150,000 eggs protected in 120 Vibert boxes are placed in the uppermost 500 m of some streams.

In summary, the annual global stocking in La Rioja is approximately 150,000 embryonated eggs, 600,000–800,000 fry, 50,000–60,000 1+ trout, and 6000–8000 2+ adults.

4 Summarizing Data Information

As aforementioned, after removing sites without assigned gauging station or habitat data, the final dataset includes 50 sites in Navarra and 38 in La Rioja. Although Navarra sites encompass data series since 1995, continuous annual quantitative data have been available for La Rioja only since 2002 (Table 1).

Finally, to homogenize the study period common to both regions, only data collected between 2002 and 2018 were used in the analyses. After removing 6 sites with <3 complete observations, the final dataset encompasses 82 sampling sites (50 sites in Navarra and 32 in La Rioja, Fig. 1) with 1136 sampling occasions in total.

5 Analyses

We fitted a density dynamics model to the quantitative time series of age-class density and mean seasonal discharge. The model was built on a multivariate non-additive linear regression that permits to distinguish the relative effect of several drivers and their interactions on age-class density at a given stream site. Moreover, we considered differences induced by habitat characteristics, stocking, and flow regulation. We compared the relative importance of every single driver and their interactions. Then we described the effects of age-class density fluctuation on the inter-annual variation of cohort density. Finally, we synthesized the effects of cohort density variations in the fluctuations of population size.

Standardized detrended 0+, 1+, and 2++ age-class densities at year $t + 1$ at every single site j were considered the response variables: $N^{0+}{}_{j,t+1}$, $N^{1+}{}_{j,t+1}$, and $N^{2++}{}_{j,t+1}$ (generalized as $N^{i+}{}_{j,t+1}$). In each case, endogenous predictors were the standardized detrended age-class density at year t, $N^{2++}{}_{j,t}$, $N^{0+}{}_{j,t}$, and $N^{1++}{}_{j,t}$ (generalized as $N^{i-1+}{}_{j,t}$) to test the stock–recruitment (SR) and cohort effects (CEs), respectively. Exogenous (discharge) predictors were, in all cases, the standardized detrended winter, spring, and autumn mean discharges, $Q\text{win}_{j,t+1}$, $Q\text{spr}_{j,t+1}$, and $Q\text{aut}_{j,t}$ at site j (hereby collectively referred to as $\{Q_{j,t}\}$). The effect of flow regulation and stocking cannot be considered independent predictors in the model, since both are highly correlated to a number of site-specific habitat features (specifically latitude, longitude, and temperature regime). Consequently, stream habitat and managerial conditions at a given site j were characterized by the first three components of the PCA run over all measured habitat features plus the stocked/non-stocked and regulated/non-regulated variables: Dim1_j, Dim2_j, and Dim3_j (hereby collectively referred to as $\{H_j\}$).

We fitted a generalized model to the whole dataset and overall, explored three alternatives: (1) linear regression model (LM), (2) linear mixed effects model (LME), and (3) generalized additive model (GAM). The first model (LM) considers only linear relationships between predictors and response variables. The second one (LME), considers nested random effects of region/stream/site and was tested to check for potential pseudo-replication. The third one (GAM) was used to test for

Table 1 Summarized description of the dataset available at every single site. Shaded cells represent a positive value (yes) in the *stocked* or *flow-regulated* columns, and data available for year (in columns)

Territory	catchment	stream	site	flow regulated	stocked	year 2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Navarra	Esca	Esca	NAV_110			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_120			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_125			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_130			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Belagua	NAV_210			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Uztarroz	NAV_320			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Irati	Salazar	NAV_710			■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_720			■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Zatoia	NAV_930			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Irati	NAV_1110			■	■	■			■	■	■	■	■		■	■	■	■		
			NAV_1130			■	■	■			■	■	■	■	■		■	■	■	■		
			NAV_1140							■	■	■	■		■	■	■	■		■	■	
			NAV_1150							■	■	■	■		■	■	■	■		■	■	
			NAV_1175	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_1180	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Legartza	NAV_1136			■	■	■			■	■	■	■	■		■	■	■	■		
		Arrañosin	NAV_1220			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Urrobi	NAV_1250			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_1260			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Sorogain	NAV_1310			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Erro	NAV_1330			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_1340			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Arga	Arga	NAV_1440			■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Ultzama	NAV_1620						■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_1625						■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Arakil	NAV_1710			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Lizarrusti	NAV_1760			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Larraun	NAV_1820			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_1830			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Basaburua	NAV_1930			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Orokieta	NAV_1940			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Ubagua	NAV_2065			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Ega	Ega	NAV_2120			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_2130			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Urederra	NAV_2220			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_2225			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			NAV_2230													■	■	■	■	■	■	■
	Oria	Araxes	NAV_2430			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Errekagorri	NAV_2480			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Erasote	NAV_2510			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Leitzaran	NAV_2520			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Urumea	Urumea	NAV_2630			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Zumarresta	NAV_2655			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Bidasoa	Baztan	NAV_2730			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Bidasoa	NAV_2740			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Aranea	NAV_2782			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Zoko	NAV_2795			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Ezkurra	NAV_2880			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Arrata	NAV_2902			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Tximista	NAV_2915			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
La Rioja	Oja-Tirón	Oja	RIO_O_1		■													■	■	■	■	■
			RIO_O_3	■	■	■	■	■	■			■	■	■	■	■						
			RIO_O_7			■	■	■	■			■	■	■	■	■	■	■	■		■	■
		Tiron	RIO_T_1			■	■	■	■				■	■	■	■	■	■	■	■	■	■
			RIO_T_3				■					■	■	■	■	■	■	■	■		■	■
	Najerilla	Brieva	RIO_Br1	■	■						■	■			■	■						
			RIO_Br2	■	■						■	■	■					■				
		Cardenas	RIO_Ca_1	■	■			■	■				■									
		Najerilla	RIO_G_N4		■												■	■	■			
			RIO_N_1								■		■	■	■							
			RIO_N_2	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
			RIO_N_3bra	■	■				■	■	■	■			■	■	■	■			■	■
			RIO_N_4	■	■	■	■				■	■	■	■	■	■	■	■	■	■	■	■
			RIO_N_5	■	■	■	■				■	■	■	■	■	■	■	■	■	■	■	■
			RIO_N_7	■	■						■		■	■	■	■	■	■	■	■	■	■
			RIO_N_8	■	■	■	■	■	■									■	■	■	■	
		Neila	RIO_Ne_2			■	■	■	■				■	■	■	■	■	■	■	■	■	■
		Urbion	RIO_U_2						■			■	■	■	■	■						
			RIO_U_5										■	■	■	■	■	■	■	■	■	■
			RIO_G_N1	■	■												■	■	■			
		Valvanera	RIO_Va1		■								■	■	■					■	■	■
	Iregua	Iregua	RIO_I_1_bis1						■			■	■	■	■			■	■	■	■	■
			RIO_I_11			■	■	■	■	■			■	■	■	■	■	■	■	■	■	■
			RIO_I_12										■	■	■			■	■	■	■	
			RIO_I_13			■	■	■	■	■	■	■	■	■	■	■	■	■	■			■
			RIO_I_14	■	■							■	■	■	■			■	■	■	■	■
			RIO_I_5	■	■	■	■	■	■	■	■											
			RIO_I_6	■	■	■	■	■	■			■	■	■	■	■	■	■	■			■
			RIO_I_8	■	■	■	■	■	■													
			RIO_I_9	■	■	■	■	■	■			■	■	■	■	■	■	■	■	■	■	■
		Piqueras	RIO_I_2			■	■	■	■			■	■			■	■	■	■	■	■	■
	Leza	Leza	RIO_L_4	■	■					■	■	■	■	■	■	■	■	■	■	■	■	■

potential non-linearities. To describe the shape of these relationships in the most unaltered conditions, these exploratory models were fitted to time series from non-stocked and non-regulated sites only. We also tested for potential interactions among predictors (non-additive effects).

The best combination of predictors and interactions was selected for every single age-class by means of an automated backward stepwise procedure by AIC (stepAIC function, MASS library). The fit of this *generalized* linear regression model provides a generalized explanation of the inter-annual variation of age-class densities and the effects of site-specific characteristics. To test for the explanatory power of the model at every single site, a set of *site-specific* models were fitted. In this case, the stocking, flow regulation, and habitat conditions, $\{H_j\}$, cannot be considered as potential predictors, thus preventing to explain of the spatial variation of the density drivers. This *site-specific* model was fitted to 14 sites in La Rioja and 45 sites in Navarra. When fitting these *site-specific* models we followed the same variable selection procedure (stepAIC function, MASS library) as in the *generalized* model.

All analyses were run in R (R Core Team 2022).

5.1 Model Formulation and Interpretation

The three *generalized* models (one per age-class i+) took the form:

$$N^{i+}_{j,t+1} = (\text{Intercept}) + a^{i+}\text{N}^{i-1+}_{j,t} + b^{i+}_{\text{win}}Q\text{win}_{j,t+1} + b^{i+}_{\text{spr}}Q\text{spr}_{j,t+1} + b^{i+}_{\text{aut}}Q\text{aut}_{j,t}$$

$$+ c^{i+}_{1}\,\text{dim}\,1_j + c^{i+}_{2}\,\text{dim}\,2_j + c^{i+}_{3}\,\text{dim}\,3_j$$

$$+ d^{i+}_{\text{win}}N^{i-1+}_{j,t}Q\text{win}_{j,t+1} + d^{i+}_{\text{spr}}N^{i-1+}_{j,t}Q\text{spr}_{j,t+1} + d^{i+}_{\text{aut}}N^{i-1+}_{j,t}Q\text{aut}_{j,t}$$

$$e^{i+}_{1}N^{i-1+}_{j,t}\text{Dim}\,1_j + f^{i+}_{\text{win},1}Q\text{win}_{j,t+1}\text{Dim}\,1_j + f^{i+}_{\text{spr},1}Q\text{spr}_{j,t+1}\text{Dim}\,1_j + f^{i+}_{\text{aut},1}Q\text{aut}_{j,t}\text{Dim}\,1_j$$

$$+ e^{i+}_{2}N^{i-1+}_{j,t}\text{Dim}\,2_j + f^{i+}_{\text{win},2}Q\text{win}_{j,t+1}\text{Dim}\,2_j + f^{i+}_{\text{spr},2}Q\text{spr}_{j,t+1}\text{Dim}\,2_j$$
$$+ f^{i+}_{\text{aut},2}Q\text{aut}_{j,t}\text{Dim}\,2_j$$

$$+ e^{i+}_{3}N^{i-1+}_{j,t}\text{Dim}\,3_j + f^{i+}_{\text{win},3}Q\text{win}_{j,t+1}\text{Dim}\,3_j + f^{i+}_{\text{spr},3}Q\text{spr}_{j,t+1}\text{Dim}\,3_j$$
$$+ f^{i+}_{\text{aut},3}Q\text{aut}_{j,t}\text{Dim}\,3_j + \varepsilon^{i+} \tag{1}$$

The summarized form of Eq. (1) is expressed in Eq. (2):

$$N^{i+}_{j,t+1} = (\text{Intercept}) + a^{i+}N^{i-1+}_{j,t} + \left\{b^{i+}\right\}\left\{Q_{j,t}\right\}$$

$$+ \left\{c^{i+}\right\}\left\{H_j\right\}$$

$$+ \left\{d^{i+}\right\}\left\{Q_{j,t}N^{i-1+}_{j,t}\right\}$$

$$+\left\{e^{i+}\right\}\left\{H_j N_{j,t}^{i-1+}\right\}+\left\{f^{i+}\right\}\left\{H_j\right\}\left\{Q_{j,t}\right\}+\varepsilon^{i+} \tag{2}$$

where $N^{i-1+}_{j,t}$ is: $N^{2++}_{j,t}$, $N^{0+}_{j,t}$ and $N^{1++}_{j,t}$ (N^{1+} and older trout),for $N^{0+}_{j,t+1}$, $N^{1+}_{j,t+1}$ and $N^{2++}_{j,t+1}$, respectively. Spring mean discharge was squared for the 0+ age-class model to account for the non-linearity observed by the fit of the exploratory GAM model (Fig. 5). The model allows interactions among endogenous and exogenous drivers, and with flow regulated–non-regulated and stocked–non-stocked conditions and site-specific habitat characteristics, $\{H_j\}$. ε^{i+} is the absolute error of the modeled $N^{i+}_{j,t+1}$, which accounts for the density variation that is not explained by the model. Since all variables were standardized, the parameters of the linear model for age-class $i+$ quantify the effect sizes of the components of population density, namely, the additive (a^{i+}) and non-additive effects ($\{d^{i+}\}$ and $\{e^{i+}\}$) of the endogenous drivers, the exogenous drivers ($\{b^{i+}\}$ and $\{f^{i+}\}$), and habitat, stocking and flow regulation conditions ($\{c^{i+}\}$).

More specifically, estimates of the parameters of the Eqs. (1 and 2) are interpreted as follows: a^{i+} influence of $i-1+$ age-class density, $N^{i-1+}_{j,t}$, on the density of the same cohort the following year (or the spawners stock for $i = 0$), when it is $i+$ age-class, $N^{i+}_{j,t+1}$, i.e., intrinsic component of the survival and recruitment rates ($N^{i+}_{j,t+1} \propto a^{i+} N^{i-1+}_{j,t}, \Rightarrow N^{i+}_{j,t+1}/N^{i-1+}_{j,t} \propto a^{i+}$);

$\{b^{i+}_{\text{win}}, b^{i+}_{\text{spr}}, b^{i+}_{\text{aut}}\} = \{b^{i+}\}$influence of the seasonal mean discharges: $Q\text{win}_{j,t+1}$, $Q\text{spr}_{j,t+1}$, $Q\text{aut}_{j,t}$ on $i+$ age-class density the following year $t+1$ ($N^{i+}_{j,t+1} \propto \{b^{i+}\}\{Q_{j,t+1}\}$); $\{c^{i+}_1, c^{i+}_2, c^{i+}_3\} = \{c^{i+}\}$ influence of the PCA components of site j specific habitat and management conditions: $\text{Dim}1_j$, $\text{Dim}2_j$, and $\text{Dim}3_j$ on $i+$ age-class density the following year ($N^{i+}_{j,t+1} \propto \{c^{i+}\}\{H_j\}$); $\{d^{i+}_{\text{win}}, d^{i+}_{\text{spr}}, d^{i+}_{\text{aut}}\} = \{d^{i+}\}$ effect of the interaction of i-1+ age-class density at year t and seasonal mean discharges: $Q\text{win}_{j,t+1}$, $Q\text{spr}_{j,t+1}$, $Q\text{aut}_{j,t}$ on $i+$ age-class density the following year $t+1$; $\{e^{i+}_1, e^{i+}_2, e^{i+}_3\} = \{e^{i+}\}$effect of the interaction of i-1+ age-class density at year t and the PCA components; $\{f^{i+}_{\text{win}}, f^{i+}_{\text{spr}}, f^{i+}_{\text{aut}}\} = \{f^{i+}\}$ effect of the interaction of seasonal mean discharges: $Q\text{win}_{j,t+1}$, $Q\text{spr}_{j,t+1}{}^2$, $Q\text{aut}_{j,t}$, and the PCA components of site j specific habitat and management conditions on $i+$ age-class density the following year ($N^{i+}_{j,t+1} \propto \{f^{i+}\}\{Q_{j,t+1}\}\{H_j\}$).

In regard to the parameters describing endogenous effects, a^{i+}, three possible effects may appear: (1) if $a^{i+} = 0$, the density of a given age-class does not depend on the density of the cohort the previous years (or recruitment is not dependent on parental stock). A year with age-class $i-1+$ density above or below the average will be followed by a year with an average density of age-class $i+$. (2). A positive value ($a^{i+} > 0$) means that a year t with i-1+ age-class density above the average will be followed by a year $t+1$ with $i+$ age-class density also above the average; and (3) if a^{i+} is negative, a year with i-1+ age-class density above the average will be followed by a year with $i+$ age-class density below the average.

Likewise, whether the effect is weaker or stronger depends on the value of the parameter. If $|a^{i+}| < 1$, the response is weak: a cohort with i-1+ age-class density above the average will produce a $i+$ age-class with density above or below the average, depending on the sign, but always nearer the average age-class density than the previous year t. Note that this does not necessarily imply a regulatory effect, the influence of N^{i-1+}_{t} on N^{i+}_{t+1} may be not so strong for the signal yielded by a higher or lower N^{i-1+} density in year t to year $t+1$. On the contrary, if $|a^{i+}| > 1$ the response is stronger, generating an amplifying response. That is, the density of an age-class i + at the year $t+1$ will deviate from the average more than the same cohort at the age-class $i-1$+, the previous year. If all these parameters of the endogenous effects, $\{a^{i+}\}$, are combined to describe the density among co-occurring cohorts, the signal of a year with age-class densities above or below the average gets an amplified response if, and only if, the product of the three parameters, $a^{0+}a^{1+}a^{2++}$, is >1 (Fig. 3e and f). If $a^{i+} = 0$, the density of age-class $i-1$+ does not influence the density of age-class i + the following year. This is not necessarily a regulatory mechanism but just a lack of effect and, age-class i + density will be on the average if no other factor operates. It follows that a non-zero value of a^{i+} means that the density of a cohort at a given year depends, to some extent, on the density of that cohort the year before and, a signal is maintained over two successive years. If a^{i+} and a^{i+1+} are both positive, the signal is maintained over a longer time interval (e.g., Fig. 3i, j, k, and l). Finally, if all $\{a^{i+}\}$ estimates are above or below zero, then the signal is consistently

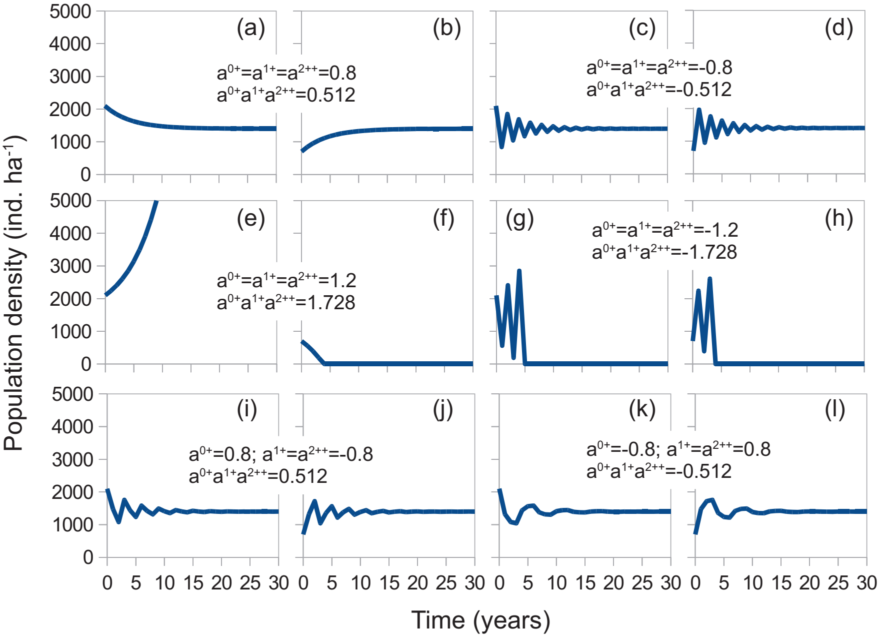

Fig. 3 Graphical representation of the hypothesis above related to the total density of a hypothetical population composed of 0+, 1+, and 2++ age-class densities averaging: 800, 400, and 200 ind. ha^{-1}, respectively (st. deviations 400, 200, 100 ind. ha^{-1}). the series commences from year 0 with all age-class densities equal 1 times the standard deviation (i.e., 1200, 600, and 30 ind. ha^{-1}, figures **a**, **c**, **e**, **g**, **i**, **k**) and equal −1 st. deviation (i.e., 400, 200, and 100 ind. ha^{-1}, figures **b**, **d**, **f**, **h**, **j**, **l**). The effect sizes of endogenous effects (a^{0+}, a^{1+}, a^{2++}) and their product is specified in the figures

maintained over time generating a sort of inertia in the density dynamics (Fig. 3a and b).

As long as the absolute value of $a^{0+}a^{1+}a^{2++}$ is <1, the population density will tend to an average after a year with higher or lower age-class densities. If the sign of all $\{a^{i+}\}$ is positive then the transition to the average will be smooth, whereas if any of them is negative, even if the product $a^{0+}a^{1+}a^{2++}$ is positive (Fig. 3i and j), then, the density will overcompensate and fluctuate around the average, showing shifts of decreasing amplitude until it eventually stabilizes. The time period of this fluctuation may last for several years, particularly if the SR relationship is negative and CE is positive. Therefore, if the estimates of $\{a^{i+}\}$ in the selected models are all non-zero provide evidence of density-dependent feedback loops. If the product $a^{0+}a^{1+}a^{2++}$ is positive a sort of inertia would yield in a smooth growth or an decrease to equilibrium. Whereas if it is negative, a weak overcompensation will lead to a damped-stable oscillation around an equilibrium.

On the contrary, if $|a^{0+}a^{1+}a^{2++}| > 1$, then age-class densities above or below the average will cause an amplifying destabilizing signal and, eventually leading the population to a collapse.

The sign and the strength of the different additive components (endogenous and exogenous) of the population density dynamics can be compared using the values of the effect sizes (i.e., parameters *a*, *b*, and *c*).

Finally, two factors may interact to change the response of age-class density to the variation caused by the effects of any of them alone. The significance of this interaction is known by the corresponding non-additive effect being selected in the final model, and its effect on the age-class density is quantified by parameters *e* and *f*.

6 Results

6.1 Site-Specific Habitat Characteristics

The network of sites analyzed encompasses a wide array of habitat conditions. The mean slope spanned between 0 and 23.4% (average 4.4%); mean site width encompasses a gradient from narrow to medium sized (range 2.5 m–19.5 m, average 8.4 m), and altitudes ranged from 110 m to 1180 m asl (average 628 m). Mean monthly stream discharge in February ranged between 0.9 and 22.4 m^3/s (average 9.2 m^3/s), and in August between 0.06 and 14.8 m^3/s (average 6.4 m^3/s) in August. Mean monthly air temperature in January ranged between 3.6 and 9.3 °C, and 9.8 and 23.4 °C in July.

The non-stocked sites were around three times (62 sites) larger than the number of stocked sites (20 sites). While the ratio of non-flow regulated to regulated sites was similar: 63 non-regulated and 19 regulated sites, respectively. According to the combined management conditions, there is a bias towards the least or most altered

Table 2 Results of the PCA with indication of the eigenvalues and variance explained by the first 5 components (Dim1 to Dim 5)

	Dim1	Dim2	Dim3	Dim4	Dim5
Stocked	0.278	−0.091	0.170	−0.049	0.048
Flow regulated	0.253	−0.209	0.112	−0.009	0.066
Slope	−0.569	0.246	−0.336	−0.175	0.682
Average width	0.021	−0.755	0.455	0.250	0.335
Longitude (UTM)	−0.860	−0.119	−0.048	0.427	0.044
Latitude (UTM)	−0.969	−0.042	0.089	−0.067	−0.126
Altitude	0.614	0.374	−0.251	0.625	0.075
Mean February flow	−0.130	−0.627	−0.675	−0.012	−0.160
Mean august flow	0.547	−0.554	−0.244	−0.075	0.062
Mean January air temp.	−0.896	−0.050	−0.013	0.223	−0.156
Mean July air temp.	0.910	0.042	−0.049	0.076	0.030
Eigenvalue	4.466	1.543	0.952	0.735	0.662
Variance (%)	48	16	10	8	7
Cumulative variance (%)	48	64	74	82	89

conditions: 60 non-stocked, non-regulated sites, and 17 stocked and regulated sites. Peculiarly, only 3 sites were stocked and non-regulated, whereas 2 sites were non-stocked and regulated.

The first three components of the PCA, including management and habitat conditions (Table 2) accounted for 74% of the total variance, and almost half of the variance (48%) was accounted only by the first component, Dim1.

The first PCA component (Dim1) highlights a gradient toward stocked and flow-regulated flat sites at higher altitudes in the southwestern end of the study area, which is subject to continental climatic conditions. Higher Dim1 values include the slope of the Ebro River basin in La Rioja, whereas lower values include Navarra's Pyrenean sites.

The epirithral-metarithral gradient is characterized by a decrease in slope and an increase in stream width. The second PCA component (Dim2) runs toward unregulated narrow section epirithral sites. Dim3 represents the gradient from narrow headwater epirithral sites toward wider lower altitude metarithral sites.

6.2 *Age-Class Densities Across Scales of Space and Time*

When sites were grouped by different management conditions, significant differences were only found among age-classes 1+ and 2++ (Kruskal-Wallis rank sum test, $p < 0.001$). The largest difference among management conditions was found in adults (2++) showing the lowest densities in the non-stocked and regulated sites (Fig. 4). However, we could not attribute this effect to flow regulation or stocking,

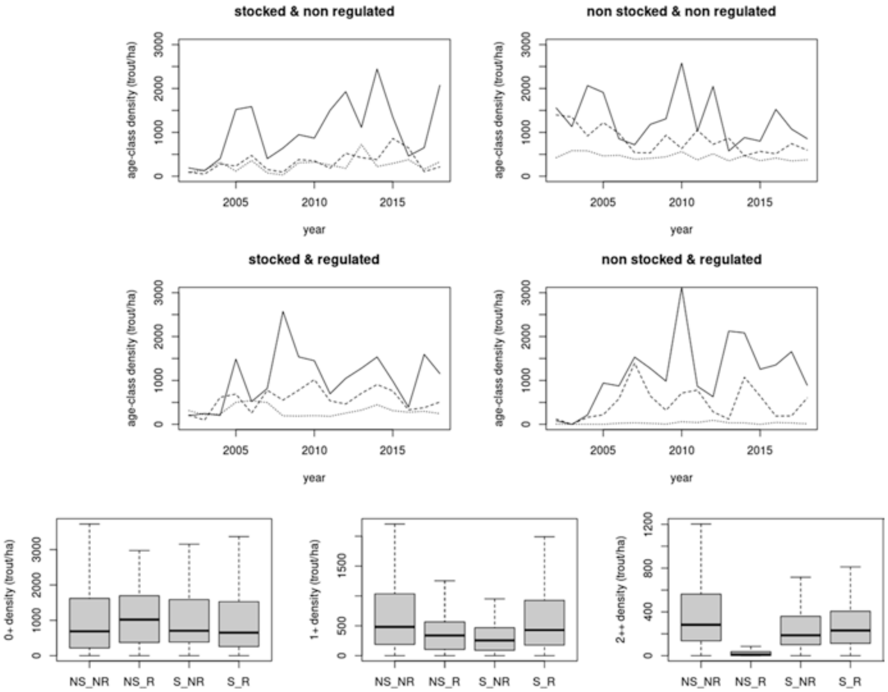

Fig. 4 Mean age-class (0+ continuous; 1+ dashed; 2++ dotted) density (ind.ha^{-1}) quantified at the sites classified by combinations of stocked (S) and non-stocked (NS), and regulated (R) and non-regulated (NR) conditions

since such management conditions covariate spatially with some relevant site-specific habitat characteristics.

6.3 *Model Analyses*

According to the Akaike Information Criterion (AIC) (Akaike 1978), the most plausible exploratory model was GAM (AIC = 2309), showing a non-linear (dome shaped) effect of $Q\mathrm{spr}_{j,t+1}$ on $N^{0+}{}_{j,t+1}$ (Fig. 5). The fitted GAM (Fig. 5) showed mainly linear responses of all age-classes densities to endogenous and exogenous drivers. Only spring mean discharge induces a non-linear response of 0+ density, being extreme mean discharges in April to June detrimental to fry densities detected during the summer surveys. The concave non-linear response of 1+ density to autumn mean discharge is weak and not easy to interpret. Therefore, this effect was assumed linear in the finally fitted non-additive linear model.

A significant effect of pseudo-replication was rejected given that LM showed better performance (AIC = 2346) than LME (AIC = 2352). Though GAM was found to be the most plausible model, GAMs cannot easily account for such

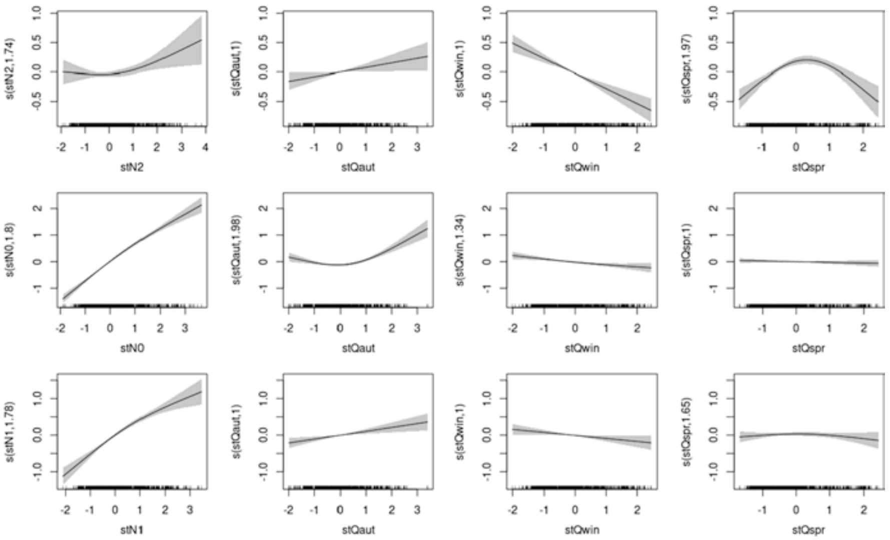

Fig. 5 Smoothed relationships obtained from the fitting of generalized additive models (GAM, $k = 3$) to time series from non-stocked—not regulated sites (saturated models with no variable selection were conducted). Response variables (lines top to bottom) are standardized densities for every age-class: 0+, N^{0+}_{t+1}, 1+, N^{1+}_{t+1}, and 2++, N^{2++}_{t+1}. Explanatory variables (columns left to right): endogenous factor, N^{i+}_{t}, and standardized seasonal mean discharges $Q\text{aut}_t$, $Q\text{win}_{t+1}$, and $Q\text{spr}_{t+1}$

non-additive effects. Therefore, we selected the linear model LM (hereby referred to as *generalized* model), though considering a quadratic effect of spring mean discharge, $Q\text{spr}^2$, to account for the observed non-linearity of this driver on 0+ age-class density (Fig. 5), and crossed interactions between $N^{i-1+}_{j,t}$, $\{Q_{j,t}\}$ and $\{H_j\}$. Habitat, stocking, and flow-regulation conditions at every single site *j* were described by means of the first three PCA components (Dim1$_j$, Dim2$_j$, and Dim3$_j$).

The fit of the *generalized* model performed differently for the three age-class densities (Table 3). It explained <10% for the inter-annual fry density variation ($R^2 = 0.09$, $p < 0.05$), and a slightly larger 20% of the adult density. The model performed better for 1+ density ($R^2 = 0.44$). The proportion of the density unexplained by the model was still larger. For the older age-class, >80% of the observed variation remained unexplained, whereas for age-class 1+, this uncertainty was slightly >50%. When fitting the model site by site (*site-specific* models), R^2 averaged 0.35, 0.63, and 0.49, for age-class densities N^{0+}_{t+1}, N^{1+}_{t+1}, and N^{2++}_{t+1}, respectively.

The *generalized* model of fry density showed a weak yet significant, positive stock–recruitment relationship ($N^{0+}_{j,t+1}/N^{2++}_{j,t} \propto a^{0+} = 0.072$), which may be understood as a positive intrinsic component of the recruitment rate. This positive value means that the greater the adult density in the summer of year *t*, the greater the fry density in the summer of year *t* + 1. Recruitment rates were higher in years of higher autumn mean discharge, the previous year, that is $N^{0+}_{j,t+1}/N^{2++}_{j,t} \propto d_{\text{aut}}^{0+} Q\text{aut}_{j,t} = 0.068\ Q\text{aut}_{j,t}$. Site-specific recruitment rate was lower in wider and lower altitude

Table 3 Estimated effect sizes of the selected non-additive linear models for age-class standardized densities (response variables, in columns)

Predictor	Parameter		$N^{0+}_{j,t+1}$			$N^{1+}_{j,t+1}$			$N^{2++}_{j,t+1}$		
			Estimate (± std. error)		*p*-value	Estimate (± std. error)		*p*-value	Estimate (± std. error)		*p*-value
(Intercept)			**0.109**	(±0.038)	0.004	0.019	(±0.022)	0.386	−0.005	(±0.027)	0.857
$N^{i-1+}_{j,t}$	a^{i+}	a^{i+}	**0.072**	(±0.029)	0.013	**0.623**	(±0.023)	<2E-16	**0.361**	(±0.028)	<2E-16
$Q\mathrm{win}_{j,t+1}$	$\{b^{i+}\}$	b_{win}^{i+}	**−0.195**	(±0.034)	8.36E-09	**−0.112**	(±0.028)	7.11E-05	−0.02	(±0.034)	0.563
$Q\mathrm{spr}_{j,t+1}{}^{2}$		b_{spr}^{i+}	**−0.126**	(±0.026)	1.13E-06						
$Q\mathrm{aut}_{j,t}$		b_{aut}^{i+}	0.025	(±0.033)	0.445	**0.145**	(±0.026)	2.29E-08	**0.067**	(±0.031)	0.033
$\mathrm{Dim1}_j$	$\{c^{i+}\}$	c_1^{i+}				−0.005	(±0.005)	0.297	−0.001	(±0.006)	0.806
$\mathrm{Dim2}_j$		c_2^{i+}	−0.001	(±0.018)	0.947	−0.0001	(±0.014)	0.995	−0.001	(±0.017)	0.929
$\mathrm{Dim3}_j$		c_3^{i+}	−0.002	(±0.03)	0.96	−0.004	(±0.024)	0.862	−0.004	(±0.029)	0.896
$N^{i-1+}_{j,t}\ Q\mathrm{win}_{j,t+1}$	$\{d^{i+}\}$	d_{win}^{i+}									
$N^{i-1+}_{j,t}\ Q\mathrm{spr}_{j,t+1}{}^{2}$		d_{spr}^{i+}									
$N^{i-1+}_{j,t}\ Q\mathrm{aut}_{j,t}$		d_{aut}^{i+}	**0.068**	(±0.027)	0.013						
$N^{i-1+}_{j,t}\ \mathrm{Dim1}_j$	$\{e^{i+}\}$	e_1^{i+}				**−0.025**	(±0.005)	3.31E-06	**−0.027**	(±0.006)	2.48E-05
$N^{i-1+}_{j,t}\ \mathrm{Dim2}_j$		e_2^{i+}				**0.037**	(±0.015)	0.011			
$N^{i-1+}_{j,t}\ \mathrm{Dim3}_j$		e_3^{i+}	**−0.059**	(±0.032)	0.064						
$\mathrm{Qwin}_{j,t+1}\ \mathrm{Dim1}_j$	$\{f^{i+}\}$	$f_{\mathrm{win},1}^{i+}$							**0.031**	(±0.008)	2.55E-04
$Q\mathrm{win}_{j,t+1}\ \mathrm{Dim2}_j$		$f_{\mathrm{win},2}^{i+}$	−0.034	(±0.021)	0.105						
$Q\mathrm{win}_{j,t+1}\ \mathrm{Dim3}_j$		$f_{\mathrm{win},3}^{i+}$	**−0.073**	(±0.032)	0.022				**−0.069**	(±0.03)	0.021
$Q\mathrm{spr}_{j,t+1}{}^{2}\ \mathrm{Dim1}_j$		$f_{\mathrm{spr},1}^{i+}$									
$Q\mathrm{spr}_{j,t+1}{}^{2}\ \mathrm{Dim2}_j$		$f_{\mathrm{spr},2}^{i+}$									
$Q\mathrm{spr}_{j,t+1}{}^{2}\ \mathrm{Dim3}_j$		$f_{\mathrm{spr},3}^{i+}$									
$Q\mathrm{aut}_{j,t}\ \mathrm{Dim1}_j$		$f_{\mathrm{aut},1}^{i+}$				**0.009**	(±0.005)	0.088	**−0.012**	(±0.007)	0.091
$Q\mathrm{aut}_{j,t}\ \mathrm{Dim2}_j$		$f_{\mathrm{aut},2}^{i+}$	**0.055**	(±0.021)	0.008	**0.041**	(±0.015)	0.005			
$Q\mathrm{aut}_{j,t}\ \mathrm{Dim3}_j$		$f_{\mathrm{aut},3}^{i+}$				**0.055**	(±0.025)	0.029			
R^2			0.09			0.44			0.2		

Predictors and interactions with $p < 0.1$ are shown in bold. $N^{i+}_{j,t}$ is $N^{2++}_{j,t}$ for $N^{0+}_{j,t+1}$, $N^{0+}_{j,t}$ for $N^{1+}_{j,t+1}$, and $N^{1++}_{j,t}$ for $N^{2++}_{j,t+1}$. The exponent 2 in $Q\mathrm{spr}_{j,t+1}{}^{2}$ denotes that this variable was squared in the 0+ age-class model ($Q\mathrm{spr}_{j,t+1}{}^{2}$), only metarithral than in narrower and higher altitude epirithral sites ($N^{0+}_{j,t+1}/N^{2++}_{j,t} \propto e_3^{0+}\mathrm{Dim3}_j = -0.059\mathrm{Dim3}_j$).

Fry density was lower in years with higher winter discharge ($N^{0+}_{j,t+1} \propto b_{\mathrm{win}}^{0+}Q\mathrm{win}_{j,t+1} = -0.195Q\mathrm{win}_{j,t+1}$) or extreme spring discharge ($N^{0+}_{j,t+1} \propto b_{\mathrm{spr}}^{0+}Q\mathrm{spr}_{j,t+1}^2 = -0.126Q\mathrm{spr}_{j,t+1}^2$). The negative effect of winter discharge was even stronger at lower altitude metarithral sites ($N^{0+}_{j,t+1} \propto f_{\mathrm{win},3}^{0+}Q\mathrm{win}_{j,t+1}\ \mathrm{Dim3}_j = -0.073Q\mathrm{win}_{j,t+1}\ \mathrm{Dim3}_j$). There was also a positive effect of higher autumn mean discharge on 0+ density at unregulated narrower epirithral sites ($N^{0+}_{j,t+1} \propto f_{\mathrm{aut},2}^{1+}Q\mathrm{aut}_{j,t}\ \mathrm{Dim2}_j = 0.055Q\mathrm{aut}_{j,t}\ \mathrm{Dim2}_j$).

For 1+ age-class density, the cohort effect, which represents the 0+ to 1+ survival rate, was the strongest driver ($N^{1+}_{j,t+1}/N^{0+}_{j,t} \propto a^{1+} = 0.623$). The 0+ age-class survival rate was independent of the seasonal mean discharge, which did not affect neither to the 0+ to 1+ survival rate nor to 1+ density. The site-specific 0+ survival rate was lower in the southwestern stocked regulated flat, higher altitude Mediterranean sites ($N^{1+}_{j,t+1}/N^{0+}_{j,t} \propto e_1^{1+}\mathrm{Dim1}_j = -0.025\mathrm{Dim1}_j$), and higher in unregulated narrower epirithral sites ($N^{1+}_{j,t+1}/N^{0+}_{j,t} \propto e_2^{1+}\mathrm{Dim2}_j = 0.037\mathrm{Dim2}_j$). The density of 1+ trout was also higher in years with higher autumn mean discharge ($N^{1+}_{j,t+1} \propto b_{\mathrm{aut}}^{1+}Q\mathrm{aut}_{j,t} = 0.145Q\mathrm{aut}_{j,t}$) and lower winter discharge ($N^{1+}_{j,t+1} \propto b_{\mathrm{win}}^{1+}Q\mathrm{win}_{j,t+1} = -0.112Q\mathrm{win}_{j,t+1}$). The positive effect of autumn discharge was stronger in wider metarithral sites ($N^{1+}_{j,t+1} \propto f_{\mathrm{aut},3}^{1+}Q\mathrm{aut}_{j,t}\ \mathrm{Dim3}_j = 0.055Q\mathrm{aut}_{j,t}\ \mathrm{Dim3}_j$), in unregulated epirithral sites ($N^{1+}_{j,t+1} \propto f_{\mathrm{aut},2}^{1+}Q\mathrm{aut}_t\ \mathrm{Dim2}_j = 0.041Q\mathrm{aut}_t\ \mathrm{Dim2}_j$), and, though marginally significant ($p = 0.088$), in southwestern stocked regulated flatter, higher altitude Mediterranean sites ($N^{1+}_{j,t+1} \propto f_{\mathrm{aut},1}^{1+}Q\mathrm{aut}_{j,t}\ \mathrm{Dim1}_j = 0.009Q\mathrm{aut}_{j,t}\ \mathrm{Dim1}_j$).

Adults density was also affected by a strong cohort effect, which represents 1++ survival rate between two successive years ($N^{2++}_{j,t+1}/N^{1++}_{j,t} \propto a^{2++} = 0.361$). As in the 0+ survival rate, the 1++ survival rate was independent of the seasonal mean discharge. Site-specific 1++ survival rate was lower in the southwestern stocked regulated, flatter, and higher altitude Mediterranean sites ($N^{2++}_{j,t+1}/N^{1++}_{j,t} \propto e_1^{2++}\mathrm{Dim1}_j = -0.027\mathrm{Dim1}_j$). Autumn mean discharge positively affected 2++ density: being higher in years in which the mean discharge during the previous autumn was higher ($N^{2++}_{j,t+1} \propto b_{\mathrm{aut}}^{2++}Q\mathrm{aut}_{j,t} = 0.067Q\mathrm{aut}_{j,t}$). The effect of higher winter discharge on the 2++ density was positive in the southwestern, stocked and regulated, flatter, higher altitude, Mediterranean sites ($N^{2++}_{j,t+1} \propto f_{\mathrm{win},1}^{2++}Q\mathrm{win}_{j,t+1}\ \mathrm{Dim1}_j = 0.031Q\mathrm{win}_{j,t+1}\ \mathrm{Dim1}_j$), and negative in wider, lower altitude metarithral sites ($N^{2++}_{j,t+1} \propto f_{\mathrm{win},3}^{2++}Q\mathrm{win}_{j,t+1}\ \mathrm{Dim3}_j = -0.069Q\mathrm{win}_{j,t+1}\ \mathrm{Dim3}_j$).

Stocking and flow regulation are represented by the first PCA component (Dim1). According to the observed effects ($N^{1+}_{j,t+1}/N^{0+}_{j,t} \propto -0.025\mathrm{Dim1}_j$, and $N^{2++}_{j,t+1}/N^{1++}_{j,t} \propto -0.027\mathrm{Dim1}_j$) these management conditions may reduce the annual 0+ and 1++ survival rates. Un-regulated flow conditions, which are represented by the second PCA component (Dim2), increase the annual 0+ survival rates ($N^{1+}_{j,t+1}/N^{0+}_{j,t} \propto 0.037\ \mathrm{Dim2}_j$). However, it is difficult to separate the specific effects of the management conditions from the effects of site-specific habitat conditions, including the biogeographical region where the sites are included. Therefore, these results should be interpreted as subtle indications that stocking and flow regulation, in combination with other habitat characteristics, may have an effect on the cohort density.

7 Discussion

We found no evidence of negative relationships between two successive age-classes nor between the parental stock and the subsequent recruitment. Nevertheless, our results provide compelling evidence that seasonal flow conditions affect recruitment whereas cohort density affects older stages more strongly than external drivers. Additionally, we highlighted evidences that seasonal flow conditions affect density only at very early stages, actually at the time of spawning, whereas site-specific habitat features (including stocking and flow regulation) affect the demographic rates only at given sites.

Fry density is the most relevant factor of cohort strength, as shown by the greater relative importance of $N^{0+}{}_{j,t}$ on the juvenile $N^{1+}{}_{j,t+1}$ year-to-year variation in density. This effect is maintained over the age-classes to the adult density, which, in turn, is also highly dependent on the juvenile density of the previous year. Recruitment is, therefore, the factor directly responsible for temporal population variation. Also, in the nearby Asturias region (northwestern Spain), it has been shown that the annual number of the youngest juveniles that incorporate into the population to initiate a new cohort is determinant of year-class strength and therefore population size (Lobón-Cerviá 2004, 2009; Lobón-Cerviá and Rincón 2004; Lobón-Cerviá et al. 2011). In addition, Cattanéo et al. (2002) found that the 1+ brown trout density was strongly related to the 0+ density the previous year, and the adult density with the 1+ density the previous year. This effect was similar across study sites in rivers across France. The positive dependence of cohort strength on the number of 0+ trout has been revealed in native resident and lake migratory brown trout (Lobón-Cerviá and Mortensen 2005), and in other populations outside its native range (e.g., North America), as much as in other salmonid species like brook trout (Zorn and Nuhfer 2007) and, golden trout (*Oncorhynchus mykiss aguabonita*) (Knapp et al. 1998). This dependence seems to be so widespread that some authors claim that recruitment dominates over post-recruitment processes as the main driver of density (Knapp et al. 1998; Cattanéo et al. 2002).

Adult density is a significant predictor of fry density in the following year. However, stream discharge accounts for a greater percent of 0+ density as indicated when comparing the effect sizes of the model (Table 3). This may be the reason why other long-term studies on recruitment dynamics at large temporal or spatial scales (Kanno et al. 2016; Lobón-Cerviá et al. 2017) did not detect relationships between the number of adults and fry in successive years.

We did not detect evidence of regulatory effects of the parental stock on recruitment, in the form of negative stock–recruitment (SR) or a negative relationship between the density of a cohort in two successive years (Elliott 1994; Nicola et al. 2009). Instead, we highlighted a positive feedback loop emerging from positive cohort effects (CE) and between parental density and recruitment. These dynamics would involve juvenile and adult densities being highly dependent on the density of the prior age class, and ultimately, by recruitment that, in turn, would be dependent on the spawners' stock. The non-regulatory responses may indicate that, if favorable external conditions prevail over several successive years, an abundant recruitment may produce abundant adult age-classes which in turn would result in the next cohort with higher recruitment.

We also found that the value of the product of the parameters that represent SR and CE was positive and < 1 ($0 < a^{0+}a^{1+}a^{2++} < 1$), implying that the population density will exhibit a sort of inertia. Under these conditions, the higher the product $a^{0+}a^{1+}a^{2++}$, the longer will take the population density to level off after years of higher or lower age-class densities. This may hold true when all other drivers remain stable at average values. Such conditions prevent the decline of the population density. But if the external conditions for recruitment are weak over several years, the parental density might not be high enough to produce an abundant recruitment, or the younger age-classes may not be abundant enough to survive to an abundant adult age-classes.

High inter-annual variability in the flow regime characterizes the Mediterranean biogeographical region. Many of the study sites located in this region are also subject to flow regulation and stocking reaches (Fig. 1). Flow regulation reduces intra- and inter-annual variability and removes winter higher discharges. Stocking further provides a regular input of recruits independently of the prevailing climatic conditions. These management practices may keep the density of those populations protected from the occurrence of unfavorable years. Non-stocked and non-regulated sites in this region, such as those in the eastern study area, i.e., Esca River, would be among the most vulnerable to successive unfavorable years. Actually, sites of the Esca River experienced a noticeable decline in density over the years 2001–2004, under prevailing higher winter discharge conditions with no evidence of recovery after a few years of moderate winter discharge (2006–2008). Apparently, the time period of favorable conditions was not long enough to overcome the ‘inertia’ of the population density.

Similar to previous studies (Warren et al. 2015; Kanno et al. 2016), higher winter discharge significantly reduces 0+ and 1+ age-class densities. The number of individuals was systematically lower in years when discharge was higher during the second winter of life. The response of adult densities to higher winter discharge was remarkably weaker probably because older individuals are more capable of taking refuge in microhabitats during extreme flow events.

Overall, our results are consistent with other studies. Too low and too high spring discharges reduce fry density at given years and sites. Flow conditions in late winter and early spring have frequently been reported as the main recruitment drivers of stream-living salmonids populations (e.g., brown trout and brook trout) including two recent large-scale analyses (Kanno et al. 2016; Bergerot and Cattanéo 2017). Discharge during fry emergence and during the early search for feeding positions, by limiting the available habitat for newly emerged fry, seems to be the main driver of annual recruitment (Daufresne et al. 2005; Lobón-Cerviá 2007). Maximum recruitment has been profusely reported to occur at the most frequent flow conditions (Lobón-Cerviá and Rincón 2004), showing a non-linear parabolic pattern. Discharge during or soon after the emergence seems to be a major determinant of recruitment in Asturias streams (Lobón-Cerviá et al. 2017). Both physiographic conditions, as well as trout phenology in Asturias, are very similar to our study area so a similar effect should be expected and actually demonstrated herein. Extreme discharge during the post-emergence period also plays a major role in the dynamics of the whole population (Capra et al. 2003). Droughts have been reported to reduce survival more markedly in 1+ than in 0+ individuals (Elliott 1987, 1994). Mortality of 1+ and older trout has been explained by the average discharge in spring (Carline 2006), although it also has been observed that for trout of the same ages, the size of the peak of spring floods does not significantly affect mortality (Jensen and Johnsen 1999). Our results, though, show that spring discharge does not affect recruitment rates or 1++ density significantly.

In contrast, higher discharge can be beneficial when they are not artificially frequent and/or occur outside the incubation and/or emergency periods (Ortlepp and Mürle 2003). Our findings indicate that autumn discharge operates on different density components depending on the life stage. Higher discharge during the spawning season increases the recruitment rate and the 1+ and 2++ age-classes densities. Strong evidence of the positive effect of higher discharge during the pre-spawning and spawning seasons on the recruitment rates have also been reported (Jensen and Johnsen 1999; Cattanéo et al. 2002; Zorn and Nuhfer 2007; Unfer et al. 2011). An increase in potential spawning areas as well as an improvement in the accessibility of adults to reach the uppermost tributaries would result in more successful spawning (Kanno et al. 2016). Average discharge in autumn during the spawning period has been positively correlated with 1+ densities (Carline 2006). Accordingly, our findings further support that higher mean discharges during the autumn are related to a higher density of all age-classes in the next summer.

It is difficult to draw conclusions on the effect of stocking and flow regulation on density because they are highly correlated to other site-specific habitat conditions. Overall, stocking and flow regulation may apparently obscure the effects of other drivers. For instance, 0+ and 1++ survival rates, whose effect sizes are positive, become reduced for higher values of the first PCA component (Dim1), which scored stocked and regulated conditions. On the contrary, Dim2 scores positively unregulated flow conditions alone, and increases 0+ survival rates. The opposing effects of Dim1 and Dim2 may suggest that an increase of the 0+ survival rate for higher values of Dim1 is due to stocking practices alone. The positive effect of higher autumn discharge on 0+ and 1+ densities is stronger in unregulated flow conditions. Therefore, flow regulation might obscure the effect of autumn discharge on 0+ density.

Our findings also enhance the importance of shelter along the stream network, specifically on upstream reaches. The negative effect of higher winter discharge on densities is significantly stronger in wider and lower altitude metarithral sites (recall Dim3 component). The same habitat-mediated response of density to higher winter discharge was also highlighted by Bergerot and Cattanéo (2017) when looking for hydrological drivers of brown trout abundance at a much larger spatial scale (whole of France). They hypothesized that the stronger effects of higher discharge in larger rivers may be caused by higher hydraulic constraints. Upstream reaches may be, therefore, natural shelters that permit individuals to escape from the negative effects of extreme discharge events. In fact, we found that recruitment rate was higher in narrower and higher altitude epirithral sites than in wider lower altitude metarithral (recall Dim3 component). Thus, headwater streams may also be safe areas for spawning, being relatively free from the negative effects of potential scouring events (Meredith et al. 2018).

The unexplained variance of the observed patterns includes changes caused by inherent moving patterns in and out the study sites, the effects of drivers not included in the model, the density estimation errors and the noisy nature of these patterns. Our analyses did not quantify the relative importance of each of these sources of uncertainty.

Moreover, we did not assess numerous other drivers, such as temperature (Merten et al. 2010; Moore et al. 2012), alone or interacting with discharge (Lobón-Cerviá and Mortensen 2005); water quality (Milner et al. 2003); other discharge details as the frequency and duration of extreme events (Halleraker et al. 2003; Alonso-González et al. 2008); and/or variables of the community dynamics as prey shifts and predators abundance (Myers et al. 1997; Hyvarinen and Vehanen 2004); and summer discharge conditions, which have been reported as a limiting factor in nearby regions (Nicola et al. 2009) and elsewhere (Elliott et al. 1997). Given the potential importance of each of these variables, further studies are needed to clarify their role and to assess the effects of changing climatic conditions in the global world.

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Salmonids in New Zealand: Old Ways in New Lands

Gerard P. Closs

Abstract The freshwater communities of New Zealand were changed forever when brown trout *Salmo trutta* was first released in New Zealand by the Otago Acclimatisation Society in 1867, derived from a mixed stock of resident and migratory fish sourced originally from England. Over the next 50 years or so, a combination of widespread introductions and natural spread resulted in brown trout becoming virtually ubiquitous in streams throughout most of the South Island, and much of the North Island. Along with brown trout, Atlantic salmon *Salmo salar*, rainbow trout *Oncorhynchus mykiss*, brook char *Salvelinus fontinalis*, mackinaw or lake trout *Salvelinus namaycush*, chinook salmon *Oncorhynchus tshawytscha*, and sockeye salmon *Oncorhynchus nerka* were also released. Although some species flourished, others such as lake char and Atlantic salmon persist only in isolated populations or are now likely extinct. Of the other species, latitude, climate, and landscape have interacted with the biology of each species to produce relatively stable patterns of co-existence, and most species are at least locally abundant in some systems and locations. Inter- and intraspecific competition and habitat segregation between salmonids, and potentially some native species, likely play a key role in determining patterns of regional and longitudinal distribution in streams, rivers, and lakes, and latitudinal patterns of distribution across New Zealand. Furthermore, complex patterns of distribution of resident and migratory potamodromous and diadromous life histories have also appeared, suggesting environment has a strong influence on life-history type. Many of the patterns of distribution of species and life-history strategies have clear parallels with similar complex patterns of salmonid life history in the Northern Hemisphere, suggesting a major factor in the success of salmonids in the Southern Hemisphere has been their ability to establish their old ways in new lands.

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1 Introduction

The release of salmonids into New Zealand waterways in 1867 led to widespread and significant changes to the ecology of New Zealand's freshwater ecosystems (McDowall 2006; Jones and Closs 2018; Jellyman et al. 2018). Today, salmonids are the most widespread, conspicuous, and abundant freshwater fish across most of New Zealand (Jarvis et al. 2019; McDowall 2006). Apart from some limited put-and-take recreational angling fisheries, most salmonid populations are sustained by natural reproduction, and without augmentation through stocking (McDowall 1990, 2006; Jarvis et al. 2019). Given the broad ubiquity of salmonids across New Zealand and the limited options available for any meaningful control, they are now an integral part of the freshwater ecosystems of New Zealand (Jone and Closs 2018; Jellyman et al. 2018). Their success has undoubtedly come about through their exceptional phenotypic plasticity (Jones and Closs 2018). Understanding how and why their biology has allowed them to integrate so effectively into New Zealand ecosystems provides some fascinating insights into the biology of salmonids and is crucial for managing both their negative effects on the native biota and their place in sustaining valuable recreational fisheries in New Zealand and elsewhere.

2 Successes and Failures

Between 1867 and 1902, seven salmonid species were imported, released and then established naturally breeding populations around New Zealand: brown trout (*Salmo trutta*; 1867), Atlantic salmon (*Salmo salar*; 1868), chinook salmon (*Oncorhynchus tshawytscha*; 1875), brook char (Salvelinus fontinalis; 1877), rainbow trout (*Oncorhynchus mykiss*; 1883), sockeye salmon (*Oncorhynchus nerka*; 1902), and lake trout (*Salvelinus namaycush*; 1906) (Stokell 1951; Scott 1964, 1984; Scott et al. 1978; McDowall 1990). Of these seven species, two are now widespread and relatively abundant (brown trout and rainbow trout), two are widespread and relatively abundant in some locations, but with evidence of decline (brook char and chinook salmon), one has a restricted distribution, but now seems to be increasing in abundance (sockeye salmon), one remains as a relict population in a single lake (lake trout), and one is now either extinct or nearly so (Atlantic salmon) (McDowall 1990; Jarvis et al. 2019). The present-day patterns of distribution and abundance reflect interactions between the history of introduction of each species, in conjunction with the influences of landscape and habitat, interactions with other salmonid species, and perhaps native species, and species-specific environmental tolerances.

3 The Widespread and Successful Species: Brown and Rainbow Trout

Today, brown and rainbow trout form the basis of the New Zealand salmonid recreational fishery (McDowall 1990; Unwin 2016). Both species are widespread, reflecting the huge efforts that were initially expended to import the species in the late 1800s, the success in rearing them in hatcheries, and the subsequent zeal exhibited by the various acclimatisation societies in releasing them widely around the country (McDowall 1990; Jones and Closs 2018; Jarvis et al. 2019). Brown trout had also entered the coastal marine environment within a few years of their release in 1867, thus enabling them to colonise new river catchments ahead of releases by the acclimatisation societies (Scott 1964). By 1921, it is estimated that around 64 million brown trout had been released into New Zealand waterways, and importations of ova from the Northern Hemisphere continued into the 1960s (Scott 1964; McDowall 1990). Similarly, around ten million rainbow trout had been released by 1921 by the Auckland Acclimatisation Society in the north of the country alone; records for other regions have not been collated (Scott et al. 1978). Brown and rainbow trout are currently so widespread and abundant across New Zealand that many consider them to be native to the region (Jarvis et al. 2019). Both species are naturally reproducing across a broad range of waterways, and only limited stocking of a relatively small number of put-and-take fisheries occurs around New Zealand (Jarvis et al. 2019).

3.1 Brown Trout

The introduction of brown trout to New Zealand has been the most successful one for salmonids (Jones and Closs 2018; Jarvis et al. 2019). Arguably, they are now the most common and widespread freshwater fish in New Zealand (Jones and Closs 2018; Jarvis et al. 2019). Although, brown trout are clearly the most widespread and abundant salmonid on the South Island, on the North Island, they are often less common than rainbow trout. In fact, brown trout are generally absent from rivers north of the city of Auckland (Jowett 1990; Jarvis et al. 2019). A remarkable feature of current brown trout distribution and life history in New Zealand is the diversity of documented migratory (potamodromous and anadromous) and non-migratory life-history strategies, which in many ways replicate patterns observed across their native range (McDowall 1990; Jones and Closs 2018). Apparently, this life-history plasticity has been a major contributor to their success (Jones and Closs 2018).

Brown trout ova released in New Zealand were originally sourced from various migratory and non-migratory stocks in England, Scotland, Germany, and Italy (Scott 1964; McDowall 1990). Little regard seems to have been given to where brown trout from these different stocks were raised or released, or subsequently relocated within New Zealand (Scott 1964; McDowall 1990). In effect, this created a fascinating natural experiment with brown trout genetics and life-history traits.

Within a few years of their release in New Zealand, brown trout were caught with increasing frequency from various coastal marine and estuarine habitats (Scott 1964), suggesting that fish were at least migrating downstream from their freshwater spawning habitats to coastal marine environments. Further, populations of brown trout also became established in rivers ahead of any anthropogenic introductions, suggesting movement from catchment to catchment through the marine environment (McDowall 1990). Concomitantly, a long-running debate ensued as to whether 'real' sea trout occurred in New Zealand, and observations of variable patterns of colouration and morphology contributed to the discussion (Scott 1964).

New Zealand comprises a relatively broad latitudinal range and associated landscape heterogeneity and large river systems, and until relatively recently, they were comparatively unaltered by intensive development. This diverse environment has formed what might be considered to be an optimal habitat template for brown trout (Lange et al. 2014; McDowall 1990). For example, brown trout in New Zealand currently exhibit a variety of life-history traits similar to those observed in migratory and non-migratory trout populations in their historic range in Europe (Jonsson and Jonsson 2011; Ferguson et al. 2019). These life-history patterns reflect habitat heterogeneity that occurs across altitudinal and latitudinal gradients (McDowall 1990; Hayes et al. 2000; Jones and Closs 2018). Headwater populations at higher altitudes comprise mainly resident non-migratory individuals that are relatively small in size and occur at comparatively low population densities (Kristensen and Closs 2008; Jones et al. 2019; Mikheev et al. 2020; Mikheev et al. 2022), traits that have been observed in populations in the Northern hemisphere (Jonsson and Jonsson 2011). Downstream populations are frequently migratory, and juvenile emigration from natal streams generally occurs during the first to third years of life (Hayes1988; Kristensen and Closs 2008, Olley et al. 2011; Holmes et al. 2014; Jones et al. 2019; Mikheev et al. 2022). Individual brown trout migrate varying distances downstream over their life history, blurring the distinction between anadromous and potamodromous populations (Kristensen and Closs 2008). Upstream migrations from the habitats where individuals grow to maturity also seem to vary, and barriers to migration appear to determine the extent of upstream movements to spawning habitats (Kristensen and Closs 2008; Mikheev et al. 2021). In the absence of major barriers, some anadromous brown trout migrate more than 50 km upstream to spawn (Kristensen and Closs 2008). Both semelparous and iteroparous life histories occur, and patterns vary with latitude and river system (Mikheev 2020).

The consistent appearance of migratory and non-migratory life-history strategies in New Zealand brown trout, despite their mixed origins, suggests a strong role of environmental cues in driving migration (Kristensen and Closs 2008; Jones et al. 2019; Mikheev et al. 2020, 2022). Migratory life histories in salmonids are initiated when juvenile fish migrate downstream, leaving their natal headwater stream and moving into larger mainstem river, estuarine, or marine habitats (Jonsson and Jonsson 2011). Summer temperatures and competition for resources have been implicated as factors driving the emigration of juveniles in New Zealand (Kristensen and Closs 2008; Holmes et al. 2014; Jones et al. 2019; Mikheev et al. 2020, 2022) and elsewhere (Olsson et al. 2006; Wysujack et al. 2009). At the northern, warmer end of the South Island, juvenile emigration has been observed to coincide with high summer water temperatures that exceed the optima for brown trout growth in small streams (Holmes et al. 2014). In contrast, summer water temperature rarely exceeds optimum temperatures for growth around the southern South Island, suggesting other environmental drivers of migration (Kristensen and Closs 2008). In streams where large migratory trout spawn, high rates of spawning success result in high juvenile brown trout densities in streams in spring, and rapid increases in trout biomass as the fish grow in late spring and early summer (Kristensen and Closs 2008; Jones et al. 2019; Mikheev et al. 2020, 2022). The subsequent accrual of brown trout biomass in streams likely plays a key role in initiating downstream migration (Kristensen and Closs 2008; Jones et al. 2019; Mikheev et al. 2020, 2022). This migration results in a cascade of juvenile fish into the downstream reaches of small tributary streams, further intensifying the competition for resources within these reaches (Kristensen and Closs 2008; Mikheev 2020; Mikheev et al. 2020; Mikheev et al. 2022). By late summer, most juvenile fish have emigrated into larger rivers, and the remaining fish may overwinter in their natal stream (Kristensen and Closs 2008; Mikheev et al. 2020, 2022).

Downstream migrating juveniles that reach lowland river and estuarine habitats will likely find themselves in highly productive habitats, often feeding on whitebait (*Galaxias* spp. juveniles) migrating in from the sea, and subsequently these juvenile brown trout are characterised by high growth rates and large sizes (Stewart et al. 2022). However, if these individuals are to successfully reproduce, they must return to headwater streams to spawn (Kristensen and Closs 2008). If successful, their large size and high fecundity will repeat the environmental resource mismatch that triggered their own initial downstream migration (Kristensen and Closs 2008; Jones et al. 2019; Mikheev et al. 2020, 2022). Thus, brown trout migratory life cycles appear to be sustained by this positive feedback loop, whereby successful spawning of large highly fecund migratory fish in small streams creates the very circumstances that initiate emigration of juveniles, and hence the next generation of migratory brown trout (Kristensen and Closs 2008; Jones et al. 2019; Mikheev et al. 2020, 2021, 2022). Further, interactions between temperature and resource competition are also likely, given that higher temperatures will inevitably increase metabolic rates up to a point, thus intensifying resource limitation and competition in the spawning streams that large migratory fish can reach (Kristensen and Closs 2008; Holmes et al. 2014; Jones et al. 2019; Mikheev et al. 2020). Although no studies have been conducted on the genetics of brown trout in New Zealand, it is also likely that there is a genetic component influencing the propensity to migrate in different individuals and across populations (see Ferguson et al. 2019).

3.2 Rainbow Trout

Rainbow trout are the other exceptionally successful salmonid translocation to New Zealand, and it is the dominant salmonid species across much of the North Island (Jowett 1990). For example, the world-renowned Lake Taupo fishery in the central North Island is largely based on rainbow trout (McDowall 1990; Dedual and Rohan 2016). Whilst rainbow trout have been stocked around the South Island, stocked populations generally do not persist in river systems lacking large lakes despite repeated releases in numerous river systems (Jowett 1990; McDowall 1990). The Pelorous River at the northern end of the South Island is an exception, however, and it supports a naturally reproducing rainbow trout population despite the absence of a large lake in the catchment (G. Closs, Pers. Obs.). In catchments with lakes, rainbow trout are abundant, and often the dominant salmonid species (e.g. the large glacial lakes and their associated tributary and outflow rivers along the eastern side of the Southern Alps on the South Island (Jowett 1990; McDowall 1990). Where rainbow trout are abundant, their winter-spring spawning life history may result in superimposition of autumn-winter spawning brown redds and in subsequent reduction, or in some cases extirpation of brown trout populations (Scott and Irvine 2000).

Rainbow trout released in New Zealand came from several sources, but details of their importation are not certain (Scott et al. 1978; McDowall 1990). Based on the records that do exist, it is likely that rainbow trout were sourced from both migratory steelhead and rainbow trout (Scott et al. 1978; McDowall 1990). However, despite the likely introduction of at least some steelhead into New Zealand (Scott et al. 1978), there is no evidence of significant anadromous rainbow trout migrations ever developing in New Zealand (McDowall 1990). Despite the lack of anadromous migrations, many rainbow trout populations in New Zealand are migratory, with extensive lacustrine-adfluvial spawning runs from lakes into tributary rivers (Dedual and Jowett 1999; Venman and Dedual 2005; Dedual 2021). Migration patterns can be complex, with some fish migrating upstream slowly prior to reaching maturity in autumn, and other mature fish migrating upstream rapidly from downstream lakes to spawn in late winter/spring (Dedual and Jowett 1999; Venman and Dedual 2005; Dedual 2021). Similarly, emigration of juveniles from their natal streams is also variable, occurring in first year or second year, depending on population and stream (Rosenau 1991; Hayes 1988, 1995). Non-migratory populations of rainbow trout also occur, with resident headwater populations present on the North Island (McDowall 1990), and shoreline lacustrine spawning occurs in some lakes (Penlington 1983).

Rainbow and brown trout likely compete for food and space in rivers and streams in New Zealand; diets and habitat use are similar for both species (McLennan and MacMillan 1984). In rivers, both species feed primarily on drifting invertebrates, but subtle differences in habitat use may occur. McLennan and MacMillan (1984) found that rainbow trout in the Mohaka River tended to occupy the head and middle parts of pools, whereas brown trout were mainly found in rapids, backwaters, and the deeper parts of pools.

In oligotrophic New Zealand lakes, a more productive shallow littoral habitat appears to be crucial, particularly for rearing juvenile rainbow trout (Graynoth 1999; Stoffels and Closs 2002). In these habitats, piscivory on native fish species seems to play a key role in enabling fish to grow to large sizes (Rowe 1984). Success of rainbow trout in North Island inland lakes has been partly attributed to the introduction of common smelt (*Retropinna retropinna*), a native planktivore more typically associated with coastal habitats, which were released into these inland lakes in the early twentieth century and where they now comprise a significant proportion of rainbow trout diet (Rowe 1984). In recent years, a fishery for spectacularly large rainbow (and brown) trout has developed in canals delivering water for the generation of hydropower to Lake Benmore, a large reservoir on the South Island. Large pens used for rearing chinook salmon (*Oncorhynchus tshawytscha)* have been placed in the canals, and trout feed on the surplus salmon feed drifting from the cages. The combination of optimum environmental conditions and unlimited food have created an environment where extraordinary growth rates and sizes have been documented (Adams 2020).

4 Still Widespread, but Declining: Brook Char and Chinook Salmon

4.1 Brook Char

Consignments of brook char were imported into New Zealand from 1877 until the early 1900s (Thompson 1922). The species was hatched and reared at hatcheries around the country, and individuals were released at multiple locations on both the North and South Islands of New Zealand, and releases continued into the twentieth century (Thompson 1922; McDowall 1990). Despite the considerable effort expended to establish the species, brook char introductions have generally failed (Dorsey 2016). Very few populations produce individuals that might be considered worth catching, and most remaining populations are in montane streams with limited access (McDowall 1990; Dorsey 2016). Although relatively few people are aware of the species' presence, brook char can be locally abundant in higher altitude streams in southern New Zealand, and they likely persist in a few streams in the central North Island (Dorsey 2016). Their distribution is slowly declining. Most extant populations are isolated in small headwater streams, and several populations have gone extinct in recent years, usually where brown trout have expanded their distribution upstream (Dorsey 2016).

Competition with other salmonids, most notably brown trout, is the most likely explanation for the failure of brook char to establish more widely in New Zealand (McDowall 1990; Dorsey 2016). Brook char rarely coexist with other salmonid species and are usually located upstream of barriers preventing the upstream dispersal of brown trout (Dorsey 2016). At the downstream end of their distribution, they may be sympatric with brown trout within streams for a short distance (McDowall 1990; Dorsey 2016), and in such cases, there is considerable overlap in diet (Fechney 1988). Brook trout persistence in higher altitude montane streams is consistent with a slightly lower optimal water temperature than either brown or rainbow trout (Carlander 1969). Populations of brook char in southern New Zealand are non-migratory. Most individuals mature within 2 years, and they generally reach only 200–250 mm (total length) after 5 years (Dorsey 2016). The scope for migration is limited given that most populations are restricted to small headwater streams (Dorsey 2016).

4.1.1 Chinook Salmon

Chinook salmon introductions to New Zealand have been generally successful, and the species is now established in multiple, large South Island river systems, particularly those draining the eastern side of the Southern Alps. Initial attempts to introduce the species that began in the 1870s were unsuccessful, and relatively small numbers were released in rivers (McDowall 1994). This strategy was revised in the 1890s by L.F. Ayson, who focused efforts on the large Waitaki River system (McDowall 1994). A hatchery was built on a tributary of the Waitaki River, and chinook salmon ova were obtained from the McCloud River (California, USA), a tributary to the Sacramento River, and more than 1.5 million salmon were produced (McDowall 1990). Individuals were released in the Waitaki River catchment, where propagation and releases continued for years (McDowall 1994). The resulting propagule pressure apparently drove their successful establishment, and by 1908, anadromous chinook salmon were spawning throughout the Waitaki and other nearby river catchments on the east coast of the South Island (McDowall 1990, 1994). Chinook salmon were released throughout New Zealand, but although chinook salmon was established in other large rivers on the south and west coasts of the South Island, the most significant salmon runs continue to occur in the east coast rivers (McDowall 1990).

Anadromous chinook salmon runs that developed in the South Island east coast rivers replicated many aspects of the life history of chinook salmon across their home range (McDowall 1990; Quinn et al. 2001). Upstream migration of salmon begins in the late spring/early summer (October–December), peaking in early Austral autumn (March) (McDowall 1990); however, catchment-specific life-history traits are evident, suggesting most fish are returning to their natal stream. Supporting evidence includes recapture of tagged fish in their natal streams and genetic structuring of the New Zealand salmon population (Quinn et al. 2001; Kinnison et al. 2011; Quinn et al. 2011). Most individuals return at age 3, reflecting the relatively short lengths of New Zealand rivers (<200 km) (McDowall 1990; Quinn et al. 2001; Kinnison et al. 2011).

Older, larger fish were historically recorded from catchments, such as the Clutha River, but runs of these large fish ceased following the construction of hydropower dams that block migration of anadromous fish into headwater spawning grounds

(McDowall 1990). Some early life-history plasticity is also evident. For example, juveniles in systems with lakes migrate to the sea at 1+ years old, but juveniles in river systems without lakes generally migrate to the sea during the first year of life (Quinn et al. 2001; Kinnison et al. 2011). Emigration from spawning streams into river main stems tends to occur in two waves: the first soon after emergence in August–November, followed by a period of emigration of larger fry from November–January (Unwin 1986). Juveniles that remain in rivers longer tend to spend more time at sea before returning to freshwater (Unwin and Lucas 1993). Unwin (1986) concluded competition for resources amongst juveniles was driving the emigration timing. Land-locked populations have also developed in several large inland lakes, including the Clutha River catchment, where hydropower dams have blocked the upstream migration of large anadromous fish into the glacial lakes in the headwaters (McDowall 1990).

Chinook salmon abundance has undoubtedly declined over the past 80 years, and artificial propagation-associated releases currently sustain the species across its range (McDowall 1990). Starting from the mid-1934 (Waitaki Dam), the construction of hydropower dams without effective fish passage in the Waitaki and Clutha rivers (the two largest rivers on the eastern side of the South Island), markedly diminished salmon runs in those systems (McDowall 1990). Excessive angler harvest, degradation of spawning habitat related to agricultural intensification, and water extraction have likely contributed to recent declines in anadromous populations (Rankin et al. 2022). Land-locked populations in lakes have also declined, and although the reasons for these declines are less obvious, subtle changes to lake ecology related to land-use change have also occurred in these systems (e.g. Bayer et al. 2016). Changes in the marine environment, including commercial fishing activities or climate change, or both, are also potentially related to the observed declines, although evidence linking cause and effect is lacking.

5 Extinct, Nearly Extinct, and Back from Near-Extinction: Atlantic Salmon, Lake Char and Sockeye Salmon

5.1 Atlantic Salmon

The widespread establishment of Atlantic salmon was undoubtedly the most cherished goal of those wishing to introduce salmonids in New Zealand (Thompson 1922; McDowall 1990). However, given the extent of the resources deployed for this attempted introduction, it was arguably a major failure (McDowall 1990). Efforts to introduce and establish Atlantic salmon began in 1864, and imports of ova periodically occurred into the 1960s (Thompson 1922; McDowall 1990). The first attempt to import live fish in 1864 failed, but from 1868 to 1910, live ova were imported into New Zealand more than 20 times (Thompson 1922). It is estimated that over 2.75 million Atlantic salmon were released. Most ova were obtained from northern Europe, but some originated from land-locked stocks in North America (Stokell 1959; McDowall 1990). Relatively small numbers of Atlantic salmon were initially released, mostly in locations around southern New Zealand, but there is no clear evidence that any persisted. Following these failures, Marine Department Inspector of Fisheries L. F. Ayson again deployed the strategy that had resulted in the successful establishment of chinook salmon (i.e., release large numbers of fish in a single catchment, the Waiau River in Southland, New Zealand; Thompson 1922; McDowall 1990). Again, it appears that high propagule pressure contributed to the successful establishment of an Atlantic salmon population at the southern end of New Zealand (Thompson 1922; McDowall 1990).

From the early 1920s, Atlantic salmon were being caught by anglers from the Waiau River system (McDowall 1990). Spawning runs were observed in tributary rivers, and there were reports of fish being caught in the lower reaches of the Waiau River (McDowall 1990). However, the focus of the fishery remained in the headwaters of the Waiau River, particularly in Lake Te Anau. In Lake Te Anau, a spawning run of 1000–2000 individuals was observed by 1930 (McDowall 1990). Atlantic salmon never grew particularly large in this system, and whilst the occasional individual was caught at sea (e.g. Phillipps 1924), there is no compelling evidence that a significant anadromous population ever developed (Stokell 1959; McDowall 1990). Furthermore, no evidence of significant Atlantic salmon runs along the length of the Waiau River exists, despite a lack of major barriers to migration between the estuary and Lake Te Anau (McDowall 1990).

By the late 1950s, it was evident that the Atlantic salmon population in Lake Te Anau was declining, and by 1963, Atlantic salmon represented only 6% of the salmonid catch from the lake (McDowall 1990). The reasons for the decline were unclear. Angling pressure on the population was substantial, and ova were harvested to rear fish for release elsewhere, but neither were likely reasons for the demise of the population (McDowall 1990). A plausible explanation for the decline of the Atlantic salmon may be competition with rainbow trout that were released into the Waiau River system in the 1920s, and soon became the most abundant salmonid species in the catchment (McDowall 1990); however, there is no direct evidence to support this hypothesis (McDowall 1990). Atlantic salmon were rare in Lake Te Anau by the 1970s, and populations that persisted in two smaller lakes (Lake Gunn and Lake Fergus) further upstream have also subsequently declined (McDowall 1990). I know of a single, small Atlantic salmon being caught from Lake Fergus in the early 2000s, and whilst that individual may have been part of the remaining wild population, it could also have been the result of the final release of hatchery fish into the upper catchment when all breeding of Atlantic salmon ceased. I can find no records of their presence since then; Atlantic salmon are, most likely, now extinct in New Zealand.

5.2 Mackinaw (Lake Trout)

In 1906, the New Zealand Government imported 50,000 mackinaw eggs that were subsequently hatched by the North Canterbury Acclimatisation Society (Thompson 1922; McDowall 1990). About 4000 mackinaw were released into Lake Pearson in Canterbury, and although 4000 were shipped to the west coast of South Island for release into Lake Ianthe, their ultimate fate is unclear (Stokell,1951). Mackinaw released into Lake Pearson persisted (McDowall 1990), with reports of catches on 'Facebook' as recently as 2015. Stokell (1951) reported individuals weighing up to 3 kg were caught in the past, but today the typical size is less than 1 kg (Stokell 1951; McDowall 1990). Lake Pearson is relatively small and shallow (approximately 17 m deep, 3 km long, and 0.5 km at its widest; Stokell 1951). Given that mackinaw is typically a fish of large deep lakes across their natural range, their persistence in Lake Pearson for nearly 100 years is somewhat surprising (McDowall 1990). The lake also supports brown and rainbow trout, and mackinaw are only occasionally caught, suggesting that only a relatively small population remains (McDowall 1990).

Mackinaw were raised in hatcheries for many years after the introduction into Lake Pearson, including the Wanaka hatchery, which is on a tributary of the large and deep, Lake Wanaka. Although it is possible juvenile mackinaw occasionally escaped downstream into the lake, there are no records of angler captures or evidence that a population was ever established. That said, as long as the Lake Pearson population exists, the risk of translocation to new locations in New Zealand remains.

5.3 Sockeye Salmon

Sockeye salmon were released into the Waitaki River system in 1902, following the acquisition of about 160,000 ova supplied without charge by the Canadian Fisheries Department (Thompson 1922; Scott 1984). Because the ova were sourced from Shuchwap Lake, British Columbia, which supported both anadromous sockeye and freshwater kokanee (non-migratory sockeye), it is likely that the fish sent to New Zealand contained progeny of both stocks (Scott 1984). By 1913, sockeye salmon were recorded in spring-fed creeks at the head of Lake Ohau, a large glacial lake in the headwaters of the Waitaki River (Thompson 1922; Scott 1984). There are also records from 1915 of larger sockeye salmon spawning further downstream in the Twizel river - there were no lakes downstream of the Twizel River at the time (there are lakes for hydropower generation there now); therefore, it is possible a small anadromous population had developed as sockeye dispersed throughout the system (Thompson 1922; Scott 1984). However, they could also have been larger individuals migrating from one of the lakes, or simply those released from hatcheries (Scott 1984).

In the decades that immediately followed their release, sockeye salmon were largely forgotten, and the construction of a hydropower dam on the Waitaki River in 1934 certainly precluded any possibility of anadromous migration (McDowall 1990). In 1969, sockeye salmon were ‘rediscovered’, with an early-autumn (March) spawning run still present in the headwater tributaries of Lake Ohau (McDowall 1990). Further hydropower development created new reservoirs downstream, and sockeye established in those lacustrine environments as well (McDowall 1990). Growth rates of fish in the more productive hydropower reservoirs was higher compared to growth in the cold, deep, and oligotrophic Lake Ohau (Graynoth 1987). Diet is diverse, but the diet of sockeye salmon contained a higher proportion of zooplankton compared to brown and rainbow trout (Graynoth et al. 1986).

The further development of hydropower generation downstream from Lake Ohau isolated the population of sockeye salmon in Lake Benmore from their upstream spawning sites, so it was assumed that populations of sockeye salmon in the lower hydropower reservoirs would decline (McDowall 1990). However, in recent years, the population appears to have boomed, with particularly large spawning runs occurring in the tributaries of Lake Benmore (https://www.youtube.com/watch?v=taOmafdHGcY). The reasons for the apparent boom in the numbers of sockeye salmon in the Waitaki reservoirs is unclear but may be related to increasing inputs of nutrients into the reservoirs related to the intensification of agriculture in upstream catchments. Large salmon farming pens in the canals that feed into Lake Benmore may also contribute to increased nutrient loading. From a beginning as a relict population that lingered for 50 years in an oligotrophic lake (Scott 1984), the booming sockeye salmon population in the Waitaki Reservoirs is a likely beneficiary of the increasingly developed and nutrient-enriched landscape of modern New Zealand.

6 Distribution and Negative Effects of Salmonids on Native Fish Species

At the landscape scale, salmonids, and particularly brown and rainbow trout, are now a nearly ubiquitous feature of freshwater fish communities in New Zealand (Jarvis et al. 2019). Brown and rainbow trout have colonised most of the available habitat through natural dispersal, and their present distributions reflect the various biotic and abiotic factors influencing their population dynamics and movements (Jones and Closs 2018; Jellyman et al. 2018; Jarvis et al. 2019). Rainbow trout dominate the North Island, whereas brown trout dominate on the South Island, reflecting the slight differences in optimal temperatures of the two species (Jowett 1990). Brook char have only persisted in higher altitude streams, upstream of brown trout. Their optimal temperature is a degree or so lower than brown trout, potentially giving them a competitive advantage in such cold, unproductive environments (Dorsey 2016).

Migrations occurs throughout occupied catchments, although the extent and magnitude of movements is strongly influenced by latitude and local landscape characteristics (Jones et al. 2019; Mikheev et al. 2020, 2021). Extensive anadromous and potamodromous migrations comprise a significant feature of brown trout population dynamics in the southern South Island, but the scale and magnitude of these movements declines further north (McDowall 1990; Kristensen and Closs 2008; Olley et al. 2011; Holmes et al. 2014; Mikheev et al. 2020). In the south, spawning by large migratory fish result in juvenile abundances that exceed the carrying capacity of the streams, likely triggering juvenile emigration downstream as available resources become insufficient to support the increasing biomass (Mikheev 2020; Mikheev et al. 2022). Abiotic factors appear to play an increasingly important role in determining distribution and movements further north (Holmes et al. 2014). This is most obvious at the northern limits of salmonid distributions, where higher peak and mean temperatures in lower-altitude systems limit the persistence of salmonids (Jowett 1990; McDowall 1990).

At finer spatial scales, patterns of salmonid distribution can be quite complex, nuanced, and dynamic, and trout are not present or dominant in all freshwater systems across New Zealand (Jarvis et al. 2019). In the smaller coastal streams and catchments of New Zealand, and particularly where natural vegetation remains intact, native fish species are often dominant (Jowett et al. 1998; Chadderton and Allibone 2000; David et al. 2002). In these smaller systems, salmonids are often rare or absent (McDowall et al. 1977; Jowett et al. 1998; Chadderton and Allibone 2000; David et al. 2002). Large aggressive giant kōkopu (*Galaxias argenteus*) and banded kõkopu (*G. fasciatus*) are often the dominant species, even in streams where there are no obvious barriers to trout movement from downstream (David et al. 2002). Although unsuitable habitat may exclude trout in some cases, suitable trout habitat is available in others (David et al. 2002).

It seems plausible that native stream fish communities that are dominated by kōkopu, exhibit a degree of biotic resistance (see Harvey et al. 2004) to trout invasion. Kōkopu live in size-structured social dominance hierarchies which are aggressively maintained by the largest fish in each pool (David et al. 2007; Hansen and Closs 2005, 2009). In smaller streams where maximum size of both kōkopu and trout is likely constrained by resource availability, kōkopu appear to have a competitive edge over trout (Hansen and Closs 2005; Akbaripasand et al. 2014). However, the competitive balance will inevitably swing in favour of trout in larger streams where trout can grow faster and attain larger sizes than the largest giant kōkopu.

Brown trout (and perhaps rainbow trout) have had severe negative effects on the various species of non-migratory *Galaxias* spp. that live in inland river and stream systems (Jellyman et al. 2018; Jones and Closs 2018). However, the dynamics of the interactions between trout and non-migratory *Galaxias* spp. are context dependent, influenced by the interaction between biotic and abiotic processes (Jellyman et al. 2018; Jones and Closs 2018).

About 20 unique species and lineages of non-migratory galaxiids are distributed across a wide range of altitudes and habitat types (Burridge and Waters 2020). Adult non-migratory *Galaxias* spp. are morphologically similar; however, a clear egg size/

fecundity trade-off related to altitude is evident amongst species (Jones and Closs 2015, 2018). High-altitude species (*G. eldoni* and *G. pullis*) produce the largest eggs and have relatively low fecundity, an adaptation for rearing larvae in cold unproductive streams (Jones and Closs 2015; Jones et al. 2016). These low fecundity species have fragmented distributions and are restricted to short headwater stream reaches upstream of barriers to trout movement (Jones and Closs 2015; Jones et al. 2016). Galaxiid distributions are rarely observed to overlap with trout, and when they are sympatric with brown trout, invariably the galaxiids are extirpated within a few years (Jones and Closs 2015). Larvae of higher altitude non-migratory galaxiid species do not disperse downstream from the spawning sites, and therefore connectivity is limited amongst populations isolated in these headwater streams, so recolonisation following extirpation does not occur (Jones and Closs 2015). Persistence of headwater galaxiid species is totally dependent on the maintenance of downstream barriers to trout movement (Jones and Closs 2015) because as barriers erode or human-assisted upstream transfer of trout occurs, native non-migratory galaxiids disappear (Jellyman et al. 2018; Jones and Closs 2018).

At lower altitudes, several species of non-migratory *Galaxias* spp. do coexist with trout to some degree, and under certain circumstances (Jones and Closs 2015, 2018). Lower-altitude species, including *G. vulgaris*, *G. anomalous*, and *G. gollumoides*, produce smaller eggs and exhibit a correspondingly greater fecundity than the high-altitude species (Jones and Closs 2015; Jones et al. 2016). Larvae may disperse considerable distances downstream from where they hatched, thus potentially creating a degree of downstream connectivity along streams (it is unknown whether there is any subsequent upstream migration) (Jones and Closs 2015). The combination of high fecundity and metapopulation connectivity appears to create a degree of resilience amongst these species to trout, potentially facilitating co-existence to some extent (Jones and Closs 2015, 2018). That resilience is likely further enhanced where there are upstream populations of galaxiids protected from trout by barriers to upstream migration, or in streams where trout populations are generally suppressed by either frequent flood- or drought-related disturbance (Jellyman et al. 2018; Jones and Closs 2018).

In large and extensive lowland systems, the negative effects of trout are both harder to discern and study (Jowett et al. 1998; Jellyman et al. 2018). In these systems, trout undoubtedly prey on a variety of native fish species, including galaxiid whitebait (mostly comprising juveniles of *Galaxias maculatus*), bullies (*Gobiomorphus* spp.), smelt (*Retropinna retropinna),* torrentfish (*Cheimarrichthys fosteri*), and eels (*Anguilla* spp.) (Stewart et al. 2022; Jellyman et al. 2018). Indeed, the ability of brown trout to migrate downstream from natal streams and exploit the rich resources of lowland rivers and estuaries no doubt contributes to the large average size of brown trout seen in many New Zealand rivers (Mikheev et al. 2021). Most of these lowland native species are highly fecund, and their population dynamics are sustained by extensively connected and poorly understood metapopulation processes that likely confer a degree of resilience to the presence of salmonids (McDowall 1990). That said, it is likely that trout had a role in the extinction of the only freshwater species known to have become extinct in the past 150 years, the

New Zealand grayling (*Prototroctes oxyrhychus*), a diadromous species that was once widespread in lowland rivers (Lee and Perry 2019). However, the causes of extinction of this species whilst others remained relatively abundant is unclear, but multiple stressors, including overfishing, land-use change, and disease, likely played a role in the demise of the New Zealand grayling (McDowall 1990; Lee and Perry 2019).

7 Salmonids: Unfortunately, an Irreversible Legacy of Colonial New Zealand

In New Zealand freshwaters, the Anthropocene undoubtedly began with the introduction of salmonids. Salmonids, particularly brown and rainbow trout, have entrenched themselves in New Zealand's freshwater communities and ecosystems (Jellyman et al. 2018; Jones and Closs 2018; Jarvis et al. 2019). They have had significant negative effects on native fish and invertebrates. Some of those effects are well-known and understood, and others will likely remain unknown (McDowall 2006; Jellyman et al. 2018; Jones and Closs 2018; Jarvis et al. 2019). Within the human population of New Zealand, feelings about this legacy are mixed (Tadaki et al. 2022). Although angling for salmonids has deep cultural roots and remains popular, particularly in the more rural South Island, participation in angling is declining, a pattern consistent with other increasingly urbanised societies (Dedual and Pickford 2018). For many native Māori, feelings towards salmonids are ambivalent. Although many Māori fish for salmonids, salmonids also negatively affect native fish and fisheries, and there has been no compensation for the loss of that cultural taonga (treasure) (Tadaki et al. 2022). A rising national awareness of the colonial legacy of introduced species, and an increasing community-wide desire to reverse the associated negative effects have also led to wider calls for salmonid control and eradication (Pham et al. 2013; Jellyman et al. 2018).

Realistic options to remove or exclude salmonids from most of the freshwater habitats occupied in New Zealand may never occur, but patterns of salmonid distribution will vary in response to a changing climate (Jellyman et al. 2018; Jones and Closs 2018; Jarvis et al. 2019). Rather than waste energy and resources on what is probably a futile debate concerning complete salmonid eradication, a more productive approach would be to consider where, when, and how salmonids can and should be managed (see Pham et al. 2013). Salmonids have had negative effects on the unique non-migratory galaxiids of New Zealand (Jellyman et al. 2018; Jones and Closs 2018), and it is demonstrably feasible that eradication and exclusion of salmonids with no significant fishery value can create trout-free galaxiid refugia in these small headwater habitats (Pham et al. 2013; Jones and Closs 2018). Such refugia would protect the most vulnerable headwater galaxiid species and increase the population resilience of lower altitude, more widespread galaxiid species (Pham et al. 2013; Jones and Closs 2018).

From a biological perspective, the introduction of salmonids to New Zealand is fascinating in so many ways. There has been, and continues to be, much to learn. Salmonids in New Zealand have revealed what it takes for introduced species to establish and spread, or conversely, marginally persist or become extinct. Native species and ecosystems have also responded in varied ways. Some species and systems have exhibited surprising resilience and resistance to the invaders (e.g. lowland coastal systems), whereas in other systems (e.g. headwater streams), salmonids often dominate, extirpating significant elements of the native fauna. Salmonids have also revealed much about themselves. Although often regarded as sensitive and vulnerable taxa across their native range, they have also exhibited extraordinary levels of adaptability and resilience following their introduction to New Zealand. Much of their success, and particularly that of brown and rainbow trout, has been associated with an ability to adapt to a new environment. The capacity of salmonids to successfully exploit a wide range of migratory and resident life-history strategies in a novel landscape is quite remarkable.

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Application of a Fine-Scale Modeling Approach to Assess Broad-Scale Changes in Stream Salmonid Habitat in a Changing Climate

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Abstract Despite abundant research exploring how climate change may affect population demographics of stream fishes (e.g., survival, growth, and relative abundance), tools are needed to provide accurate, fine-scale stream temperature predictions over large spatial extents encompassing multiple fisheries management agencies and jurisdictions. As such, a fine-scale modeling approach based on artificial neural networks was developed to forecast reach-specific thermal conditions under different climate-change scenarios across the Upper Midwest, USA (i.e., Michigan, Minnesota, and Wisconsin). Specifically, models collated landscape and climatic data to predict individual stream temperatures across watersheds and states with relatively high accuracy ($r^2 = 0.71–0.76$). Collectively, models predicted widespread increases in stream temperature across the study region averaging 1.5 °C through 2087, with substantial warming in Wisconsin and Minnesota but moderate warming in Michigan streams. For instance, the extent of warm-transitional (July mean water temperature 19.5–21.0 °C) and warmwater (>21.0 °C) habitats in Wisconsin—currently 40% of stream kilometers—was projected to reach up to 63% in 2042 and 71% in 2087, with concomitant reductions in growth and survival of stream salmonids (e.g., brook charr *Salvelinus fontinalis*, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss*). Overall, our modeling approach provides managers with a stream-specific yet spatiotemporally broad tool for predicting the magnitude and distribution of stream warming amid climate change that can be used to prioritize efforts for stream salmonid management and conservation. Such information is critical for developing state and regional climate adaptation strategies for Upper Midwest streams and coordinating thermal habitat management activities (e.g., groundwater conservation and riparian/watershed rehabilitation) among fisheries and aquatic resource agencies and across jurisdictions.

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1 Introduction

Freshwater ecosystems are increasingly threatened by climate change and other anthropogenic stressors such as land-use alteration, species invasion, harmful algal blooms, and microplastic pollution (Carpenter et al. 1992; Palmer et al. 2009; Woodward et al. 2010; Taniwaki et al. 2017; Reid et al. 2019). Due to anticipated changes in precipitation patterns as well as generally increasing air temperatures, global climate change is expected to have substantial effects on streams by altering flow regimes and increasing water temperatures (Eaton and Scheller 1996; Meyer et al. 1999; Allan 2004; van Vliet et al. 2013). Water temperature is one of the most important factors influencing the reproduction, abundance, and distribution of stream fishes (Magnuson et al. 1979; Wehrly et al. 2003, 2007; Lyons et al. 2009; Arismendi et al. 2013; Armstrong et al. 2021). Stream temperature affects fishes

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directly by influencing biological processes including metabolism, feeding, and growth (Elliot 1981), as well as indirectly by influencing prey availability and competitive interactions (Taniguchi et al. 1998). Changes in stream temperature regimes can alter fish abundance and distribution (Jackson and Mandrak 2002; Lyons et al. 2010; Stewart et al. 2015, 2016a), sometimes resulting in declines of stream salmonids near the upper end of their thermal tolerances (Keleher and Rahel 1996; Carlson et al. 2017a, 2017b). Therefore, forecasting stream temperature alterations is imperative for predicting how stream salmonid populations may respond to climate change and prioritizing management actions from local to regional scales (Snyder et al. 2015; Carlson et al. 2019, 2020).

Most research exploring effects of climate change on stream temperature and fishes has focused on smaller regions such as single stream reaches (Caissie et al. 2001; Caissie 2006; Dugdale et al. 2018; Lee et al. 2020), local stream watersheds (Meisner 1990; Gardner et al. 2003; Arismendi et al. 2014; Selbig 2015), or individual basins/sub-basins (Sahoo and Ray 2008; Isaak et al. 2010; Ficklin et al. 2013). Increasingly, researchers are assessing climate-change effects at larger spatial extents (Buisson et al. 2013; van Vliet et al. 2013; Pletterbauer et al. 2015; Detenbeck et al. 2016; Isaak et al. 2016; Ruiz-Navarro et al. 2016; Comte and Olden 2017; Tsang et al. 2021). Some studies have evaluated impacts of climate change on lake and stream fishes throughout the Great Lakes basin (Meisner et al. 1987; Collingsworth et al. 2017), the Muskegon River watershed (Michigan, USA, Steen et al. 2010), and the North Platte River drainage (Wyoming, USA, Rahel et al. 1996, Acharya et al. 2012). Similarly, Eaton and Scheller (1996) and Mohseni et al. (2003) assessed fish-habitat responses to climate change at over 1700 stream gauging stations in the contiguous United States. While these large-scale assessments provide important information for planning at the national level, they are often less focused on characterizing the implications of stream temperatures at finer scales (e.g., reaches and watersheds) for fisheries conservation and management strategies at local, state, and regional levels, particularly in the Upper Midwest, USA (Michigan, Minnesota, Wisconsin).

Geographic information systems (GIS) approaches have emerged as a valuable tool for extrapolating results at smaller scales to make predictions about stream temperature and subsequent fish-species changes across broad geographic regions (Keleher and Rahel 1996; Lyons et al. 2010; Stewart et al. 2015, 2016a; Isaak et al. 2017). However, integration of small- to large-scale thermal habitat information is relatively uncommon and has not been performed for all streams across Michigan, Minnesota, and Wisconsin, USA, highlighting an important knowledge gap that motivated the present study. Moreover, small- to large-scale thermal habitat models could be improved by developing a flexible approach that synthesizes diverse data sources to identify associations between stream habitats (e.g., thermal and physical) and fish communities across varying spatiotemporal scales, including stream reaches, watersheds, and regions at daily, monthly, and yearly time steps. Such an approach could serve as a foundation for integrative stream research and management programs involving local, state, regional, and national partnerships that are necessary for conserving salmonids and other stream biota and habitats in a changing climate.

The goal of this study was to develop a fine-scale modeling approach that incorporates landscape, climate, and stream temperature data across broad spatial extents to predict stream temperature under different climate-change scenarios and evaluate implications for stream salmonid populations in the Upper Midwest, USA. This study is part of an effort to assess riverine-ecosystem vulnerability to climate change in the Great Lakes region (Stewart et al. 2016a) and builds on work of Lyons et al. (2010) and Stewart et al. (2015) in Wisconsin by integrating diverse data sources into a common approach for forecasting stream temperature metrics (e.g., July mean temperature) for every stream reach in Michigan, Minnesota, and Wisconsin. Our objectives were to: (1) model current mean daily stream temperatures and thermal habitat conditions for all streams in Michigan, Minnesota, and Wisconsin; (2) quantify the relative change in July mean stream temperatures across multiple future time steps in a changing climate; (3) evaluate future changes in stream salmonid thermal habitat suitability and associated management implications; and (4) discuss limitations and potential uses for this small- to large-scale thermal habitat assessment. Given our focus on stream salmonids and their management in the Upper Midwest, USA—a region where fisheries and aquatic resource management is primarily a state-level enterprise—inclusion of state-level models was essential to address the objectives of this chapter. Recognizing that state-centric models can be considered hydrologically uninformative (i.e., state boundaries *per se* have little influence on hydrology), we selected a modeling approach that is most relevant for salmonid management in our part of the world.

2 Methods

2.1 Study Area

The study area covers approximately 645,000 km^2 across the states of Michigan, Minnesota, and Wisconsin in the midwestern United States (Fig. 1). Spanning all streams in these states, the study area falls within the Temperate Plains and Upper Midwest super ecoregions, which comprise aggregated Level III sub-regions (Omernik and Griffith 2014). Agricultural land use occurs throughout the study area, and urbanization is common, although portions of northern Michigan, Wisconsin, and Minnesota remain forested with many glacially formed lakes and wetlands. Streams in the study area are generally surrounded by wetlands, forests, or grasslands, but agricultural and urban streams were included in the study when they encompassed natural flow paths (i.e., no canals, ditches, drains, pipelines, coastlines, or diversions, see full inclusion criteria below).

The study area has heterogeneous geology and hydrology, ranging from groundwater-fed, hydrologically stable streams draining deep sand and gravel

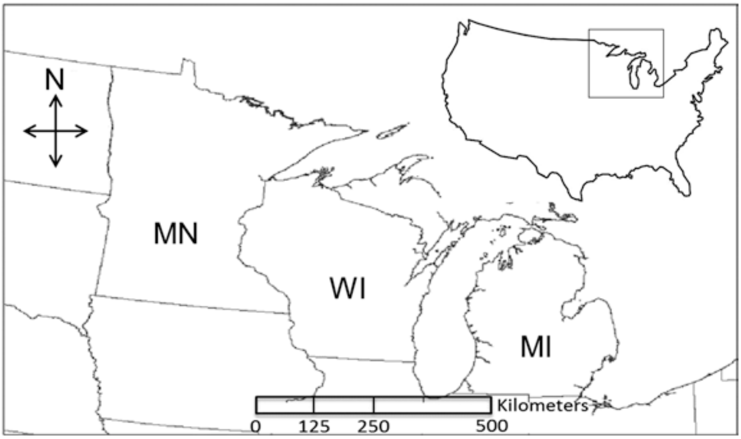


Fig. 1 Map of Michigan (MI), Minnesota (MN), and Wisconsin (WI) where stream temperatures were modeled

deposits to flashy, runoff-dominated streams draining clay or bedrock deposits (Zorn 2018). The streams containing robust populations of salmonids generally receive large inputs of groundwater, which provides temperature and flow stability as it moves through deep, coarse-textured glacial drifts with high hydraulic conductivity (Wiley et al. 1997; Krider et al. 2013; Mundahl 2017; Zorn 2018). However, hydraulic conductivity is variable across the study area due to diverse landforms, including areas of ice contact (100 m/day), coarse-textured moraines (30 m/day), and fine-textured moraines (conductivity <0.005 m/day; Seelbach et al. 2011). Across this landscape, variability in stream temperature is mostly explained by heterogeneity in landform and hydrology (Zorn et al. 2002; Wehrly et al. 2006; Seelbach et al. 2011). Michigan contains some of the most hydrologically stable streams in the United States, including renowned salmonid streams such as the Au Sable and Manistee rivers. However, there is a million-fold range in hydrologic stability (as measured using 90% exceedence flow yield per catchment area) between Michigan's most stable and most flashy streams (Zorn et al. 2002). Likewise, Minnesota and Wisconsin feature diverse stream types, ranging from groundwater-fed salmonid streams of the Driftless Area—an unglaciated region with sedimentary bedrock containing sequences of limestone, dolomite, shale, and sandstone—to agricultural and urban streams that tend to have warmer water temperatures, finer-textured geology, and more immediate anthropogenic influences (Krider et al. 2013; Mundahl 2017).

The study area has a temperate climate featuring warm to mild summers and cold winters, with mean annual air temperature varying from 1 °C in northern portions of the region to nearly 13 °C in southern areas, and precipitation ranging from 40 to 119 cm/year. Proximity to the Great Lakes produces dissimilarities in local climate conditions (Ordonez and Williams 2013; Zorn 2018). For instance, Michigan exhibits wide-ranging growing season length (87–163 days), mean annual air temperature

(4.2–9.3 °C), mean summer (May–September) air temperature (14.4–19.3 °C), and mean summer precipitation (36–50 cm, Zorn 2018). The study area's diverse streams support coldwater and warmwater fish assemblages (Brenden et al. 2006; Lyons et al. 2009).

2.2 *Modeling Approach*

A modeling approach was developed to incorporate landscape, climate, and stream temperature data from multiple sources to forecast stream temperature changes under predicted climate-change scenarios (Fig. 2). This approach was designed to be applicable across a broad geographic range encompassing all streams in the states of Michigan, Minnesota, and Wisconsin. The modeling approach included: (1) identifying and assembling available data; (2) integrating data into an appropriate spatial framework that reflected the research questions and scales of analysis; (3) fitting models for each state to empirical relationships between landscape, climate, and stream temperature data; (4) fine-tuning models with empirical and simulated climate data to allow fine-scale forecasting; and (5) forecasting stream temperatures under multiple projected climate scenarios.

The 1:100,000 scale National Hydrography Dataset Plus Version 1 (NHDPlusV1) was used to acquire, manage, and analyze data for the stream thermal habitat modeling approach (USEPA and USGS 2005). The base spatial unit was the stream reach, defined as an NHDPlusV1 confluence-to-confluence or origin-to-confluence segment and its associated local drainage catchment (Wang et al. 2011). Landscape and

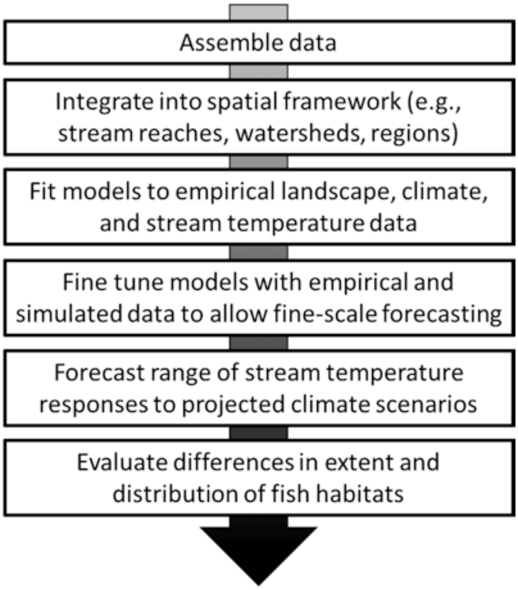


Fig. 2 Conceptual approach for forecasting stream temperature responses to projected climate scenarios

land-use variables were attributed to approximately 165,000 individual stream reaches throughout the three states and aggregated throughout network catchments, which included the local catchments of the target reach and those of all upstream reaches. The nested hierarchy built around NHDPlusV1 allowed for delivery of results at scales ranging from local catchments to hydrologic units (HUCs), an entire state, and the three-state region. See Wang et al. (2011) for more information on the hierarchical spatial approach used in the present study.

2.3 Stream Temperature Data

To accurately describe relationships between climate, landscape attributes, and stream temperature, long-term U.S. Geological Survey (USGS) stream temperature data (>10 years) were acquired from the National Water Information System (USGS 2022) and supplemented with short-term (1–5 years) stream temperature data (temperature loggers) from other sources (Table 1, *sensu* Mantua et al. 2010, McKenna et al. 2010, Stewart et al. 2015). These additional data included continuously collected (hourly or finer) stream temperatures from 1996 to 2010 for Michigan, Minnesota, and Wisconsin from the Michigan Department of Natural Resources (DNR), Michigan State University, Minnesota DNR, Wisconsin DNR, and Minnesota Pollution Control Agency (Stewart et al. 2015, 2016a, 2016b). Integrating long- and short-term stream temperature data made it possible to model distributions of fish thermal habitats (McKenna et al. 2010; Stewart et al. 2016a, 2016b) and to overcome systematic limitations in the USGS stream temperature data (e.g., low representation of headwater streams and large rivers), allowing characterization of landscape-pattern influences on stream-fish habitats across spatial scales (DeWeber et al. 2014). All stream temperature data were summarized as mean daily values for 1 May to 30 September of each year (i.e., “summer”). Summer was emphasized because warm conditions and low water levels common during summer are thermally stressful for coldwater fishes, and data outside the summer months were sparse. Many sites had only a single year of data, but several had multiple years; none of the sites had data for all years between 1996 and 2010. It was assumed that stream temperature data collected in any given year (or years) were representative of typical thermal conditions at particular sites. Variability in Midwestern stream temperatures is determined in large part by landform and hydrology (e.g., groundwater input, Zorn et al. 2002; Wehrly et al. 2006; Seelbach et al. 2011), which generally do not change over geologically short time spans such as 1996–2010. Groundwater recharge was calculated using a soil water balance (SWB) model encompassing precipitation, air temperature, land-use conditions, hydrologic soil group, groundwater flow direction, and soil-water capacity. The SWB model calculated groundwater recharge at a daily time step (Thornthwaite and Mather 1957), but only for Wisconsin due to limited data availability in other states; groundwater recharge was estimated using soil permeability in Michigan and Minnesota (Swartz et al. 2003).

Table 1 Number of sites containing stream temperature data by state (Michigan [MI], Minnesota [MN], Wisconsin [WI]) and year

State	Year	# Sites w/data	# Classifier models	Total # sites
MI	1996	38	3	809
	1997	40	3	
	1998	66	3	
	1999	48	3	
	2000	60	2	
	2001	133	4	
	2002	99	3	
	2003	88	3	
	2004	184	4	
	2005	187	3	
	2006	137	3	
	2007	116	3	
	2008	176	2	
	2009	104	3	
MN	2000	35	3	507
	2001	55	4	
	2002	59	3	
	2003	79	4	
	2004	83	4	
	2005	80	4	
	2006	96	3	
	2007	92	2	
	2008	175	3	
	2009	110	4	
WI	1998	49	3	371
	1999	62	3	
	2000	70	2	
	2001	73	3	
	2002	72	3	
	2003	NA	NA	
	2004	72	3	
	2005	53	3	
	2006	53	2	
	2007	58	3	
	2008	62	3	
	2009	30	3	
	2010	40	4	

The number of classifier models used to evaluate the importance of static variables for each year in the absence of inter-annual climate effects is also presented. Data that are not available are marked “NA”

Stream sites were excluded from data analyses if: (1) the stream reach was an artificial flow path (i.e., canal, ditch, drain, pipeline, coastline, or diversion) in NHDPlusV1; (2) daily stream temperature values were more than three standard deviations from the reach's seasonal mean; (3) the stream reach did not have data for the entire month of July; or (4) a stream's respective aggregated upstream catchment was ≥25,000 km^2 (i.e., "great river" *sensu* Wang et al. 2011). Further, only one stream temperature time series was attributed to each monitored stream reach. If multiple data sources (i.e., logger locations) were present within a given stream reach for the same time period, their daily values were averaged (geospatial averages, McKenna et al. 2010). If the time series occupying the same stream reach did not overlap temporally, they were combined into a single time series.

2.4 Empirical Climate Data

Empirical daily air temperature and precipitation data for Michigan and Minnesota from 1990 to 2010 were obtained from the National Climate Data Center (http://www7.ncdc.noaa.gov/CDO/cdo), now included in the National Centers for Environmental Information (https://www.ncdc.noaa.gov/). Wisconsin data were from the Midwest Regional Climate Center (https://mrcc.illinois.edu/) for the same time period. Data from individual climate stations were included if they contained at least 10 continuous years of air temperature and/or precipitation data. Because climate stations were relatively sparse and unevenly distributed throughout the region, daily climate data could not be attributed to stream reaches with measured temperature. Hence, a K-means clustering approach was used to develop a set of de-correlated daily air temperature and precipitation time series to be used as inputs for predictive stream temperature modeling (Risley et al. 2003; Stewart et al. 2015). Although two climate stations may be geographically close, their climate data may exhibit markedly different trends due to complex terrain or local land cover (Turner et al. 1996; Risley et al. 2003; Stewart et al. 2015). Clusters of time series were based on regional climate behavior (due to geology, topography, etc.), so clusters were composed of time series that were dynamically similar to one another. Clustering air temperature and precipitation time series made it possible to reduce the number of climate sites used in the analysis and thereby vastly reduce the data burden compared to attributing daily climate data to individual stream reaches. Further, using clustered climate data facilitated accurate depiction of regional weather patterns and, therefore, reliable evaluation of the relationship between climate conditions and stream temperature (Risley et al. 2003; Stewart et al. 2015).

2.5 Modeled Climate Data

Grids measuring 15 km^2 and containing daily air temperature and precipitation data generated from downscaled atmospheric and oceanic general circulation models (AOGCMs) were used to predict thermal conditions of Midwest streams at "current" and future time steps. Forecasted air temperature and precipitation spatial grids were overlaid on the aforementioned empirical climate station locations. The AOGCM climate data were only attributed to climate stations used to calculate the empirical climate time-series clusters. Air temperature and precipitation time-series clusters were then recalculated with forecasted climate data from each AOGCM and time-series step. The subsequent time-series clusters were then used as inputs for stream temperature modeling runs. Deviations between stream temperature predictions calculated using empirical and modeled "current" climate data made it possible to develop correction factors for individual stream reaches to improve predictions of fine-scale stream temperatures under projected climate scenarios (see "Model predictions" below, Stewart et al. 2015).

Climate data included backcasted and forecasted regional climate conditions for periods of the late twentieth and twenty-first centuries (Table 2). Downscaled (RegCM3) air temperature and precipitation data were derived from the following AOGCMs: GENMOM (Alder et al. 2011), MPI ECHAM5 ("ECHAM5," Roeckner et al. 2003), and GFDL CM 2.0 ("GFDL," Delworth et al. 2005, Table 2). Downscaled data also included root-zone soil moisture (RZSM) from the aforementioned AOGCMs. The RZSM is a measure of water content in the root zone of the soil (~2 m, Hostetler et al. 2011, 2018) and was summarized as an annual average for each stream reach for the 1997 time period and then treated as a static variable for all modeling forecasts. Despite the limitations of RZSM for capturing future changes in soil moisture which could vary substantially with differences in storage occurring across the landscape in a changing climate, this variable was used to capture the conceptual importance of soil moisture to stream temperature. Forecasted climate variables for all AOGCMs were produced under the A2 emissions scenario developed for the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (IPCC 2007). The A2 family of relatively high-emissions scenarios assumes a continually increasing global population and large greenhouse gas

Table 2 Range of years corresponding to each time step and climate model: GENMOM (Alder et al. 2011), MPI ECHAM5 ("ECHAM5," Roeckner et al. 2003), and GFDL CM 2.0 ("GFDL," Delworth et al. 2005)

Time step/model	Range of years
Current	1995–1999
2032	2030–2034
2042	2040–2044
2062	2060–2064
2087	2085–2089
GENMOM	1968–1999 & 2010–2089
ECHAM5	1968–1999 & 2010–2089
GFDL	1980–1999 & 2038–2069

emissions and is widely used in climate-change research (IPCC 2007). This study focused on the A2 scenario, rather than a combination of scenarios, for several reasons. The AOGCMs employed in this study already encompass wide-ranging climate futures. In addition, there were logistical constraints to applying a detailed modeling methodology to multiple AOGCMs and multiple emissions scenarios across every stream in three US states; such an analysis was not consistent with the study's scope and objectives. Moreover, considering the study's focus on stream salmonid management, it was deemed preferable from a management perspective to "assume the worst" and develop corresponding strategies to proactively conserve vulnerable fisheries, rather than assume lower-emissions scenarios and contend with "unexpected" effects of climate change *ex post facto*.

2.6 Landscape Variables

Landscape analyses began with 40 static variables describing physical and geological attributes (e.g., slope, elevation, and lithography) of Michigan, Minnesota, and Wisconsin at the local and network-catchment scales (see Wang et al. 2011 for a full description of static variables). Land use was based on the 2001 National Land Cover Dataset (NLCD) to describe current land uses for the following aggregated categories as a percentage of total land use within stream catchments: urban, agriculture, forest, wetland, grassland, and open water. All land-cover percentages were held constant at 2001 levels for all modeling simulations. To avoid including multicollinear variables in state-level stream temperature models, we performed Pearson correlation analyses to first identify the variables that explained significant variation in daily stream temperatures (p <0.05) and then ascertain pairs of static variables that were highly correlated (≥0.75); only variable from each pair was retained for further analysis. Generally, aggregated variables describing the network catchment of a particular stream reach (e.g., network slope) were retained in lieu of variables describing local conditions.

Classifier models were constructed in the iQuest v2.03 (Advanced Data Mining, LLC, Greenville, South Carolina) modeling environment to further examine static variables for possible inclusion into each state-level stream temperature model (Risley et al. 2003; Stewart et al. 2015). In particular, classifier models were used to identify a manageable set of 14 static variables that best explained the intra-annual variation in stream temperature. Up to four classifier models were constructed for each year for stream reaches with available stream temperature data (Table 3). The number of classifier models developed per year depended on the number of stream temperature time-series clusters required to describe the temperature regime of monitored reaches included for that particular year. Stream temperature time series were calculated in the same manner as air temperature time-series clusters. For example, in 2002, three clusters sufficiently described the stream temperature time series for 99 stream reaches in Michigan. Use of classifier models ensured that

Table 3 Model performance and static/dynamic variables for each state-level artificial neural network (Michigan [MI], Minnesota [MN], Wisconsin [WI])

Model	Training r^2	Testing r^2	RMSE	Variables
MI	0.753	0.717	1.70	Stream order, area L, stream slope L, area N, soil permeability L, groundwater index L, root zone soil moisture, land use urban N, land use agriculture N, TA
MN	0.720	0.750	1.67	Stream order, stream slope L, soil permeability N, area N, land use urban N, land use agriculture N, root zone soil moisture, TA
WI	0.710	0.760	1.95	Area N, land use urban N, land use agriculture N, land use wetland N, land use open water N, darcy N, darcy N buffer, stream sinuosity, TA, SWB

"L" indicates that the variable is attributed to the local catchment of each stream reach, and "N" indicates attribution to the upstream network catchment of each stream reach. "TA" represents the air temperature time-series clusters as described in the Methods. "SWB" represents the clusters predicted by the soil water balance model (Wisconsin only)

stream reaches exhibiting similar thermal behavior in response to static variables would be adequately represented by such variables.

To select static variables for inclusion in stream temperature models, classifier models were used to rank all static variables based on: (1) the number of state-specific classifier models including each variable; and (2) the average and maximum r^2 increase resulting from inclusion of each variable (Stewart et al. 2006, 2015). These rankings were then averaged to determine the overall rank of each variable. The 14 highest-ranked variables for each state were retained because they best explained the intra-annual variation in stream temperature due to landscape factors. The actual number of variables used in the final state-level models was determined later through the model training process (see below). Percent urban and agricultural land cover were included in each state-level model, and additional land-cover variables were added to models based on their performance in the aforementioned ranking process.

2.7 *Model Development and Evaluation*

Artificial neural networks (ANNs) were used to develop stream temperature models for several reasons: (1) ANNs require less intensive, and hence more widely available, datasets than mechanistic models (Chenard and Caissie 2008); (2) ANNs use similar data to statistical models (McKenna et al. 2010); and (3) ANNs can perform better than statistical regressions (Sahoo and Ray 2008), especially when predicting daily values (Ahmadi-Nedushan et al. 2007). ANN-based modeling uses reach-scale information to generate local, watershed, and regional stream temperature predictions for a large region (i.e., Michigan, Minnesota, and Wisconsin), which is valuable for management but uncommon in the published literature (Stewart et al. 2006, 2015; DeWeber and Wagner 2014).

Stream reaches with temperature data were partitioned into training (90% sites) and testing (10% sites) datasets. The training and testing datasets consisted of relatively equal percentages (~25%) of stream thermal types: coldwater (July mean water temperature < 17.5 °C), cold-transitional (17.5–19.5 °C), warm-transitional (19.5–21.0 °C), and warmwater (>21.0 °C, Lyons et al. 2009). The training dataset was used to develop models consisting of a backpropagation algorithm with a maximum of three hidden layers and one output using the iQuest v2.03 software package (Stewart et al. 2006). Initial learning rates were identical for each neural network (Table 4) but were modified independently during the training process. The neural-network learning rates were modified by a factor of 10 (i.e., 0.075 ➔ 0.0075) when the training r^2 values did not improve by ≥0.001 over each 100-epoch interval (refresh rate). This procedure was used to prevent model over-fitting based on the training dataset and to ensure global convergence (McKenna et al. 2010). For each learning-rate change, the stability of the included static variables was monitored to ensure their utility in developing useful relationships within the neural networks. Learning rates were modified a maximum of three times during training for each state-level model.

Each model-training process began with an output variable (empirical daily stream temperature) and the following inputs: the six most highly ranked static variables (of the top 14), empirical daily air temperature time-series clusters, urban and agricultural land-use values, and SWB clusters (Wisconsin model only). Static variables were then iteratively removed or added until models had: (1) the highest possible training and testing r^2 values; (2) a list of variables that remained stable throughout the training process; and (3) minimal "wobble" around a desired 1:1 relationship in the plot of observed versus predicted daily stream temperatures. Variable standardization was unnecessary as iQuest automatically performed this step.

After the final list of variables was determined for each state-level model, the training ability of each model was further improved by removing outlier-data years and sites. Although the stream temperature datasets generally satisfied the aforementioned criteria for the modeling approach, thermal data from some sites did not

Table 4 Initial training parameters and values for neural network creation

Training parameter	Value
Max # training epoch	10,000
O learning rate	0.075
H learning rate	0.075
T learning rate	0.01
IO learning rate	0.01
Alpha	0.08
Hidden layer addition	Fixed
All else	Default

always behave consistently relative to other sites (e.g., anomalous years). Hence, a one-time removal of outlier-data years and sites was performed during the training process if >30% of the predicted daily stream temperatures were >5.0 °C warmer or colder than empirical observations. Depending on the number of data years a particular site contained, this process sometimes led to the removal of an entire site. Overall, a total of 1687 sites across the three states fit criteria for inclusion (Table 1). Using the final list of sites, each stream temperature model was re-trained a final time. Each finalized state-level ANN was then exported as a feedforward neural network and later used to predict current and future daily stream temperatures for all stream reaches within the respective state (Stewart et al. 2015).

2.8 Model Predictions

Mean daily stream temperature (°C) was the primary output for each state-level model. An R script (R Development Core Team 2013) was used to iteratively run all stream reaches and their associated attributes in each state through their respective ANNs to calculate daily stream temperatures of current and future time steps. Future climate data were simulated using AOGCMs, and current stream temperatures were modeled using empirical climate data, so the two could not be directly compared. Backcasted climate predictions did not always match empirical climate records, making it important to develop a correction factor to standardize AOGCM predictions with empirically observed climatic conditions; correction factors were then applied to predict future stream temperatures for each AOGCM. This process assumed that deviations between empirical and modeled climate predictions remained consistent throughout climate forecasts.

To develop correction factors, each state-level ANN was calibrated using empirically derived current climate data for all stream reaches in the corresponding state. Then, each state-level ANN was calibrated using AOGCM-derived current climate data for each of the three AOGCMs. Reach-specific correction factors were determined based on the difference between the AOGCM-derived and empirically derived current July mean temperatures. Finally, each state's entire suite of stream reaches was run through its respective state-level ANN for each AOGCM and time step, and correction factors were subsequently applied to daily stream temperature values. After daily stream temperatures were forecasted and correction factors applied for each time step within each AOGCM, another R script was used to calculate summary statistics characterizing the predicted temperature regime of each stream reach over time (e.g., temperature magnitude, variability, and rate of change, Tsang et al. 2016). Here, July mean stream temperature is reported because it is an important driver of fish population dynamics in general, and stream salmonid reproduction, growth, and survival in particular (Lyons et al. 2009; Carlson et al. 2017a, 2017b, 2019, 2020). July mean stream temperature was used to categorize streams into thermal classes (i.e., coldwater, cold-transitional, warm-transitional, and warmwater) that were developed based on Michigan and Wisconsin fish assemblages

(Lyons et al. 2009) and were relevant for fisheries management and environmental regulation.

3 Results

3.1 Model Performance

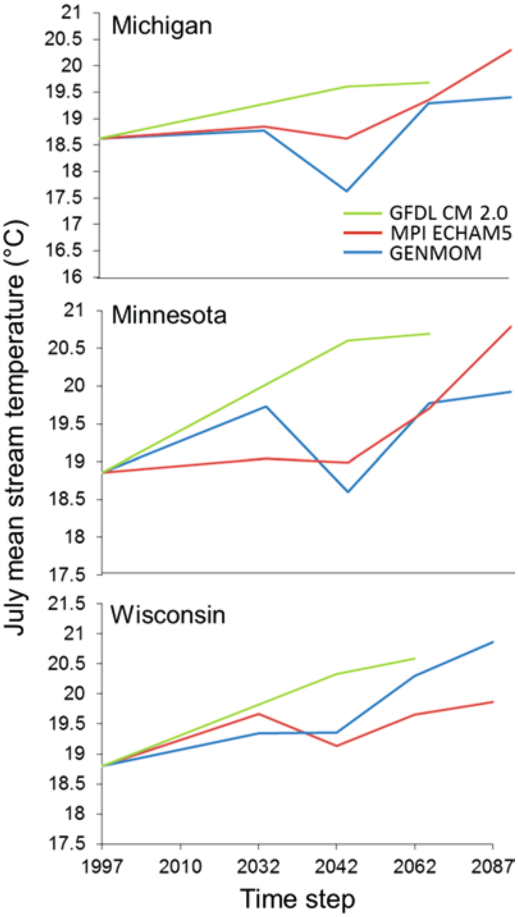
The three state-level models predicted mean daily stream temperature reasonably well. Model fit (r^2) ranged from 0.71 to 0.76 for both testing and training datasets. Root mean square error (RMSE) was consistently low and ranged from 1.53 to 1.95 °C. Static variables used in final models included parameters measuring groundwater, catchment area, and stream size (Table 3). For all three state-level models, plots of predicted versus observed daily stream temperatures showed slight deviation from 1:1; predictions for the coldest streams were slightly warmer than observed, whereas predictions for the warmest streams were slightly colder than observed.

3.2 Model Predictions

Average statewide stream temperatures increased in nearly all time steps regardless of the climate model used (Fig. 3). Downscaled GFDL models predicted the greatest changes in stream temperature across the study region, whereas GENMOM and ECHAM5 yielded less-pronounced and relatively consistent changes in stream temperature. Interestingly, the latter two models predicted a reduction in July mean stream temperature from 2032 to 2042 in Michigan and Minnesota (Fig. 3). Predicted stream temperature changes based on the ECHAM5 climate model involved warming throughout the twenty-first century and the most rapid warming after 2042 (Fig. 4). Collectively, the models predicted substantial warming throughout Wisconsin and Minnesota but moderate warming in Michigan. Across the study region, stream temperatures increased by an average of 0.57 °C through 2042 and 1.45 °C through 2087.

Model predictions showed a common increasing trend in stream temperature throughout the twenty-first century (Fig. 5). However, predicted changes in mean July water temperature from 1997 to 2062 were spatially heterogeneous within the study region, depending on the AOGCM used (Fig. 5). Downscaled GENMOM climate data yielded the smallest changes in regional stream temperature and predicted nearly consistent stream warming (~0.2° decade^{-1}) across Minnesota and Wisconsin, with lower warming rates for the majority of streams in Michigan (~0.1° decade^{-1}). In comparison, the ECHAM5 model projected consistent stream warming in Minnesota and Michigan (~0.1–0.2° decade^{-1}) but higher warming rates in

Fig. 3 Mean statewide July mean stream temperature changes for all time steps and each climate model: GENMOM (Alder et al. 2011), MPI ECHAM5 (Roeckner et al. 2003), and GFDL CM 2.0 (Delworth et al. 2005)



the southern two-thirds of Wisconsin (~0.3–0.4° decade^{-1}). In contrast, the GFDL model predicted greater and more heterogeneous stream warming rates in Minnesota and Wisconsin (~0.3–0.4° decade^{-1}) than in Michigan (~0.2° decade^{-1}, Fig. 5).

Stream warming decreased the spatial extent (river km) of cool and coldwater habitats in all future time steps relative to past and current time steps for all AOGCMs (Table 5). Estimates of current percentages of coldwater, cold-transitional, warm-transitional, and warmwater habitats in the region were 27%, 39%, 22%, and 12%, respectively. In future time steps, state-level models collectively predicted a widespread shift from colder to warmer habitat categories across the study region (Tables 5 and 6, Fig. 6). By 2042, coldwater streams were more likely to change into cold-transitional (range 5.4–58.7%) than warm-transitional (<1%) streams. Similarly, by 2087, coldwater streams were predicted to change primarily into cold-transitional systems (range 44.7–68.9%, 2.9% warm-transitional). However, warm-transitional and warmwater habitats were predicted to cover a considerable portion of the study region in the future. In Wisconsin, for example, the extent of warm-transitional and

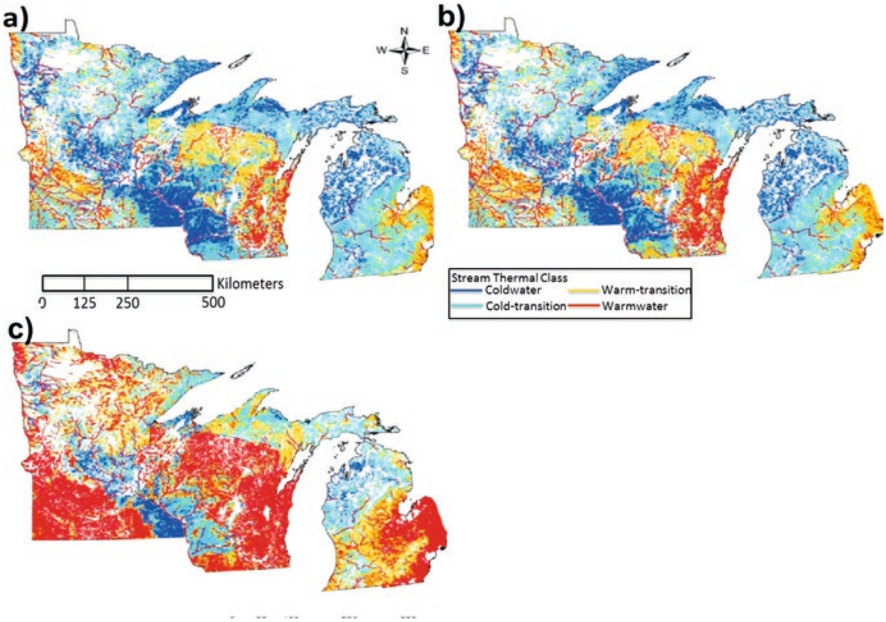


Fig. 4 Thermal classification of every stream reach in the study region for (**a**) 1997 ("current"), (**b**) 2042, and (**c**) 2087 using the MPI ECHAM5 climate model (Roeckner et al. 2003)

warmwater habitats (currently 40% of stream kilometers) was projected to reach up to 63% in 2042 and 71% in 2087.

Although streams throughout the study region were generally predicted to become warmer in the future, some stream thermal classes were projected to warm to a greater degree than others. Based on all three AOGCMs, absolute changes in stream temperature from 1997 to 2062 were the greatest in warmwater streams followed by warm-transitional, cold-transitional, and coldwater thermal classes (Fig. 7). The ANN model-predicted July mean stream temperatures and other stream temperature metrics are described and available for download on the project website (https://ccviewer.wim.usgs.gov/FishVis/, Stewart et al. 2016a, 2016b).

4 Discussion

Our fine-scale modeling approach was effective for assessing broad-scale changes in stream thermal habitats and effects on stream salmonids and other fishes in a changing climate. Models developed herein are conducive for local, state, and regional assessments of diverse stream temperature metrics (e.g., summer mean, daily/weekly/monthly range, spring warming rate, and fall cooling rate) encompassing multiple aspects of fish thermal habitat requirements. Hence, our modeling

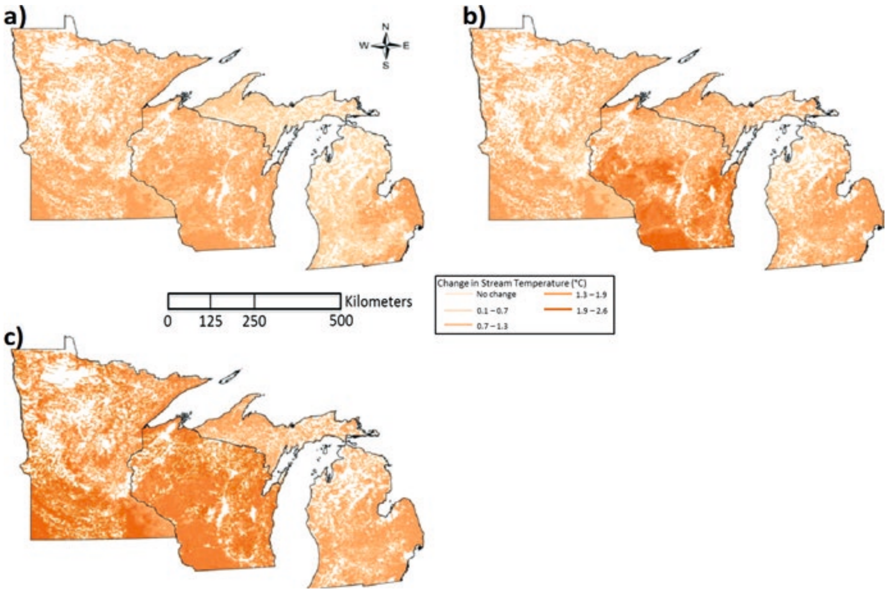


Fig. 5 Change in stream temperature (°C) from 1997 to 2062 using downscaled air temperature data from climate models, including (**a**) GENMOM (Alder et al. 2011), (**b**) MPI ECHAM5 (Roeckner et al. 2003), (**c**) and GFDL CM 2.0 (Delworth et al. 2005)

Table 5 Predicted losses of coldwater and cold-transitional habitat (i.e., cool-cold) expressed as river segment percentage and river kilometers for each time step and climate model: GENMOM (Alder et al. 2011), MPI ECHAM5 ("ECHAM5," Roeckner et al. 2003), and GFDL CM 2.0 ("GFDL," Delworth et al. 2005)

Model	Time step	% cool-cold lost	km cool-cold lost
GENMOM	2032	17.9	32,688
	2042	(−1.1)	(−3166)
	2062	23.8	43,211
	2087	28.1	50,405
ECHAM5	2032	10.1	17,917
	2042	7.5	12,981
	2062	29.7	52,230
	2087	53.3	93,655
GFDL	2042	38.8	68,040
	2062	41.3	72,323

For comparison, "current" cool-cold habitats spanned 79,612 segments and 168,747 km. Values in parentheses indicate predicted gains in cool-cold habitat

approach is an improvement over stream temperature models that do not integrate stream temperature predictions across local, state, and regional scales and thus provide a more spatially limited picture of factors influencing fish thermal habitat requirements (Wehrly et al. 2009; McKenna et al. 2010). Models that simultaneously account for fine- and broad-scale stream temperature patterns are becoming

Table 6 Predicted changes in thermal classification (coldwater, cold-transitional, warm-transitional, warmwater) over time for streams in Michigan (MI), Minnesota (MN), and Wisconsin (WI), expressed as a percentage of total stream km

State	Model	Time step	Change in Thermal classification (% of total)			
			Coldwater	Cold-transitional	Warm-transitional	Warmwater
MI	Empirical	Current	22.6	48.2	23.9	5.3
	GENMOM	2032	19.4	48.3	25.7	6.6
		2042	24.2	48.9	22.4	4.5
		2062	11.1	46.3	29.4	13.2
		2087	10.0	44.9	29.5	15.6
	ECHAM5	2032	18.1	48.2	26.5	7.3
		2042	22.7	47.8	24.1	5.5
		2062	10.5	45.6	29.5	14.4
		2087	3.7	26.6	36.0	33.7
	GFDL	2042	7.5	42.8	31.2	18.5
		2062	7.2	41.4	30.8	20.6
MN	Empirical	Current	28.3	38.1	19.1	14.4
	GENMOM	2032	17.4	31.4	26.2	24.9
		2042	32.5	39.1	15.9	12.4
		2062	17.5	30.1	26.1	26.2
		2087	16.4	28.8	25.6	29.3
	ECHAM5	2032	25.6	36.5	21.5	16.4
		2042	26.4	37.2	20.7	15.7
		2062	18.3	30.6	26.0	25.1
		2087	11.4	20.5	22.2	45.9
	GFDL	2042	12.3	22.2	22.5	43.0
		2062	11.6	21.6	22.6	44.2
WI	Empirical	Current	29.8	30.0	24.5	15.8
	GENMOM	2032	21.0	26.3	25.2	27.5
		2042	25.7	28.8	25.5	20.0
		2062	20.4	25.4	24.4	29.8
		2087	17.8	24.8	23.9	33.6
	ECHAM5	2032	21.8	27.5	28.8	21.9
		2042	22.3	26.8	28.1	22.7
		2062	10.9	23.7	25.4	39.9
		2087	7.0	22.0	19.2	51.7
	GFDL	2042	13.1	24.4	20.7	41.9
		2062	11.1	24.3	19.4	45.2

Current percentages were generated using empirical climate data. Future percentages were predicted using the following climate models: GENMOM (Alder et al. 2011), MPI ECHAM5 ("ECHAM5," Roeckner et al. 2003), and GFDL CM 2.0 ("GFDL," Delworth et al. 2005)

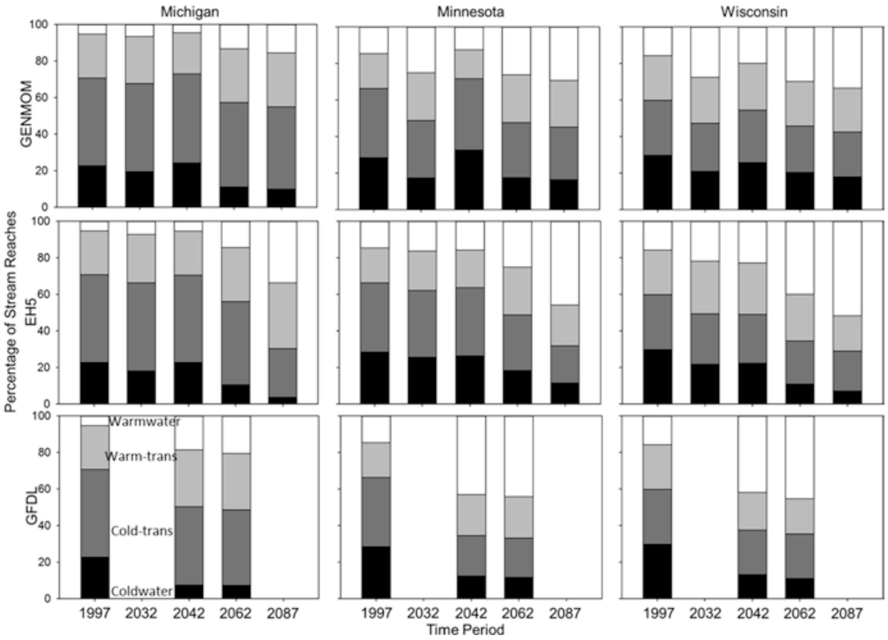


Fig. 6 Current and projected future percentage of stream reaches by state (Michigan [MI], Minnesota [MN], Wisconsin [WI]) organized by thermal category. As illustrated in the figure, coldwater streams are black, cold-transitional streams are dark gray, warm-transitional streams are light gray, and warmwater streams are white. The 1997 time step represents the "current" conditions and depicts empirical climate data. Future values were predicted using the following climate models: GENMOM (Alder et al. 2011), MPI ECHAM5 ("EH5," Roeckner et al. 2003), and GFDL CM 2.0 ("GFDL," Delworth et al. 2005)

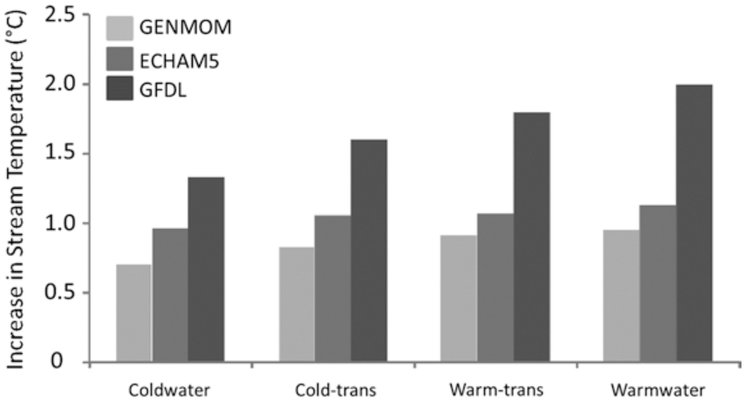


Fig. 7 Average increase in stream temperature predicted across stream thermal classes and climate models: GENMOM (Alder et al. 2011), MPI ECHAM5 ("ECHAM5," Roeckner et al. 2003), and GFDL CM 2.0 ("GFDL," Delworth et al. 2005). Cold- and warm-transitional streams are denoted by "cold-trans" and "warm-trans", respectively

more prevalent (Isaak et al. 2016; Jackson et al. 2018), although not in the context of stream salmonid management in the Upper Midwest, USA. Moreover, stream temperature metrics resulting from our modeling approach can be derived from one model per state, which is more efficient and informative for fisheries management amid resource limitations (e.g., time, money, and personnel) than building multiple models. Our approach involved reach-level stream temperature predictions, accounting for the unique landscape context of each reach while generating spatially extensive temperature projections for all streams across the Upper Midwest. Such integration of small- to large-scale thermal habitat information has not been performed for Upper Midwest streams in the context of stream salmonid management and conservation. This approach is informative for predicting how climate change may affect the abundance and distribution of stream salmonids and other fishes within and across management jurisdictions (Steen et al. 2008, 2010), and thereby developing management strategies that are appropriately scaled.

Our state-level ANNs performed well, and their accuracy was generally consistent with or better than other studies using fine-scale approaches applied over small and large spatial extents. Although we did not intend to create models with equivalent accuracy to stream-specific models, the RMSE reported herein (1.53–1.95 °C) was similar to that reported for system-specific models in New Brunswick, Canada (RMSE 0.59–1.62 °C, Caissie et al. 1998) and central Idaho, USA (root mean square prediction error 0.74–2.75 °C, Isaak et al. 2010). It is important to note that our models were somewhat less accurate than other applications of deep- and machine-learning approaches for modeling stream temperatures, such as long short-term memory network models (RMSE 1.13–1.20 °C, Rahmani et al. 2021) and random forest models (RMSE 0.60–1.00 °C, O'Sullivan et al. 2021). However, the accuracy of our modeling approach was similar to or better than previous studies that predicted stream temperature metrics rather than daily values, as in the present study. For instance, McKenna et al. (2010) predicted stream thermal classes (cold, cool, warm) using ANNs that explained approximately 90% of the data variation compared to our range of 71–75%, but the study spanned only one state (New York) and was based on averages within small subwatersheds. Wehrly et al. (2009) predicted July mean stream temperatures for Michigan streams using several modeling approaches and reported higher RMSE (2.0–2.6 °C) than our models (1.53–1.95 °C).

Models created herein generally predicted that Midwest streams will become warmer for all time steps evaluated. Stream temperature declines between 2032 and 2042 were consistent across all three AOGCMs and likely a product of the AOGCMs themselves, rather than the ANNs. As expected in a warming climate, a substantial amount of coldwater and cold-transitional habitat was predicted to change to warm-transitional or even warmwater habitat. Shifts in stream temperatures and thermal classes will likely alter thermal habitat suitability for stream salmonids and other fishes. For instance, coldwater streams that become warm-transitional or warmwater streams will likely become less thermally suitable for brook charr *Salvelinus fontinalis*, although thermal refugia arising from groundwater inputs may provide locally suitable conditions for growth and survival (Wilbur et al. 2020; O'Sullivan et al. 2021). Even if coldwater streams become cold-transitional and still support coldwater fishes such as brook charr, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss*, growing conditions may become suboptimal, contributing to changes in fish community composition (Carlson et al. 2017a, 2017b, 2019, 2020). Clearly, populations of stream salmonids and other coldwater fishes will decline if climate change causes water temperatures to exceed species-specific thresholds for survival or reproduction and thermal refugia become limited. In some streams, these thermal changes could create novel habitat for more thermally tolerant species such as smallmouth bass (*Micropterus dolomieu*, Paukert et al. 2016; Carlson et al. 2017b). This may further reduce cold- and cool-water fish populations through shifts in species interactions such as predation and competition (Van Zuiden et al. 2016). Combined with managers' firsthand knowledge of the systems they manage, the modeling approach developed herein will allow managers to discern between streams or reaches that will be "lost" to warmwater and warm-transitional habitats, and those that can be successfully managed for thermal resilience via groundwater conservation, riparian/watershed rehabilitation, and related management activities. The modeling approach developed herein will facilitate such efforts for stream salmonids and other fishes.

Despite the efficiency and utility of our modeling approach and associated data, they had limitations. First, an AOGCM-based modeling approach, although consistent with previous climate-change research in fisheries, inherently favors certain climatic "futures" over others because different models represent different climatic conditions. For this reason, we used multiple AOGCMs—chosen specifically to represent a wide range of projected future climatic conditions—to predict stream temperatures and associated changes in thermal habitats and fish communities. In future studies, researchers could integrate multiple AOGCMs with multiple emissions scenarios to gain deeper insights on how climate change may affect stream salmonids, particularly in the Upper Midwest, USA. Second, thermal-class predictions did not always match state boundaries (e.g., "coldwater" in Michigan changed abruptly to "cold-transitional" in Wisconsin) because each state was modeled independently. This is to be expected given that each state-level ANN was constructed using a separate (although not mutually exclusive) list of variables, not all variables were available for all three states (e.g., measures of groundwater movement were not available for Minnesota), and variables in common had distinct ranges in each state. Overall, thermal-class predictions are useful in allowing managers to anticipate future stream temperature conditions within and across states. Such projections could support existing (or foster new) inter-state partnerships and thermal habitat management efforts for stream salmonids and other fishes.

The difficulty of discerning trends in site-specific empirical data (e.g., increasing or decreasing water temperatures) was another limitation of predicting stream temperatures over a large spatial extent. We faced a modeling trade-off between spatial expansiveness and site-specific temporal resolution, as very few stream sites herein had more than a few years of empirical stream temperature data. Likewise, the relatively sparse distribution of climate stations made it necessary to cluster air temperature and precipitation time series, an approach that likely reduced model accuracy compared to using site-specific climate data, which are uncommonly available in studies of this spatial extent. However, our results are valuable in combination with research that has site-specific components (e.g., Carlson et al. 2017a, 2017b) because our findings provide a multi-scale perspective for interpreting thermal trends observed at individual stream sites. In a stream salmonid management environment marked by resource limitations (e.g., time, money, and personnel), pairing large-scale and site-specific research is important for effective decision-making at both the regional and local scales where management takes place (Carlson et al. 2017a, 2017b, 2019, 2020). Finally, although ANNs are sometimes considered "black boxes" that do not allow extrapolation—making them less reliable at the "ends" of datasets, as observed herein—and do not provide users with equations or coefficients for defining relationships among variables, they are more effective thermal prediction tools than statistical regressions (Chen and Kim 2006). In addition, ANNs characterize nonlinear relationships among many factors influencing stream temperature (Sivri et al. 2007) without requiring numerous, high-density temperature monitoring sites (Chenard and Caissie 2008). These models also enable calculation of multiple (rather than single) stream temperature metrics and thereby offer useful insights into the numerous factors influencing fish thermal habitats, including thermal and flow resilience of groundwater, which are highly complex and heterogeneous (even across single catchments, O'Sullivan et al. 2019, 2020). For these reasons, ANNs were ideal for stream temperature prediction in the Upper Midwest in a manner that was useful for stream salmonid management and accounted for fine-scale heterogeneity in stream thermal regimes across a large spatial extent and multiple time steps.

Developing a functional, fine-scale stream temperature modeling approach for use by stream salmonid managers and other stakeholders across broad spatial scales is important for addressing effects of climate change. The modeling approach developed herein provides a mechanism for fisheries managers to leverage the copious amount of available climate data to manage stream salmonids in a changing climate. In addition, our modeling approach is informative for developing stream salmonid management priorities and recommendations based on potential changes in stream thermal habitat that arise from changes in climate. For instance, fisheries managers from Michigan, Minnesota, and Wisconsin could collaboratively use our modeling approach to integrate stream thermal habitat management strategies across local, state, and regional scales to enhance protection of coldwater habitats and stream salmonid populations. By providing insights about the specific stream reaches, watersheds, basins, and time scales at which management activities (e.g., groundwater conservation, riparian/watershed habitat rehabilitation) are most needed, our modeling approach can help improve stream salmonid management and conservation.

Our modeling approach allows fisheries and aquatic resource professionals to quantify spatial variability in stream temperatures, and thereby identify which stream types will warm the most and where they are located—critical information for proactive fisheries management (Arismendi et al. 2012). These spatial insights are important in an Upper Midwest landscape with abundant streams spanning a wide range of current and projected future temperatures (Wehrly et al. 2003; Lyons et al. 2010; Carlson et al. 2017a, 2017b). Our reach-specific temperature predictions provide useful information for development of state and regional climate adaptation strategies in Upper Midwest lotic systems, particularly in the context of salmonid management. By not treating all streams the same, our approach allows managers to account for different stream thermal drivers (e.g., groundwater, precipitation, and riparian/watershed land cover), thermal regimes, and associated fish communities within and across states. In turn, our modeling approach can be used to prioritize streams for thermal habitat protection and rehabilitation and develop thermal habitat management strategies that are informed by both regional and local stream temperature conditions. For instance, rehabilitation of forested and grassland watersheds, in combination with site-specific groundwater conservation or riparian habitat protection, may be needed to protect coldwater habitats and sustain stream salmonid populations on regional and local scales. Despite these insights and applications for stream salmonid management, it could be beneficial to expand the focus on July mean stream temperatures to include thermal maxima and minima, which affect fish physiology and metabolism and may have an important influence on how stream salmonid populations respond to climate change.

In conclusion, our fine-scale stream temperature modeling approach is effective for predicting broad-scale changes in stream thermal habitats, salmonid populations, and other fish populations and communities in a changing climate. Climate change is unlikely to influence stream thermal habitats exclusively at local scales or affect all streams in the same manner. Instead, streams spanning large spatial extents face a range of potential outcomes that are realized at local scales and can have cumulative effects throughout watersheds. Our stream temperature modeling approach fulfills the need for a tool that can provide fine-scale predictions over large, multi-jurisdictional spatial extents encompassing multiple management agencies, political boundaries, and laws and regulations. In turn, our modeling approach can facilitate partnerships among local, state, and federal agencies and associated stakeholders that are necessary for advancing management and conservation of stream salmonids and other fishes in a changing climate.

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Conflict of InterestThe authors declare that they have no conflict of interest.

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Determinants of Productive Capacity for Stream Salmonids

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Abstract Trout growth and production are controlled by (1) the area and quality of habitat for sequential life history stages, (2) the availability and production of invertebrate prey, and (3) stage-structured population dynamics, in particular, the degree of recruitment limitation associated with serial habitat bottlenecks or stochastic disturbance events like floods or droughts. These controls are influenced by stream habitat structure, water chemistry (which controls primary production), and flow regime, as modified by riparian and watershed-scale influences. Production is optimized when channel structure maximizes both the production (flux) of drifting invertebrates and the efficiency with which trout can harvest drifting prey, and when habitat heterogeneity minimizes the occurrence of limiting habitat bottlenecks for critical life history stages. While habitat structure and prey abundance set maximum potential habitat capacity, recruitment acts as a control on whether maximum production is realized; stochastic events like floods that result in egg or juvenile mortality may limit production below capacity. Range contraction and declining production

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are associated with a warming climate, increasing eutrophication, and habitat impacts that degrade channel complexity (loss of riparian forest, watershed development, flow regulation). Effective protection of productive capacity requires moving beyond generic policy prescriptions to implementation of controls on cumulative development impacts at watershed scale.

Keywords Trout production · Trout growth · Stream habitat · Habitat limitation · Habitat bottleneck · Invertebrate drift · Fish food

1 Introduction

Skilled anglers and keen observers of the carnival that is life recognize that trout streams provide very different angling opportunities, and that some streams support a much higher abundance of fish than others. Fisheries managers, scientists, and anglers alike have invested great effort in trying to understand the root causes of this variation. Any consideration of trout production must be grounded in an understanding of (1) the principles of habitat limitation, and (2) the factors that drive variation in abundance of their invertebrate prey. Stream-dwelling trout are predators that feed on aquatic invertebrates floating in the water column (e.g., mayflies and stoneflies), terrestrial invertebrates that fall onto the surface of streams, and the occasional fish (although some wild trout stocks are highly piscivorous, particularly as adults larger than 30 cm; Keeley and Grant 2001; Hughes et al. 2018; Monnet et al. 2020). Stream productivity—the number or biomass of fish that can be produced per unit area of stream per year (Ivlev 1966)—depends strongly on nutrient levels in the water column, which ultimately drive algal and aquatic invertebrate production, and is a function of watershed geology and hydrology (Fig. 1). However, fish production is also sensitive to direct habitat limitation (Hayes et al. 1996; Rosenfeld and Hatfield 2006), i.e., the area of stream habitat that is available to fish for rearing (useable habitat), which depends on the physical structure of the stream channel (depth, velocity, substrate). The proportion of useable stream habitat also strongly influences the proportion of invertebrate biomass that can be harvested by fish. For instance, in a turbulent, steep gradient boulder-bed channel much of the habitat may be beyond the swimming abilities of most salmonids, thereby reducing the proportion of available prey flux that can be consumed (e.g., Nislow et al. 1999). Historically, variables related to physical habitat structure dominated predictive models of trout abundance (e.g., Binns and Eisermann 1979). However, productivity in trout streams is best understood as jointly limited by prey abundance (bottom-up processes) and the availability of suitable physical habitat (Chapman 1966; Poff and Huryn 1998; Rosenfeld et al. 2014); consequently, correlates of prey production are being included in predictive models of productive capacity in increasingly

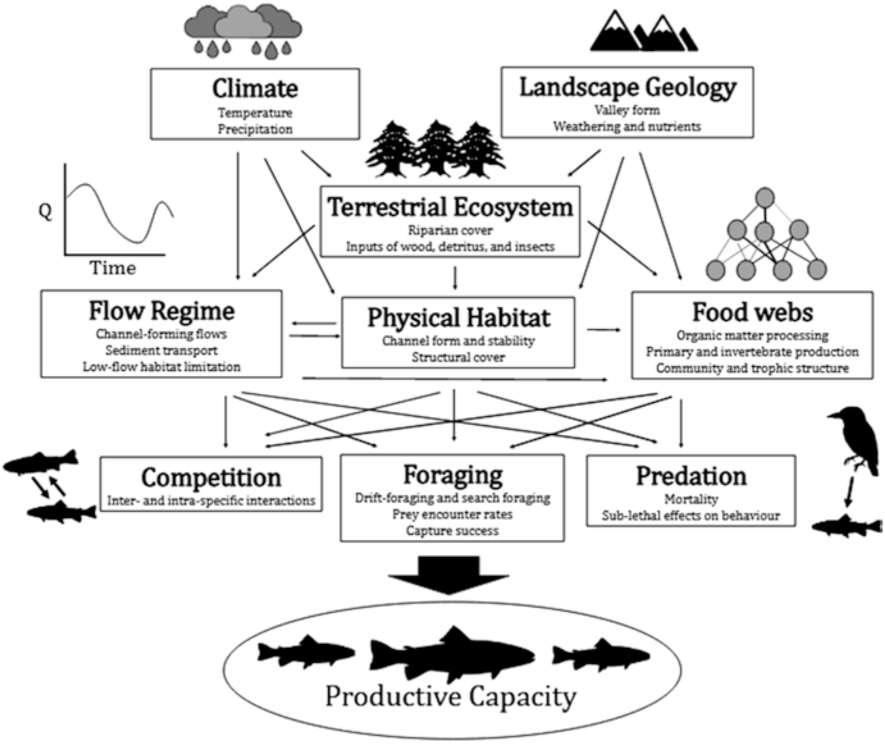

Fig. 1 The productive capacity of a stream to support trout depends on a hierarchy of landscape-scale drivers of channel morphology like climate and geology, physical habitat structure and flow regime, controls on prey abundance like terrestrial vegetation and aquatic food web structure, and biotic interactions like predation and competition from conspecifics, other native species, and exotics

sophisticated ways (e.g., Hayes et al. 2016; Naman et al. 2020c; Railsback et al. 2021a).

In this chapter, we first describe fish production and how it is commonly measured, and then explore the many determinants of trout production within the context of prey abundance and channel physical habitat structure, paying particular attention to how the effects of habitat are mediated by the properties of turbulent flow and the drift-foraging strategy of salmonids. This perspective provides a useful framework for understanding human impacts on trout production because human activities (excluding harvest mortality) primarily affect water quality (via nutrient inputs and eutrophication) and habitat structure (through channel dredging and sediment inputs, for example). Stream flow and temperature also exert strong effects on trout production, and streams are subject to severe modification of flow regime by dams and water abstraction for human use, as well as climate change; the impacts of flow alteration can also be well understood within the context of changes in available habitat and available prey. We then consider ecological strategies to maintain, restore, and protect the productive capacity of trout streams, which are under increasing pressure from human development and climate change impacts.

1.1 What Is Production and How Is It Measured?

Fish biomass ($g \cdot m^{-2}$) or abundance ($\text{number} \cdot m^{-2}$) are measures of standing stock. Fish production is a rate, and is generally defined as the rate of increase in biomass over a specified time interval, including the biomass of individuals that may not survive the production interval (Ivlev 1966; Chapman 1978a; Hayes et al. 2007a). Typical units of production for stream fish are $g{\cdot}m^{-2}{\cdot}yr^{-1}$ for juveniles or $kg{\cdot}Ha^{-1} \cdot yr^{-1}$ for larger fish, but production may also be expressed in terms of energy per unit time (J or $Kcal{\cdot}yr^{-1}$) or numbers of individuals; for instance, production of out-migrating smolts can be expressed as number per year for an entire population, which can also be standardized to number of smolts per area of habitat (e.g., $smolts{\cdot}m^{-2}{\cdot}yr^{-1}$; Roni et al. 2006) or number of smolts per linear km of stream channel (e.g., $smolts{\cdot}km^{-1}{\cdot}yr^{-1}$; Bradford et al. 1997). Production can be estimated for an entire fish community (Downing and Plante 1993) or for individual cohorts or populations (Fig. 2). Production rate should not be confused with the intrinsic rate of population growth, since a population that is stable (births = deaths) will still be producing considerable biomass as animals grow and cohorts recruit through sequential age classes.

Production rate of young-of-the-year (yoy) fish is easy to conceptualize as the product of density and average individual fish weight at the end of the growing season, since all yoy biomass is elaborated in their first year of life. For older age classes, fish production is the product of abundance (density) and average growth increment throughout the year; production of the population is the sum of production of all age classes. However, this simplified conceptualization of fish production neglects the biomass generated by fish that die before the end of the growing season; because self-thinning (mortality through competition) can be substantial within a trout cohort (e.g., Lobón-Cerviá and Mortensen 2006), non-survivors may represent a significant amount of additional production, particularly for yoy fish. This production can be accounted for by measuring the abundance and average individual weight of a cohort at shorter (e.g., monthly) intervals as the population self-thins. A more accurate estimate of cohort production can then be obtained graphically using an Allen curve (Fig. 2; Chapman 1978a; Lobón-Cerviá 2009a), which plots decreasing fish abundance as a function of increasing body weight over a specified growth interval; the area under the curve corresponding to a specific increase in fish weight can be used as a direct estimate of production over the associated time interval (Fig. 2). Chapman (1978a) and Hayes et al. (2007a) provide simple equations for directly calculating production (i.e., the area under the curve) if initial and final weight and abundance are known, assuming that both mortality rate and instantaneous growth rate are exponential; Newman and Martin (1983) provide additional guidance for variance estimation.

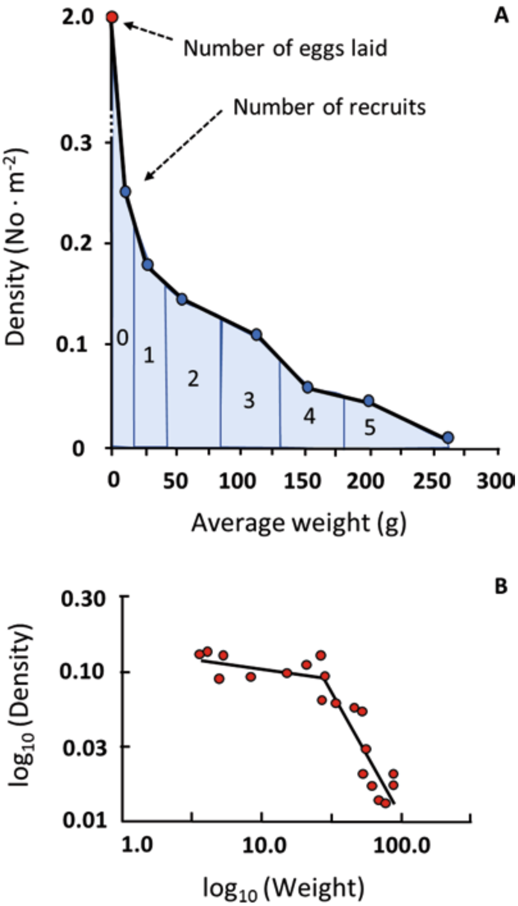

Fig. 2 Allen curve illustrating changes in average density and weight for a hypothetical cohort as it ages over time (**A**; after Lobón-Cerviá 2009a). Total area under the curve represents cumulative cohort production, including production of fish that did not survive to maturity; production for any given age class equals the area inside the specific year class polygon. When density vs. weight are plotted on a log scale they generate a characteristic self-thinning curve, and may indicate non-linearities in survival such as the 2-stage curve illustrated in panel **B**, which may be a consequence of non-linear changes in survival associated with habitat limitation for older age classes (after Rincón and Lobón-Cerviá 2002)

Biomass (mean standing stock, g·m^{-2}) is often used as a surrogate of production, with the assumption that higher biomass reflects higher production. The correlation between yoy biomass and production should be higher than for older age classes because of their negligible initial biomass (i.e., egg weight) relative to their final weight at the end of the growing year. The ratio of production : biomass (P/B) can be used as a shortcut for estimating production (Mertz and Myers 1998; Randall 2002); P/B is defined as the ratio of production to mean standing stock (Waters 1969; Hayes et al. 2007a) over the life cycle of a species, and if mean biomass is known then generic P/B ratios can be used to infer average production rate. For freshwater invertebrates with one generation a year P/B averages approximately 3.5, indicating that production is generally in the range of 3.5 times mean standing crop measured over their life cycle. P/B for salmonids is typically in the range 1–2 (Chapman 1978b; Clarke and Scruton 1999; Lobón-Cerviá et al. 2011); however, fewer small fish survive to the end of any time so that P/B is higher for smaller size classes, and population P/B therefore declines as the number of year classes in a population increases (e.g., P/B decreases from ~1.8 to 0.7 as age classes increase from 2 to 7; Kwak and Waters 1997).

1.2 Determinants of Productive Capacity

Productive capacity defines the upper limit of trout production that can be supported within a given area (e.g., stream reach or watershed) based on intrinsic habitat conditions. For size-structured populations like trout, productive capacity depends on the ability of habitat to support the growth and production of each life history stage while generating sufficient recruits to saturate available habitat for the next life stage (Rosenfeld 2014). Productive capacity represents a potential that may not be realized if habitats are under-recruited due to external factors like overharvest, migration barriers, or poor marine survival (for anadromous species). The productive capacity of trout streams is an emergent property of multiple constraints ranging from watershed-scale geology, to biological processes, climate, and physical habitat structure (Fig. 1). We consider these controlling factors in more detail below.

Prey Abundance (Bottom-up Effects) The energy that drives stream ecosystems originates from both internal and external sources. Autochthonous production of benthic algae through photosynthesis supports grazing aquatic invertebrates like mayflies, chironomids, and snails (Vadeboncoeur and Power 2017), and reach-scale variation in primary production can be a strong predictor of variation in salmonid abundance (Saunders et al. 2018). Algal production may dominate energy inputs in open-canopied streams with higher light availability, and may also contribute significantly to production in forested streams because of the high quality of algal food sources relative to terrestrial detritus (Bilby and Bisson 1992). Terrestrial (allochthonous) inputs of organic matter (leaves, wood) are also a major source of carbon that supports shredding, detritivorous, and collector-gathering invertebrates like stoneflies, mayflies, and caddisflies (Cummins 1973), all of which are prey for stream salmonids. In addition to providing leaves as a carbon source at the base of aquatic food chains, terrestrial insects falling off of riparian vegetation provide an additional prey source for salmonids (e.g., caterpillar larvae falling out of trees, ants, spiders, beetles, and adult flies; (Nielsen 1992; Baxter et al. 2005; Sotiropoulos et al. 2006)).

The magnitude of algal production is directly influenced by nutrient availability (i.e., nitrogen and phosphorous) and light levels (canopy cover; Hill and Knight 1988). Algal resources can enter the food chain through direct consumption by grazing herbivores like mayflies, or when senescent algae enter the detrital pool to be consumed by detritivores (Cummins 1973). Trout are often confined to cool mountainous headwaters, and are therefore frequently associated with oligotrophic (low-nutrient) conditions that may severely limit both algal and trout production (Stockner and Shortreed 1976); nutrient limitation is well demonstrated by the positive effects of nutrient additions on salmonid production (Johnston et al. 1990; Peterson et al.

1993). Regional geology affects water chemistry and thermal regimes (Huryn et al. 1995; Koetsier et al. 1996; Lobón-Cerviá 2003), and regional differences in both trout and invertebrate biomass are often correlated with alkalinity (Krueger and Waters 1983; LaPerriere 1983; Kwak and Waters 1997; Almodóvar et al. 2006). Consequently, trout production can be expected to be higher in regions where the underlying bedrock has higher weathering and nutrient delivery rates (Poff and Huryn 1998; Almodóvar et al. 2006). Trout production may also increase substantially with moderate inputs of nutrients from agricultural or urban sources (Askey et al. 2007; Jonsson et al. 2011). However, the positive effects of mild nutrient enrichment often transition to negative impacts of eutrophication when excessive primary production creates high biological oxygen demand and hypoxic (low oxygen) conditions (Anderson et al. 2006; Pardo and García 2016; Rosenfeld et al. 2021). A gradient of increasing trout production from headwaters to valley bottom is frequently associated with a transition to warmer temperatures and nutrient enrichment but is often sharply truncated by high temperatures, eutrophication, or degraded physical habitat at lower elevations, often associated with concentrated human development on valley bottoms (Pess et al. 2002; Sinnatamby et al. 2020b). Nutrient levels are thus a major driver of natural variation in trout production at a landscape scale, and anthropogenic fertilization mediates a transition to eutrophic streams dominated by algal blooms and low dissolved oxygen in highly developed landscapes (Jenny et al. 2016; Rosenfeld et al. 2021).

Although terrestrial detritus generally has lower food quality (higher C:N ratio) than algae (Guo et al. 2016; Brett et al. 2017), it may be the dominant basal energy source in heavily shaded oligotrophic streams with low algal production (Wallace et al. 1997, 2015). The standing stock of organic detritus in a stream depends on the dynamics of input, storage, and downstream transport, much like inorganic sediment dynamics (i.e., transport of sand, gravel, and boulders; Rosenfeld et al. 2011). The efficiency of energy transfer from detritus to fish is strongly influenced by the retentiveness of the stream channel; a channel that stores detritus with minimal export will have more complete consumption of detritus by benthic invertebrates, allowing processing chains of shredding invertebrates to convert leaves into fine particulates that are then consumed by collector–gatherers and filter–feeders (Huryn and Wallace 1987; Heard 1994). Mechanisms of organic matter retention include deposition (settling) in low velocity habitats (Walde and Davies 1984) and impingement and entrapment by the force of flowing water in high-velocity habitats (e.g. riffles; Speaker et al. 1984). In practical terms, retentiveness generally increases with channel roughness and complexity, which increases hydraulic diversity and depositional microhabitats (Humphries et al. 2020). Key locations of organic matter deposition are unembedded substrate interstices (Rosenfeld 2000), slow-velocity microhabitats in pools or behind boulders (Wallace et al. 1995; Negishi and Richardson 2003; Richardson et al. 2005), and slow-velocity channel margins. Key locations of storage by impingement are in riffles where terrestrial leaf packs accumulate on the upstream face of rocks, on small debris dams (Speaker et al. 1984), or associated with log jams (Wallace et al. 1995; Diez et al. 2000). Retention also varies at reach scales, with less confined floodplain segments acting as key storage and processing areas within watersheds (Bellmore and Baxter 2014; Ciotti et al. 2021; Wohl et al. 2018). Experimental additions and reductions of organic matter have clearly demonstrated their pivotal impacts on benthic invertebrate production (Cuffney et al. 1990; Wallace et al. 1997, 2015), but positive responses of salmonid production to detrital manipulation are less well demonstrated.

Although stream trout will forage on the benthos when drift abundance is low (Nislow et al. 1998; Harvey and Railsback 2014; Rossi et al. 2021), drift-feeding (foraging on invertebrates suspended in the water column) is their preferred strategy which generally maximizes rate of net energy intake and growth relative to other foraging modes (Nielsen 1992; Rosenfeld and Raeburn 2009). Drift abundance is therefore a key factor influencing trout production. Invertebrate drift is usually assumed to be proportional to benthic production (e.g., Koetsier et al. 1996); while this is a reasonable inference, data in support of it is inconsistent. For instance, Karen et al. (2003) found weak relationships between benthic abundance and drift, suggesting that local drift rate depends greatly on local per capita resource availability for invertebrates, predation risk, and benthic community structure (Rader 1997; Naman et al. 2016). Nevertheless, it is probably reasonable to assume that, on average, higher benthic invertebrate production does translate into higher average drift production (e.g., Esteban and Marchetti 2004), an inference which is indirectly supported through stream fertilization experiments (e.g., Warren et al. 1964; Johnston et al. 1990) where increased benthic biomass results in increased growth of drift-feeding fish. Drift production is also closely linked to changes in discharge, since hydraulic forces associated with increasing or decreasing flows can lead to differential scour or deposition of benthic substrate and associated invertebrates (Gibbins et al. 2007; Hayes et al. 2018; Rashidabadi et al. 2022). Flow variation is therefore highly consequential for flux and delivery of drifting invertebrates to trout (see the *Flow Effects on Trout Production* section below).

Effects of Habitat Structure on Useable Habitat (i.e., Population Limitation) Animal populations are frequently limited by the availability of suitable habitat (Hayes et al. 1996; Rosenfeld and Hatfield 2006). For size-structured populations, the availability of habitat for any life stage may act as a bottleneck limiting the size of the adult population (Reeves et al. 1989; Greene and Beechie 2004; Cantin and Post 2018). For instance, inadequate spawning habitat may cause insufficient egg production for larval fish to saturate available rearing habitat (Fig. 3). If there is an overabundance of spawning habitat, then a limiting bottleneck may be displaced to a later life history stage, up to the availability of habitat for adults (Fig. 3). Because the area and energy requirements of individual fish generally increase with body size, later life stages generally demand the greatest proportion of available habitat for a stable population structure**.** Habitat limitation can generally be recognized by significant deviation of channel structure from a generic optimal habitat ratio (e.g., absence of pool habitat), or by a population increase in direct response to manipulation of a limiting habitat factor (e.g., through creation of increased rearing habitat (Moore and Gregory 1988a). This forms the basis of many stream habitat restoration programs, which seek to restore productive capacity by

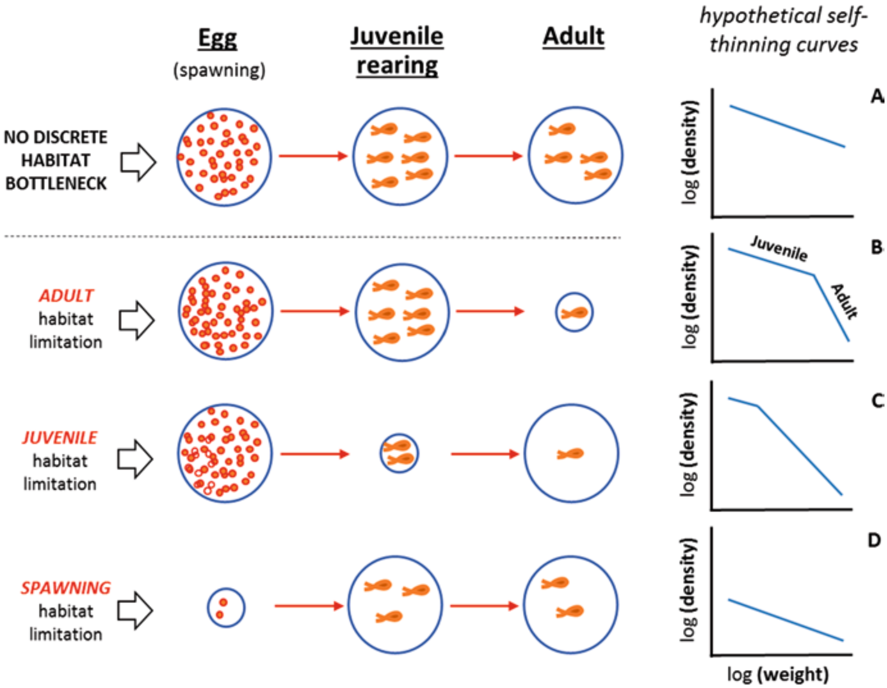

Fig. 3 Illustration of sequential habitat limitation for different life-history stages in an aging fish cohort over time. Circle size represents the relative amount of habitat available for a cohort, where a smaller circle indicates limiting habitat; note that circle area does not represent actual areal habitat requirements for a cohort, which generally increase with individual mass. Self-thinning curves on the right represent different hypothetical self-thinning patterns associated with different types of habitat limitation, where a 2-stage curve (**B**, **C**) indicates a transition to strong size-specific habitat limitation. Constant reduction in abundance over time in the upper and lower self-thinning curves (**A**, **D**) is assumed to be due to density-independent factors (i.e., predation and disease) rather than habitat limitation (Rosenfeld 2014)

increasing the area or quality of suitable habitat (Reeves et al. 1989; Roni and Beechie 2012). Success of such endeavors rests heavily on correctly identifying limiting habitat or associated stressors (MacPherson et al. 2023).

Stream salmonids generally spawn in clean, unembedded gravel substrate, which is most abundant in stream channels of intermediate gradient. Spawning habitat may be absent in low-gradient streams dominated by fines, and limited in steep boulder-bed channels with high sediment transport rates (Montgomery et al. 1996), or landscapes with very low rates of erosion and gravel recruitment (Kondolf et al. 1991; Palm et al. 2007). Slow velocity near-shore habitat may also be essential for the growth and survival of immediately post-emergent trout (Moore and Gregory 1988b; Armstrong and Nislow 2006; Kennedy et al. 2008), and may be limited in channelized streams that lack habitat complexity (Humphries et al. 2020). Trout typically shift to deeper, faster habitats as they grow (Nislow et al. 1999), and older life history stages usually require deeper habitat to avoid predators and meet their greater energy demands (Lonzarich and Quinn 1995; Hansen and Closs 2009; Rosenfeld and Taylor 2009). Because deeper pool habitat is often scarce in smaller streams, it may become increasingly limiting for older age classes of fish. This may contribute to a characteristic decline in abundance of older cohorts as fish grow in size, commonly known as self-thinning (Steingrimsson and Grant 1999; Lobón-Cerviá 2008). Self-thinning is usually a sign of density-dependent competition and a diagnostic of habitat limitation (Figs. 2 and 3); 2-stage self-thinning, where self-thinning only becomes evident at older age classes, is typical for streams with limited pool habitat, and indicates the importance of deeper pools for production of larger fish (Rincón and Lobón-Cerviá 2002; Rosenfeld 2014). Deep pools in most intermediate-gradient second to third order streams are usually created by large wood of riparian origin (Fig. 4a; Montgomery et al. 1995; Rosenfeld and Huato 2003; Johnston et al. 2011), which has been severely depleted in many European and North American trout streams as a consequence of deforestation, greatly reducing productive capacity for salmon and trout (Fig. 4b and c; Murphy and Koski 1989). However, there remains significant variation in stream-specific slopes of self-thinning curves that may be difficult to attribute to a single cause because of the variety of interacting factors that affect fish survival (Lobón-Cerviá 2008).

The productive capacity of a stream depends on both the area of useable habitat and its quality, where quality is manifest in terms of the realized growth, survival, or density of fish in a given habitat area (Hayes et al. 1996; Rosenfeld 2003; Greene and Beechie 2004). Habitat quality increases with the abundance of available prey as well as the availability of cover from predators, which comes in the form of undercut banks, root wads, large wood, unembedded substrate, and other forms of habitat complexity (Finstad et al. 2007; Penaluna et al. 2021). Historically, human activities tend to reduce habitat complexity in streams by removing the riparian forest (the main source of instream wood; (Martin and Benda 2001; Johnston et al. 2011), channelizing and dredging streams to maximize conveyance of logs (Sedell et al. 1991; Nilsson et al. 2005), and by increasing sediment loads that clog substrate interstices (Wood and Armitage 1997). Habitat restoration is generally focused on land-use practices and instream habitat projects that reverse these trends to restore productive capacity (Beechie et al. 2010; Jorgensen et al. 2021). Habitat restoration may focus on increasing the area of available habitat (e.g., by removing barriers that prevent access to upstream rearing habitat; e.g., (Hill et al. 2019) or by improving the quality of existing habitat.

Effects of Habitat on Prey Production and Availability to Trout Habitat structure affects the availability of useable habitat for trout, but it also affects the production and delivery of their invertebrate prey. This is mediated in part through the storage and retention of organic matter that subsidizes benthic invertebrate production, as described earlier. However, all habitats do not contribute equally to prey production, and it is generally thought that faster-velocity riffle habitat contributes disproportionately to the production of invertebrate drift (Poff and Huryn 1998). This is partly because benthic invertebrate biomass is often higher in riffles than in pools

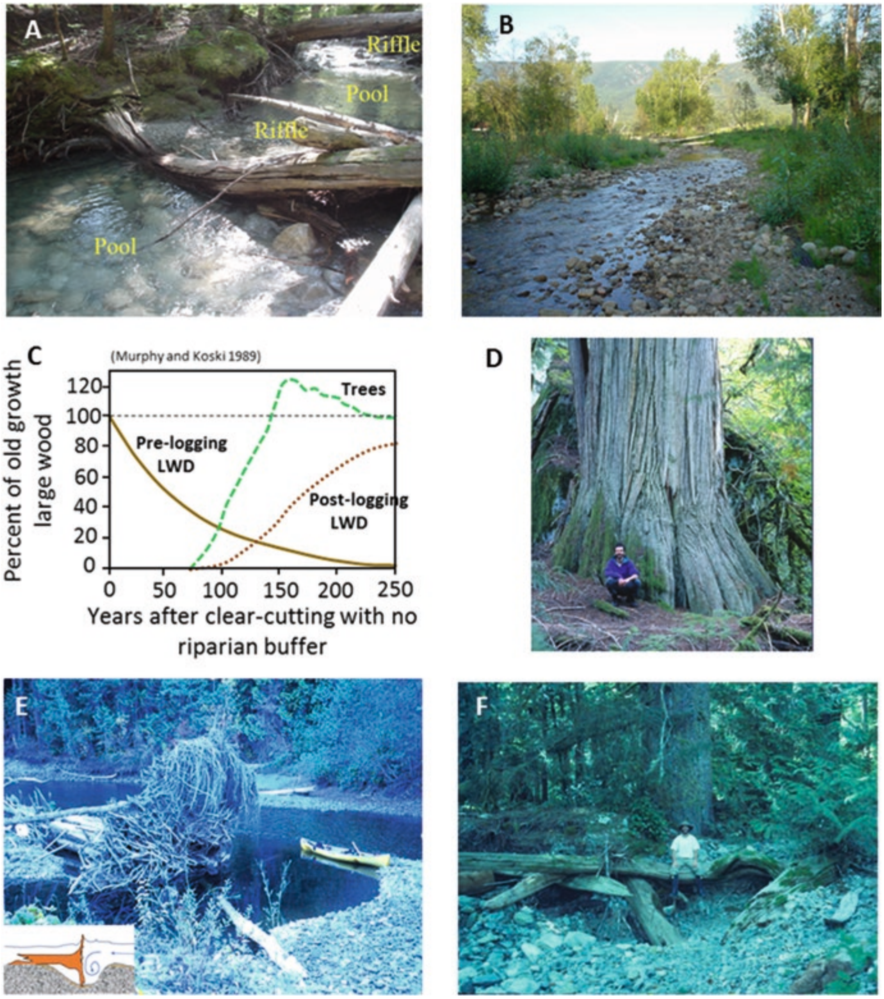

Fig. 4 Effects of large wood on channel structure in a side channel to the Nahatlach River, British Columbia, Canada (**A**); note spawning gravel retained immediately upstream of the log jam, the scour pool below it, and the dammed pool above the log jam. Panel **B** illustrates a channel with low complexity through historic loss of riparian forest, resulting in depletion of instream wood. This process is illustrated in **C**, where the decay of instream wood (solid line) is modelled over time following clear-cutting of the riparian forest, resulting in a century-long depression of wood abundance until riparian trees grow to sufficient size (broken line) to recruit to the stream channel through mortality and renew instream wood (dotted line). Large old-growth trees can create fish habitat even in larger rivers (**D**, **E**; inset to panel **E** illustrating pool formation by scour at the root wad from Buffington et al. (2002). Panel **F** illustrates the joint dependence of available habitat on channel structure and flow; absence of water during drought creates poor habitat, despite complex structure with abundant large wood and diverse substrate

(Rosenfeld and Hudson 1997), because riffles support not only detritivores that feed on interstitial detrital accumulations but also filter-feeding insects like black fly larvae (Simuliids) and grazers like *Baetis* which feature prominently in the diet of drift-feeding trout (Rader 1997). Empirical measurements of drift also indicate larger individual size and higher drift concentrations in riffles than in pools, and that drift concentrations increase with riffle length (Hansen and Closs 2007; Naman et al. 2017b), implicating long riffles as important sources of drift production to downstream pools.

Because many juvenile salmonids are adapted to low-velocity pool habitats where swimming costs are low, while shallow high-velocity riffles tend to be less hydraulically suitable, riffles tend to be net sources of drifting invertebrates which subsidize trout production in downstream pools (Poff and Huryn 1998; Rosenfeld and Raeburn 2009; Naman et al. 2017b, 2018). In contrast, net consumption of drift in pools by trout and other drift-feeders tends to make pools sink habitats for drifting prey (Rosenfeld and Raeburn 2009; Naman et al. 2018), and areas of high intraspecific competition. The disproportionate generation of prey in riffles therefore sets up a trade-off between a habitat that generates prey (riffles) and a habitat that is more suitable for rearing (pools), suggesting that an intermediate pool:riffle ratio will optimize trout production (Poff and Huryn 1998; Rosenfeld 2014). Such optimal habitat ratios have rarely been quantitatively defined for salmonids, although rules of thumb have been proposed (e.g., an optimal pool area of 30–55% to maximize juvenile salmonid production; Fig. 4a; Johnston and Slaney (1996). Experiments and modelling of juvenile salmonid abundance and energy flux in pools vs. riffles generally support this inference, but also demonstrate that the structure that maximizes trout production is very sensitive to the magnitude of terrestrial prey subsidies (Naman et al. 2018). As subsidies of terrestrial invertebrate prey increase, reliance of fish on riffles for prey generation declines, and the optimal habitat structure shifts to a higher proportion of habitat suitable for juvenile rearing (i.e., pools; Naman et al. 2018).

The trade-off between habitat for foraging and habitat for producing prey can also be understood in terms of the foraging arena concept (Walters and Juanes 1993; Ahrens et al. 2012). The foraging arena is the area of the stream where a fish can effectively forage and intercept prey, and is jointly constrained by predation risk (i.e., water depth or proximity to cover) as well as the swimming capacity of the fish, which excludes it from habitats with velocities that exceed its swimming performance. When the foraging arena (i.e., useable habitat) is small relative to the area of the stream that generates prey (as may be the case for smaller trout in large high-velocity rivers), prey flux into the foraging arena may be high and essentially donor-controlled (i.e., fish does not reduce the drift supply rate; Matte et al. 2021). A relatively small foraging arena would result in a low overall transfer efficiency of total energy flux of suspended prey to the fish trophic level. In contrast, if the stream habitat is hydraulically benign (i.e., lower velocity), then the foraging arena may encompass much of the channel, allowing strong top-down effects of trout on prey abundance and also allowing trout to harvest a relatively high proportion of drifting prey (Huryn 1996; Leung et al. 2009; Naman et al. 2018), resulting in high efficiency of energy transfer to the fish trophic level. The foraging arena constitutes a high proportion of the available habitat area in small, moderate gradient (e.g., 1–3%) trout streams, which represent a large proportion of the linear stream area in a watershed (Naiman et al. 1987; Rosenfeld et al. 2002). These second–third order streams may be very important for trout production, even if larger resident fish are rearing in deeper downstream habitats. Small streams represent a particularly productive habitat for the juveniles of anadromous fish (Elliott 1984; Murphy 1995; Rosenfeld et al. 2000), which emigrate as smolts at comparatively small sizes. Unfortunately, most non-biologists and land managers fail to appreciate the importance of small streams to trout production within a watershed, and their small size makes them extremely vulnerable to land-use impacts including drainage and infilling, which contributes to their disproportionate loss in developed landscapes (Langer et al. 2000; Rosenfeld et al. 2021).

A key influence on prey availability at the microhabitat scale is the effect of velocity on prey capture success (Hill and Grossman 1993; Grossman and Rincon 2002). Drift-feeding involves a sequence of prey detection, interception, and capture, all of which are strongly affected by velocity and turbulence (Hughes and Dill 1990). While prey encounter rates increase at high velocity, capture success declines sharply, and fish experience elevated costs of swimming and maneuvering (Hill and Grossman 1993; Hayes et al. 2007b), making high-velocity microhabitats energetic sinks. However, by selecting microhabitats behind flow obstructions drift-feeding fish can minimize swimming costs in a hydraulic refuge while maintaining access to adjacent elevated drift (Hayes and Jowett 1994; Naman et al. 2020a; however, see Johansen et al. 2020 for a divergent perspective). Preferred microhabitats are therefore characterized by strong lateral or vertical velocity gradients (low focal velocity, high adjacent prey velocity), and are usually associated with roughness elements like boulders or transition zones where riffles enter pools, which are frequently selected by dominant individuals (Nakano 1995). The strong influence of velocity on capture success highlights the critical importance of hydraulic heterogeneity to trout production; roughness elements such as large substrate may create critical hydraulic refuges that allow fish to harvest drifting invertebrates that would otherwise be unavailable.

Drift-feeding Strategies Although most stream salmonids are drift feeders, drift-foraging strategies differ in significant ways that may impact fish production. Some species are highly surface oriented, and disproportionately consume terrestrial prey (e.g., juvenile coho salmon *Oncorhynchus kisutch*; Nielsen 1992; Rosenfeld and Raeburn 2009); these species typically hold relatively high in the water column and therefore select lower velocity (e.g., pool) habitat to minimize their swimming costs while maximizing access to the stream surface, and to exploit a less turbulent water surface that maximizes detection of surface drop. In contrast, other taxa focus on prey drifting in the low or mid-water column, and select higher velocity habitats that maximize drift flux rather than surface prey detection. These taxa typically hold closer to the stream bed to exploit lower velocities near the boundary layer, where they may exploit particles that are saltating along the stream bed as well as those in complete suspension (Fig. 5), and consequently, they may consume fewer terrestrial prey. Taxa adopting this strategy include juvenile steelhead trout *Oncorhynchus mykiss* and Atlantic Salmon *Salmo salar*, the latter using their pectoral fins to anchor themselves to the surface of a home rock to minimize swimming costs, rather than holding in the water column (Arnold et al. 1991). Although anecdotal and somewhat speculative, these associations suggest that drift-foraging in lower velocity habitats

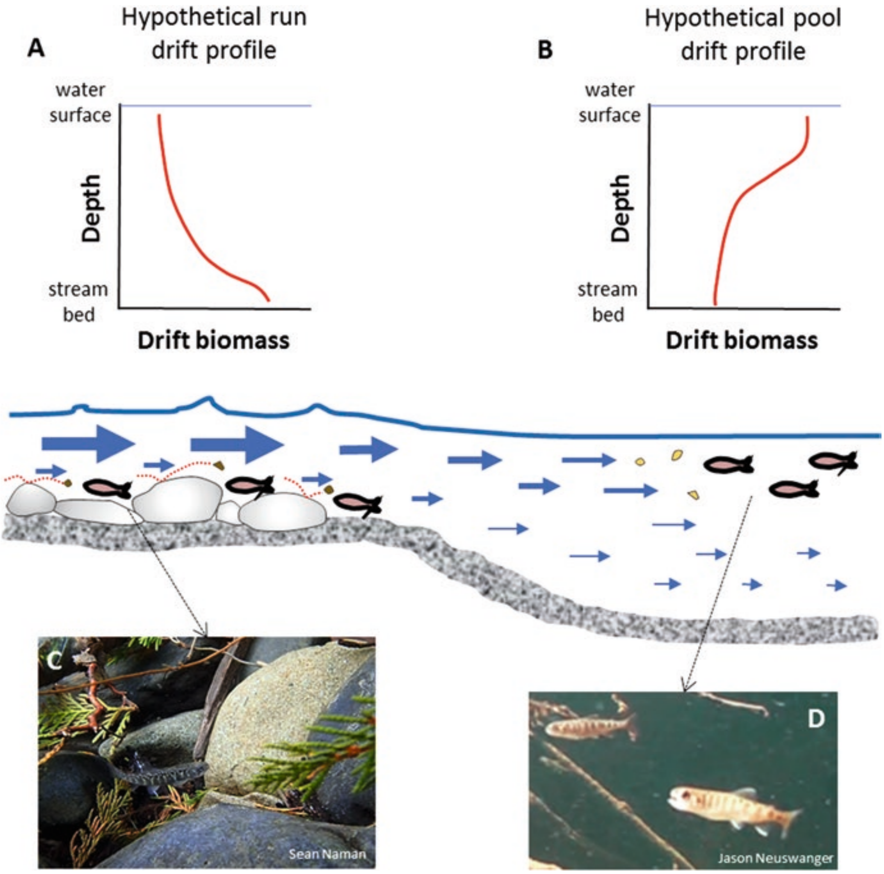

Fig. 5 Benthic-oriented vs. surface oriented drift-foraging strategies. Drift-foragers adapted to high-velocity habitats (e.g., juvenile bull trout *Salvelinus confluentus*, Atlantic salmon *Salmo salar*) will hold at a focal point near the stream bed to exploit low-velocity refuges in the boundary layer (left side of figure and panel **C**, bull trout juvenile). Because of high bed shear stress in these habitats, saltating particles may hypothetically increase drift abundance close to the stream bed (panel **A**; see https://vimeo.com/288824145 for a dynamic example). In slower deeper pool habitat that lacks the energy to entrain bedload particles (right side of figure), drift may be highest near the water surface where it is further subsidized by terrestrial inputs, supporting a surface-oriented drift-foraging strategy (e.g., juvenile chinook salmon; panels **B**, **D**). Arrow size indicates relative velocity. Panel **D** from Neuswanger et al. (2014)

is dominated by a strategy oriented toward feeding on the surface and suspended drift with a relatively high terrestrial component; whereas the optimal drift-foraging strategy in a very high-energy riffle or cascade habitat is to hold closer to the stream bed where swimming costs are lower, and where saltation of organic bedload that briefly enters the water column may elevate drift closer to the stream bed (e.g., see https://vimeo.com/288824145; Fig. 5). Nielsen (1992) observed a similar divergence in foraging strategy among individuals within a species, with dominant drift-feeding juvenile coho holding territories at higher velocities, and subordinate floaters without territories feeding in low-velocity habitats and foraging primarily on the terrestrial surface drop, with lower realized growth rates. Grant and Noakes (1987), Nakano (1995), and Nakano and Furukawa-Tanaka (1994) observed similar within-population variation in foraging strategies for brook charr *Salvelinus fontinalis*, spotted charr *Salvelinus leucomaenis*, masu salmon *Oncorhynchus masou*, and Dolly Varden *Salvelinus malma*, with faster-growing territorial individuals drift-feeding in contrast with slower-growing non-territorial fish. Experimental reductions in drift typically result in a shift from drift to benthic foraging (Nislow et al. 1998), indicating that drift-feeding is generally the preferred strategy that generates the highest net energy intake.

There is also some evidence of taxonomic differentiation in attributes that integrate both foraging strategy and metabolism. Species that exploit higher-flux microhabitats like fast riffles may adopt a rate-maximizing strategy, with high-energy intake, elevated energy expenditures, and relatively low growth efficiency (Monnet et al. 2020, 2022; Rosenfeld et al. 2020). In contrast, the juveniles of species like coho salmon that occupy lower velocity and lower energy flux pool habitat appear to adopt an efficiency maximizing strategy, with lower energy expenditures, lower maximum daily ration, and higher growth efficiency (Monnet et al. 2022; Sullivan et al. 2000; Rosenfeld et al. 2020). It is unclear whether other salmonid species that exploit similar high- and low-flux environments show similar habitat matching of metabolic strategies. However, a similar contrast in growth efficiency strategies along a productivity gradient has been observed between brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*; Arctic charr are efficiency maximizers, growing at the same rate as brown trout on 40% less food (Finstad et al. 2011), and appear to be adapted to low productivity environments that cannot support brown trout. However, brown trout are much more aggressive, which allows them to outcompete Arctic charr in more productive habitats despite their low growth efficiency, which Finstad et al. (2011) attribute, in part, to the high-energy costs of aggression. In principle, the higher growth efficiency of Arctic charr should allow greater production per unit area than brown trout in allopatry, although the enhanced aggression of brown trout should cause their phenotype to predominate in sympatry. Similarly, the higher growth efficiency of coho should increase their production per unit area or food ration relative to steelhead; however, in this case their divergent habitat tolerances (pools vs. riffles, respectively) should allow complementarity, reducing competition and potentially enhancing overall salmonid production in sympatry. Overall, drift-foraging strategies tend to match environmental or microhabitat specializations, which likely maximizes the production of a species assemblage by allowing more efficient exploitation of multiple habitats.

Relative to feeding on the benthos, drift-feeding may also reduce exclusive dependence on the aquatic food chain, allowing trout to achieve levels of production that might not otherwise be possible in oligotrophic streams. In principle, benthic-feeding fishes like sculpin (*Cottus* sp.) should have access to a larger pool of invertebrate prey than do drift-foragers, because only a fraction of benthic invertebrates enter the drift at any moment. However, in highly oligotrophic streams production of benthic fishes will be severely limited, while drift-feeders may be able to maintain a larger biomass based on subsidies of terrestrial invertebrates (e.g., Huryn 1996). This facultative dependence on terrestrial production would allow drift-foraging fishes to achieve higher production in oligotrophic headwater streams than might otherwise be expected. This also likely facilitates the early colonizing ability of salmonids in newly exposed glacial landscapes (e.g., Milner et al. 2000), and stabilizes variation in prey abundance associated with disturbance events like floods or benthic scouring that may interrupt the supply and production of aquatic prey.

Flow Effects on Trout Production Channel structure and stream flow are the main habitat axes that jointly control physical habitat availability for trout. High stream flows are the dominant channel-forming process in streams, and the magnitude, frequency, and timing of peak flows are a primary control on habitat structure; they also set the background disturbance rate that affects basal production of invertebrates and may act as a direct source of mortality to incubating eggs or larval trout (Schuett-Hames et al. 2000; Carline and McCullough 2003). At the opposite end of the hydraulic spectrum, low flows determine the physical area of habitat available for fish rearing, and low flows may generate a habitat bottleneck that strongly limits recruitment to older age classes (Lobón-Cerviá 2009b).

Channel-forming flows in streams are generally considered to be bankfull and higher; even though rare floods well in excess of bankfull can transport more bedload per unit time, bankfull flows occur more frequently and with a longer cumulative duration, and are therefore thought to have a larger net effect on substrate movement (Doyle et al. 2005; Doyle and Shields 2008). Scour and sediment transport at high flows creates habitat (e.g., pools associated with large wood and side-channel habitats; Fig. 4; Wohl et al. 2018), and plays a significant role in mobilizing and reworking the stream bed substrate, which removes fines and cleans spawning gravel (Kondolf and Wilcock 1996). Lack of periodic bed mobilization leads to infilling of substrate interstices with fines, which greatly reduces benthic invertebrate abundance (Suttle et al. 2004), quality of spawning habitat for salmonids, and overall productive capacity (Ligon et al. 1995; Kondolf 1997). Loss of high flows is a serious source of habitat degradation below reservoirs on regulated rivers where normal seasonal flows are truncated to retain water for power generation or flood control. The importance of high flows for maintenance of channel structure is a key dimension of the natural flow regime paradigm (Poff et al. 1997).

Although high flows are necessary for proper channel functioning, they can also have direct negative impacts on salmonids in terms of egg mortality through redd scour, stranding of redds laid at high river stage, and displacement or mortality of juvenile fish (Erman et al. 1988; Carline and McCullough 2003). Salmonids preferentially lay their eggs in unembedded gravel substrate, which permits interstitial flow to deliver oxygen to eggs during the incubation period. Habitats with these characteristics (e.g., the tailouts of pools or heads of riffles) are often subject to scour-and-fill over a flood cycle, and if this occurs when eggs are in the gravel it can lead to significant egg mortality (Lapointe et al. 2000; May et al. 2009). If the stream bed is sufficiently unstable and disturbance frequent enough, this can conceivably limit juvenile recruitment in a stream; otherwise, egg mortality through redd disturbance represents a stochastic process that reduces spawning success to varying degrees depending on flow regime and channel structure. Once fry have hatched, their limited swimming ability also makes them vulnerable to downstream displacement or mortality during spring floods. This also represents a stochastic process, and depends on the timing of egg hatch and high flows (Armstrong and Nislow 2006). Regional hydrology and climate will dictate the coincidence of these events, as in Colorado where high spring flows from snowmelt often correspond with fry emergence and limit year-class strength of brown trout (Wilding and Poff 2008). This effect is also well documented for brown trout recruitment in southern Europe, where both excessively high and low flows can reduce recruitment of young-of-the-year trout (Cattanéo et al. 2002; Lobón-Cerviá and Rincón 2004; Lobón-Cerviá 2009b). This highlights the hierarchical nature of controls on salmonid production in streams; even if habitat structure and prey abundance create favorable conditions for salmonid growth, stochastic flow variation during the critical post-emergence period (Armstrong and Nislow 2006) may result in variable recruitment and production that is often well below capacity (e.g., Lobón-Cerviá 2003, 2014). Higher growth and survival at lower fish densities tend to stabilize variation in production (Lobón-Cerviá 2009a); however, there are limits to compensatory density-dependent dynamics, and production will decline at very low recruitment levels.

Scouring flows also affect basal production in stream food chains. Intermittent spates during prolonged low-flow periods may be important for exporting nuisance algal growths in eutrophic trout streams (Jowett and Biggs 2006), and may partially reset the algal community from filamentous algae to diatoms that are more easily consumed by grazing invertebrates (Davie et al. 2012; Vadeboncoeur and Power 2017). Periodic spates may cause higher mortality to cased caddisflies that are well-defended against predation but vulnerable to floods, shifting the benthic invertebrate community toward invertebrates with higher vulnerability to predation (e.g., mayflies), thereby enhancing energy transfer to fish (Wootton et al. 1996). Severe floods may also cause a significant reduction in benthic invertebrate biomass in high-velocity areas of the stream bed, although depositional areas will retain both invertebrates and detrital resources (Lancaster and Hildrew 1993), and recolonization of scoured habitat is generally relatively fast (order of 2–4 weeks). Bed scour may also lead to lagged increases in benthic invertebrate production, as a consequence of sediment removal and increased interstitial habitat (Korman et al. 2011).

The limiting effects of summer low flows on trout populations are well documented (Kovach et al. 2016; Jespersen et al. 2021), particularly in Mediterranean climates with prolonged summer low-flow recessions associated with seasonal drought (Nicola et al. 2009; Beecher et al. 2010; Grantham et al. 2012; Fig. 4f). As flows decrease during summer periods with low rainfall, fish become increasingly confined to a smaller habitat area, where they will experience greater competition for limiting resources (prey and space; Grant and Kramer 1990; Imre et al. 2005; Ward et al. 2007). These effects will be particularly pronounced in smaller streams, especially if fish are unable to disperse downstream to larger mainstem habitats (e.g., because of downstream barriers or excessively high downstream temperatures). Although low flow negatively impacts available habitat, it may also lead to increased summer water temperatures as the inertial capacity of the water to resist warming declines with flow (Poole and Berman 2001). Elevated summer temperatures may increase trout production in extremely cold streams, but reduce it in streams above optimal temperatures, particularly if prey abundance does not increase with warming (Ayllón et al. 2019). Low flows can also result in depressed dissolved oxygen, and declining water quality may limit trout production at higher flow thresholds than those that trigger habitat limitation, particularly in eutrophic streams (Graeber et al. 2013; Rosenfeld 2017; Zinn et al. 2021). Incubating eggs are particularly sensitive to hypoxia and low flows because they lack mobility and are dependent on interstitial flows for oxygenation (Martin et al. 2017). Winter low-flow periods may also be stressful for fish in cold temperate climates where precipitation falls as snow rather than rain, and overwinter survival may decrease at low winter flows (Mitro et al. 2003; Hvidsten et al. 2015). Low winter flows will reduce available habitat as surface and anchor (bed-attached) ice forms in marginal habitat and at the stream surface (Cunjak 1996), compounded by the formation of frazil ice (ice suspended in the water column) that can harm gills, and the physiological stress of low temperatures and minimal food (Cunjak et al. 1998; Bradford and Heinonen 2008).

Variation in flow regime also has important effects on flux and delivery of drifting invertebrates to trout. Stomach contents of stream salmonids are often fuller following rainfall events, when increased flows induce scour and elevate drift, or dislodge terrestrial invertebrates from overhanging vegetation. This may be particularly important during prolonged periods of declining or stable low flows, when intense competition in shrinking habitats may limit growth (Harvey et al. 2006) and drive strong patterns of density-dependence (Matte et al. 2021). Periodic spates that elevate flows and temporarily increase drift may be critical to the survival of subordinate fish that might otherwise starve over the low-flow period, although the importance of these periodically pulsed prey subsidies has yet to be demonstrated empirically. The effects of declining flows on non-catastrophic background drift are also potentially consequential; several studies have shown a reduction in drift concentration as flows decline over the summer low-flow period (Rashidabadi et al. 2022), indicating that the negative consequences of reduced habitat area on trout production are compounded by a decrease in prey abundance per unit discharge (Romaniszyn et al. 2007; Hayes et al. 2019).

Competition, Predation, and Diversity Competition from conspecifics and other fish species will affect trout production, as will the abundance of terrestrial and aquatic predators. Competition generally takes place through exploitative (scramble) or interference competition (territoriality). In exploitative competition, individuals are unable to monopolize resources, and depletion of a shared resource reduces per capita energy intake and growth for all individuals equally; this is often the case in pelagic zones of lakes, where fish are unable to defend territories. In contrast, the structural stability of streams allows interference competition, where dominant individuals can monopolize resources (e.g., through territoriality or dominance hierarchies; Nakano and Furukawa-Tanaka 1994; Elliott 2002), leading to a skewed distribution of per capita energy intake, growth, and size distributions (Jenkins et al. 1999; Imre et al. 2005). Exploitative competition can reduce overall individual fitness at high densities; in contrast, territoriality in streams allows a subset of dominant individuals to maintain relatively higher fitness despite high fish densities (Jenkins et al. 1999), which should help stabilize population fluctuations under low per capita resource availability (i.e., if overwinter survival is size-dependent, larger territorial individuals will experience higher survival than their smaller-bodied sub-dominant conspecifics).

Competition among trout species is also common, but the factors that mediate competitive abilities are poorly understood. Species differ in the degree to which they exhibit territoriality; some species, like Atlantic salmon or brown trout, are strongly territorial (Keenleyside and Yamamoto 1962; but see also Roy et al. 2013), while other species like Arctic and brook charr are behaviorally flexible and often defend foraging stations temporarily or non-exclusively (Grant and Noakes 1987; Gunnarsson and Steingrímsson 2011; Matte et al. 2021). Some of the variation in competitive ability among species is related to differences in habitat tolerances (e.g., preference for pools vs. riffles; Glova 1986; Young 2001), divergence in hatch timing that generates priority effects when establishing foraging territories, or differences in timing of spawning and fry emergence that affects vulnerability to spring floods (Fausch et al. 2001; Hasegawa 2020). Differences in thermal performance may also mediate species replacement along downstream thermal gradients; this has been observed for many species pairs of trout, including bull trout *Salvelinus confluentus* and rainbow trout in western North America (Parkinson et al. 2016) and spotted charr and Dolly Varden in Japan (Taniguchi and Nakano 2000). Temperature has also been demonstrated to mediate competitive outcomes between steelhead trout and redside shiner *Richardsonius balteatus*, a cool water cyprinid that outperforms steelhead at warmer temperatures (Reeves et al. 1987). Differences in competitive outcomes among salmonids are especially evident following introduction of trout outside of their native range, where invasive species often outcompete native (often endangered) trout (e.g., Harig et al. 2000). Although introduced salmonid species have severe negative impacts on native species, stocking of domestic or alien strains of trout within their native range can have equally negative impacts on native trout diversity and production (Araki et al. 2007; Buoro et al. 2016).

Although information on the relationship of salmonid diversity to community productivity is limited, evidence suggests that species diversity may match habitat diversity; for example, Montgomery (2000) argues that the higher native diversity of trout and salmon in Western relative to eastern North America relates to the greater physical diversity of stream habitats and hydrology in western North America. In principle, habitat diversity should favor specialization, reduced competition, and complementarity (i.e., higher salmonid community production; Loreau and Hector 2001). This would manifest in the use of different habitats by species in sympatry (e.g., rainbow trout rearing in riffles while coho rear in pools; Bisson et al. 1988). Complementarity may also involve facilitation, where the presence of one salmonid species benefits another. The widely documented positive effects of pink salmon *Oncorhynchus gorbuscha* and chum salmon *Oncorhynchus keta* on sympatric trout populations is one example. Pink, chum, and sockeye salmon *Oncorhynchus nerka* are numerically dominant as adults in the North Pacific Ocean (Ruggerone and Irvine 2018) and spawn in large numbers. Consequently, their eggs and fry are important resource subsidies for resident and anadromous trout in many rivers. For example, Armstrong and Bond (2013) found that Dolly Varden in an Alaskan river derived most of their annual energy intake by gorging on sockeye salmon eggs over a 5-week period. Bailey et al. (2018) also observed a positive correlation between steelhead smolt production and spawning pink salmon in the Keogh River, British Columbia. These and other studies indicate that production of trout is often strongly linked to predictable resource pulses associated with spawning salmon. This contrasts with adults, where exploitative competition with over-abundant adult pink salmon in the ocean may reduce the body size of other anadromous species (Ruggerone and Nielsen 2004).

Terrestrial predators may also have significant impacts on trout production. Avian predators like herons, kingfishers, mergansers, cormorants, and even owls may consume large numbers of juvenile trout or out-migrating smolts (Lonzarich and Quinn 1995; Harvey and Nakamoto 2013). River otters and mink can have similar effects, particularly in smaller streams (Heggenes and Borgstrom 1988). Mortality rates are often mediated by physical habitat; in general, deeper water, instream cover, and habitat complexity provide refuge from predation (Lonzarich and Quinn 1995; Harvey and White 2017).

Predation risk from aquatic predators, including cannibalistic conspecifics, has well-documented effects on trout habitat use, behavior, and survival (e.g., Furey et al. 2016). Many trout species become opportunistic piscivores as they grow larger, but some species and populations have evolved to specialize as piscivores. For example, adult bull trout are predators of other trout species, but will also cannibalize smaller conspecifics (Pinto et al. 2013). Piscivorous populations of rainbow trout have also evolved in lakes with kokanee (land-locked sockeye), where piscivore trout grow to exceptionally large sizes feeding on kokanee (Monnet et al. 2020). A similar evolution of sympatric piscivore, planktivore, and benthic ecotypes is common in northern populations of charr (Jonsson et al. 1988). Although predators exert direct mortality that may limit prey populations, the effects of predation risk on behavior and habitat use likely has more significant limiting effects on production than actual mortality (Preisser et al. 2005). In particular, the foraging arena available to juvenile trout will be limited to areas of low predation risk (Walters and Juanes 1993); for juvenile rainbow trout in lakes, this includes shallow littoral areas with abundant cover in the form of coarse substrate or submerged vegetation. Stream-rearing salmonids will also be limited to marginal habitats with heavy cover or shallow riffles in the presence of high predation risk (Rosenfeld and Boss 2001; Harvey and White 2017). Time windows of lower risk may also select for crepuscular or nocturnal foraging behavior (Naman et al. 2022; Railsback et al. 2021b).

There is some anecdotal evidence that juvenile salmonids rearing in streams with large resident trout may experience more predation risk than salmonids rearing in anadromous streams. Observations of juvenile coho salmon and steelhead (anadromous rainbow trout) in coastal streams in British Columbia indicate that juveniles forage freely in the open water column during daylight (Naman and Rosenfeld, pers obs.). However, juvenile resident rainbow and bull trout in non-anadromous streams (e.g., the Skagit River, British Columbia) appear to be restricted to foraging under cover during the day, and only forage in the open at dusk and dawn (Naman et al. 2022), presumably because of the high risk of predation from adult bull trout which are known to be visual predators that alter the distribution of their juveniles (Pinto et al. 2013). While it is not well understood whether restriction of juvenile trout to a smaller foraging arena limits population size and production in streams (e.g., Vik et al. 2001), it is well documented in lake populations of rainbow trout (Biro et al. 2003).

Water Quality (Temperature, Nutrients, Hypoxia) Water quality is a key limiting factor in trout distribution and production, with temperature, nutrients, and dissolved oxygen of greatest consequence. Temperature acts as a primary filter on the regional distribution of trout across landscapes and within drainage basins (Wenger et al. 2011; Armstrong et al. 2021). Trout may be present throughout a watershed in cold-water glacial-fed rivers, or in north-temperate climates with low to moderate average air temperatures. However, trout become increasingly confined to colder high-elevation streams in warmer climates near the southern edge of their distributions. Background nutrient levels (e.g., nitrogen and phosphorous, often indexed using conductivity or alkalinity as a surrogate) determine algal productivity in streams, driving invertebrate production at the base of the aquatic food chain and therefore directly affecting carrying capacity for trout (Poff and Huryn 1998). The trophic state is also very sensitive to nutrient inputs from human sources, which are pervasive in developed landscapes (Gordon et al. 2008).

Like all aerobic animals, trout require oxygen to metabolize food, and low dissolved oxygen levels can directly limit growth (Herrmann et al. 1962; Hrycik et al. 2017; Rosenfeld and Lee 2022) or cause direct mortality (Vaquer-Sunyer and Duarte 2008, 2011). Low dissolved oxygen (hypoxia) may occur naturally in trout streams but is generally rare in pristine systems because cool temperatures are associated with high oxygen saturation and low oxygen demand. Exceptions include temperate lakes that freeze over in the winter, limiting gas diffusion at the lake surface and often resulting in winterkill when respiration from lake sediments depletes available oxygen; this may also impact water quality in the outlet stream below the lake, depending on stream gradient and the rapidity of re-aeration. Hypoxia can also occur in naturally productive streams at low flows where biological oxygen demand of the ecosystem exceeds oxygen supply through surface diffusion (Fellman et al. 2015; Pardo and García 2016).

Trace nutrient inputs from urban, agricultural, and industrial sources can stimulate production in oligotrophic trout streams (Johnston et al. 1990), but excessive nutrients can trigger severe eutrophication leading to hypoxia and water quality issues, particularly in developed landscapes. Increased nutrients elevate algal production as well as microbial breakdown of stream detritus; nocturnal respiration by algae and microbial respiration of dead algal tissue greatly elevates biological oxygen demand (Pardo and García 2016) and can lead to severe hypoxia and fish mortality (Vaquer-Sunyer and Duarte 2008). Hypoxic effects of eutrophication also tend to be non-linear, and elevated fish and invertebrate production by nutrient inputs may mask an impending transition to a hypoxic state (Rosenfeld 2017). Increased temperature, nutrients, and decreased flows tend to have synergistic impacts on hypoxia; elevated temperatures reduce saturation levels of dissolved oxygen and increase respiratory demand, while the low flows that often accompany hot dry weather reduce turbulence and re-aeration at the air–water interface (Rosenfeld et al. 2021). These factors collectively reduce trout production in valley bottom areas of intense human development, unless stream temperatures are extremely low.

Acidification also remains a serious threat to trout production in some areas; inputs of sulfates and nitrates from industrial pollution (e.g., coal-fired power stations) acidifies streams and causes stress or mortality to benthic invertebrates, salmonid eggs, and may inhibit growth and survival of fry (Schindler 1988; Lacoul et al. 2011). Although great progress has been made in reducing acid-causing emissions, many systems have not recovered because the soil buffering capacity of the watershed has been lost, and streams remain acidic without artificial additions of calcium or other buffering agents (Clair and Hindar 2005; Clair et al. 2011). These legacy effects are widespread in some areas; approximately 40% of trout and salmon streams in the province of Nova Scotia, Canada, remain at or near pH levels that cause mortality to larval salmonids as a consequence of historic acid deposition (Dennis and Clair 2012; Department of Fisheries and Oceans Canada 2013).

Not all changes in water quality negatively impact trout production. In fact, the productivity of very cold oligotrophic streams may be enhanced by increased water temperatures or mild eutrophication (Askey et al. 2007; Sinnatamby et al. 2020b). However, for the many populations that are near their thermal optimums elevated temperatures and nutrient levels will have negative impacts. Optimal temperature for salmonid growth also tends to be ration-dependent, with fish selecting low temperatures to minimize respiration rate when food is scarce, and higher temperatures to maximize digestion when food is abundant (Hughes and Grand 2000; Hughes 2009; Armstrong and Bond 2013). Armstrong et al. (2021) argue for the importance of thermal diversity to salmonid production, promoted by the adjacency and availability of cool and warmer habitats within a reach or drainage basin (Brewitt et al.

2017). Thermal diversity allows trout to maximize production by selecting the optimal thermal environment to match their particular life history stage, physiological state, or satiation level.

1.3 Effects of Climate Change on Trout Production

Salmonids are highly vulnerable to climate warming because of their cool water physiology and ecology, with optimal growth typically in the range of 12–19°C; e.g., Bear et al. 2007; Kovach et al. 2019); this vulnerability is exacerbated for stream-dwelling populations confined to dendritic networks with limited ability to migrate to more suitable climates (Kovach et al. 2019; Sinnatamby et al. 2020a). Climate warming constrains the physiology of all salmonids as they cannot live outside their lower and upper incipient lethal temperatures, and within these thermal boundaries different functions (e.g., feeding, growth, reproduction) are restricted to even narrower ranges beyond which performance declines (Elliott and Elliott 2010). However, even though most research has focused on the thermal consequences of climate change for stream salmonids, warming is just one dimension of the problem. In fact, stream flow is more consistently related to trout demography and individual growth than temperature (Kovach et al. 2016), and hydrologic change may be a more critical dimension of climate change for population persistence (Ayllón et al. 2019; Kovach et al. 2019). In this section, we describe the consequences of ongoing and future climate-driven temperature and stream flow changes for trout growth and demography. We close the section by highlighting the behavioral, plastic, and evolutionary mechanisms that provide stream salmonids with important resilience to climate change.

Increased Temperatures Beyond certain thresholds, climate warming directly decreases individual performance in foraging, growth, reproduction, immune competence, and competitiveness (Pörtner and Farrell 2008). Climate warming affects fish growth and development through direct effects of temperature on energetic processes such as metabolism (e.g., costs) and food intake (benefits), although the direction and magnitude of an individual's net response (i.e., benefits minus costs) is determined by the thermal optimum relative to the currently experienced environmental temperature and the magnitude of warming (Ohlberger 2013). Therefore, summer growth rates are predicted to increase in very cold rivers with sub-optimal temperatures and short growing seasons (Jonsson and Jonsson 2009; Elliott and Elliott 2010; Al-Chokhachy et al. 2013). For example, O'Gorman et al. (2016) showed that warming enhances brown trout individual growth and population production at high latitudes, where current ambient temperatures are sub-optimal for their physiological performance.

In contrast, warming would lead to depressed growth during the summer months in rivers currently at or near optimal temperatures (Al-Chokhachy et al. 2013; Ayllón et al. 2019; Gallagher et al. 2022). If warming pushes temperatures beyond the species-specific growth optimum, then growth efficiency will decrease because metabolic costs increase faster than consumption (Crozier et al. 2010). Since different life stages have different thermal sensitivities, depending on the magnitude of change warming can negatively affect some life stages but not others (Ohlberger 2013; Myrvold and Kennedy 2015). However, at very high temperatures, fish growth becomes impaired by insufficient energy or oxygen supply at all developmental stages (Pörtner 2010). Since saturation levels of dissolved oxygen drop with increasing temperatures, warming concurrently produces oxygen limitation while exponentially increasing metabolic demand; thus, changes in the aerobic scope of fish with temperature are highly non-linear (Pörtner 2010; Rosenfeld 2017), and the limiting effect of temperature on aerobic scope becomes greater as body size increases (Breau et al. 2011). Strong warming therefore leads to reduced mean body size at the population level as a direct consequence of decreased size-at-age of individuals (especially of adults; Cheung et al. 2012) and/or an increasing proportion of young life stages relative to adults (Daufresne et al. 2009; Ohlberger 2013; Ayllón et al. 2019).

Elevated temperatures also affect resource acquisition, as prey capture success by drift-feeding salmonids is highly driven by swimming ability, which depends on fish size and is affected by water temperature (Hill and Grossman 1993; Watz and Piccolo 2011). There is typically a humped response of critical and maximum sustainable swimming speed to temperature, with peaks around 14–17 °C for salmonids (e.g., Myrick and Cech 2004; MacNutt et al. 2006). Therefore, strong climate warming impacts swimming performance and consequently foraging success, impairing feeding, growth, and ultimately survival.

Thus, strong warming results in increased fish mortality by starvation (i.e., fish are not able to meet their increased metabolic demands; e.g., Ayllón et al. (2019), while extreme temperatures lead to the breakdown of physiological processes (Pörtner 2010), with stronger effects on larger fish. Reduced size and number of breeders diminish total egg production of the population; in addition, high temperatures can be directly lethal to trout eggs (Jonsson and Jonsson 2009) which have much lower critical temperatures for survival than alevins, juveniles, or adults (Elliott and Elliott 2010). These mechanisms strongly affect recruitment, a main driver of production dynamics in stream salmonids (Lobón-Cerviá 2009a). Decreased recruitment and survival from ongoing climate warming have already caused trout population declines in thermally limited rivers (Ayllón et al. 2013; Bassar et al. 2016; Gallagher et al. 2022), and mechanistic simulations predict strong reductions in biomass and production even in headwaters that are currently experiencing temperatures well below thermal optima for trout (Ayllón et al. 2019).

Hydrologic Change Shifts in hydrologic regimes are predicted to have considerable effects on the growth and demography of stream salmonids, and will in many cases exacerbate the impacts of warming (Kovach et al. 2019). However, there is a strong spatial and temporal (seasonal) heterogeneity in current and projected changes in hydrologic regimes. In trout populations, stream flow is generally positively associated with growth and abundance of all age classes in the summer and autumn (see review by Kovach et al. (2016)). In contrast, decreased summer flows reduce both available habitat—increasing competition for food and space—and drift food availability at the time when temperature-driven metabolic requirements are highest, and thus produce strong impacts on trout populations. For example, in Southern Europe, where droughts will start earlier and last longer and stream flow is projected to maintain current declining trajectories in all seasons, brown trout individual growth rates and population biomass and production are expected to rapidly decline, and local population extirpations are predicted (Ayllón et al. 2019). Likewise, decreased summer low flows in western North America and an extended low flow season in the Northeast and Midwest (Kovach et al. 2019) are also predicted to impact trout population dynamics and trigger local extirpation in streams already experiencing summer temperatures that exceed physiological optima (e.g., Letcher et al. 2015). However, in contrast with rain- or snow-dominated catchments where summer low flows may create a limiting habitat bottleneck, elevated summer flows triggered by accelerated glacial melt may reduce suitable habitat in glacier-dominated watersheds (e.g., Neuswanger et al. 2015), highlighting the sensitivity of climate impacts to hydrologic context (Beechie et al. 2013).

Not all hydrologic change will be negative, and increased autumn flows may buffer the demographic impacts of warming in systems where autumn flows are projected to increase (Kanno et al. 2016). However, high winter precipitation and flows may cause reduced growth (Xu et al. 2010) and survival (Letcher et al. 2015; Kanno et al. 2016) because of depressed foraging success from elevated water velocities and reduced swimming ability at low temperatures. Thus in northern regions, the projected increase in winter flows may reduce or offset the predicted growth and demographic benefits of strong winter warming.

Changes in winter and spring stream flow conditions can also have strong demographic impacts via spawning success and subsequent effects on impaired recruitment. In many regions like northern Europe and western North America, winter precipitation and flows will increase (Kovach et al. 2019), particularly where less precipitation falls as snow with rising freezing levels. Increased frequency of winter high-flow events is predicted to cause repeated recruitment failures for fall/winter-spawning trout (Jonsson and Jonsson 2009; Wenger et al. 2011; Kanno et al. 2016) because of redd scour (Gauthey et al. 2017) and spawning disruptions (Strange et al. 1992). In contrast, in southern Europe it is reduced flows and elevated temperatures in late autumn and winter that are expected to degrade hydraulic and thermal habitat for spawning (Kovach et al. 2019; Santiago et al. 2020), compounded by increased egg mortality from limited oxygen exchange at low water velocities (Martin et al. 2017). Both very low and very high flows during or immediately after emergence decrease the survival rate of recruits by reducing food intake and availability of suitable habitat (Cattanéo et al. 2002; Nicola et al. 2009; Lobón-Cerviá 2014). Thus, decreasing spring flows coupled with increasing temperatures may limit recruitment, and thus production, of fall-spawning trout in southern Europe (Ayllón et al. 2019).

The frequency of moderately extreme river floods (i.e., those with a 30-year return interval) is projected to decrease throughout the distribution of most salmonids (e.g., northern Europe, the Mediterranean basin, western and eastern North America), with some exceptions (e.g., central North America) (see review by Death et al. 2015). However, the intensity of very extreme floods (those with a 100-year return interval) has been increasing in recent decades in many temperate regions, for example, in northern and central Europe (Blöschl et al. 2019). Increased intensity and frequency of extreme floods might produce biologically relevant geomorphic responses in rivers (Death et al. 2015), including: (1) increased fine sedimentation from elevated bank and catchment erosion, affecting available cover and suitable substrate for spawning as well as the diversity and composition of invertebrate communities; (2) channel straightening and entrenchment, reducing both structural diversity and the availability of pool habitats, thereby diminishing the quantity and quality of food and habitat available to stream salmonids. In fact, local extinctions of marble trout *Salmo marmoratus* populations caused by flash floods and landslides have already been documented (Vincenzi et al. 2016). In contrast, a reduction in ecologically important moderate-sized floods (i.e., 30-year return period) that periodically mobilize substrate and reduce embeddedness will decrease the abundance and diversity of invertebrates and facilitate fish invasions (Death et al. 2015). Climate change is also shifting the timing of extreme river floods (e.g., Blöschl et al. 2017), potentially increasing the risk of egg and fry scouring and periodic recruitment failure (Death et al. 2015).

Indirect Effects of Increased Temperatures and Hydrological Change While the direct abiotic effects of climate change are relatively clear (i.e., temperature effects on physiological limits), the existing literature suggests that indirect effects—i.e., altered species interactions—are more important drivers of population change (Ockendon et al. 2014). First, climate change effects on stream salmonids are contingent on parallel changes in food availability, since metabolic rates and optimal temperatures for growth vary in response to food abundance (Huey and Kingsolver 2019; Archer et al. 2020). However, predicted changes in prey availability are quite uncertain. Empirical studies indicate that aquatic macroinvertebrate production increases with individual body mass and water temperature (Morin 1997); aquatic mesocosm experiments also suggest an increase in the biomass of lower trophic level organisms with warming (e.g., Yvon-Durocher et al. 2011). Terrestrial invertebrate subsidies also appear to increase in warmer environments (O'Gorman et al. 2016). Under the assumption that higher temperatures elevate invertebrate production (at constant mean body mass and energy content), mechanistic simulations predicted no warming-induced changes in brown trout production in Mediterranean headwaters and dampened declines in thermally limited mainstem habitats (Ayllón et al. 2019). However, climate warming is also likely to alter the composition of food resources available to stream salmonids, with the loss of invertebrate species beyond their thermal limits and invasions of warm-adapted and generalist taxa (e.g., Domisch et al. 2013). In fact, shifts in macroinvertebrate assemblage composition and declines in abundance due to ongoing warming have already been reported (e.g., Durance and Ormerod 2007). Whether increasing invertebrate production can keep up with increasing metabolic demands of trout in warming waters is unclear. This uncertainty is compounded by the fact that invertebrate taxa differ in their propensity to drift (Rader 1997) and therefore their vulnerability to trout predation, and unexpected shifts in community composition may have profound impacts on prey availability.

While floods and droughts can radically change the composition of invertebrate assemblages (Wootton et al. 1996), flow changes can also alter the entry rate of individuals from the benthos into the drift. The experiments of Naman et al. (2017a) and others (e.g., James et al. 2008; González et al. 2018) show that total drift concentration increases immediately after flow reductions, but only for the most mobile taxa, suggesting a behavioral response of benthic invertebrates most likely related to reduced velocity and secondarily to decreased wetted area. Hence, climate-driven flow reductions might initially cause brief increases in drift production at a cost of decreased longer-term drift and benthic production. In addition, mean body size of drift appears to decrease with flow reductions (Caldwell et al. 2018), further reducing energy availability to drift-feeding trout. Thus, while stream flow reduction can clearly alter food availability for drift-feeding fish in the short term, and multiple lines of evidence suggest strong potential for negative impacts on prey abundance, the long-term effects of altered flow regimes on food availability for stream salmonids remain unclear.

Second, climate warming is already facilitating (or will enable) the expansion of both native and invasive cool- and warm-water species into salmonid-dominated cold rivers (Almodóvar et al. 2012; Zillig et al. 2021), and thus increasing negative interactions with native populations, through competition (e.g., (Kovach et al. 2017), predation (e.g., Lawrence et al. 2014), or hybridization (e.g., Muhlfeld et al. 2014). Projected climate-driven hydrological changes are also predicted to alter fish assemblage composition and promote invasions (Rahel and Olden 2008). For example, earlier flooding and decreasing spring flows have facilitated the expansion of nonnative rainbow trout and its hybridization with threatened native Westslope cutthroat trout *Oncorhynchus clarkii* populations in western North America (Muhlfeld et al. 2014; Sinnatamby et al. 2020a).

Third, climate change can alter disease dynamics: with continuous warming, several fish diseases will become more virulent while salmonids become more thermally stressed, reducing their disease resistance (Jonsson and Jonsson 2009). For example, the prevalence and intensity of proliferative kidney disease and darkened syndrome are clearly linked to water temperature in wild brown trout populations; thus climate warming might have triggered the spread of those diseases and contributed to the ongoing decline of trout populations in central Europe (Lewisch et al. 2018; Arndt et al. 2019; Rubin et al. 2019). Importantly, infectious diseases can induce evolutionary responses (e.g., in maturation schedules; Ohlberger et al. 2011), which might limit the scope of local adaptation to climate change.

Behavioral, Plastic, and Evolutionary Responses to Warming and Hydrologic Change Stream salmonids possess a variety of mechanisms that confer resiliency to cope with climate change (Kovach et al. 2019). First, there is growing evidence that salmonids can adapt to ongoing climate change via natural selection (Crozier and Hutchings 2014). For example, various salmon species show local adaptation of cardiorespiratory (Eliason et al. 2011) and other physiological traits associated with thermal performance (Fraser et al. 2011). Genomic data indicates that rainbow trout populations in desert environments have evolved an adaptive heat shock response to deal with thermal stress at lower physiological costs (Narum et al. 2013). Mechanistic simulations predict evolutionary changes in trout life history traits (reduced size at maturity and size at emergence) as a response to climate warming and stream flow decline (Ayllón et al. 2019); however, river warming would select for larger maturity size thresholds in Atlantic salmon, leading to less frequent river maturation (Piou and Prévost 2013). Finally, there is evidence for rapid climate-induced adaptive evolution in phenological traits, such as timing of seaward migration in different salmon species (Crozier et al. 2011; Kovach et al. 2012).

Second, phenotypic plasticity provides an additional avenue for adaptation, and likely underlies most documented phenotypic responses to climate change in salmonids (Crozier and Hutchings 2014). However, most observed plastic responses in life history (growth, size at maturity/smolting) and phenological traits (migration timing) have been reported for anadromous populations. Simulations predict earlier fry emergence both in fall- and spring-spawning trout under climate warming (Penaluna et al. 2015; Ayllón et al. 2019; Santiago et al. 2020). Earlier emergence would extend the growing season for recruits and thus have positive effects on individual growth rate and survival (Ayllón et al. 2019), as long as climate-induced trophic mismatches do not occur (see Jonsson and Setzer 2015). However, strong warming and flow reduction in late autumn is predicted to delay spawning, which would result in later emergence and smaller size at the end of the first growing season (Ayllón et al. 2019). Delayed spawning phenology in response to elevated stream temperatures has already been described in different stream salmonids, such as brook trout (Warren et al. 2012), brown trout (Riedl and Peter 2013) or cutthroat trout (Bennett et al. 2014).

Third, there is also strong evidence that density-dependence can create compensatory dynamics that buffer the negative effects of climate change on trout growth and demography. In particular, density-dependent growth appears to be a key mechanism for coping with climatic changes (Bassar et al. 2016) or recovering from extreme climatic events (Vincenzi et al. 2016). Indeed, recent studies (Bassar et al. 2016; Ayllón et al. 2019) indicate that, thanks to density-dependent feedbacks, young-of-the-year, and juvenile individuals do not necessarily get smaller under continuous warming, contrarily to theoretical expectations (Daufresne et al. 2009). Higher growth at low density, coupled with strong selection for smaller size at maturity, leads to earlier maturation, which helps reduce negative impacts on recruitment caused by the loss of large, old breeders under climate change (Ayllón et al. 2019).

Finally, stream salmonids actively respond to environmental change through behavioral plasticity. For example, fish can behaviorally adapt to more energetically challenging conditions by selecting more profitable foraging habitats, although at the cost of higher predation risk (Ayllón et al. 2019). Fish can change not only where but when they feed to adapt to new environmental conditions: for example, to balance higher metabolic costs more diurnal and crepuscular (compared to nocturnal) feeding are expected at elevated temperatures, low flows, or when food is limited (Railsback et al. 2020, 2021b). In addition, due to the asynchrony of temperature and prey abundance across the river network, stream salmonids can optimize their growth potential by seasonal movement among habitats to track favorable growth conditions, i.e., by residing during the non-summer periods in seasonally warm downstream habitats, which can enhance annual fish production (Armstrong et al. 2021). Thus trout have a suite of behavioral, evolutionary, density-dependent, and plastic strategies that allow some degree of population stability under climate change (Amat-Trigo et al. 2023); however, there are limits to this resilience, as evidenced by ongoing range contractions, particularly when climate change synergizes with other forms of human impact.

1.4 Quantitative Models and Limits to Salmonid Production

Fish production in lakes around the world can be predicted empirically using variables related to system fertility (Downing et al. 1990; Downing and Plante 1993), including phytoplankton production, chlorophyll a concentration, phosphorus, and water temperature. Although simplified trophic models for streams and rivers have also been developed based on biogeochemical drivers (i.e., nutrients; see PCDitch and Delft3D-ECO; Janse 1998; Mooij et al. 2010), they are largely based on lake models (e.g., PCLake; Janssen et al. 2019), and are applied primarily to ditches or large rivers and estuarine habitats (Delft3D) rather than salmonid streams; they focus on biogeochemical drivers and primary producers in slow or stratified water bodies, rather than habitat or food web issues that are more relevant to quickly flowing streams (Ayllón et al. 2018). Models have also been developed to capture longitudinal changes in salmonid productive capacity associated with idealized downstream trends in velocity, depth, and gradient along the River Continuum (Laliberte et al. 2014, 2016). However, simple, generalizable trophic-based habitat capacity models have yet to be developed for trout streams, perhaps due to a lack of interdisciplinarity (i.e., a failure to integrate physical, biochemical, and trophic processes; but see the Aquatic Trophic Production Model (Bellmore et al. 2017; Whitney et al. 2020) for a simulation-based trophic modelling approach that includes channel features). Perhaps the most successful early model for trout streams, Binns and Eisermann (1979), explained 96% of the variation in trout biomass in Wyoming trout streams. However, this model performed poorly at predicting trout biomass in southern Ontario streams (Bowlby and Roff 1986), and is likely not broadly transferable to other locations.

Why have general models for stream salmonid productive capacity not been developed? Fausch et al. (1988) suggested that early attempts focussed on correlational approaches that neglected the mechanistic relationship between habitat variables and fish abundance. Furthermore, these models were developed for particular geographical regions, based on small sample sizes, and were not broadly transferable (Fausch et al. 1988). Unlike models for lakes, stream biologists also tend to focus on physical habitat variables rather than bottom-up trophic approaches (Wurtsbaugh et al. 2015), even though fish production in streams is positively correlated with indicators of underlying fertility (e.g., N, P, conductivity; Binns and Eisermann 1979; Bowlby and Roff 1986; Ptolemy 1993; Randall et al. 1995). Thus, the broader failure of stream ecologists to develop more generalizable models of productive capacity may reflect: i) neglect of the role of basal system productivity, as indexed by water chemistry or prey abundance; ii) a narrow regional focus in the development of habitat capacity models, with a small range in underlying water chemistry relative to the continental scale of lake productivity datasets; and iii) a focus on physical habitat features, which may limit transferability depending on underlying regional geomorphology and site-specific channel structure.

The comprehensive approach to production advocated in this chapter will perhaps encourage others to develop more general models to predict salmonid production worldwide. One promising avenue might be to treat bottom-up and physical habitat effects as sequential limiting filters: nutrient levels (e.g., N, P, or correlates like alkalinity or conductivity) determine maximum production potential, while physical habitat (e.g., percent pool, and reach gradient) determines the degree to which productive potential based on water chemistry is fully realized (Cade and Noon 2003). These could be strictly empirical correlative models like the simple lake productivity regressions (e.g., Ptolemy 1993; Kwak and Waters 1997), or they could incorporate explicitly mechanistic approaches (e.g., Bellmore et al. 2017). Explicitly mechanistic approaches may model the effects of territoriality on growth and self-thinning (Grant and Kramer 1990; Ayllón et al. 2012a), or the effects of invertebrate drift on carrying capacity or individual net rate of energy intake (NREI) using drift-foraging theory (Hayes et al. 2007b; Weber et al. 2014; Laliberte et al. 2016). Drift-foraging bioenergetic models (e.g., Hayes et al. 2007b; Hayes et al. 2016; Naman et al. 2020c) estimate NREI (energy consumption less metabolic expenditures) by explicitly linking energy intake and metabolic costs to instream hydraulics (i.e., focal velocity and depth), temperature, and prey abundance (invertebrate drift; Hughes and Dill 1990; Naman et al. 2020b, 2020c). These models have been used to assess the bioenergetic consequences of habitat restoration (Hafs et al. 2014; McHugh et al. 2017), longitudinal trend in salmonid habitat capacity along the downstream River Continuum (Laliberte et al. 2016), and climate change impacts (Ayllón et al. 2019). While drift-foraging models capture the influence of physical habitat using generalizable foraging mechanisms, the key parameter that sets maximum productive capacity is invertebrate drift biomass ($mg{\cdot}m^3$); however, factors governing spatial variation of invertebrate drift remain poorly understood (Rosenfeld et al. 2014). Individual-based models like inSTREAM (and its eco-genetic version, inSTREAM-Gen; Railsback et al. 2021a) go a step further to predict emergent population responses by incorporating drift-foraging bioenergetics in simulations of individual fish behavior, growth, survival, and reproduction, and in principle can be used to predict the effects of changes in physical habitat structure, flow, temperature, or prey abundance on salmonid abundance, persistence, or even the evolutionary trajectory of populations (Ayllón et al. 2016; Railsback et al. 2021a). Basal system productivity in InSTREAM is represented by two key input parameters: invertebrate drift biomass, and the rate of benthic invertebrate production, which affects the rate of drift biomass generation.

The shared information gap for these and other mechanistic models remains an empirical relationship between the basal production input parameter (e.g., drift entry rate, invertebrate drift abundance, or benthic invertebrate production) and a landscape-scale proxy of stream fertility (e.g., water chemistry). For example, using a drift-foraging bioenergetic model to predict landscape-scale variation in habitat quality (in terms of NREI or fish biomass) requires some relationship between invertebrate drift ($mg \cdot m^3$) and regional drivers like N, P, alkalinity, landuse, or underlying geology (LaPerriere 1983). Consequently, developing these relationships is a research and management priority. Coupling a trout drift-foraging bioenergetic model with an aquatic ecosystem model that mechanistically or empirically links biogeochemical processes with primary and secondary production might be another path forward.

A more empirical approach to salmonid production is useful in the absence of general trophic or habitat models. While an upper limit to salmonid production has been hypothesized for some time, the suggested limit has been increasing over time: 12 $g \cdot m^{-2} \cdot y^{-1}$ (Le Cren 1969); 30 $g \cdot m^{-2} \cdot y^{-1}$ (Mann and Penczak 1986; Elliott 1993; Kwak and Waters 1997); and 40 $g \cdot m^{-2} \cdot y^{-1}$ (Lobón-Cerviá 2009a). At least three streams exceed this highest limit: 40.2 for a Cantabrian stream (Lobón-Cerviá et al. 2011), 46.1 for River Ucero, Spain (Lobón-Cerviá 2003), and 54.7 for the Horokiwi Stream, New Zealand (Allen 1951). In addition, salmonid biomass was 37.3, 55.5, and 63.4 $g \cdot m^{-2}$ in South Brook and the Virginia River, Newfoundland (Gibson and Colbo 2000), and Sand Creek, Wyoming, respectively (Binns and Eisermann 1979). Assuming a P/B ratio of 1.3 (Mann and Penczak 1986), salmonid production in these three streams is conservatively estimated at 48.5, 72.2, and 82 $g \cdot m^{-2} \cdot y^{-1}$, respectively. Except for Lobón-Cerviá (2009a), however, all these estimates come from short-term studies that ignore temporal variation in biomass or production. Longer-term studies (e.g., Elliott 1993; Lobón-Cerviá et al. 2011) indicate dramatic temporal variation in production within a single site that can rival the spatial variation in production observed globally among streams; much of this temporal variation is driven by variation in recruitment (Lobón-Cerviá 2009a; Lobón-Cerviá et al. 2011). A review of these longer-term studies suggests that the best salmonid streams in the world produce an average of 30–40 $g \cdot m^{-2} \cdot y^{-1}$ (Elliott 1993; Lobón-Cerviá et al. 2011).

Social behavior, in the form of territoriality, has been hypothesized to be the primary mechanism limiting salmonid density and biomass (Chapman 1966; Allen 1969; Le Cren 1969). Assuming that territory size is inflexible, allometric territory size data can be used to predict the maximum density of fish (Grant and Kramer 1990). Using this approach, a maximum biomass of 30 g/m^2 is predicted, which translates to a production of 39 $g \cdot m^{-2} \cdot y^{-1}$, assuming a P/B ratio of 1.3 (Mann and

Penczak 1986). This value is eerily similar to the maximum annual production of 40 g·m^{-2}, as noted above. This apparent coincidence does not necessarily mean that territoriality actually limits density. Rather, territory size may simply predict the minimum space required for a salmonid fish of a given size in its ideal habitat. Nevertheless, the predictive power of territory size is potentially useful (see Cramer and Ackerman 2009; Ayllón et al. 2012b).

Stage-structured population models that incorporate habitat effects on growth and survival are a widely used framework for modelling population dynamics of stream salmonids (e.g., Nickelson and Lawson 1998; Scheuerell et al. 2006). They also rely on empirical relationships that relate habitat conditions (e.g., water temperature, flows, and habitat quality) to productive capacity, rather than the mechanistic modelling that drives bioenergetic drift-foraging or individual-based models. Their focus is on population dynamics in response to environmental change and harvest management rather than modelling production per se (Battin et al. 2007; Jorgensen et al. 2021), and their strength lies in the ability to project the outcome of different management scenarios on population dynamics (and by implication production), rather than prediction of productive capacity in different streams.

An intriguing approach would use self-thinning theory to predict salmonid production. Self-thinning is caused by density-dependent population responses to limited habitat or energy, perhaps mediated by territoriality. Self-thinning theory posits that if the energy available to a cohort is fixed through time, then as individuals age and grow their greater individual energy requirements will cause density to decline through mortality or emigration (Fig. 2). The slope of the self-thinning curve can be predicted by the allometry of energetic requirements (e.g., Elliott 1993; Bohlin et al. 1994), territory size (Steingrimsson and Grant 1999), or habitat requirements (Rincón and Lobón-Cerviá 2002). The intercept of the self-thinning curve is generally understood to reflect the number of recruits (i.e., fry), and it is well demonstrated that the intercept is related to aspects of habitat structure and flow that affect egg survival and recruitment success (Lobón-Cerviá 2008, 2009b). However, the elevation of the intercept—and the entire self-thinning line—should be sensitive to underlying system productivity; i.e., if higher water nutrients support greater prey biomass, the number of spawners that produce recruits should increase, as well as the capacity of the habitat to support recruits. The key challenge is to relate parameter values (i.e., slope and intercept of the self-thinning curve) to metrics of habitat and water chemistry that influence productive capacity, as has been done with habitat and flow (Lobón-Cerviá 2009b). Whether such an integrative approach can produce generalizable models to predict salmonid production across the globe remains to be seen, but some promising regional models already exist (e.g., Cramer and Ackerman 2009; Rincón and Lobón-Cerviá 2002).

1.5 Human Impacts on Productive Capacity: Habitat Degradation and Restoration

Human activities pervasively degrade the productive capacity of trout streams, leading to global imperilment of many populations (Dauwalter et al. 2020; Tickner et al. 2020), and significant investment to restore streams and their watersheds (Bernhardt and Palmer 2005; Acreman and Ferguson 2010). Human impacts on streams and corresponding restoration priorities can be understood in terms of direct and indirect habitat effects; for instance, activities such as dredging and channelization directly degrade stream habitat. However, streams integrate all upstream land-use impacts in a watershed, ranging from removal of riparian forest to diffuse land-use impacts on water quality, such as urbanization, agriculture, and logging. These indirect, cumulative effects are difficult to detect and manage, and traditional restoration approaches have typically focused on instream habitat. While reach-scale instream habitat restoration can improve local habitat capacity, these effects may be transient if the larger-scale riparian and land-use issues that are causing reach-scale degradation are not addressed (Beechie et al. 2010; Roni et al. 2015; Young et al. 2017). Streams and their watersheds are integrated systems (Voulvoulis et al. 2017) and effective protection and restoration require a functional approach that focuses on recovering the upslope processes that create and maintain stream habitat (Roni et al. 2002; Kondolf et al. 2006; Beechie et al. 2010). We briefly consider these issues below.

Instream Habitat Like many taxa that span orders of magnitude in body mass through ontogeny, trout production is optimized in habitat with a moderate to high degree of habitat heterogeneity (Poff and Huryn 1998; Naman et al. 2018). Salmonids have distinct life history stages with diverse habitat requirements (e.g., adults need faster-velocity riffle or run habitat for spawning; post-emergent fry need shallower marginal areas for rearing; adults need deeper pool habitat; and all life stages need low-velocity hydraulic refuges during floods; (Tschaplinski and Hartman 1983; Moore and Gregory 1988b; Schlosser 1995). Habitat diversity ensures that any single habitat type is less likely to be a limiting population bottleneck in most streams. Diversity in depth and water velocity is usually associated with alternating pool and riffle channel units, the frequency and diversity of which increases with the abundance of large wood, boulders, or other obstructions (Fig. 4a; Lisle 1986; Montgomery et al. 1995). The tendency of streams to meander introduces an additional lateral dimension to diversity, which manifests as important side-channel and floodplain habitat (Morley et al. 2005; Kondolf et al. 2013).

Most human impacts tend to homogenize streams and reduce habitat structural diversity (Gorman and Karr 1978; Schlosser 1991; Death et al. 2015; Bouwes et al. 2016; Wohl et al. 2018). Dredging to improve agricultural drainage has a pervasive impact on developed landscapes (Wohl 2019). Habitat structural complexity (e.g., large wood and meander bends) provides resistance to flow, increasing water depth and water volume in the stream channel. While this moderates downstream flooding by retaining water in the channel and floodplain, it also delays drainage of upstream areas. Channel dredging and straightening that removes structure decreases resistance to flow, resulting in higher velocities and discharge, and a much less hospitable habitat for fish (Death et al. 2015). Elevated sediment inputs from unstable banks fill in pools and reduce variation in depth and velocity, which further reduces bedform roughness and resistance to flow. Infilling of coarse substrate also reduces bed surface roughness, reducing bed friction and increasing velocities close to the stream bed. In general, hydraulic roughness and complexity tend to match habitat diversity, and simplified channels lack the diversity in hydraulic habitat necessary to support diverse life history activities, such as drift-feeding, spawning, and refuging during floods (Bouwes et al. 2016; Humphries et al. 2020). Channel straightening also often results in the loss or disconnection of floodplain habitats that may be critical rearing and overwintering habitat (Wohl 2019; Wohl et al. 2021).

Instream restoration typically focuses on restoring the structural elements that contribute to habitat heterogeneity (e.g., Bouwes et al. 2016). This may include the placement of boulders in streams or additions of large wood to compensate for the loss of riparian tree inputs (Slaney and Zaldokas 1997; Whiteway et al. 2010; Roni et al. 2015; Pess et al. 2023). The addition of large wood may be particularly useful in restoring habitat and structure (e.g., Fig. 4a), but its long-term effectiveness is contingent on the restoration of upstream processes that take place at larger spatial scales (Roni et al. 2015). For instance, very high sediment input rates will destabilize and infill stream channels, reducing the effectiveness of reach-scale large wood additions in forming pools (Rosenfeld et al. 2011); and a restored channel will revert to a simplified one once added large wood decays, unless the natural upstream processes that supply large wood are restored (Murphy and Koski 1989).

Diking and channelization of streams is a pervasive impact driven by floodplain development (e.g., housing and agriculture on valley bottoms, or construction of linear corridors like logging roads next to streams). These activities isolate the stream from its floodplain (Florsheim et al. 2008; Kondolf et al. 2013), and cut off lateral habitats that are essential for overwintering or rearing trout (Cunjak 1996); once a river can no longer meander across its floodplain, natural formation of side channel as a dynamic process ceases (Ciotti et al. 2021). In situations where intense human development precludes recovery of processes that create side-channels (for example, by moving dikes back from the river to allow channel migration), construction of stable engineered floodplain and side-channel habitats may be necessary to re-establish habitat diversity (Beechie et al. 2010).

Riparian Habitat The riparian forest that naturally grows adjacent to streams provides bank stability, an important source of large wood that generates channel structure (Fig. 4b, c), shading that moderates temperature and provides cover, and a direct source or terrestrial insect prey and organic detritus to the stream channel (Allan et al. 2003; Micheli et al. 2004; Collins et al. 2012). Riparian zones also act as a buffer to filter out fine sediment and nutrients from upslope processes (Richardson et al. 2010). Human activities often result in the removal of riparian vegetation, either through direct harvesting as timber, to allow machine access for dredging, to reduce shading that impairs crop growth, as an indirect effect of livestock grazing, or when streams are buried as sewers to allow urban development. The critical role of riparian forest in maintaining stream ecosystem function is well recognized (e.g., Richardson et al. 2010), and is reflected in legislation that protects riparian buffers of varying widths in many jurisdictions (Young 2000). However, riparian habitat remains unprotected on private and public land in many developed countries, and riparian reforestation remains one of the most effective and high-priority ways of protecting trout streams and re-establishing the natural habitat-generating processes that will stabilize habitat capacity and enhance the likelihood of persistence (Chase et al. 2016; McHugh et al. 2017). In particular, riparian reforestation is a key management intervention that can restore or maintain thermal habitat in degraded streams (Broadmeadow et al. 2011; Beechie et al. 2013; McHugh et al. 2017). For example, modelling has demonstrated that restoring shade in some watersheds could result in future water temperatures that are colder than those today, even under a warming climate (Wondzell et al. 2019).

Removal of riparian forest has legacy effects on stream habitats that operate with significant time lags. Murphy and Koski (1989) showed that the effect of clear-cut logging on instream wood volumes takes decades to manifest as wood slowly decays, with modelled instream wood volumes reaching a minimum of 20% of old-growth levels 125 years post-harvest, and taking another 125 years to recover to 80% of pre-harvest wood volume as the riparian forest regrows (Fig. 4c). Repeated removal of riparian forest results in permanent depletion of instream wood and simplification of channel structure (Fig. 4b; Collins et al. 2012). Although this effect is most pronounced in landscapes like Europe that have been inhabited for millennia, it is still evident in regions subject to much more recent deforestation (e.g., North America; Herdrich et al. 2018). Until the critical role of large wood in streams was identified (e.g., Sedell and Froggatt 1984), wood in streams was broadly viewed as harmful or an aberration even by many ecologists, providing an illustration of the shifting baseline effect (Soga and Gaston 2018) whereby the dominant scientific perception and societal aesthetic associated with a healthy stream is an artifact of historic land-use practices rather than a true reference condition (Piégay et al. 2005; Walter and Merritts 2008; Wohl 2019).

Human Appropriation of Flow Increasing water demand for drinking, irrigation, power generation, and industry generates conflict with instream flow needs for trout production (Postel et al. 1996), and this is most severe during periods of seasonal drought (i.e., summer) when out-of-channel water use is highest. Determining the minimum flows required to protect trout production is an important dimension of applied fisheries science (Jowett et al. 2008). Traditionally, guidelines for minimum flows are established based on loss of habitat at benchmark flows expressed as a proportion of annual mean flows (e.g., flows less than 10% of mean annual discharge are likely to be severely limiting to trout production; Tennant 1976). These rules of thumb are easily applied with limited resources, but streams differ substantially in their response to altered flows depending on channel morphology, natural hydrology, and the habitat requirements of the fish community (Arthington et al.

2006). More sophisticated habitat modelling approaches like the Physical Habitat Simulation Model (PHABSIM), River 2D, and their variants (Gopal 2013; Williams et al. 2019) capture stream-specific idiosyncrasies in how physical habitat changes with flow, but their application is demanding in terms of time and resources, and they are generally only applied to streams and rivers with high fishery values or regulated rivers with a revenue stream (e.g., hydroelectricity) to pay for the costs of modelling and impact assessment (Gouraud et al. 2001; Jowett and Biggs 2006; Campbell et al. 2021). Habitat simulation models have also been heavily criticized based on theoretical shortcomings (e.g., Mathur et al. 1985; Castleberry et al. 1996), and because they only account for the effects of flow on habitat and ignore the effects on prey availability and basal production (Railsback 2016; Railsback et al. 2021a; Rosenfeld and Naman 2021). More recently, bioenergetic modelling approaches are being applied that better integrate the joint effects of flows on physical habitat and the flux of drifting invertebrate prey (Ayllón et al. 2016; Naman et al. 2020b; Railsback et al. 2021a) Although they require further validation, drift-foraging bioenergetic approaches have the potential to integrate the multiplicative effects of changing flows, prey abundance, and temperature under climate change scenarios (Laliberte et al. 2016; McHugh et al. 2017; Ayllón et al. 2019).

Minimum flow regulations vary regionally and may be discretionary guidelines rather than regulations, or entirely absent in many jurisdictions. Although flow regulations usually focus on protecting minimum low flows as a critical rearing period in trout streams, it is also important to recognize that flow needs vary among life stages, and it may be important to identify minimum flow thresholds associated with spawning, bed mobilization to maintain substrate, fish passage, and other ecological functions (Jowett and Biggs 2006; Horne et al. 2017). The natural flow regime paradigm (Poff et al. 1997) suggests that maintaining the general attributes of the natural flow hydrograph is the best default precautionary approach to maintaining natural processes in streams, including trout production. This is generally true, however it is important to recognize that not all natural flow regimes are optimal for the production of a given fish species, and altered ("designer") flow regimes may in some cases enhance trout production (Jowett and Biggs 2006; Acreman et al. 2014; Hvidsten et al. 2015). To the extent possible, regional agencies responsible for the management of trout production need to establish how trout production changes with local flow regimes, ideally by empirical measurement of changes in trout biomass or production with flow alteration, and use this knowledge to better guide local instream flow management to protect trout (for example, see Jowett and Biggs (2006) and Kendy et al. (2012)).

Watershed-Scale Effects Human activities in a watershed impact key physical, hydrologic, and ecological processes underlying trout production (Sinnatamby et al. 2020b). Changing landcover alters surface permeability, which in turn controls the rate of groundwater recharge vs. surface runoff, as well as the nutrients or contaminants that are absorbed as rainfall makes its way to the stream. Land use will therefore affect both water quality (temperature, nutrients, suspended solids) as well as hydrology, in particular how flashy the stream is (i.e., how quickly flows peak following rainfall) and how low discharge becomes during drought (Allan 2004; Poff et al. 2006). Temperature and flow management are therefore intimately linked to watershed-scale land-use processes that affect runoff and infiltration. Not all areas of a watershed contribute equally to maintaining baseflow (Dralle et al. 2023), and protecting wetlands and recharge areas that deliver groundwater to streams during drought is a critical element of trout stream management (EPA 2015; Kurylyk et al. 2015; Bouwes et al. 2016). Similarly, because thermal inertia increases with discharge, restoring or enhancing stream flow is an important temperature management strategy.

Urbanization is probably the most dramatic form of land use alteration because of the high proportion of impermeable surfaces (e.g., road surfaces and rooftops); this results in the urban stream syndrome, whereby surface runoff increases dramatically, leading to flashy streams with high peak flows and low baseflows because of reduced groundwater recharge (Wang et al. 2001; Walsh and Webb 2016). This effect is compounded by toxic chemicals that build up on roadways during dry periods and are released into streams following rainfall, such as recently discovered quinone derivatives from wear of rubber automobile tires that can cause direct mortality to salmonids (Tian et al. 2021). Urbanization is also a major source of nutrient inputs to streams, primarily through sewage outfalls, and has been identified as the primary factor initiating early lake eutrophication in Europe (Jenny et al. 2016). Although urbanization may seem irrelevant given the association of many trout streams with mountainous headwaters, this partially reflects a shifting baseline; contemporary loss of trout from urban streams is common in recently developed cities (e.g., Vancouver, Canada; Proctor and Harris 1989), but may have occurred so long ago in areas of eastern North American and Europe that the original reference state is lost to memory. Urban stream restoration is possible but is contingent on adequate baseflows and water quality improvements in the upstream watershed.

Forestry impacts on streams generally involve elevated rates of sediment delivery from logging roads or landslides, reduced large wood inputs from poor riparian protection, and altered hydrology if too much of a watershed is logged (Hartman and Scrivener 1990; Hartman et al. 1996; Thomas and Megahan 1998). Regulations that protect riparian buffers, constrain the design and construction of logging roads, and limit the area of a watershed that can be logged can mitigate many of these effects (Pike et al. 2010). Recovery of watersheds damaged by past logging practices is also possible because most forestry lacks the permanent infrastructure impacts associated with urbanization. Agriculture impacts streams through sediment input from exposed soil, nutrient inputs from fertilization, and direct water withdrawals for crop irrigation (Montgomery 2007; Miller et al. 2011; Saalfeld et al. 2018; Sinnatamby et al. 2020b). Low flows and eutrophication are common consequences of intensive agriculture, all of which may negatively impact salmonids (Ayllón et al. 2012b). Mitigating agricultural impacts requires watershed-scale changes in the management practices that deliver sediment and nutrients to streams, which may come at considerable cost (Johansson and Kaplan 2004; Gordon et al. 2010). The appropriate suite of management practices to reduce nutrient inputs and restore water quality are relatively well understood (Sharpley et al. 2006, 2013). The main barriers to sustainable land management to protect trout streams are (1) the wicked nature of cumulative effects, which require complex negotiations among many stakeholders to arrive at a solution (Freeman 2000) and (2) the reluctance of government, landowners, and society to forego the future economic benefits of development and bear the socio-economic costs of sustainable watershed management.

Protection of trout productive capacity requires that society value trout more than the economic benefits associated with degrading their habitat. Most loss of trout productive capacity is associated with the cumulative effects of incremental development, where an accumulation of diffuse impacts leads to a trajectory of habitat loss. While higher-level policy directives recognize the importance of conserving aquatic habitats (e.g., the EU Water Framework Directive), there are persistent gaps in actual implementation of conservation measures (Voulvoulis et al. 2017; Ruhl et al. 2021). In particular, our existing regulatory structures are not well-suited to dealing with diffuse impacts at a watershed scale; most resource management agencies evaluate and approve single development applications over a limited time horizon, and ignore cumulative effects. This is problematic because the protection of trout habitat requires explicit management of development at a watershed scale by projecting the long-term outcomes of different management scenarios into the future within the context of a changing climate (Martinuzzi et al. 2014; Ayllón et al. 2019). The science, spatial tools, and analytic approaches to do this are now well established; however, resource management planning lags far behind other applied sectors in use of predictive technology (e.g., climate prediction: Bauer et al. 2015; navigation: Amirian et al. 2016) and requires a paradigm shift. Resource management agencies need to accelerate the adoption of widely available spatial modelling approaches that are currently used for other routine tasks (e.g., integration of spatial data by Google Maps to instantaneously compute optimal travel routes). Ultimately, the long-term protection of trout habitat will require careful land-use modelling over appropriate time horizons, and deliberate, transparent, and considered trade-offs with other societal values to ensure that the future of trout production is not the random outcome of cumulative effects from serial development approvals (the current modus operandi for most government agencies).

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Determinants and Dynamics of Production Rates of Stream-Dwelling Salmonids: The Importance of Intrinsic Factors

Javier Lobon-Cervia and Gorm Rasmussen

Abstract Based on published and unpublished long-term data sets covering a wide range in size, growth, density, and production rates reported for resident, sea-migratory, and lake-migratory stream-dwelling salmonid populations, we examined, revisited, and summarized cohort and annual production rates and turnover ratios at a global scale, including most of the production rates variability reported worldwide, within the range 0.01–45 g m^{-2} year. Major highlights include strong recruitment-dependent cohort production rates and density-dependent annual production rates. Moreover, when combining a heterogeneous suit of slow-growing, high-density and fast-growing, low-density populations, we observed striking trade-offs along a continuum of recruitment, growth, and production rates: lowest recruitment is strongly related to highest growth and lowest production rates, whereas, at the opposite extreme, highest recruitment is related to lowest growth and highest production until an asymptotic value upon which production rates remain constant. In addition, asymptotic recruitment-dependent cohort and density-dependent annual turnover rates suggest a maximum cohort production-to-biomass ratio = 6 and annual production-to-biomass ratio = 2. Previous assessments of discharge-dependent recruitment relationships in combination with the patterns elucidated here revealed dramatic year-to-year variations in recruitment and cohort production rates, implying that annual production rates only maximize over several successive favorable years for recruitment, a most unlikely event. These processes suggest that annual production rates appear to have a maximum limit at approximately 40–45 g m^{-2} year across stream-dwelling salmonid populations. All patterns high-

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lighted here are summarized in simple linear and nonlinear models that may be steadily applied to a variety of predictive purposes.

Keywords Cohort production rates (PC) · Annual production rates (PA) · Turnover rates · Cohort Pc/Bc ratios · Annual Pa/Ba ratios · Stream salmonids · Long-term studies

1 Introduction

The production rate is a measure of the speed upon which the biomass of a population is growing over time in a given space, irrespective of whether individuals migrate or die during the time interval selected (Ivlev 1966). This rate is considered one of the best measures of population success because it is a composite of population structure, density, biomass, growth, reproduction, survival, and development time (Benke 1983), and as such, it is linked to the habitat quality and is a major component of the energy budgets and trophic webs and commonly included into fishery models, either those directed at optimizing production for human consumption or to provide sound fisheries management.

The assessment of production rates of stream-dwelling fishes was a major research focus from the beginning of the 1950s to the end of the 1990s, enhanced primarily by the International Biological Programme (i.e., Gerking 1967). Following the appealing interest to disentangle the complex dynamics of production rates and its application to fishery management, Hunt (1974), in his pioneer 11-year study on the production rates of brook trout *Salvelinus fontinalis* in a Wisconsin stream, recalled that "*Efforts by fishery biologists to assemble useful models of the dynamics of fish populations are analogous to the task of assembling an unusual puzzle—a puzzle having an unknown number of pieces, the shapes of which keep changing.*" Apparently, five decades later, the puzzle is still incomplete.

Since the seminal studies by Ricker and Foerster (1948) and Allen (1951), a diversity of studies on stream-living fishes were reviewed by Mann and Penczak (1986). These authors, among other fish species, reported 83 estimates of annual production rates of eight salmonid species within a broad range of 0.01–30.0 g m^{-2} year with the only exception of 54.7 g m^{-2} year for the New Zealand Horokiwi stream (Allen 1951). The latter, however, was considered an overestimation by Chapman (1967) and Le Cren (1969) and reduced these rates to 38 and 45 g m^{-2} year, respectively. Peculiarly, all studies available focused on annual production rates with no estimate of cohort production rates reported, a limitation given the essential role of the cohort dynamics for understanding the annual production rates (Figs. 1 and 2).

Mann and Penczak (1986) emphasized that the need for successive estimates of growth and density and the environmental heterogeneity of the streams represent major limitations for the accurate estimation of these rates. Moreover, in standard studies where the populations are quantified in selected stream sites with

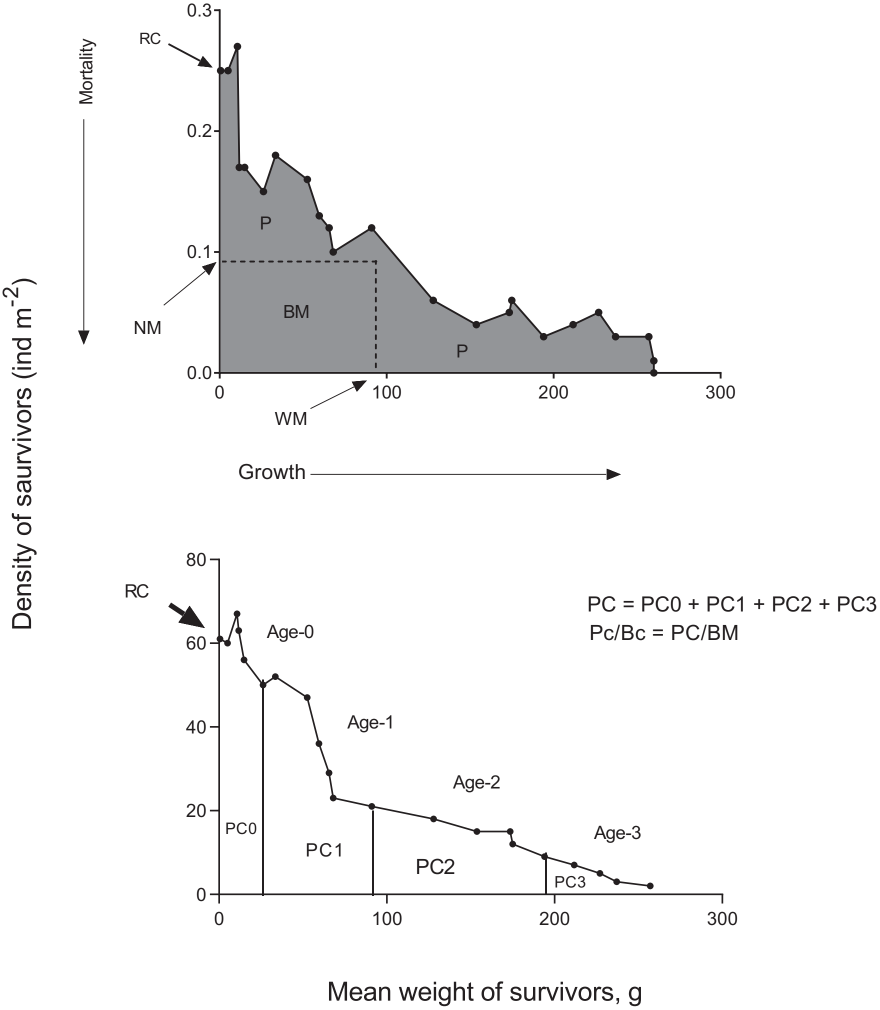


Fig. 1 An Allen graph of a hypothetical cohort (or year-class or generation) from the time of recruitment (RC, ind m^{-2}) to its total disappearance by natural mortality with indication of the total cohort production rate. *Top panel*: PC, g m^{-2}, dark area below the curve of cohort decay, cohort mean number (NC, ind m^{-2}), and mean weight (WC, g), age-classes, age-0 to age-3 composition. *Bottom panel*: The corresponding age-class-specific production rates (PC0 to PC3) and the turnover rate or the Pc/Bc ratio

electrofishing techniques, the young-of-the-year (YOY) may be systematically underrepresented even if they may be a significant part of these rates. They finally appealed for the need for long-term studies, even if these are costly, labor-intensive, and time-consuming.

Note that since production rates are the ultimate expression of a complex interaction among several population attributes, any factor, biotic or abiotic, operating on

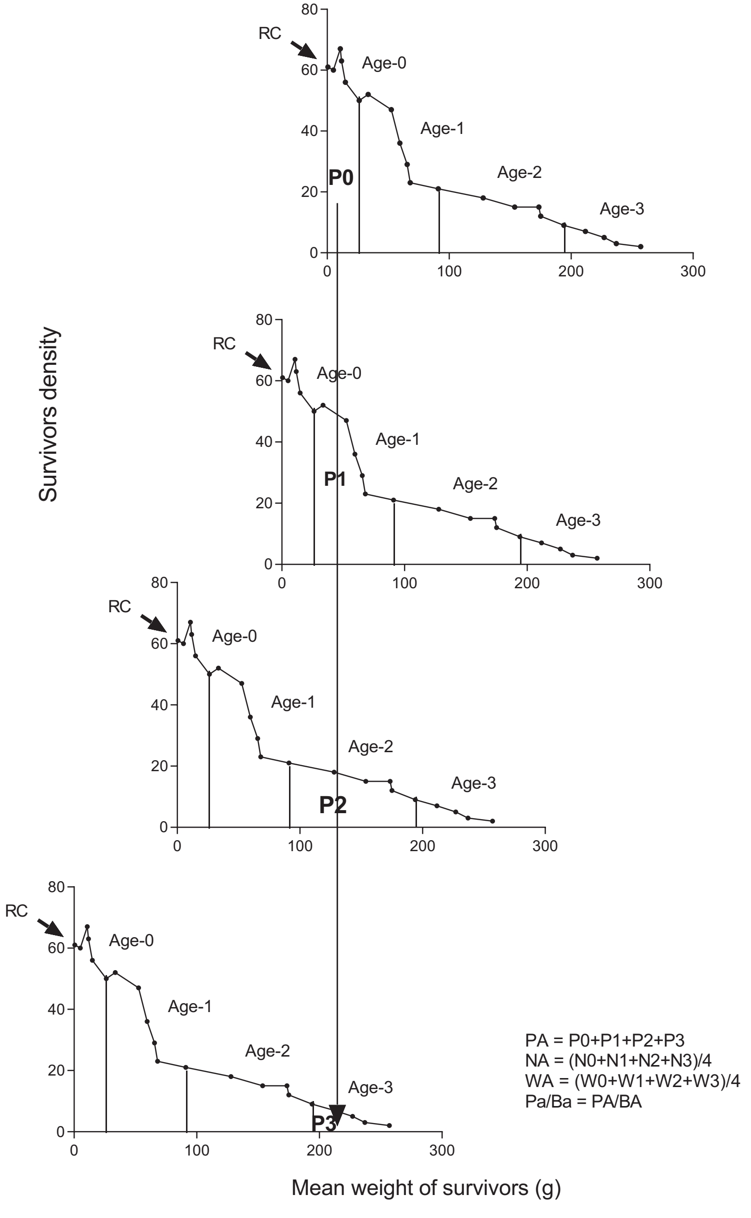


Fig. 2 Composite annual production rates in a four age-classes population with the same cohort dynamics over 4 years. Annual production (PA, g m^{-2} year) is indicated with an arrow as the addition of the four age-classes growing simultaneously in a given year. The corresponding mean annual density (NA, ind m^{-2}), mean weight (WA, g) and turnover Pa/Ba ratios are indicated

either attribute might also affect these rates. As a consequence, a potentially widely varying array of factors and their interactions may underpin these rates. Some of these factors are extrinsic to the fish population, for example, prey production, temperature regimes, or the water chemistry that drive basal system production (see Rosenfeld et al. 2024, chapter 21), while other factors are intrinsic, such as the operation of density dependence over the lifetime and ultimately recruitment to the adult population.

Recently, a wealth of long-term studies on stream-living salmonids have become available and currently permit meta-analytical approaches at broad spatial and temporal scales in order to highlight patterns of cohort production rates, the identification of major production attributes, and their subsequent role as determinants of annual production rates and to uncover the underlying mechanisms.

In this study, encompassing published and unpublished data sets, we reviewed, updated, revisited, and synthesized the cohort and annual production rates of stream-living salmonids, with an emphasis on brown trout *Salmo trutta,* and attempted to identify intrinsic factors underlying these rates. More specifically we focus on the cohort production rates PC (g m^{-2}) and the annual production rates PA (g m^{-2} year) and extend this analysis to the weight-specific rates or the ratio of production (P) to biomass (B), namely the cohort Pc/Bc ratio or the total production rate of a cohort over the entire lifetime divided by its corresponding mean biomass. We also focus on the annual Pa/Ba ratio or the annual production rate divided by the mean annual biomass (Figs. 1 and 2). Note that the easiest approach to estimate production rates is as the product of the instantaneous growth rate, G, multiplied by the mean biomass, B, as P = B * G; therefore, the turnover rates (P/B = G) are a measure of population growth.

2 Production Rates and Methods

In age-structured populations with annual reproduction, subsequent cohorts (often referred to as year-classes in fishery sciences and more generally as generations) are subject to natural mortality and undetermined growth such as in many fishes (Fig. 1—known as the "Allen graph," Allen 1951). The Allen graph depicts the decay of a cohort of individuals from the time of recruitment (the initial number of individuals that commence the cohort, Cushing 1996) to its total disappearance by natural mortality as they grow in weight over four complete years, that is, in a cohort composed of four age-classes. Production rate is a direct function of density N and biomass B, and the total production rate of that cohort, PC (g m^{-2}), is the area below the curve describing this decay. In numerical terms, this area or the cohort production rate is the integral between the initial and final number of survivors during the lifetime as a function of weight or:

$$PC = \int N dW$$

In turn, the annual production rate, PA (g m^{-2} year), is the addition of the production rates of all cohorts growing simultaneously in a particular year, as shown in

Fig. 2, for a hypothetical population also composed of four similar age-classes, where PA = P0 + P1 + P2 + P3.

Graphical, analytical, and more simplified mathematical methods to estimate production rates and their components have been summarized by Gerking (1978) and Mertz and Myers (1998). Unlike the tedious graphical calculation methods, the simplified analytical ones also have the advantage that they permit the estimation of the variances of the production rates and their corresponding confidence intervals (Newman and Martin 1983).

In this study, all our estimates first focused on the production rates of single cohorts (Fig. 1). As an early step, we defined recruitment of every cohort as the first quantification of the cohort numbers by April or May, depending on the population (Cushing 1996), and used this early estimate or recruitment as an independent variable over successive analysis. These cohort rates were calculated for each time interval between two successive quantifications of numbers and weights from the second sample until the total disappearance of the cohort. For every single time interval between samples, we calculated the initial biomass (b1, g m^{-2}) as the mean weight (g) * density (ind m^{-2}) and the mean biomass as (b1 + b2) / 2, where b1 and b2 are the initial and final biomass of that time interval and calculated the daily instantaneous growth rates (G), as: log (w2 / w1) / t, where w1 and w2 are the mean weights at the beginning and at the end of that time interval and t, the number of days. The production rates were then estimated as mean biomass *growth rate *number of days and the total cohort production rate PC as the addition of those rates over the lifetime. Annual production rates were then estimated as the corresponding addition of the production rates of every single age-class growing simultaneously in a given year (see Fig. 2).

Throughout our analyses, the mathematical models used and fitted to specific data sets were the following:

Linear: $Y = a + b X$	Model 1
Or its log–log version: $\text{Log}(Y) = a + b \text{Log}(Y)$	Model 1.1
Power: $Y = a + b X^C$	Model 2
Multivariate: $Y = a + b \text{Log} X - c \text{Log} Z$	Model 3
Asymptotic: $Y = As (1 - \exp^{-K(X-U)})$	Model 4
Two-phase linear: $Y = a + b \cdot c (X < M) + a1 - b1 (X > M)$	Model 5

In all models, a, b, c, a1, b1, K, U, As, and M are constants to be estimated. Each of these constants, estimated for each model fitted to specific data sets, are summarized in Table 1.

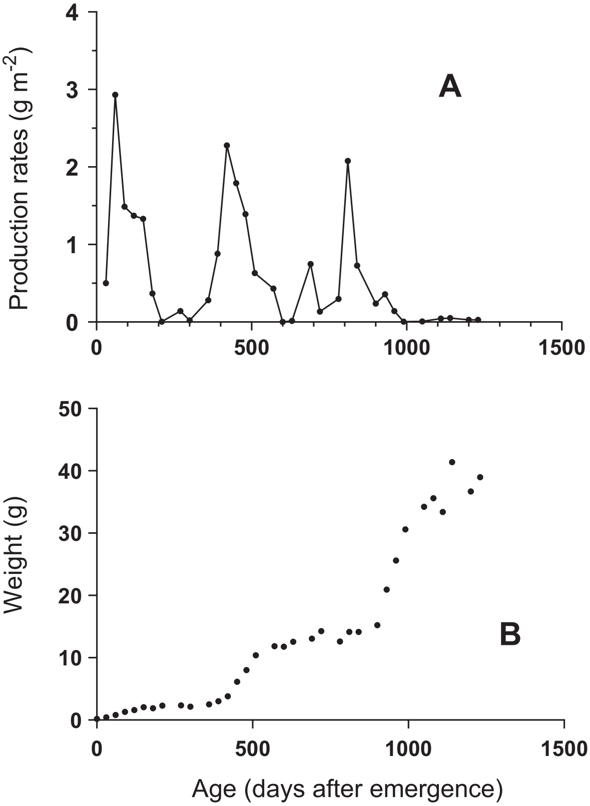
These linear and nonlinear models were fitted to data with an iterative quasi-Newton algorithm and were selected for parsimony by applying the Akaike information criterion. We made pairwise comparisons and calculated the corresponding Akaike values, w1 and w2, for each model. Overall, the model with the lowest value

Table 1 Estimates of the constants a, b, c, K, U, and As for Models 1–5 indicated as M1–M5 below, fitted to specific data sets and graphically represented in Figs. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, and 21 indicated as F1–F21 for each single relationship below, in brackets. R^2, coefficient of determination. All significant in at least $0.01 > P > 0.001$

		a	b	c	K	U	As	R^2
(A) Cohort production PC, *vs.*								
RC (M4, F6)					−0.68	0.07	48.1	0.74
WC (M1.1, F7)		2.0	−0.3					0.33
		1.7	−0.1					0.20
		1.4	−0.2					0.26
RC-WC (M3)		−0.6	0.6	−1.2				0.81
		1.0	0.7	−0.3				0.87
		1.1	0.5	−0.1				0.60
Cohort production PC, two sets of populations, *vs.*								
RC (M4, F8)	Southern Pop.				−2.1	−0.05	31.7	0.76
	Northern Pop.				−0.35	−0.04	28.0	0.79
WC (M1.1, F9)	Southern Pop.	4.6	−1.9					0.50
	Northern Pop.	2.1	−1.0					0.48
(B) Annual production PA *vs.*								
NA (M2, F11)	Southern Pop.		27.5	0.9				0.77
	Northern Pop.		23.0	0.5				0.84
NA, WA (M3)	Southern Pop.	−0.5	25.8	−0.1				
	Northern Pop.	2.2	25.9	−0.1				
(C) Cohort Pc/Bc ratios *vs.*								
RC (M4, F13)	Rio Esva				−4.0	−0.2	6.0	0.46
	Two sets of Pop.				−2.0	−0.1	6.1	0.60
(D) Annual Pa/Ba ratios *vs.*								
NA (M4, F15)	Rio Esva				−2.5	−0.2	2.1	0.42
NA (M2, F15)	Pop. D2	1.5	0.5					0.55
(E) Site-specific relationships (M1.1, F16)								
Pa/Ba *vs* RC		1.2	0.8					0.52
Pc/Bc *vs.* RC		4.4	2.2					0.78
NA (*10) *vs.* RC		1.4	6.7					0.94
PC *vs.* RC		2.6	22.9					0.83
PA *vs.* RC		−2.4	47.1					0.88
(F) Annual production PA *vs.*								
Cohort production PC (M1, F17)			0.99					0.93
(G) Pa/Ba ratios *vs*								
Pc/Bc ratios (M1, F18)		0.25	0.25					0.33

is the most plausible. However, we calculated the likelihood that one of the two models was better, based on the differences between the two values and selected the most plausible when the difference $w2 - w1 > 2$, which is equivalent to a $\geq 75\%$ probability that the model selected is the top model (Motulsky and Christopoulos

Fig. 3 Month-to-month variation of: (**a**) Production rates (g m^{-2}) and (**b**) individual growth in weight (g) during the lifetime of a cohort (from recruitment to the time of complete disappearance, some 1250 days after emergence) of the Bisballe Baeck brown trout population in central Denmark



2004). All analytical and graphical analyses were made with Statistica version 10.0 and GraphPad Prism version 9.0.

3 Results

After Mann and Penczak (1986), several short-term (<5 years) studies on single salmonid populations or on fish assemblages including salmonids (i.e., Freeman et al. 1988; Kwak and Waters 2011) and experimental populations (i.e., Zalewski et al. 1985) reported values ?? within similar but not identical ranges. The majority of these studies are summarized in Gibson and Cutting (1993) and Almodóvar et al. (2011).

More recent studies, based on accurate multi-sample procedures across seasons and years quantified with efficient electrofishing techniques and applying depletion methods (Lobon-Cervia 1991), contributed to our understanding of cohort and annual patterns of production rates and facilitated identifying several underpinning factors. Among these, factors external to the populations such as those related to

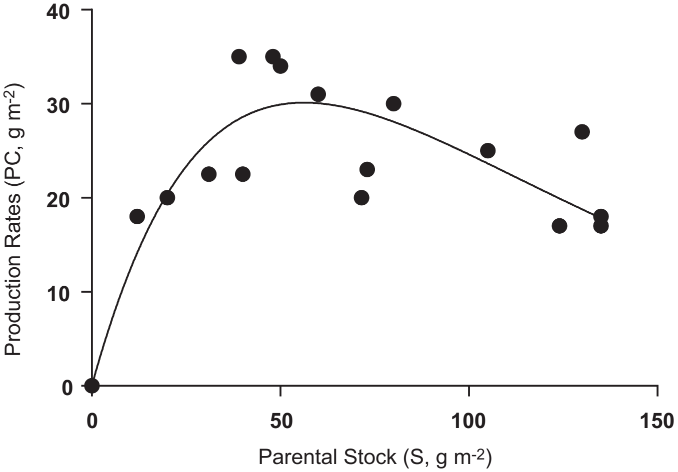


Fig. 4 Cohort production rates (PC, g m^{-2}) of the Black Brows Beck (UK) brown trout *Salmo trutta* population plotted *vs.* the parental component of the population (S) quantified as the number of eggs per m^{-2} with a dome-shaped relationship in the form PC = A * S exp (− B * S) fitted to data. Constants A and B are 1.512 and 0.0180, respectively, and $R^2 = 0.378$. Redrawn from Elliott (1985) with permission

habitat quality and variability, human impacts, the effects of global change and warming, and other related issues are dealt with by Rosenfeld et al. (2024, chapter 21). As aforementioned, here we focus on production rates *strictu sensu* and related intrinsic factors.

Notably, with very few exceptions (i.e., Kwak and Waters 2011; Scarnecchia and Bergensen 1987; Benjamin and Baxter 2011), most recent short- and long-term studies have focused on brown trout, including resident, sea-migratory, and lake-migratory populations within their native distributional range. These populations rarely occur as single species but are accompanied by 1–3 additional species, most commonly by European Eel *Anguilla anguilla* and Atlantic salmon *S. salar*. Typically, these brown trout populations are composed of 3–5 age-classes and vary extensively in size, growth, and density.

3.1 Cohort Production Rates

The few studies reporting cohort production rates have assessed brown trout populations sampled in selected, fixed stream sites around 100 m long and are based on detailed long-term monitoring procedures.

To date, the only known detailed, month-to-month determination of production rates across the lifetime was quantified during the freshwater phase of a lake-migratory brown trout population inhabiting Bisballe Baeck in central Denmark

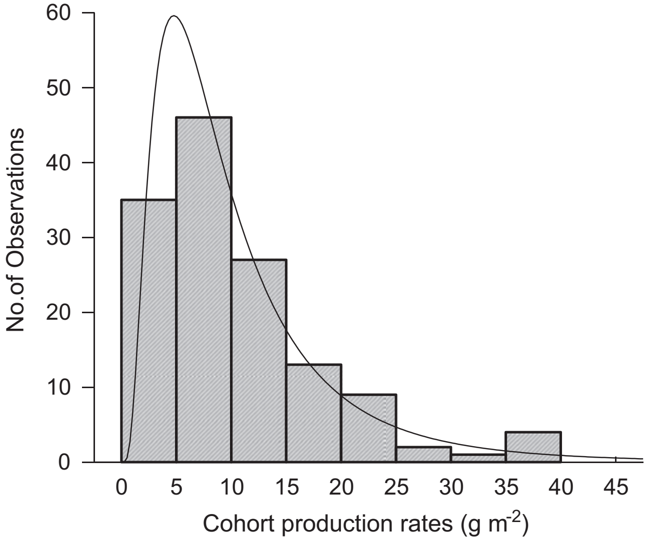


Fig. 5 Frequency distribution of 127 cohort production rates of brown trout quantified at 12 sites over 21 years distributed along four tributaries of the Rio Esva (northern Spain) with a continuous log-normal distribution fitted to data

(this study). These data permit the examination of monthly patterns of production rates in relation to growth.

As shown in Fig. 3, the monthly production rates track tightly with the sigmoidal growth that typify seasonality in northern hemisphere climates with intense growth and production rates since the very beginning of the commencement of growth in spring and lower in the summer and early autumn. The most productive stage occurs during the earliest spring growth from April to June, followed by the second and the third peaks in the second and third spring seasons, whereas production is zero or near zero during the three successive winters.

Elliott (1985, 1993) pioneered cohort production rate studies summarizing 22 successive cohorts of a slow-growing, high-density, sea-migratory brown trout population inhabiting a 60 m^2 site of Black Brows Beck, a northern England stream. As a major determinant of cohort production, he described a nonlinear parental density (quantified as the number of eggs laid at the study site, eggs m^{-2}) determination where, excluding three exceptionally drought years, these rates increase with increased density until a maximum upon which they declined with increased parental density tracking a dome-shaped relationship (Fig. 4). This relationship explained 57% of the total cohort production rates variation, within the range of 7.6–33.9 g m^{-2}, and further related a minor effect of growth to this variation.

Interestingly, independent of the mortality and/or migration during the lifetime, the abundance of the spawning parental component of the population determines the total cohort production rates. This dome-shaped relationship predicts that a low parental density of 20 eggs m^{-2} recorded in the 1979, 1980, and 1987 cohorts yield

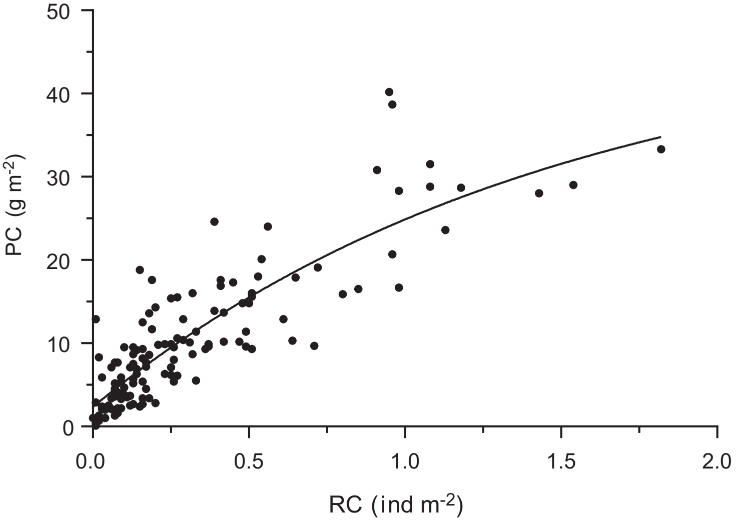


Fig. 6 Asymptotic relationship between recruitment (RC, ind m^{-2}) and the total cohort production rates (PC, g m^{-2}) of 127 cohorts of brown trout quantified, over 20 years, at 12 sites spread along four tributaries of Rio Esva in northern Spain

the same production rates, around 20 g m^{-2}, as the maximum parental densities, i.e., 130 egg m^{-2}, observed in the 1974 and 1982 cohorts, with intermediate rates at around 50 eggs m^{-2}.

Lobon-Cervia et al. (2011) also monitored the dynamics of a combined suit of slow- and fast-growing, low- and high-density, resident brown trout populations at 12 sites of four tributaries of the Rio Esva Basin in northern Spain over the long term.

Due to an extremely low number of recruits in several years and sites, cohort growth and production rates could not be estimated, yet 127 complete cohorts from recruitment to their total disappearance by natural mortality permitted a meta-analysis.

Cohort-to-cohort production rates varied widely within a broad range of 1.2–40.2 g m^{-2} with an average of 16.3 g m^{-2}. However, an earlier exploration demonstrated that the frequency distributions of these rates fitted a log-normal distribution (Fig. 5), in which cohorts with rates <10 g m^{-2} predominate and those >30 g m^{-2} were scarce.

Based on a nested ANOVA of the effects of stream, site, and year, all three factors were significant ($P < 0.001$) but explained rather low and similar % of the variance of each single factor with 19.8%, 22.0%, and 22.5% for the stream, site, and year, respectively, with a 35.7% of the variance left unexplained.

Unlike Elliott (1985, 1993), visual inspections and nonlinear models analysis definitively showed no relationship between the parental density—quantified in this study as the number of spawning females and the subsequent number of eggs laid at each site and year (Lobon-Cervia and Rincon 2004)—and the cohort production rates (Lobon-Cervia 2007). We therefore explored the role of the two major

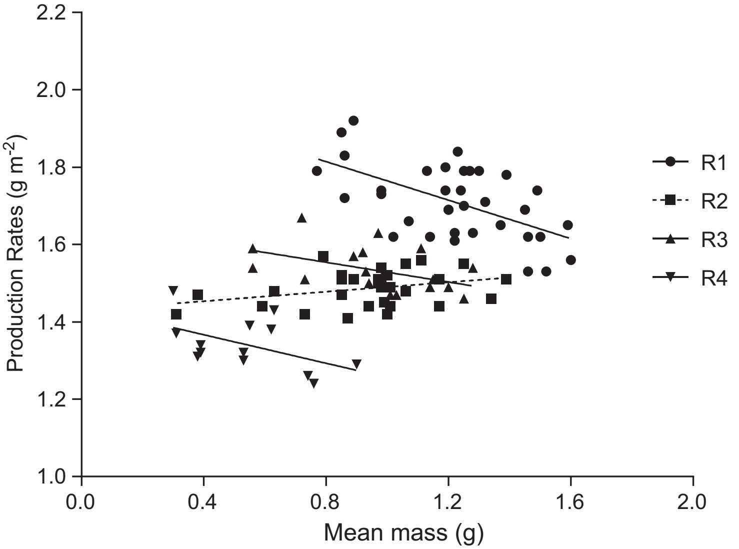


Fig. 7 Negative weight-dependent cohort production rates of brown trout at the four streams (R1 to R4, sites pooled) studied in Rio Esva in northern Spain. Broken line at R2 = nonsignificant

attributes intrinsic to the populations, namely, growth, in the form of the mean weights of individuals over the lifetime (WC, g), and density, in the form of recruitment (RC, ind m^{-2}), (see Fig. 1) as potential determinants of these rates.

Plots of the production rates *vs.* recruitment, at a site scale, indicated positive relationships where these rates appeared to increase faster at lower rather than at higher recruitment. When all sites and cohorts were pooled together, we observed a curvilinear trajectory as shown in Fig. 6.

The fit of several nonlinear models indicated an asymptotic Model 4 as the most plausible. Fit of this model (constants in Table 1) explained a remarkable 74% of all the variation of these rates across the recruitment range with an asymptotic value at PC = 48.1 when recruitment attained a maximum at around RC = 2.0 ind m^{-2}.

Thus, at any spatial (stream or stream site) and temporal (among cohorts) scale, recruitment (RC) predicts correctly cohort production rates (PC). These rates increased faster at lower than at higher recruitment until an asymptotic value upon which production rates remained constant, independent of the effects of any ancillary factor during the lifetime.

We further explored the potential effects of the mean weights (WC, g). At a site scale, we detected no consistent relationship between PC and WC, with only a few exceptions where there appeared to be a negative relationship. However, when we analyzed streams with sites pooled, we detected (Fig. 7) two significant ($P < 0.01$) negative relationships in streams R1 and R4, but that only explained 33% and 21% of the variation, respectively. Another stream, R3, was fairly significant at $P = 0.09$, but that only explained 7% of the variation; we observed a nonsignificant ($P = 0.32$) relationship in stream R2 (see Table 1 for constants, R^2, and significant levels).

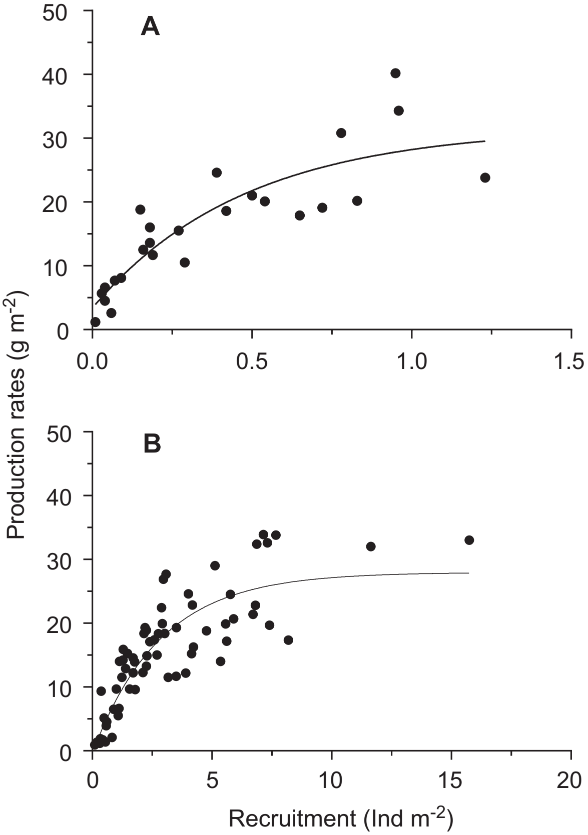


Fig. 8 Asymptotic relationships between recruitment (RC, ind m^{-2}) and cohort production rates (PC, g m^{-2}) for two sets of brown trout populations: (**a**) The two faster-growing populations (CH). (**b**) The slow-growing populations (D1, D2, and BR) pooled. Note different recruitment ranges between the two sets of populations

We further fitted a multivariate regression for the two effects combined, RC and WC. Fits of Model 3 showed to be highly significant for streams R1, R3, and R4, at $P < 0.001$ with a variance explained 81.4%, 87.2%, and 60.0%, respectively. The variance explained by these two effects combined, even though highly significant, was only 13% higher than the variance explained by the effect of recruitment alone (constants, for Model 3, R^2, and significant levels in Table 1).

3.1.1 A Comparison Across Populations

Given the consistency of the patterns highlighted for a large-scale data set of the Rio Esva populations, with strong recruitment-dependent cohort production rates and minor, but significant, negative effects of mean weights, as an index of the lifetime growth, we explored whether this pattern was consistent across a suit of contrasting, slow- and fast-growing, high- and low-density brown trout populations, including resident, sea-migratory, and lake-migratory life histories across the natural distribution range.

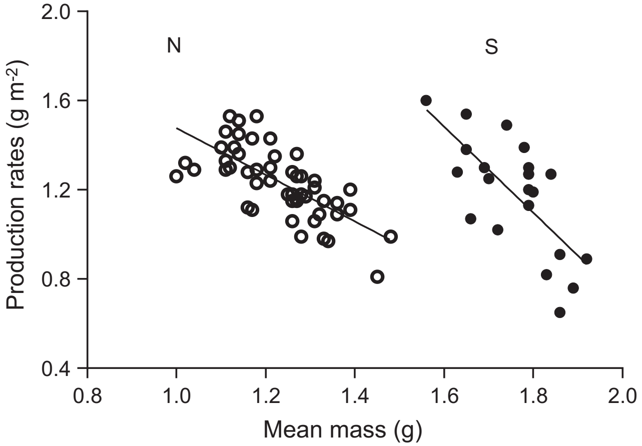


Fig. 9 Negative linear log–log relationships between cohort production rates (PC) and the corresponding mean weight (WC) for the two sets of brown trout populations, the fast-growing, southern (S) and the slow-growing, northern populations (N)

To this end, we examined long-term data sets from six populations belonging to the three life histories exhibited by brown trout located at the extreme range of environmental conditions, habitat quality conditions, and temperature regimes within its natural distributional range, namely, (1) the two fast-growing, low-density, resident populations selected among the tributaries of the Rio Esva analyzed above (hereafter CH) located 2400 km (2) a slow-growing, high-density, lake-migratory population inhabiting Bisballe Baeck, a small tributary of Lake Hald in central Denmark (hereafter D1), (3) two slow-growing, low-density sea-migratory populations inhabiting Brandstrup and Tjaerbaeck Baecks also in central Jutland (hereafter D2), and finally (4) a slow-growing, high-density, sea-migratory population inhabiting Black Brow Beck in northern England (hereafter BR) reported by Elliott (1993), located 1000 km distance from the Danish populations.

This meta-analysis encompassed 101 complete cohorts in total, 26 cohorts of the two southern CH populations, 15 cohorts of D1, 16 cohorts of BR, and 28 and 16 cohorts of two D2 populations. Despite substantial differences in size, density, and life history, all the populations were composed of 3–5 age-classes.

The two population attributes whose effect on production rates we examined differed by several orders of magnitude among populations. Recruitment was remarkably lower in the southern CH populations with RC = 0.34 ind m^{-2} (range 0.3–1.2 ind m^{-2}) and in the Danish D2 populations with RC = 1.3 (range 0.1–2.2 ind m^{-2}) relative to being several times higher in the BR population with RC = 5.3 (range 2.2–7.7 ind m^{-2}) and a disproportionally high recruitment in the Danish D1 population with RC = 15.8 ind m^{-2} within also with a disproportionally broad range (0.9–15.8 ind m^{-2}). In turn, the mean weights of the southern CH population (WC = 60.3 g) were more than double the magnitudes of the slow-growing D1, D2, and BR populations with WC = 19.3 g, 19.1 g, and 13.1 g, respectively.

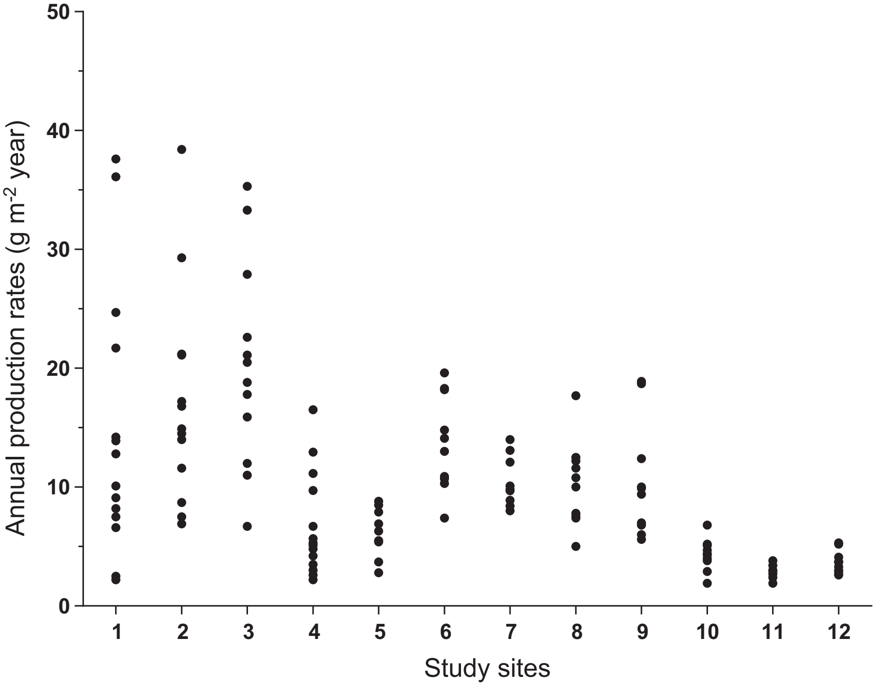


Fig. 10 Annual production rates (PA, g m^{-2}, 137 estimates) of brown trout across 12 sites of four streams, R1 (sites 1–4), R2 (sites 5–7), R3 (sites 8–10), and R4 (sites 11–12) tributaries of Rio Esva (northern Spain) over the years 1986–2001

Note, however, that a slight difference in the total cohort production rates among populations is that the southern population (CH) includes these rates from the egg stage to recruitment, which is missing in all other populations. No data on the production rates of every single age-class within cohorts (Fig. 1) were available for BR, but a comparison among all other populations revealed that the youngest juveniles YOY typically contribute a remarkable amount (Hunt 1974; Mortensen 1977). On average, these rates from recruitment until the first birthdate (i.e., YOY) represented 42% of the total production in the southern populations and 32% in the northern ones, and the two youngest age-classes combined contribute to approximately 75% of the total cohort production rates in all populations.

Moreover, in the southern CH population, the production rates of the successive age-classes were strongly recruitment-dependent, with a declining effect with increased age. Recruitment explained a substantial 81% of the cohort production variations in age-0 individuals, 57% of the variation in age-1, and a significant 20% in age-2 individuals. A very low number of survivors apparently obscures this effect on age-3 individuals. A similar effect was observed in the slow-growing D1 and D2 populations in which recruitment significantly explained 62% and 43% in age-0 and age-1 production rates but was not significant for the age-2 and age-3 individuals.

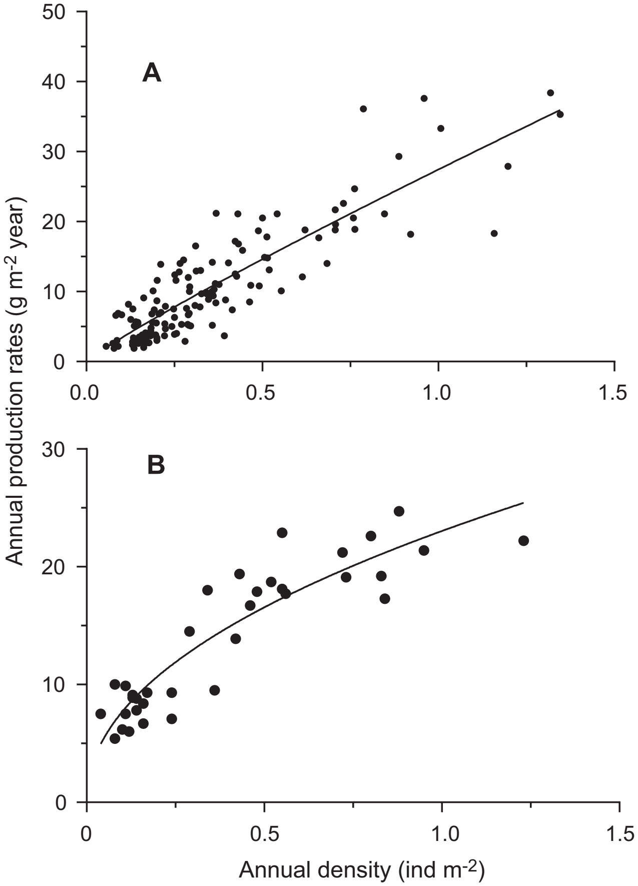


Fig. 11 (**a**) Annual production rates (PA, g m^{-2} year) *vs.* mean annual densities (NA, ind m^{-2}) of brown trout determined at 12 sites of four streams spread along the Rio Esva, over 15 years. (**b**) Annual production rates (PA) *vs.* mean annual density (NA) for two slow-growing, D2 northern populations

An exploration of the six populations pooled showed that the cohort production rates, unlike in the Rio Esva studied sites, the frequency distribution rather a normal distribution (Chi-squared 7.7, $P = 0.05$) with a mean at PC = 17.0 g m^{-2} with the lowest and highest rates being most unlikely. Nonetheless, there were highly significant differences among populations (ANOVA, $P < 0.001$), with the mean rates being highest in BR = 24.8 g m^{-2}.

As in the above analysis, we first visually inspected the plots of cohort production rates (PC) *vs.* recruitment (RC) for each single population separately that showed consistent positive linear trends. We ran correlations and linear regressions and highlighted significant positive linear relationships where recruitment significantly explained ($0.01 > P > 0.001$), between 30% in D2 and 57% in CH of the

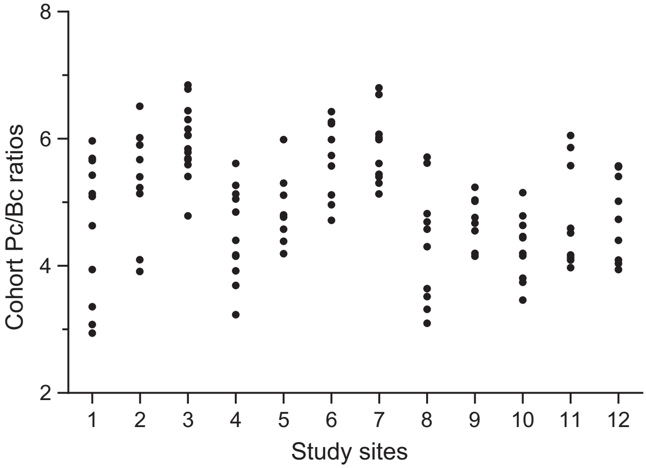


Fig. 12 Values of the cohort Pc/Bc ratios for brown trout estimated at 12 sites spread along four tributaries of Rio Esva over 20 years

temporal variations of these rates indicating a consistent role of recruitment as determinant of the production rates in all populations. Nonetheless, based on an ANCOVA, we detected significant differences among the slopes of the six populations, and a post-hoc Bonferroni test grouped two sets of populations. One set included the two fast-growing CH populations, and a second set included the four slow-growing populations D1, D2, and BR.

Plots of these cohort production rate*s versus* recruitments for the two sets of populations separately highlighted asymptotic trajectories with slower increments at higher than at lower recruitment, increasing toward an asymptotic value (Fig. 8) that matches exactly the pattern highlighted for the Rio Esva (Fig. 6). Subsequent fits of Model 4 were highly significant (Table 1) albeit the asymptotic values and the recruitment upon which production rates attained those asymptotes differed substantially between the two sets of populations (Fig. 8).

The asymptotic value for CH at PC = 31.7 g m^{-2} was attained at a recruitment around RC = 1.5 ind m^{-2}, whereas for the second group of populations this value was lower at around PC = 28 g m^{-2} but a much higher recruitment PC = 8 ind m^{-2}. Note that the asymptotic values predicted by these two regressions are rather similar to those currently observed PC = 40 g m^{-2} and 38 g m^{-2}, respectively and lower than the asymptote predicted by the very same model fitted to 127 cohorts of the Rio Esva sites, Pc = 48 g m^{-2} (Fig. 6). Remarkably, these two similarly shaped nonlinear regressions predicting cohort production rates (PC) from recruitment (RC) within an extremely broad range of values, i.e., RC = 0.1–15.6 ind m^{-2}.

To further examine the effects of growth on the production rates of these two sets of populations, we used the mean weights as above (See Fig. 7). Plots of cohort production rates versus mean weights clearly indicate two different, separate trajectories for each set of populations. Log–log linear regressions (Model 1) revealed

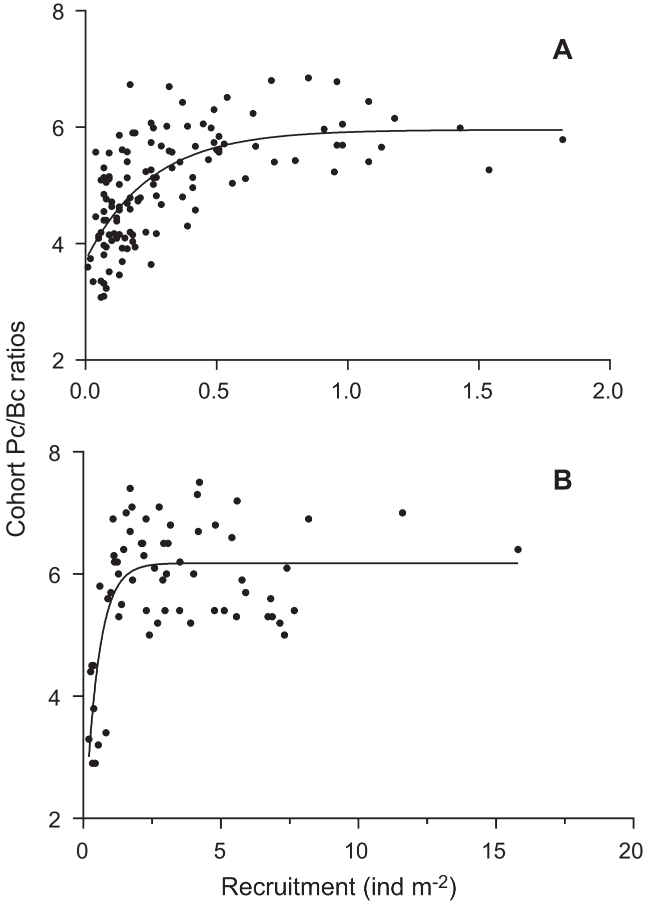


Fig. 13 (**a**) Asymptotic relationships between the cohort Pc/Bc ratios and recruitment (RC, ind m^{-2}) for 127 cohorts of brown trout estimated at 12 sites spread along four tributaries of the Esva River. (**b**) Asymptotic relationship between the cohort Pc/Bc ratios and recruitment (RC, ind m^{-2}) for 82 cohorts of four slow-growing, northern populations

that in northern and southern populations, the mean weights were significantly negatively related, and the models explained half of the variations, 50% and 48%, respectively (Fig. 9), with highly significantly different slopes (ANCOVA, $P < 0.001$) being markedly steeper in the CH populations (Table 1).

A markedly steeper slope in the fast-growing populations indicates that any increase in growth brings about a substantial decrease in these production rates relative to markedly weaker effects in the slow-growing populations. An interesting additional highlight is that in the two sets of populations, highly recruited cohorts of higher production rates are related to slower growers, and at the opposite extreme, the least productive cohorts are related to faster growers.

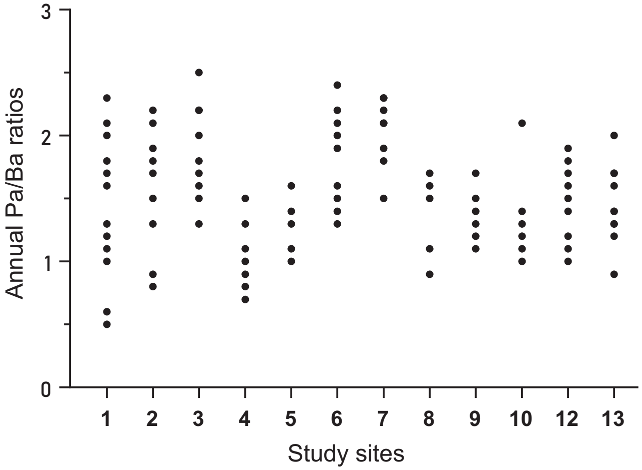


Fig. 14 Estimates of annual Pa/Ba ratios for brown trout at 12 sites of four streams spread along four tributaries of the Rio Esva in northern Spain, over 16 years

Consistent with the analysis of the Rio Esva sites above, the analysis of these six populations, which includes a wide range in variation of recruitment, growth, and density reported for stream-dwelling brown trout throughout its distributional range, leads to the following conclusions: (1) growth rates differed widely among populations and may typify populations among fast-, intermediate-, and slow-growing populations. Such a pattern suggests there is not a homogeneous effect of recruitment on cohort production rates across populations. Nevertheless, higher production rates are not necessarily associated with fast-growing populations. Slow-growing, high-density populations (i.e., BR) may exhibit cohorts with production rates of magnitudes similar to fast-growing, low-density populations (i.e., CH). (2) The monthly and seasonal patterns of production rates track tightly with the sigmoidal growth patterns that typify brown trout in temperate climates. (3) Consistent with other studies, the production rates of the two youngest age-classes contribute >70–75% of the total cohort production rates in all populations. (4) Recruitment plays an overwhelming role as determinant of cohort production rates, independent of the post-recruitment processes that may occur during the lifetime, a pattern which shows a strong tendency to asymptotic values at high recruitment. And (5) growth appears to play a minor, yet significant, negative role as determinant of cohort production rates.

3.1.2 A Look at Sea-Migratory Populations

Further consideration of sea-migratory salmonid populations with two different life stages may be insightful. In these populations, after 3 or 4 years of in-stream life, smolts migrate downstream to marine waters, where they spend a variable number

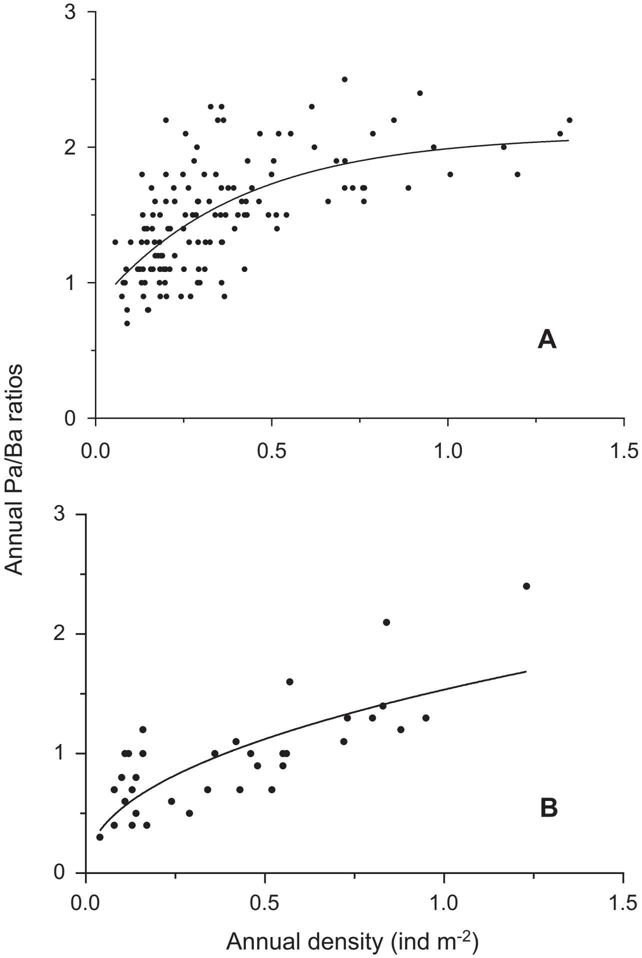


Fig. 15 (**a**) Estimates of annual Pa/Ba ratios of brown trout across 12 sites spread along four Rio Esva streams vs. mean annual density (NA, ind m^{-2}) with an asymptotic model fitted to data. (**b**) Annual Pa/Ba ratios vs. mean annual density for the two slow-growing D2 populations with the model fitted to data

of years before returning to their natal streams for spawning. To our knowledge, no previous study has attempted to evaluate cohort production rates of these populations over the two life stages, nor has anyone investigated the relative importance of the disparate body growth experienced by individuals during the marine life stage to cohort production rates. Here, by monitoring individuals of the two life stages over the lifetime, we attempted to quantify these rates during both the fresh- and marine stages of the Brandstrup Baeck brown trout population (central Denmark) that migrate to the Skagerrak-Kattegat Sea.

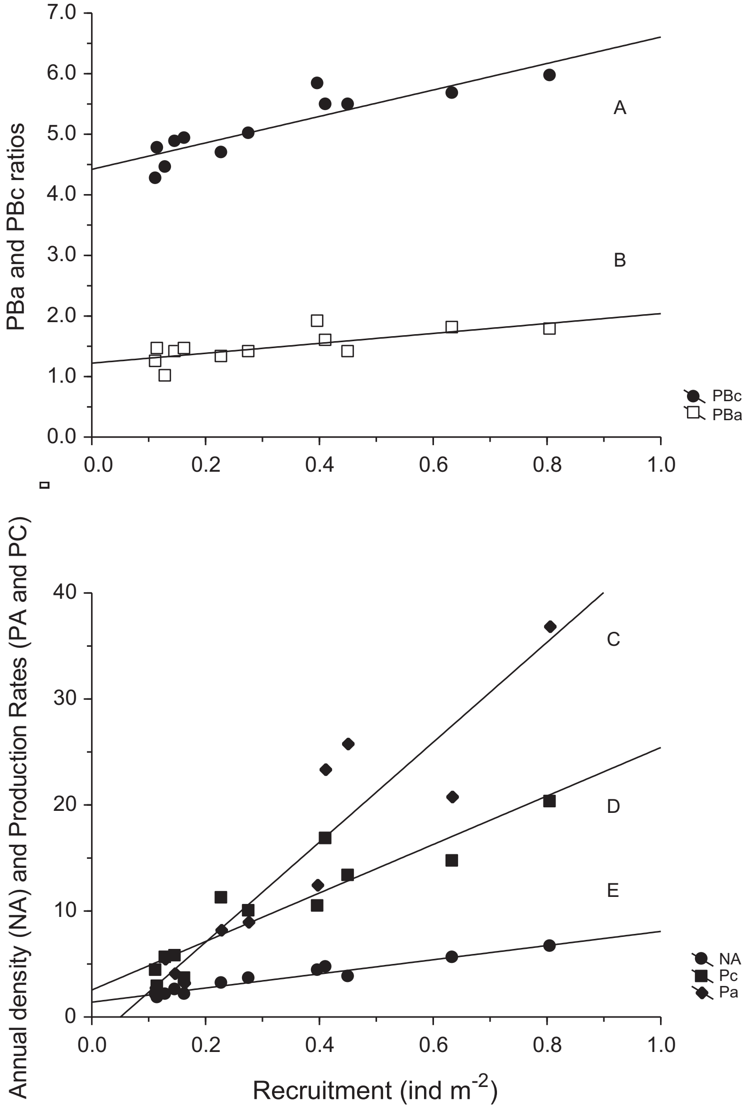


Fig. 16 *Above*: Site-specific recruitment-dependent Pa/Ba and Pc/Bc ratios for brown trout at 12 sites examined in four Rio Esva tributaries (north Spain). *Below*: Site-specific linear recruitment-dependent annual density (10* NA, ind m^{-2} re-scaled), cohort production (PC, g m^{-2}), and annual production (PA, g m^{-2} year) for the same sites, years, and cohorts

Our approach was the following: we monitored the number of individuals in the stream up to the smolt stage over the years, and then we tracked individual emigrants subject to a fishery as sea trout and we considered the following: the mean recruitment was 1.69 ind m^{-2} and from these individuals, 0.16 smolts migrate to the

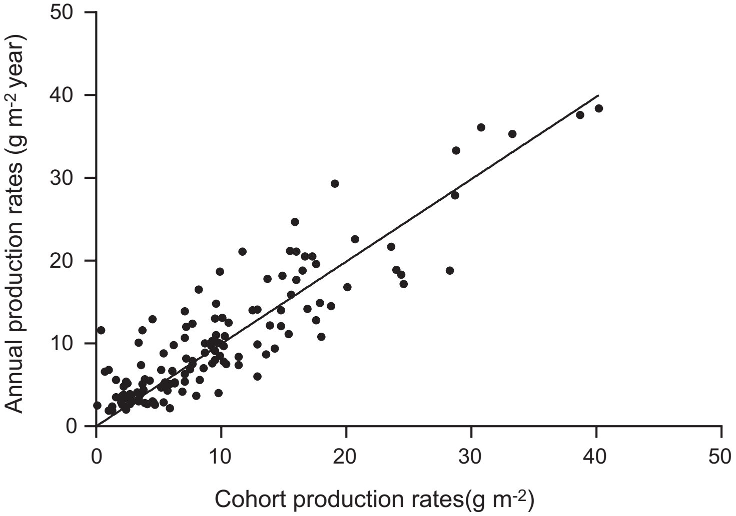


Fig. 17 Annual production PA (g m^{-2} year) vs. cohort production PC (g m^{-2}) for brown trout in four Rio Esva tributaries with a linear regression with zero intersect (see Table 1)

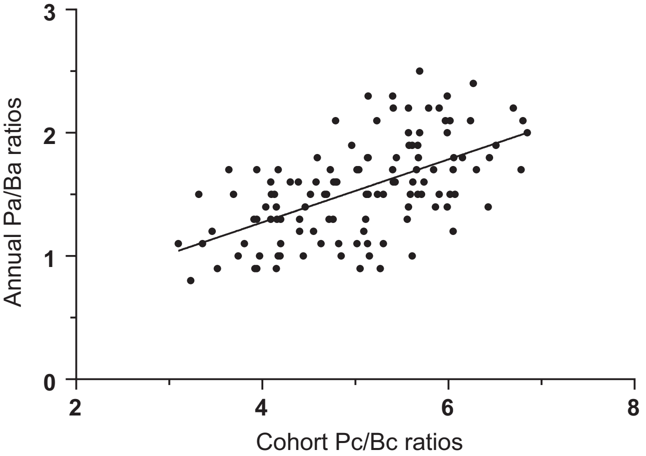


Fig. 18 Annual Pa/Ba ratios vs. Cohort Pc/Bc ratios for 122 estimates of brown trout across cohorts and years in four Rio Esva tributaries of northern Spain with a positive linear regression fitted to data (for details see Table 1)

sea. In freshwater, only natural mortality (M) regulates the number of individuals until the total disappearance of the cohort in the stream. In marine waters, the total mortality of individuals is Z = M + F + S, where F is fishery mortality and S is the spawning mortality.

From data of sea trout—as reported by Christensen et al. (1993) and Rasmussen and Pedersen (2018, Table 2)—we calculated the total production in saltwater of a

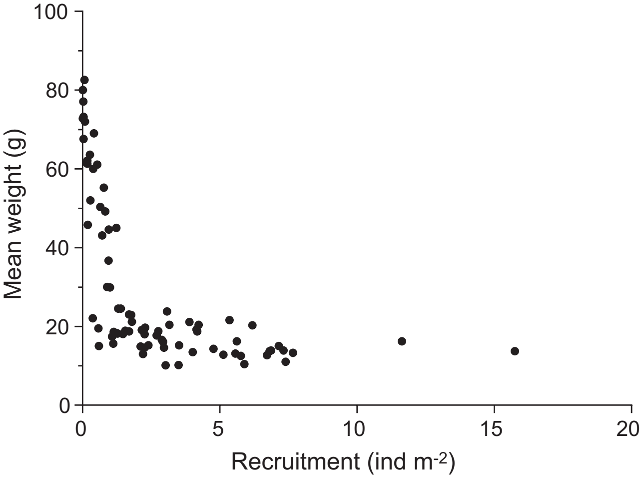


Fig. 19 Mean cohort weights (WC, g) vs. recruitment (RC, ind m^{-2}) for all data pooled of six populations of brown trout studied: two CH populations, one D1, two D2, and one BR populations

cohort starting from a number of smolts = 0.16 ind until the extinction of that cohort. Total mortality Z was calculated from the number of succeeding age-classes given in Rasmussen and Pedersen (2018, Table 2). The production rates for each cohort were calculated from the instantaneous growth rate, G * mean mass (Rasmussen and Pedersen 2018, Table 2). Smolts mostly recruit from age 3 and 4, and that explains why the number of individuals increases in the first ages 2 and 3 in marine waters (Table 2). The total cohort production rates in freshwater (FW) (Rasmussen 2018) were estimated as $PC_{FW} = 15.9$ g m^{-2}, whereas the total cohort production rates in marine water (MW) yielded $PC_{MW} = 238.3$ g (details in Table 2). Disregarding area we can say that 1 recruit produced 9.4 g in freshwater and 141.0 g in saltwater. Likewise, these calculations could be done for each smolt cohort; herein, we pooled them and the production in marine waters should be nearly the same. Though our analysis may be biased due to simplifying assumptions, it provides a good demonstration of the substantially higher production rates of individuals in marine waters relative to freshwater, which drives the disproportionately high growth at sea. These differences are most likely a result of marine individuals feeding upon fishes, whereas, in streams, they feed largely upon invertebrates with lower energy content.

3.2 *Annual Production Rates*

As aforementioned, the annual production rates (PA) refer to the addition of all cohorts growing simultaneously during a year and are expressed in g m^{-2} year (Fig. 2). Relative to the poorly documented cohort production rates, both short-term and long-term estimates of annual production rates have been assessed across a

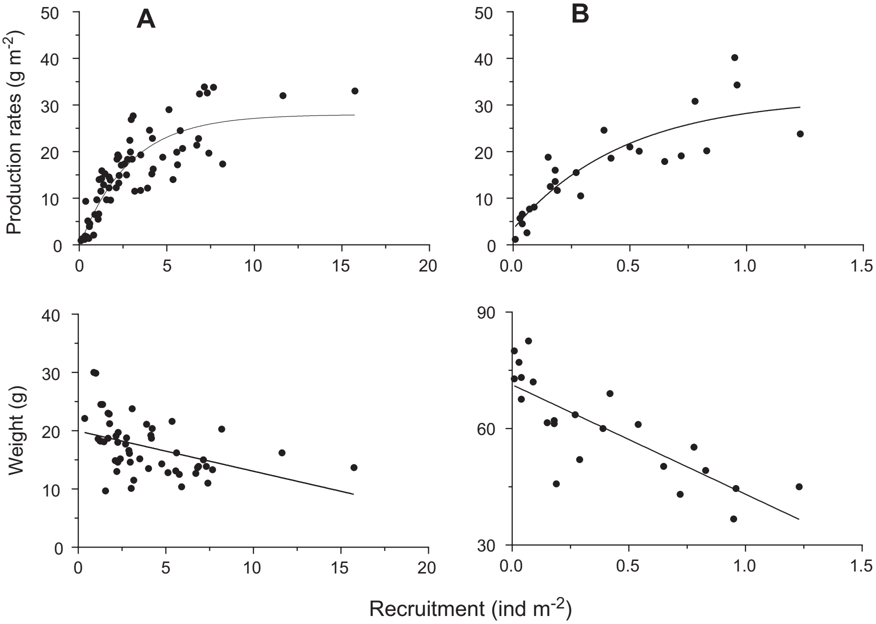


Fig. 20 Relationships between recruitment and cohort production rates of brown trout with asymptotic functions fitted to data (redrawn from Fig. 8) and growth in the form of mean weights (g) with negative linear regressions fitted to data for (**a**) the three northern populations and (**b**) the two southern populations

diversity of salmonid populations and temporal (years) and spatial (geographical) scales. The latter ranges from single to multiple sites along heterogeneous streams within and among contrasting river basins and up to continental scales.

Nevertheless, as emphasized by Mann and Penczak (1986), elucidating non-equivocal patterns of annual production rates across spatial and temporal scales and disentangling the interacting factors is rather complicated. Major handicaps include at a minimum: First, stream variability appears to be the rule rather than the exception. Habitat quality along the stream gradients and across temporal scales may vary in in-stream features, temperature, and primary and secondary food production with subsequent consequences for salmonid growth rates and density. Second, in a given year, the same annual production may be attained by populations composed of different relative contributions of age-classes; for example, the same rate may be attained by two strong age-classes added to a weak and to a still weaker age-class than four intermediate age-classes. Third, as aforementioned, these patterns may be further complicated by the fact that the same annual rates may be attained by populations composed of a few, fast-growing individuals and by those composed of many, slow-growing individuals. Despite these shortcomings, several authors have attempted to assess habitat-quality related spatial patterns and have further assessed the extent to which these rates remain rather constant and/or vary over temporal scales as follows.

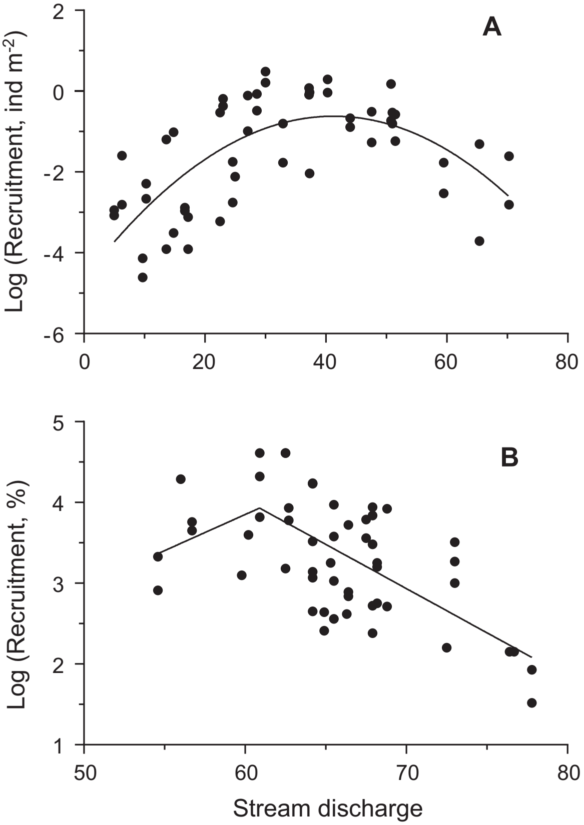


Fig. 21 (**a**) Discharge-dependent brown trout recruitment with a parabolic function fitted to data for the fast-growing, southern populations (CH), over 30 years (1986–2015). (**a**) Discharge-dependent brown trout recruitment with a two-phase function fitted to data for the two slow-growing Danish populations (D1 and D2), over 21 years

Table 2 Mean number of individuals since recruitment (ind m^{-2}), mean weight (W, g), and production rates (g) estimated for each age-class of the fresh-stage and estimated production rates for the marine life stage (g) of the Brandstrup Baeck brown trout population (central Denmark). Number and production is m^{-2} in freshwater

		Mean N	Mean W, g	Age-class P, g
Stream	Age 0	1.63 m^{-2}	0.83	2.36 m^{-2}
Stream	Age 1	0.72 m^{-2}	6.26	6.93 m^{-2}
Stream	Age 2	0.28 m^{-2}	20.85	3.96 m^{-2}
Stream	Age 3	0.08 m^{-2}	47.06	1.67 m^{-2}
Stream	Age 4	0.01 m^{-2}	98.49	0.99 m^{-2}
Sea	Age 2+3	0.14	116.9	47.9
Sea	Age 4	0.098	592.5	61.0
Sea	Age 5	0.057	1211.3	47.0
Sea	Age 6	0.028	2089.5	48.8
Sea	Age 7	0.008	3406.6	31.4
Sea	Age 8	0.0016	4381.5	2.3

Long-term assessment of annual production rates was pioneered by Hunt (1974), who reported annual rates of brook trout in Lawrence Creek (Wisconsin) during an 11-year time period. He studied four uncommonly long 1.1–1.7 km sites selected along the stream and reported rather stable annual rates across years with only a 20% difference within the range 10.6–12.9 g m^{-2} year and a maximum rate in one of the study sites subject to some "habitat improvement" practices that attained 25.8 g m^{-2} year. He further suggested these rates were regulated through compensatory adjustments in growth and survival rates of varying importance among age groups.

Elliott (1985, 1993) reported these rates over 24 years for brown trout at the BR site mentioned above. These rates attained a rather high value at 33.9 g m^{-2} year, yet varied almost by 350% among years from 8.9 to 33.9 g m^{-2} year.

Waters (1999) reported a 21-year study of a more complex salmonids assemblage composed of brook trout, rainbow trout *Oncorhynchus mykiss* and brown trout co-occurring in a single Minnesota stream site. Owing to the replacement of brook trout by brown trout, following floods and sedimentation and environmental disturbance over the years (details in Waters 1983), the annual rates varied widely, but in no cases did the maximum rates, including all three species, exceed the standard values reported by Mann and Penczak (1986). At the end of the study, the annual production of brown trout, representing 93% of the total, attained 32.2 m^{-2} year.

Higher production rates by nonnative salmonids appeared not to be an exception. A replacement of salmonids was also observed by Benjamin and Baxter (2011) in Teton River (Idaho), and they reported that the invasive, nonnative brook trout replaced the native cutthroat trout *O. clarkii* over a 4-year period and showed 2.1 times higher production rates. Furthermore, several studies have also attempted to quantify annual production rates across spatial (geographical) scales. At small scales, as selected sites within or among nearby streams annual rates are summarized by Mann and Penczak (1986), Gibson and Cutting (1993) and Almodovar et al. (2011, Table A.1 and references therein) and overall, the authors reported scattered, environmentally induced spatial patterns and rather low to intermediate rates, with a maximum at 18.4 g m^{-2} year in ten Colorado streams, 8.0 in a British stream, 15.3 in several Irish streams, 5.9 in a Canadian stream, 13.5 in several Portuguese streams, and a higher rate at 38.6 g m^{-2} year in one Spanish stream (Lobon-Cervia 2003 and this study).

At a larger spatial scale, Newman and Waters (1989) evaluated annual rates of brown trout in eight contiguous 300 m long sites that constituted the entire length of South Branch Creek, a limestone bedrock flowing stream of southeastern Minnesota, over 3 years. These rates differed among sites, but the relative differences remained fairly constant over the years, with the most productive sites being 1.5–2 times higher than the least productive sites and with no obvious effects of growth among sites. Overall these rates increased over the 3 years studied from 9–10 g m^{-2} year to 15–17 g m^{-2} year, values that may be considered low to intermediate according to Mann and Penczak (1986).

At a substantially large spatial scale, Randall and Chadwick (1986) examined Atlantic salmon in 27 sites in Miramichi and 16 sites in Restigouche Rivers of New Brunswick (Canada) over 11 years. Annual production rates were typically low in the two rivers within the range 0.4–16.1 g m^{-2} year. Inter-annual variation was essentially determined by density that explained 82% of the variation in these rates for the two streams pooled, whereas growth accounted only for <10% of those inter-annual variations.

Moreover, Kwak and Waters (1997) focused a broad-scale study on stream water fertility related to limestone bedrock geology. They examined 13 populations and compared their production rates with other populations across the USA to conclude that increased rates were related to increased stream alkalinity. They admit, however, that the overall maximum rate may be governed by water quality, but factors other than water fertility may limit fish production. Also, Almodovar et al. (2011) examined populations inhabiting streams flowing over different types of bedrock of central Spain, and after comparing contrasting European populations, they highlighted a positive correlation between alkalinity and annual production rates. In either case, however, the maximum rates, 27.9 and 25.0 g m^{-2} year, for the two studies, respectively, were below those reported by Mann and Penczak (1986).

The consistency of these alkalinity-related patterns was, however, challenged by several authors who assessed brown trout annual production rates across different European streams and reported markedly higher rates in non-alkaline streams. For example, Elliott (1993) reported 33.9 g m^{-2} year for a population inhabiting a slate bedrock stream of the UK; Mortensen (1978) reported 33 g m^{-2} year for a moraine-dominated streams of central Denmark, and still higher rates at 38.6 g m^{-2} year were reported for populations inhabiting streams flowing over quartzite bedrock of northern Spain by Lobon-Cervia et al. (2011). It is also worthwhile to mention that Rasmussen (1986) estimated rates as high as 43.0–49.8 g m^{-2} year for brown trout and rainbow trout co-occurring in another moraine-dominated Danish stream, slightly enriched by a fish farm located just upstream of the study site.

Lobon-Cervia et al. (2011) highlighted an overwhelming variability in the annual production rates of resident brown trout in streams of northern Spain at a rather large spatial and temporal scales, 12 sites across four streams over 15 years (134 estimates in total). Variability across years was overwhelming with a Coefficient of Variation for annual production CV = 74% and for numbers CV% = 120% (see Dauwalter et al. 2009). When all sites and years were examined together, the range of variation, 1.9 and 38.6 g m^{-2} year, included all the variations in the annual production rates reported for stream salmonids inhabited by one or several species worldwide. Earlier exploration of the frequency distribution of these 134 estimates (Fig. 10), highlighted a log-normal distribution (quite similar to Fig. 5) where low rates around PA = 5–10 g m^{-2} year predominate and the highest PA = >30 g m^{-2} year were rather uncommon.

The productive potential of the Rio Esva tributaries appears spatially and temporally heterogeneous (Fig. 10). Sites differed significantly (ANOVA $P < 0.01$) in their productive capacity with several sites characterized by systematically higher annual production rates, i.e., Sites 1–3 (R1) and at the opposite extreme, sites with lowest rates, i.e., Sites 11–12 (R3); other sites demonstrated intermediate values. Differences among the four streams were five times higher and differences among sites were three times higher within and six times higher among streams and, despite remarkable temporal variations, the relative differences remain fairly similar over the years. Temporal shifts from year to year showed disproportionally higher variations in the most productive sites (i.e., sites 1–3, Fig. 10).

Based on a nested ANOVA for the effects of stream, site, and year, we observed significant effects (at $P < 0.001$) of the three factors with similar % of annual production variance explained, 32%, 27%, and 27% by the stream, site, and year, respectively, leaving 14% unexplained.

"*A priori*" there was no obvious factor to explain so much spatial and temporal variability. Following the relative importance of recruitment and growth for cohort production rates highlighted above, we explored the role of mean annual density (NA, ind m^{-2}) and mean annual growth (WA, g) for these annual rates (PA, g m^{-2} year).

At a site scale, there were consistent positive relationships between these rates and mean density, where typically, these rates increase linearly. Nonetheless, when we pooled all sites and years and visually inspected the corresponding plots, we observed an interesting potential relationship. We tested several linear and nonlinear models and the most plausible was Model 2; the fit of this model (Fig. 11) highlighted an intersect = zero, which was significant at $P < 0.001$ and explained a remarkable 77% of the annual production variations across the whole range of densities values available (Fig. 11a). Constants for Model 2 fitted to data are given in Table 1.

Among the set of slow-growing northern populations, only D2 included annual rates and mean densities permitting a comparison. These populations, 37 estimates of these rates in total, were also potentially related (Model 2), and a fit of this model also showed an intersect = zero with a declining increase at high-density values; this model yet explained a higher 84% of the variation along a rather broad range of density values (Fig. 11b). Constants for the corresponding fits, R^2 and significant levels are given in Table 1.

For the Rio Esva and for two northern populations where data were available, no consistent relationships were detected between the annual rates and the mean weight. We ran multiple correlations including the two factors, PA *vs.* NA and WA that highlighted significant effects at $P < 0.001$ with positive and negative effects for NA and WA, respectively, and explained 84.6% and 85.0% of the variations for the southern and northern populations, respectively just a 7% and 1% more than the density alone (Table 1).

Overall, these PA-NA relationships were strongly consistent with each other and with several studies discussed above, where density was the major determinant of annual production rates across spatial scales (sites, streams, and populations) and years with only a weak effect of the mean annual weights, despite substantial differences in growth among populations.

3.3 Turnover Rates: Cohort Pc/Bc Ratio and Annual Pa/Ba Ratio

3.3.1 Cohort Pc/Bc Ratios

The overall lack of information on cohort production rates underlies an overall lack of information on cohort Pc/Bc ratios. As expected from the month-to-month variation in the cohort production shown in Fig. 3, the monthly Pc/Bc ratios precisely match the sigmoidal growth patterns. In this sigmoidal pattern, monthly Pc/Bc ratios maximize at around Pc/Bc = 1 from April to June and decline nearly linearly down to the mid-autumn or early winter when growth, production, and these ratios are nil.

Elliott (1993) for the BR study site reported a rather constant value at Pc/Bc = 5.5 within the range Pc/Bc = 4.8–7.8 over 22 cohorts. Lobon-Cervia et al. (2011) reported a similar range Pc/Bc = 3.0–7.0 over 16 years at 12 sites of the Rio Esva in northern Spain, shown in Fig. 12.

Based on a new nested ANOVA for this Rio Esva data set, we observed significant differences ($P < 0.001$) among sites and among cohorts with a >60% difference among sites, Pc/Bc = 7 relative to Pc/Bc = 4.3, and less different, but still significant, among cohorts, Pc/Bc = 5.7 relative to Pc/Bc = 4.4 (Fig. 12). A more detailed visual analysis and fits of several nonlinear models highlighted an asymptotic relationship where at low recruitment, these ratios increase more or less linearly until they reach an asymptotic value that remains constant at higher recruitment levels. An asymptotic Model 4 proved to be the most plausible fit for the whole data set pooled and demonstrated a significant ($P < 0.001$) fit explaining 46% of the variation among sites and years (Fig. 13a), with an asymptotic value at Pc/Bc = 6 (see Table 1 for details).

Interestingly, in a comparison of the Pc/Bc ratios between the two sets of populations, 82 cohorts of the slow-growing D1, BR, and D2 populations *vs.* 127 cohorts of the fast-growing populations, we observed significant differences (ANOVA, $P < 0.001$) with higher Pc/Bc = 5.7 in the slow-growing populations relative to Pc/Bc = 4.7 in the fast-growing populations. We detected no relationship between these ratios and the mean weights; however, visual inspections and fits of the asymptotic Model 4 to the 82 cohorts of the northern populations (Fig. 13b) were also significant and explained 60% of the variations of Pc/Bc ratios (see Table 1 for model parameters).

A comparison between the plots and fitted models of Fig. 13a, b emphasizes that the asymptotic values were very similar at Pc/Bc = 6. However, these ratios are typically <6 in the fast-growing populations, whereas values = >6 appear the rule rather than exception in the slow-growing populations. Moreover, the recruitment values upon which the trajectories change direction toward an asymptotic or constant value differed markedly between the two sets of populations. While in the fast-growing populations this threshold occurred at around RC = 0.5 ind m^{-2}, in the slow-growing populations, a disproportionally higher number of recruits is needed to reach the asymptote at around RC = 2.5 ind m^{-2}. Independent of other ancillary factors operating at a population scale, the Pc/Bc ratios = 6 appear to be near the maximum in all populations and depend tightly on recruitment.

3.3.2Annual Pa/Ba Ratios Since Chapman (1978), it has been currently assumed that values of Pa/Ba ratios are typically around two and may otherwise be species-specific (Kwak and Waters 1997), depending on the population age structure (Waters et al. 1990; Waters 1992), and vary somewhat in relation to warmer/colder habitats (Chapman 1978) and across years (Elliott 1993). Several authors have further suggested several patterns of Pa/Ba, including declining Pa/Ba with the increased number of age-classes (Waters 1992), being the reciprocal of mean age and mean life span (Allen 1971, Leveque 1978); a weight-at-maturity dependent log–log negative relationship (Banse and Moser 1980) and an allometric form as: Pa/Ba = a $W^{-0.35}$ (Randall and Minns 2000; Randall 2002).

Several studies have reported on stream salmonid Pa/Ba ratios, including native and introduced populations. Mann and Penczak (1986) summarized a range of Pa/Ba = 0.48–2.7 for stream salmonids, similar to Pa/Ba = 0.6–2.5 for three salmonids in two Minnesota streams (Waters et al. 1990). A similar range of Pa/Ba = 1.0–1.6 was reported for brown trout populations of central Spain (Almodovar et al. 2011), whereas Kwak and Waters (1997) reported an average of Pa/Ba = 1.03 for 13 brown trout populations of Minnesota streams; for a 3 age-classes of a brown trout population, Elliott (1993) reported consistently higher mean values at Pa/Ba = 2.73 within the range 2.28–4.02.

Based on the aforementioned large-scale study of resident brown trout in Rio Esva streams, Lobon-Cervia et al. (2011) examined Pa/Ba ratios at the same 12 sites over 16 years and observed an intriguing, extensive range of Pa/Ba between 0.8 and 2.5 (Fig. 14).

Based on a new, nested ANOVA for the effects of the stream, site, and year, we observed rather unclear results with a significant ($P < 0.001$) effect of the site that only explained 36.7% of the variance, of year that only explained 20.2% and a non-significant effect of stream. Remarkably, an analysis of the potential effects of weight on these ratios at any spatial and temporal scale also detected no consistent relationships. Our analyses were fully inconsistent with any negative relationship of these ratios with the mean age and mean life span even more inconsistent with a negative, allometric relationship and still less consistent with a warmer-cooler relationship, that is, between the southern warmer streams *versus* the northern cooler streams.

A plot of all the data set pooled versus the mean annual densities (NA, ind m^{-2}) highlighted that typically, most Pa/Ba values were under the expected Pa/Ba = 2 but highlighted a consistent trajectory, quite similar to that in Fig. 13. The values of Pa/Ba increase linearly at low densities and shift direction toward an asymptotic value at a threshold around NA = 0.7 ind m^{-2}, beyond which Pa/Ba remains constant at around Pa/Ba = 2. The fit of Model 4 to this relationship significantly explained 42% of the variation of Pa/Ba across the broad range of density variations (constants in Table 1) shown in Fig. 15a, where the asymptotic value equal two is attained at the highest NA = 1.5 ind m^{-2}.

Data available for the D2 populations indicated that, with a few exceptions, Pa/Ba values were also typically <2 (Fig. 15b) probably because this is a 5 age-classes population. A plot of these ratios *versus* annual density highlighted a quite similar trajectory where, unlike Rio Esva, Model 2, proved to be the most plausible (constants in Table 1) with a predicted Pa/Ba = 2 at the maximum density observed NA = 1.5 ind m^{-2}.

4 Relationships Between Cohort PC and Annual PA Production Rates and Between the Turnover Rates, Cohort Pc/Bc and Annual Pa/Ba

Given that annual production rates and the Pa/Ba ratios depend on cohort production rates, we deemed that an exploration into potential relationships between them was worthwhile. The similarity between the PA and PC with a mean at PC = 12 g m^{-2} and PA = 11.0 g m^{-2} year and a maximum at 35–40 g m^{-2} suggests potential relationships as much as between the Pc/Bc and Pa/Ba ratios. The analysis previously reported by Lobon-Cervia et al. (2011) for the Rio Esva sites highlighted several patterns we revisit here.

Given that "site" was demonstrated to have strong effects on all these production rates attributes, we focused on site-specific relationships. A simple exploration revealed that mean annual density (NA ind m^{-2}), cohort production (PC, g m^{-2}), annual production (PA, g m^{-2} year), and the Pc/Bc and Pa/Ba ratios were highly, linearly related with site-specific recruitment (RC, ind m^{-2}), as shown in Fig. 16 (see Table 1 for details).

Finally, we examined relationships between cohort and annual production rates estimated from the years of emergence and between the Pc/Bc and Pa/Ba ratios. As expected based on the patterns observed in Fig. 15, there was a direct, positive linear relationship between annual, PA and cohort production PC rates. This relationship showed to be very close to equality and the fits of a regression with intersect at zero ($PA = b \cdot PC$), *vs.* a linear Model 1 ($PA = a + b*PC$), which demonstrated the same probability (50%) to the correct model. So, in Fig. 17, these rates PA and PC are plotted under the regression PA = 0.99 PC, significant at $P < 0.001$ (see Table 1 for details).

The turnover rates, Pa/Ba, and Pc/Bc were also positively linearly related following Model 1 that proved to be the most plausible model, given the data, yet only explained 33% of the variation (see Table 1 for details). At high recruitment values, this is roughly equivalent to a relation Pa/Ba = Pc/Bc − 4, where 4 is the number of age-classes (Fig. 18).

Overall, all production-related attributes examined above are strongly interrelated within and among populations. Apparently, along the environmental heterogeneity of the streams gradients, the quality of the habitat capable to sustain recruits is site-specific and varies from year to year in determining site-specific and annual-specific recruitment levels that, in turn, determine the subsequent density and production rates during the lifetime and the corresponding the Pc/Bc ratios. While recruitment, density, and production rates vary widely within and among populations, both the Pc/Bc and Pa/Ba ratios increase toward fixed maximum values at Pc/Bc = 6 and Pa/Ba = 2. Interestingly, the heterogeneity of the streams with sites of low, intermediate, and high recruitment levels persists over the years, and this pattern also explains why differences among sites also persist over time.

5 Is There a Maximum Limit of Production Rates in Stream Salmonids?

This question of whether or not there is a maximum limit of production rates in stream salmonids may be asked in several different ways. For example, this and other studies coincided to report maximum annual rates at around 40–45 g m^{-2} year. Is this the maximum production rate of stream-dwelling salmonids? Or alternatively, is it possible to find natural populations with higher recruitment and higher growth rates determining higher production rates than those observed?

The first issue to be revisited is the role of growth on cohort production rates, whose relations are plotted in Fig. 7 for the Rio Esva data set and in Fig. 9. The two groups of populations appeared to demonstrate significant negative relationships, but the relationships explained less variance than expected, perhaps suggesting weak effects of growth. Given such big differences in growth within and among populations, such fuzzy relationships confuse more than clarify the role of growth.

A visual inspection of the mean cohort weights (WC, g) plotted versus recruitment (RC, ind m^{-2}) for the two sets of populations pooled, including an overwhelming range of both mean weights (16.0–82.0 g) and recruitment (0.1–15.6 ind m^{-2}), highlighted a continuous and rather intriguing relationship (Fig. 19), where growth appears to be related to recruitment in two different, separate phases. An early, very steep phase at low recruitment values followed by a shallow slope separated by a breakdown? threshold, upon which recruitment appeared to have a weak or practically no effect on growth.

In this two-phase recruitment-dependent growth relationship, a very steep declining slope on the left wing implies severe growth declines with a small increment of recruitment until a breakdown threshold point at a recruitment around RC = 1.5 ind m^{-2} that abruptly separates the two phases. The opposite occurs along the right-side wing suggesting a rather constant growth with increased recruitment, where increments of recruitment affect little or do not affect growth.

To determine the real effect of recruitment on growth, we estimated the slopes of this two-phase relationship. We explored several nonlinear regressions and the most plausible was a broken line (Model 5), whose fit yielded the following slopes and breakdown threshold:

slope for the left-side wing, b = −28.2,
slope for the right-side wing, b1 = −0.55,
breakdown point M = 1.3

The two slopes, b and b1, were highly significant at $P < 0.001$ indicating that the second slope was significantly different from a slope = 0 or non-constant, meaning that growth decreases significantly with increased recruitment above the breakdown threshold, or in other words at high recruitment levels.

These data split into two sets from above and below the breakdown point and plotted *versus* recruitment, and then compared with the recruitment-dependent production rates of Fig. 8, highlighted a particularly striking pattern, strongly consistent in the two sets of populations (Fig. 20). Despite remarkable differences in recruitment and growth between the two sets of populations, a declining recruitment-dependent growth and an increasing recruitment-production rates enhance the occurrence of a continuous trade-off between recruitment, growth, and production. The lowest recruitment is consistently related to the highest growth and to the lowest production rates. At the opposite extreme, the highest recruitment is related to the lowest growth and the highest production until asymptotic values at the highest recruitment, upon which the interaction between recruitment and growth does not yield any higher production rates and remains constant.

On the other hand, previous studies on the fast-growing, southern (Lobon-Cervia and Rincon 2004; Lobon-Cervia 2007) and the slow-growing northern populations (Lobon-Cervia et al. 2017) have shown that recruitment is essentially determined by the discharge conditions of the streams soon after emergence, when the youngest juveniles abandon the redds in search for feeding positions in the water column.

In the fast-growing populations, year-to-year variation in recruitment describes a parabolic trajectory over stream discharge in March (Hm^3 month^{-1}), the month that covers the earliest life stages of the youngest juveniles, and increases from a minimum in years of lowest discharge up to maximum at average discharge. At this point, recruitment maximizes and then declines toward the years of increased discharge to attain minimum values again, in years of maximum discharge. Thus, recruitment is similarly low in the years of lowest and highest discharge and maximizes in years of average conditions (Fig. 21a). For parabolic model fitting and constants see Lobon-Cervia et al. (2017).

Likewise, discharge-dependent recruitment also occurs in the three Danish, D1 and D2 populations, which are subject to the same rainfall-fed discharge regime and fluctuate simultaneously over time. Given huge differences in recruitment among these populations (see above), we re-scaled recruitment for the years 1979–1999 as the % of the highest recruitment considered to be 100 for every single population and described the new values after log-transformation. A quite similar two-phase discharge-dependent recruitment was highlighted for this set of populations (Fig. 21b). Note that here, discharge refers to the month of April when trout emerge in these colder streams, a month later than in the southern populations and is expressed in l/s. In these populations, rather than a parabolic trajectory, recruitment described an ascent/descent, threshold-like patterns where, similar to the fast-growing populations. Recruitment attained the lowest values in years of minimum discharge on the left-side wing of this relationship and increased up to a threshold at intermediate discharge, upon which it declined linearly in the years of increased discharge (Lobon-Cervia et al. 2017).

In the two sets of populations, the rainfall-discharge conditions shift from year to year, sometimes dramatically, but for the most, show rather intermediate conditions with the extremes, too rainy or too dry being less common (Fig. 21a, b). Apparently, the study time periods of the two sets of populations appeared long enough to have captured the maximum ranges of rainfall-discharge conditions and, therefore, the maximum variations where recruitment was highest in years of intermediate discharge and lowest at the two extremes of discharge.

Shifts from year to year in stream discharge imply that recruitment and the subsequent cohort production rates vary from year to year following the vagaries of the spring rainfall. Thus, in the most common populations composed of 3–5 age-classes, the maximum annual production may only be attained when 3–4 successive years of intermediate discharge conditions enhance successive maximum recruitment that, in turn, maximizes cohort production and subsequently, annual production rates.

During the study years of the fast-growing populations, this set of conditions only occurred 1 or 2 years before the commencement of the study, i.e., 1984–1985, and continued during four successive 1986–1989 years when discharge matched successively intermediate conditions around 30 and 50 Hm^3 and recruitment attained an average >0.9 ind m^{-2}. Subsequently, the cohorts production rates maximized at PC = 35 g m^{-2} and the annual production rates maximized at around >35 g m^{-2} year. Somewhat surprising, these environmental circumstances never happened again during the 30 years of study.

A similar process occurred in the slow-growing populations where during the years 1976–1979, discharge attained intermediate conditions, around 60 L/s, recruitment maximized at 3–4 ind m^{-2} and the subsequent cohort and annual production attained the highest rates. Apparently this occurred again in the years 1989–1992 when discharge attained rather intermediate values and the subsequent recruitment, cohort production and annual rates maximized.

The unpredictable character of the discharge-recruitment relationships, the strong recruitment- and density-dependent cohort and annual production rates and the trade-offs between recruitment, growth and production rates explain consistently why production rates observed in this study and in those reported by other studies across populations and geographical scales show maximum rates at around 40–45 g m^{-2} year. These observations also explain why the majority of the studies including this one, have reported low to intermediate production rates. As a consequence, it is probably conceivable but certainly most unlikely, that other, natural, populations may attain production rates >40–45 g m^{-2}, nor should they exhibit Pc/Bc ratios >6 and Pa/Ba ratios >2.

6 Concluding Remarks

Here, we have attempted to add pieces to the Hunt (1974) puzzle by examining, in the very long term and at large geographical scales, unexploited, natural populations with no human impact and that covered a wide range of size, growth, density, and production rates of stream-living resident, lake-migratory and sea-migratory salmonid populations. We summarized production rates in the form of PC and PA and their relationships with major population attributes, recruitment, and density, in the form of RC, NA, NM, growth, in the form of WC and WA, and the cohort and annual turnover rates, Pc/Bc and Pa/Ba and their asymptotic relationships with recruitment and density. We described all these relationships in simple linear and non-linear mathematical models and further argued that the maximum production rates in other natural populations might not be higher than those already observed across available populations and studies.

We expect that, in a variety of different ways, our findings may be applied for predictive purposes with no need of additional ancillary, environmental, or intrinsic factors operating on growth and mortality—as they necessarily do, but in no case we considered were their effects sufficiently strong to affect any of these relationships—when developing energy budgets for specific populations, to develop fishery models, for environmental impact assessments, and as reference for restoration programs.

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Influence of Streamflow on Productivity of Stream Type Chinook Salmon Populations in the Salmon River Drainage, Idaho

James V. Morrow Jr and David L. Arthaud

Abstract We compared whole life cycle population productivity to population density and streamflow experienced by rearing juveniles for ten Chinook salmon populations in the Salmon River drainage of central Idaho, USA. Three of the populations were in drainages with heavily developed water resources (developed drainages) and seven were in drainages with very little water use (undeveloped drainages). For two of the populations, one in a developed and one in an undeveloped drainage, we also compared productivity measured at the juvenile outmigrant and smolt life stages to population density and rearing streamflow. Productivity was positively related to flow experienced by rearing juveniles across the entire range of flows. The strength of the relationships increased with age, with the weakest and strongest relationships, respectively, for the outmigrant and adult return life stages. Both population size and productivity were substantially higher in undeveloped than in developed drainages, but the relationships of population productivity and rearing flow were similar. Productivity was negatively related to population density in both developed and undeveloped drainages and, as with flow, the strength of the relationships increased with age. Adding population density to the regression models usually did not improve relationships for flow, possibly due to high leverage of the low population density data points, especially for undeveloped drainages. Removing all data points in the lowest 25 percentile population density increased the strength of the productivity versus rearing flow relationships in both developed and undeveloped drainages, but did not appreciably change the slopes of the relationships. The positive relationships across the entire range of flows suggest that instream flows should be protected and enhanced whenever possible.

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Keywords Instream flow · Flow restoration · Density dependence · Chinook salmon · Population productivity · Climate change

1 Introduction

Anadromous salmonids have been an important part of the culture and economy of the Pacific Northwest for thousands of years (NRC 1996; Campbell and Butler 2010; Gislason et al. 2017). Large-scale water diversion for irrigation began in the 1860s and there are currently more than 2 million hectares of irrigated lands in the Columbia River drainage (NWPPC 2021). The adverse effects of flow depletion on anadromous salmonid fisheries have been known since at least the early 1950s (Gooding and Hatch 1951), and efforts to regulate streamflow to protect aquatic resources began in the mid-twentieth century (Giger 1973). Although efforts to protect flows needed to support anadromous salmonids have been ongoing for approximately 70 years, there remains considerable controversy on the methods used to determine flows needed to protect aquatic resources (Railsback 2016, 2017).

Habitat-based flow models were developed in the 1970s (Railsback 2016) and continue to be widely used. However, when applied to stream dwelling salmonids, habitat-based models often produce outputs that are negatively related to standing stock (Shirvell 1986; Bourgeios et al. 1996) or population productivity (Beecher et al. 2010) and often predict "optimal" flows that are "irrationally low" (Hardy et al. 2006). Efforts to improve habitat-based models have been ongoing, with typical solutions being to add hydrologic and/or habitat parameters to better approximate the ecological processes that drive salmonid growth and/or survival. Some of the recently described flow models incorporate two-, and sometimes three-, dimensional hydrologic models; invertebrate drift; bioenergetic-based habitat suitability curves; and holistic habitat descriptions. These refinements have improved the ability of habitat-based flow models to predict salmonid numbers, distribution (Hayes et al. 2007), and production (Rosenfeld et al. 2016), but even relatively sophisticated models can underestimate optimal flows (Rosenfeld et al. 2016; Rosenfeld and Naman 2021). Recent efforts have focused on causes of, and possible solutions for, biases of habitat-based flow models (Railsback et al. 2021; Rosenfeld and Naman 2021).

Although relatively sophisticated habitat-based flow models are needed to accurately predict production or productivity of stream dwelling salmonid populations, the relationships of fish population demographics and discharge can often be described using relatively simple statistical models. Studies comparing salmonid growth or population demographics to streamflow, or precipitation, were ongoing as early as the late 1930s (Smoker 1953). These studies typically indicate that low spring, summer, or fall flow during juvenile rearing is correlated with low growth, year class strength, production, or population productivity (Smoker 1953; Mathews and Olson 1980; Nislow et al. 2004; Elliott et al. 1997; Deegan et al. 1999; Arthaud et al. 2010; Beecher et al. 2010; Hvidsten et al. 2014; Lobón-Cerviá 2014; Kovach et al. 2016; Uthe et al. 2019). Most describe positive relationships across the range of flows studied, but at least two describe curvilinear relationships, with both high and low flows corresponding to relatively low population productivity (Lobón-Cerviá 2004, 2014). Although most studies describe positive salmonid/flow relationships, some describe negative relationships (Smith 2000; Lobón-Cerviá and Mortensen 2005; Neuswanger et al. 2015), and one study described a positive effect of precipitation, but a negative effect of flow, on population productivity (Jones et al. 2020). The relative ease of detecting population versus flow relationships for a wide variety of salmonid populations suggests that flow is a key driver of habitat quality and/or quantity for stream dwelling salmonids.

In 2010, we published a paper describing the relationships of productivity and flow experienced by rearing juveniles for two Chinook salmon populations (the Lemhi River and Marsh Creek) in the Salmon River drainage in Idaho, USA (Arthaud et al. 2010). That paper described productivity at three life stages: Outmigrants from the natal tributaries, smolts surviving to the first mainstem dam on the Snake River, and adults returning to the natal tributaries; for the 1995–2005 brood years. Since Arthaud et al. (2010) was published, juvenile production estimates have been completed for an additional 8 year classes for the Marsh Creek population, and for an additional 11 year classes for the Lemhi River population. Other developments that have occurred since publication of Arthaud et al. (2010) include an improved knowledge of the effects of population density on juvenile production of Salmon River Chinook salmon (Walters et al. 2013), improved knowledge of the effects of climate change on Salmon River Chinook salmon (Crozier et al. 2021), and completion of numerous habitat restoration actions in the Lemhi River drainage. In this chapter, we incorporate the longer time series, and population density, into the productivity versus flow relationships described in Arthaud et al. (2010). We also expand on Arthaud et al. (2010) by comparing population productivity to flow experienced by rearing juveniles for ten Salmon River Chinook salmon populations. Three of these populations spawn and rear in drainages with heavily developed water resources, and seven spawn and rear in drainages that are essentially unaffected by water use.

2 The Salmon River

The Columbia River is the largest river, by volume, in the Pacific drainage of North America and the Snake River is the largest tributary of the Columbia River. The Salmon River is the largest tributary, by drainage area, of the Snake River, encompassing 36,000,000 ha, all within the state of Idaho, USA (Fig. 1). The mouth of the Salmon River is 825 km upstream from the Pacific Ocean and the mainstem is approximately 647 km long, making it one of the longest remaining undammed rivers in the contiguous USA. The Salmon River drainage contains large areas of

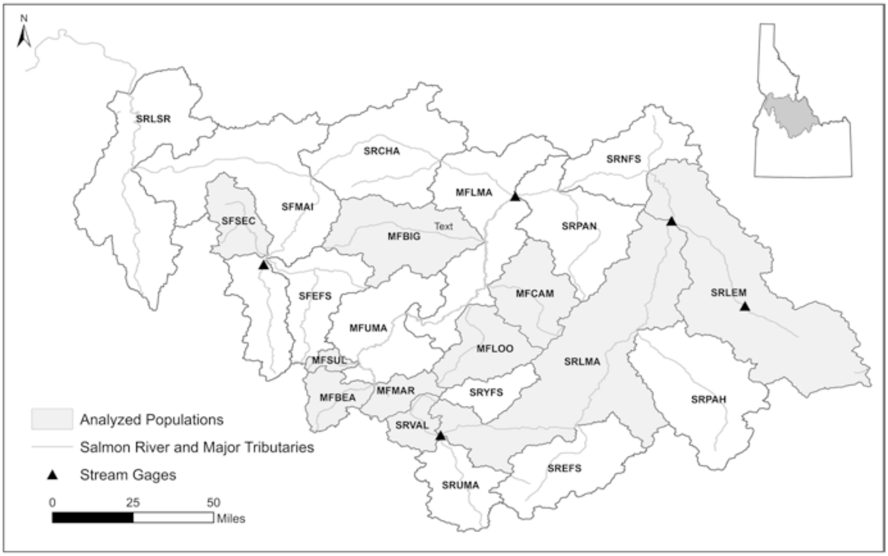

Fig. 1 Boundaries of the 22 spring/summer Chinook salmon populations in the Salmon River drainage, Idaho. The ten shaded populations were analyzed in this chapter. These are: South Fork, Secesh River (SFSEC); Middle Fork, Big Creek (MFBIG); Middle Fork, Sulphur Creek (MFSUL); Middle Fork, Bear Valley Creek (MFBEA); Middle Fork, Marsh Creek (MFMAR); Middle Fork, Loon Creek (MFLOO); Middle Fork, Camas Creek (MFCAM); Salmon River, Valley Creek (SRVAL); Salmon River, lower mainstem (SRLMA); and Salmon River, Lemhi River (SRLEM). The 12 unshaded populations were not analyzed. These are: Salmon River, Little Salmon River (SRLSR), South Fork, mainstem (SFMAI), South Fork, East Fork South Fork Salmon River (SFEFS); Salmon River, Chamberlin Creek (SRCHA); Middle Fork, upper mainstem (MFUMA); Middle Fork, lower mainstem (MFLMA); Salmon River, Panther Creek (SRPAN), Salmon River, North Fork Salmon River (SRNFS); Salmon River, Pahsimerio River (SRPAH); Salmon River East Fork Salmon River (SREFS), Salmon River, upper mainstem (SRUMA); and Salmon River, Yankee Fork Salmon River (SRYFS)

undeveloped land, including 1,070,000 ha of designated wilderness, but it also has large developed areas with approximately 75,728 ha of irrigated agriculture. Most of the irrigation is via surface water diversions and most of the irrigated land is in the upper portion of the drainage. Water diversion for irrigation reduces flow throughout the mainstem Salmon River and many tributary streams. Prior to restoration activities in the late 1990s and early 2000s, the upper mainstem Salmon River and two major tributaries, the Lemhi and Pahsimeroi Rivers, were regularly dewatered during the irrigation season. Although the mainstem Salmon, Lemhi, and Pahsimeroi Rivers are no longer completely dewatered, many smaller tributaries remain completely dewatered during the irrigation season, and flow throughout the mainstem Lemhi River, Pahsimeroi River, and the upper 266 km of the mainstem Salmon River remains greatly reduced. Although flow is greatly depleted throughout much of the upper portion of the Salmon River drainage, water resources in the lower portion of the drainage are relatively undeveloped, and flow in the two largest

Salmon River tributaries, the Middle Fork and South Fork Salmon Rivers, is largely unaffected by water use.

The Salmon River drainage supports six native and several introduced salmonid species.[1] Of the introduced salmonid species, only brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) are widespread, and the others are currently confined to high mountain lakes. There are two stocks of Chinook salmon (*Oncorhynchus tshawytscha*) in the Salmon River drainage, Snake River fall Chinook salmon and Snake River spring/summer Chinook salmon. Snake River fall Chinook salmon are part of a single population that spawns in the lower 140 km of the mainstem Salmon River[2] and that typically exhibit an "ocean type" life history with juveniles migrating to the ocean during the spring of emergence. In contrast, there are 22 independent populations (21 extant[3]) of Snake River spring/summer Chinook salmon in the Salmon River drainage. They spawn in the upper 229 km of the mainstem Salmon River, in all of the major tributaries, and in many of the smaller streams distributed throughout the drainage; and they typically rear for a year in freshwater (i.e., stream type) before migrating downstream to the ocean. Both Snake River fall Chinook salmon and spring/summer Chinook salmon are listed as threatened under the Endangered Species Act. For the remainder of this chapter, Snake River spring/summer Chinook salmon will be referred to as simply "Chinook salmon."

Although there are no mainstem dams in the Salmon River drainage, there are eight mainstem dams on the Snake and Columbia Rivers that Chinook salmon must negotiate on their migration to and from the Pacific Ocean. Dam construction began in 1933 and extended through 1975, when the Lower Granite Dam was completed on the Snake River. Chinook salmon redd surveys in the Salmon River drainage began in the early 1950s and were standardized in 1957. The populations generally declined from the beginning of standardized redd surveys through the early 1990s, when Chinook salmon were listed under the ESA and received Federal protection.

Hatchery supplementation of Chinook salmon in the Salmon River drainage began in the late 1960s and the current stocking rate is 2–3 million juveniles per year. However, stocking has largely been confined to eight populations, with most populations receiving no supplementation for many years and at least nine

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[1] The salmonid species that are native to the Salmon River drainage are: mountain whitefish (*Prosopium williamsoni*), cutthroat trout (*Oncorhynchus clarki*), bull trout (*Salvelinus confluentus*), rainbow trout/steelhead (*O. mykiss*), sockeye salmon/kokanee (*O. nerka*), and Chinook salmon (*O. tshawytscha*). Introduced salmonid species that are established in the Salmon River drainage are: brook trout (*S. fontinalis*), lake trout (*S. namaycush*), Arctic char (*S. alpinus*), Arctic grayling (*Thymallus arcticus*), and brown trout (*Salmo trutta*).

[2] Currently occupied habitat for the single extant population of Snake River Fall Chinook salmon includes the lower 398 km of the mainstem Snake River and the lower portions of the larger tributaries to the lower Snake River, including the lower 140 km of the Salmon River.

[3] Mine discharge in the 1960s degraded water quality in Panther Creek and the Panther Creek Chinook salmon population was declared functionally extinct in the 1990s. However, Chinook salmon began spawning in Panther Creek again in 2001 and habitat in the Panther Creek drainage may eventually contribute to recovery of Snake River spring/summer Chinook salmon.

populations that have never been supplemented with hatchery fish. Most directed harvest of wild Chinook salmon stopped in the 1980s and is currently limited to a few small, and very localized, tribal fisheries. The low levels of directed harvest, the large number of populations with no hatchery supplementation, and the long time series of standardized population surveys make the Salmon River drainage ideal for investigating habitat-related drivers of annual variability in population productivity. The heavy development of water resources in large portions of the drainage, and the relative abundance of streamflow gage data, makes the drainage particularly well suited for investigating the effects of variations in streamflow on Chinook salmon.

The 22 populations of Chinook salmon in the Salmon River drainage are grouped into three major population groups (MPGs). These are: (1) The upper Salmon River MPG that includes nine populations that spawn in the main Salmon River and tributaries upstream from the confluence of the Middle Fork and main Salmon Rivers; (2) the Middle Fork Salmon River MPG that includes eight populations that spawn in the Middle Fork Salmon River drainage and one that spawns in Chamberlin Creek; and (3) the South Fork Salmon River MPG, that includes three populations that spawn in the South Fork Salmon River drainage and one that spawns in the Little Salmon River. Eight of the nine populations in the upper Salmon River MPG, and the Little Salmon River population, are affected by surface water diversions to the extent that flows are substantially reduced in large portions of the spawning and rearing areas. In contrast, the nine populations in the Middle Fork Salmon River MPG, and the three populations in the South Fork Salmon River drainage, spawn and rear in habitat that is nearly unaffected by water diversions. Twenty of the 21 extant Chinook salmon populations in the Salmon River drainage are currently at high risk of extinction due to low abundance and productivity (NMFS 2017).

3 Impacts of Streamflow on the Lemhi River and Marsh Creek Chinook Salmon Populations

The Lemhi River drainage is in the upper Salmon River MPG. Water in the Lemhi River drainage is diverted to irrigate approximately 24,000 ha of agricultural lands. Prior to habitat restoration, this water use dewatered the lower reaches of all but three Lemhi River tributaries, and a portion of the lower mainstem Lemhi River, during portions of the irrigation season. The mainstem Lemhi River is no longer dewatered and at least five tributary streams have been partially reconnected to the mainstem, but water use continues to dewater most of the Lemhi River tributaries and greatly reduces flow in the mainstem. Marsh Creek is a tributary of the Middle Fork Salmon River and the Marsh Creek Chinook salmon population is part of the Middle Fork Salmon River MPG. The Marsh Creek drainage historically contained approximately 129 ha of irrigated land, which reduced flow in one tributary stream (Knapp Creek) and had a small effect on flow in mainstem Marsh Creek. But due to habitat restoration, only 16 ha of irrigated agriculture remains. Consequently, flows in the Marsh Creek drainage are essentially unimpaired by water diversions.

Chinook salmon spawn in late summer and juveniles emerge from the spawning gravel during late winter or early spring of the subsequent year. Juveniles typically rear until the following spring before migrating downstream to the ocean. Arthaud et al. (2010) compared egg-outmigrant and egg-smolt survival to rearing flow for 9- and 10-year classes, respectively, for the Marsh Creek and Lemhi River Chinook salmon populations. In these comparisons, outmigrants were enumerated at the juvenile screw traps located at the downstream end of the spawning reaches, smolts were defined as juveniles migrating past Lower Granite Dam, and rearing flow was characterized as average May and average August flow in the natal tributary during the year of emergence (i.e., Brood Year + 1). Arthaud et al. (2010) found a significant relationship between juvenile survival and flow at the outmigrant stage for the Lemhi River population, but not until the smolt stage for Marsh Creek Chinook salmon. Arthaud et al. (2010) also found that survival versus rearing flow relationships were similar for flows measured in May and August and that rearing flow influenced adult returns for both populations.

Since Arthaud et al. (2010) was published, accessibility of Chinook salmon population and streamflow data has improved dramatically. We obtained estimated numbers of juvenile outmigrants, and the number of smolts surviving to Lower Granite Dam, from the Idaho Department of Fish and Game (IDFG) Anadromous Emigrant Monitoring annual reports. We obtained redd survey data from IDFG Salmon Spawning Ground Survey reports, IDFG Natural Production Monitoring and Evaluation reports, IDFG Adult Chinook Salmon Monitoring reports, and unpublished data obtained from the Idaho Fish and Wildlife Information System (IFWIS). We used streamflow gage data from the Middle Fork Salmon River near Shoup gage (USGS 13310199) for the Marsh Creek comparisons, and from the Lemhi River at McFarland Campground gage for the Lemhi River comparisons. The reports and websites used to obtain data for this chapter are listed in Table 1.

We compared juvenile productivity to rearing flow for 21-year classes of Lemhi River Chinook salmon and 17-year classes of Marsh Creek Chinook salmon. We used two measures of juvenile productivity: (1) Outmigrants, enumerated at the screw trap per redd (outmigrants/redd), which is analogous to egg-outmigrant survival in Arthaud et al. (2010); and (2) smolts surviving to Lower Granite Dam per redd (smolts/redd), which is analogous to egg-smolt survival in Arthaud et al. (2010). We also compared whole life cycle productivity (return redds/stock redds) to rearing streamflow for 19-year classes of Lemhi River Chinook salmon and 18-year classes of Marsh Creek Chinook salmon. We log transformed all productivity measures.

We used gage data from the Middle Fork Salmon River near Shoup (USGS 13310199) and the Lemhi River at McFarland Campground gages, respectively, to characterize rearing flow in Marsh Creek and the Lemhi River; and we defined rearing flow as average May through August flow during the year of emergence (i.e., brood year + 1). We used the average May-August flow to address the year-to-year variability in hydrographs in the Lemhi River, where any month during the

Table 1 Data sources for Chinook salmon outmigrants, Chinook salmon redds counted in spawning reaches, and streamflow in Chinook salmon habitat

Data type	Source
Juvenile outmigrants	Idaho Department of Fish and Game—Idaho Anadromous Emigrant Annual Reports for 2016, 2017, and 2018.
Smolts surviving to Lower Granite Dam	
Redds counted in spawning habitat	Idaho Department of Fish and Game—2000 Salmon Spawning Ground Surveys
	Idaho Department of Fish and Game—Idaho Natural Production Monitoring and Evaluation, 2012 and 2014 Annual Reports
	Idaho Department of Fish and Game—Idaho Adult Chinook Salmon Monitoring, 2015, 2016, 2017, and 2018 Annual Reports
	Unpublished data from Idaho Department of Fish and Game—Idaho Fish and Wildlife Information System, idfg.idaho.gov/data
	Unpublished data from the United States Forest Service, Rocky Mountain Research Station
Streamflow gages	United States Geological Survey gages: 13310700, 13310199, 13305000, 13302500, 13295000.
	Idaho Department of Water Resources—Aqua Info, https://research.idwr.idaho.gov/apps/hydrologic/aquainfo/Home/Data#!/

irrigation season can have the highest or lowest average flow, depending on year. For example, for the 21-year classes in this study, average flow was highest in May during 6 years, June during 8 years, July during 2 years, and August during 5 years and was lowest in May during 3 years, in June during 5 years, in July during 6 years, and in August during 7 years.

Productivity versus rearing flow relationships for the Lemhi River and Marsh Creek Chinook salmon populations are given in Fig. 2. Productivity of the Lemhi River Chinook salmon population, measured as outmigrants/redd, smolts/redd, and return redds/stock redd, was related to rearing flow. For the Marsh Creek population, productivity measured as outmigrants/redd was not related to rearing flow, the relationship of smolts/redd and rearing flow was suggestive, and the relationship of return redds/stock redd was significant. These results are consistent with Arthaud et al. (2010) in that productivity of both populations is influenced by rearing flow, but the relationships are apparent earlier in the life cycle for the Lemhi River population (Fig. 2). The trend of better relationships in later life stages could be due to the influence of flow on growth (see Harvey et al. 2006; Davidson et al. 2010; Teichert et al. 2010; Uthe et al. 2019) that manifests as survival in later life stages. For both populations, the relationships for the longer time series were more variable than those reported in Arthaud et al. (2010).

For both the Marsh Creek and Lemhi River Chinook salmon populations, the effect of population density on productivity became more pronounced as the life cycle progressed (Fig. 3), with relatively poor relationships for the outmigrant and smolts stages. This is possibly because population density initially influences size of rearing salmonids and only manifests itself as survival later in the life cycle (Lobon-Cervia 2007). Regardless, incorporating population density into the regression

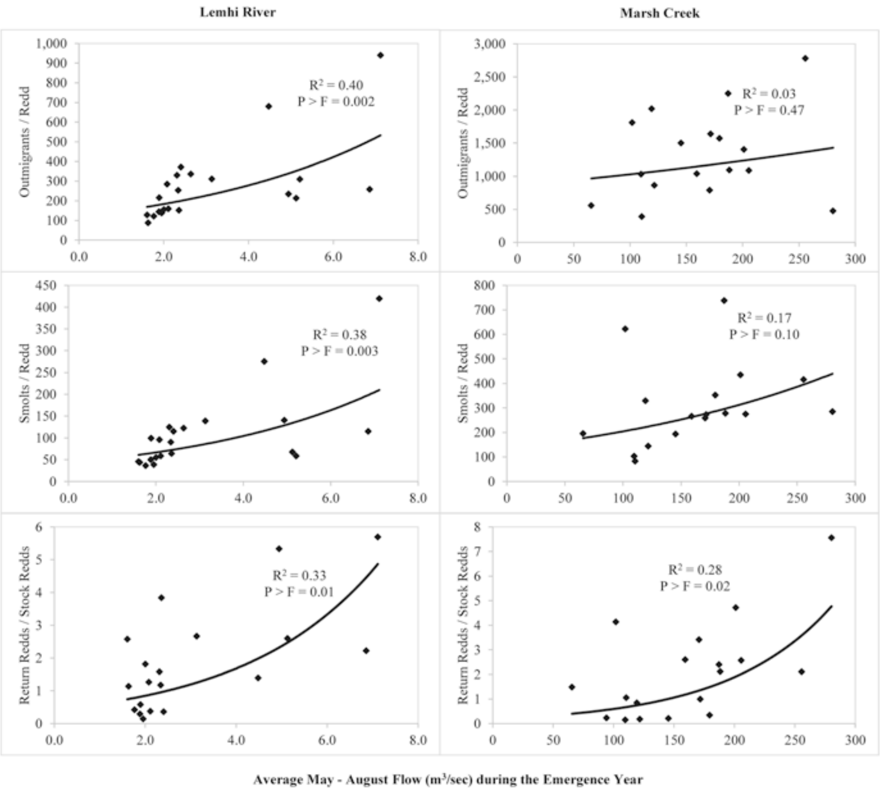

Fig. 2 Productivity of Lemhi River and Marsh Creek Chinook salmon populations versus average May–August flow (m^3) during the emergence year (i.e., the year following the brood year)

models did not improve the relationships of flow and outmigrants/redd or smolts/redd, for either population, probably due to the poor productivity versus density relationships for those life stages. Population density improved the relationship of flow and return redds/stock redds for the Lemhi River population (Fig. 4), but not for the Marsh Creek population. The lack of improvement for the Marsh Creek population could be due to high leverage of the data point with the lowest density (Fig. 3, Return Redds panel) and/or due to correlation between population density and flow for the Marsh Creek population. Neither of those conditions was as pronounced for the Lemhi River population.

Inclusion of population density improved the relationship of whole life cycle productivity and flow for the Lemhi River population but otherwise, it did not change the results. The comparison of population productivity versus rearing flow with the longer time series resulted in essentially the same findings as Arthaud et al. (2010), which are: (1) Flow during the juvenile rearing life stage is an important determiner of year class strength for both the Lemhi River and Marsh Creek Chinook salmon populations; (2) effects of rearing flow are more pronounced and are

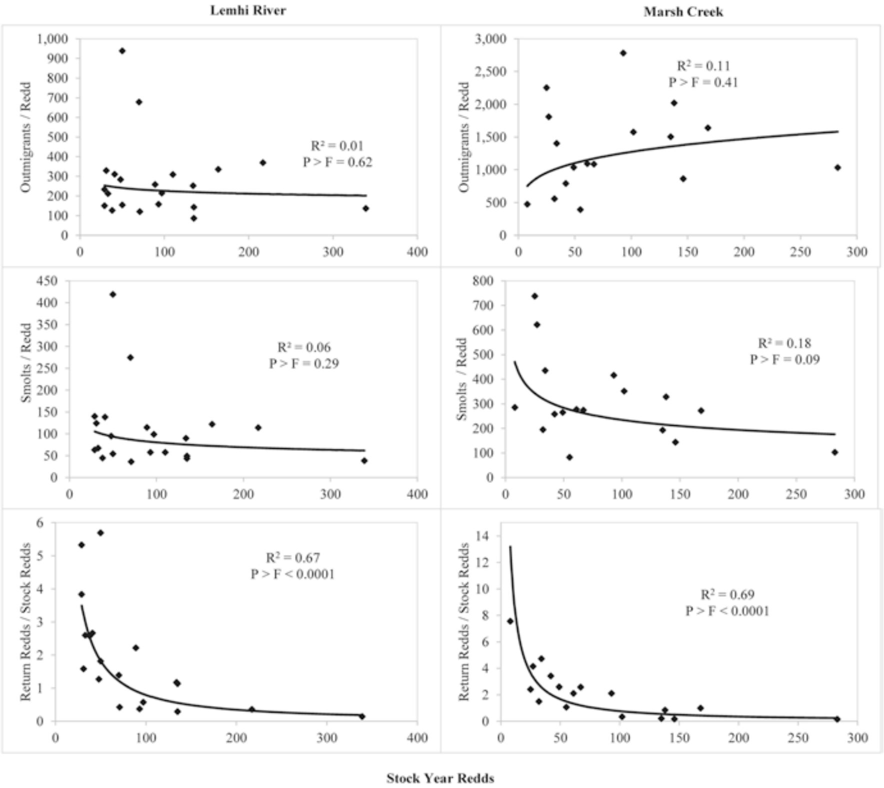

Fig. 3 Population productivity, measured at three life stages, versus population density (stock year redds) for the Lemhi River and Marsh Creek Chinook salmon populations

apparent at earlier life stages in the Lemhi River than in Marsh Creek; (3) there is no indication that population productivity is reduced by high flows during rearing; and (4) productivity of the Marsh Creek population is 2.4–2.8 times higher than productivity of the Lemhi River population. Streamflow appears to be a scarce resource for juvenile Chinook salmon rearing in habitat that is impaired by water diversions as well as those rearing in habitat with unimpaired flow.

4 Effects of Streamflow on Ten Salmon River Chinook Salmon Populations

Ten Salmon River Chinook salmon populations have had little or no hatchery supplementation since 1990 and have had consistent redd surveys since 1996 (Shaded in Fig. 1). Three of these populations are in the upper Salmon River MPG, five are in the Middle Fork Salmon River MPG, and one is in the South Fork Salmon River

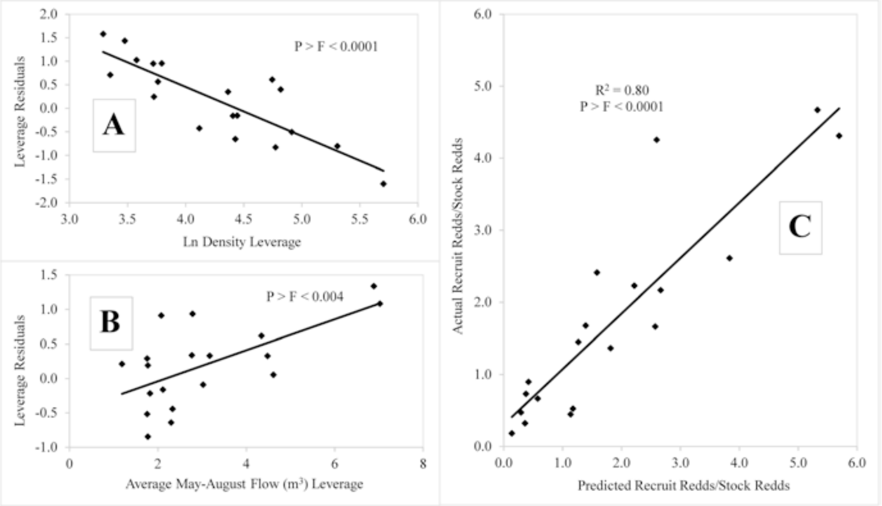

Fig. 4 Leverage plots for population density (**a**) and percent of average May through August flow during the emergence year (**b**); and the relationship of actual versus predicted population productivity (**c**) for a multivariate regression of Lemhi River Chinook salmon whole life cycle productivity (i.e., return redds/stock redds) versus population density (stock year redds) and average May through August flow during the emergence year

MPG. The populations in the Middle Fork Salmon River and South Fork Salmon River MPGs are minimally affected by water diversions and are termed “undeveloped” for this chapter. In contrast, flow in spawning and rearing habitat in the three upper Salmon River populations is substantially reduced during the irrigation season. These three populations are termed “developed” for this chapter. All ten of populations are at high risk of extinction due to low abundance and productivity (NMFS 2017).

We obtained redd survey data for populations in the upper Salmon River and the South Fork Salmon River MPGs from IDFG reports and the IDFG IFWIS website. For populations in the Middle Fork Salmon River MPG, we obtained redd survey data from the USFS for 1996–2017 and from IDFG reports for 2018–2019 (Table 1). We treated redds as individuals and treated the number of redds counted as an absolute population size. We calculated population productivity by dividing return redds by brood year redds. Salmon River Chinook salmon typically spend 1–3 years in the ocean and return to freshwater as 3- to 5-year-old adults (Camacho et al. 2019). Based on Chinook salmon age data presented in Camacho et al. (2019), we assumed that 75% of adult returns would be 4 years old and 25% would be 5 years old. We therefore calculated the number of return redds as the sum of 0.75 times the number of redds counted 4 years after the brood year and 0.25 times the number counted 5 years after the brood year. Three-year-old returns are usually males that contribute little to population productivity and we therefore did not consider 3-year-old returns in the analysis.

In undeveloped drainages, average population size ranged from 41 redds to 306 redds (mean 143) and productivity (recruit to stock ratio) ranged from 2.0 to 12.6 (mean 4.4). In developed drainages, average population size ranged from 48 redds to 88 redds (mean 71) and average productivity ranged from 1.7 to 2.7 (mean 2.1). Because population size and productivity varied substantially among the populations, we normalized both values by dividing each data point by the population-specific average for the time series. Normalizing the data facilitated comparison of the populations on a common scale.

We compared population productivity to rearing flow (i.e., Average May through August flow during the year following the brood year) measured at the closest gage with a period of record covering the rearing years (i.e. 1997–2015). For each gage, we normalized the data by dividing the rearing flow for each year by the average rearing flow for the period of record. We used data from five gages: Valley Creek at Stanley, Idaho (USGS 13295000); Salmon River at Salmon, Idaho (USGS 13302500); Lemhi River at McFarland Campground (IDWR gage); South Fork Salmon River near Krassel Ranger Station, Idaho (USGS 13310700), and the Middle Fork Salmon River near Shoup, Idaho (USGS 13310199). We compared the Valley Creek and Lemhi River populations, respectively, to flow measured at the Valley Creek and McFarland Campground gages, which are located within the spawning reaches of those populations. We compared the SRLM population to flow measured at the Salmon River gage, which is located at the lower end of the historic spawning reach of the SRLM population and is approximately 50 km downstream from the current downstream extent of spawning. We compared the Secesh River population to flow measured at the South Fork Salmon River gage, which is located in the South Fork Salmon River approximately 5 km upstream from the mouth of the Secesh River. The Bear Valley Creek, Marsh Creek, Loon Creek, Camas Creek, and Big Creek populations all spawn in tributaries of the Middle Fork Salmon River and were all compared to flow measured at the Middle Fork Salmon River gage, which is located near the mouth of the Middle Fork Salmon River.

Population productivity was positively related to flow in both developed and undeveloped drainages. The slope was slightly steeper in developed drainages, with each percent increase in flow corresponding to a 0.78% increase in population productivity, compared to a 0.40% increase in productivity in undeveloped drainages (Fig. 5 Panel a). Productivity was also strongly related to density (i.e., stock redds) in both developed and undeveloped drainages, with extremely high productivity at very low population density (Fig. 6). This was especially apparent in undeveloped drainages, where productivity was never below 1.8 when the number of stock redds was in the lower 25 percentile. High productivity of Salmon River Chinook salmon populations at low population density is well documented (ISAB 2015) and is apparent at both the smolt (Walters et al. 2013) and adult return (ISAB 2015) life stages.

Because of the very high population productivity at very low population density, population density has the potential to confound the productivity versus flow relationships; however, inclusion of population density in the regression models did not improve the relationships for flow, possibly due to the high leverage of the low

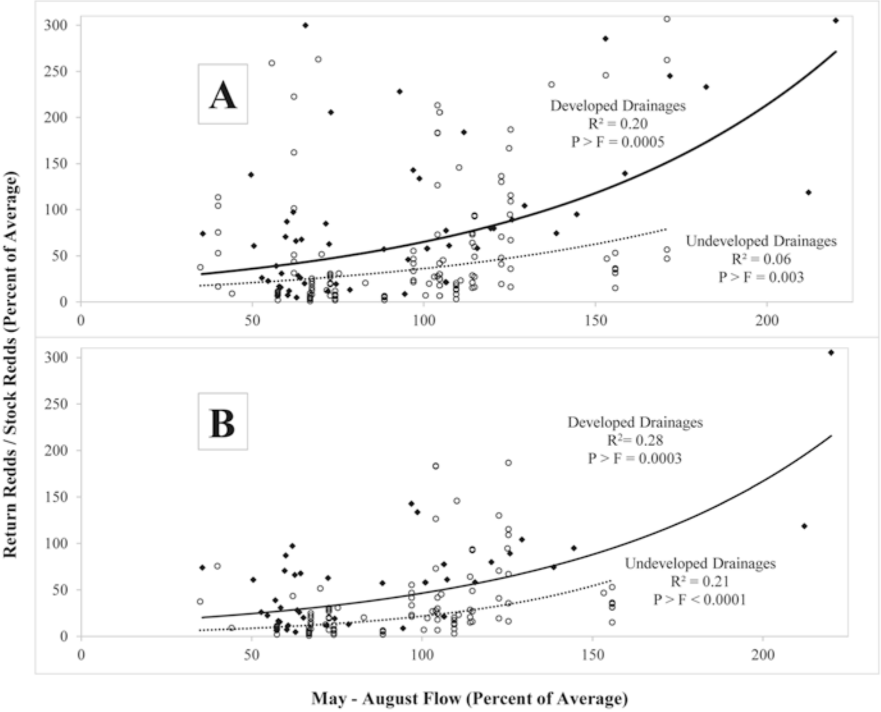

Fig. 5 Productivity versus flow relationships for Salmon River Chinook salmon in three developed drainages (diamonds and solid lines) and seven undeveloped drainages (circles and dotted lines) with all stock sizes (Panel **a**) and with all data points fewer than 25 percentile stock redds (normalized) removed (Panel **b**). Note: Some of the low population density data points for undeveloped drainages are above the scale and therefore not shown on Panel **a**

population density data points. Because recovery of Salmon River Chinook salmon populations will require improving population productivity at higher than the current population densities (NMFS 2017), knowing the overall influence of density on the flow-productivity relationships is not as important as knowing how flow influences productivity at higher population densities. We therefore ran the regressions with all data points with fewer than 25 percentile stock redds removed. Removing the low population density data points improved the flow-productivity relationships, especially for undeveloped drainages, but did not appreciably change the slopes. With the low population density data points removed, each percent increase in rearing flow corresponded to a 0.60% increase of productivity in developed drainages and a 0.40% increase in undeveloped drainages (Fig. 5 Panel b). Although removing the lowest density data points improves the description of the effects of flow at higher densities, the highest population densities in this study are well below the minimum needed to meet recovery objectives and are a small fraction of historic levels (Thurow et al. 2020).

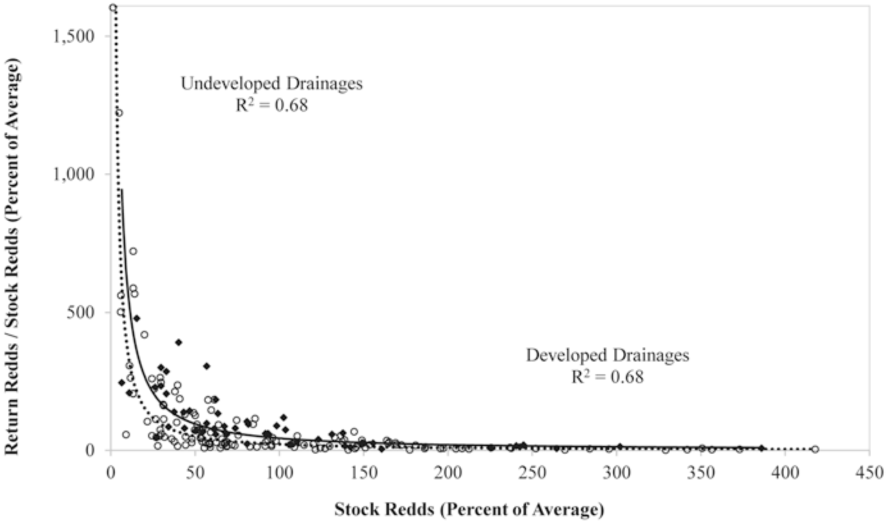

Fig. 6 Productivity versus population density relationships for Salmon River Chinook salmon in three developed drainages (diamonds and solid line) and seven undeveloped drainages (circles and dotted line)

The highest flows in developed and undeveloped drainages were 220% and 170%, respectively, of the average flow. Either with the low population density data points included or removed, the relationships indicate increased productivity with flow throughout the range of flows. The relationships with the low population density data points removed indicate that flows less than 75% of average are detrimental for populations in both developed and undeveloped drainages, and there are no indications that the highest flows recorded during the time series were detrimental. The higher maximum flows, compared to average, in developed drainages, were likely due to a depression of average flows due to water use.

5 Implications for Flow Management

Population size and productivity were more than twice as high in undeveloped as in developed drainages. Although flow impairment is only one of the many habitat differences between developed and undeveloped drainages, the greater abundance and productivity in undeveloped drainages is an indication that reducing flow impairment will improve population performance in developed drainages. Normalizing the data allowed depiction of the productivity versus flow relationships on the same scale, which revealed that Chinook salmon population productivity is positively related to flow, over the entire range of flows, in both developed and undeveloped drainages. This suggests that increasing flow will increase population productivity and that further development of water resources would likely reduce population productivity. In undeveloped drainages, where opportunities for improving flows are extremely limited, flow management should entail protection of existing flows from future development. In developed drainages, flow management should also entail protection of existing flows from additional development, but should also include restoration of flow in depleted reaches.

The developed portions of the Salmon River drainage have numerous stream reaches that are extremely depleted, many to the extent that they are dried during portions of the irrigation season. Restoring streamflow typically has positive effects on salmonid populations (Pierce et al. 2013) and adding even small amounts of flow to depleted stream reaches can have substantial positive effects (Kiernam et al. 2012). In addition, the most flow impaired stream reaches in the Salmon River drainage are often the lowest reaches of tributary streams, between the lowest diversion and the tributary mouth. Dewatering those reaches disconnects habitat in the tributary and impairs important tributary functions, such as cold water refugia and delivery of invertebrate drift. Likewise, reestablishing even partial habitat function can have disproportionally large positive impacts, especially if connectivity to high quality habitat is reestablished.

In developed drainages, flow in Chinook salmon spawning/rearing habitat can be improved by changing irrigation infrastructure or by reducing irrigation. Changes in irrigation infrastructure, such as improving irrigation and/or water transmission efficiency, moving points of diversion downstream or to groundwater sources, etc., can improve flows in some reaches, but improvements are often less than expected and, in the case of improved efficiencies, the changes can result in increased consumptive use and less water available for streamflow (Grafton et al. 2018; Linstead 2018). Reducing irrigation will increase the amount of water available for streamflow, but it may also reduce agricultural production, which can have substantial economic and social costs. Flow restoration in the Salmon River drainage has generally taken a focused approach wherein the most flow depleted reaches are targeted with the goal of reconnecting habitat and/or reestablishing tributary functions, such as cold water refugia. Monitoring in the Lemhi River drainage suggests that this focused approach has improved conditions for rearing Chinook salmon (Uthe et al. 2017) without appreciably reducing the amount of water available for irrigation. However, failure to reestablish use of tributary habitat by adult Chinook salmon suggests that there are limits to habitat restoration that can be achieved without reducing irrigation.

Flow restoration efforts in the Salmon River drainage should also consider long-term trends and should anticipate declining water availability. Spring and summer flow in the Salmon River drainage has been gradually declining for at least 60 years (Fig. 7). Although some if this decline is probably due to increased consumptive use by irrigation, the reduction in Johnson Creek (Panel c of Fig. 7), which has very little water development, suggests that some of the reduction is also due to climate change. Climate change is likely to continue for the foreseeable future and will likely result in a long-term decline in summer flow in the Salmon River drainage (Crozier et al. 2021). Although current restoration efforts are focused on the most flow depleted reaches, the declining water availability and the positive production/

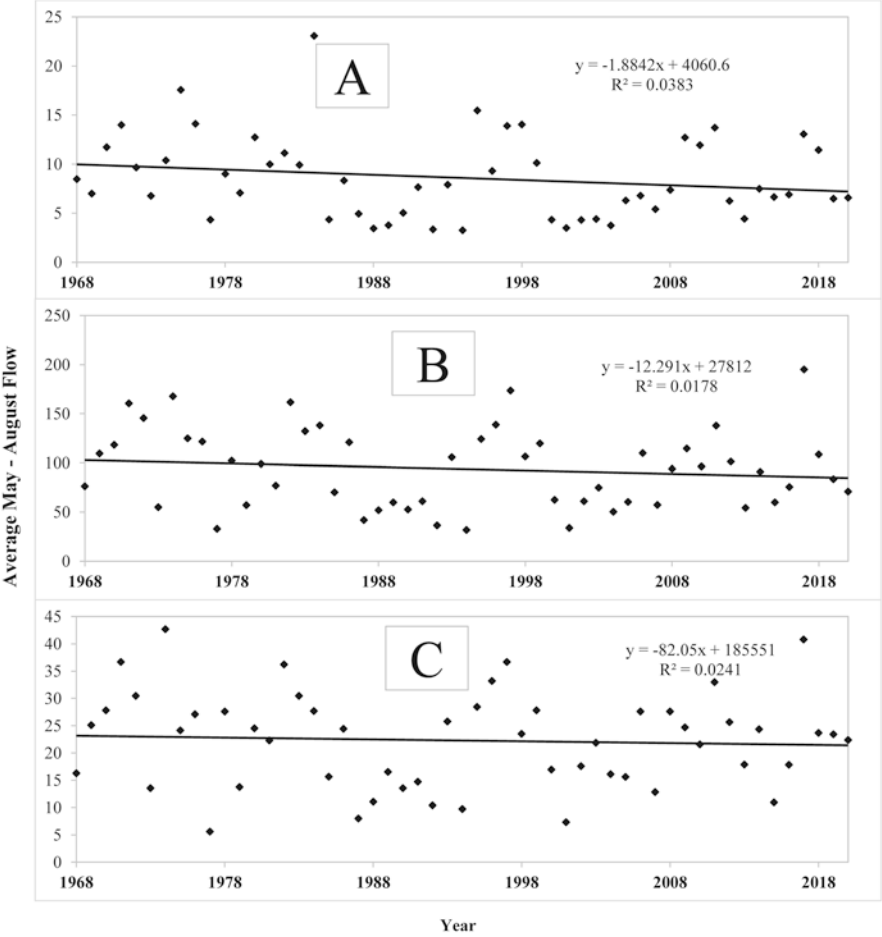

Fig. 7 Average May–August flow measured at the Lemhi River near Lemhi gage (USGS 13305000) (Panel **a**), the Salmon River at Salmon gage (USGS 13302500) (Panel **b**), and Johnson Creek at Yellow Pine (USGS 13313000) (Panel **c**), from 1968 through 2020. The Lemhi and Salmon Rivers are heavily influenced by irrigation diversions whereas there is little water use in the Johnson Creek drainage

flow relationships suggest that flows should be protected and enhanced whenever possible and that water acquired for flow restoration should be protected as far downstream as possible.

6 Conclusions

Large-scale development of surface water resources in the Pacific Northwest has been ongoing since the 1860s and adverse effects of water use on anadromous salmonids have been recognized since at least the 1950s. Relationships between Snake River spring/summer Chinook salmon population productivity and flow experienced by rearing juveniles are positive across the Salmon River drainage and across the entire range of flows. This suggests that any improvement in flow in developed drainages is likely to benefit Chinook salmon and that any further degradation of flow anywhere in the drainage is likely to further impair population productivity and abundance. A focused approach to flow restoration, wherein the most flow depleted reaches are targeted for restoration, will likely have the most benefit with the least amount of water allocated to streamflow. However, the continual reduction of mainstem flows throughout the Salmon River drainage indicates that more systematic measures, such as acquiring water rights and allocating them to instream flow, may also be needed to conserve Chinook salmon populations in the Salmon River drainage.

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The Increasing Threat Posed by Nonnative and Hatchery-Reared Salmonids to Japanese Wild Native Salmonids

Koh Hasegawa

Abstract Japan has eight native salmonid species, and stocking with nonnative salmonids from foreign and domestic regions is posing problems for the conservation of these native species. In particular, species replacement of native white-spotted charr by nonnative brown trout and rainbow trout is now a serious issue in some streams. Interspecific interactions such as competition and hybridization are thought to be the prime mechanisms of this replacement. Moreover, recent studies suggest that stocking with hatchery-reared native species also damages wild populations of native species. Hatchery-reared fish outcompete wild fish, and hybridization between them transmutes the genuine genetic background of wild populations. Hybridization sometimes also alters the life history of wild populations. These stockings have been conducted for fisheries purposes and for civic environmental education, but they are likely to have results opposite to those expected by fisheries managers. From a Buddhist perspective, many Japanese people believe that allowing animals to escape from cages is an act of goodwill, and especially this belief is a cause of widespread stocking as civic environmental education. To solve these problems, we need to develop not only government systems but also public education campaigns based on biological knowledge.

Keywords Biological invasions · Competition · Hybridization · Stocking

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1 Introduction

The four main islands—Hokkaido, Honshu, Shikoku, and Kyushu—forming the Japanese archipelago account for 97% of the area of Japan (Fig. 1). This archipelago spans a distance of 1800 km between about 30°N and 45°N latitude, and the northern region above 37°N is categorized as subarctic (Beck et al. 2018). Anadromous populations of native salmonids, which are cold-water fish species, are very common in the coastal side of the northern region. These species—especially those of the genus *Oncorhynchus* (chum salmon *O. keta*, masu salmon *O. masou masou*, and pink salmon *O. gorbuscha*)—have been major targets of commercial fisheries and are the basis of local and traditional food culture (Irvine 2018; Oishi et al. 2021). In the northern region, salmonids occur even in urbanized rivers (Fig. 2) (Aruga et al. 2021; Suzuki et al. 2021). In contrast, the southern region of Japan is nearly the southern limit of the salmonid range, and the distributions of native salmonids (white-spotted charr *Salvelinus leucomaenis* and masu or red-spotted masu salmon *O. masou ishikawae*) are limited to cold-water streams at high altitude in this region. Although the commercial scale of these southern fisheries is smaller than that of the northern ones, they are still important as targets of aquaculture and recreational fishing (Fig. 3). As is the case for many other organisms, populations of these salmonids on the margins of the species' ranges are under threat from anthropogenic impacts such as global warming and habitat fragmentation (Nakano et al. 1996; Tsuboi et al. 2013).

Fig. 1 Locations of prefectures described in the main text. Inset shows the location of the Japanese archipelago and the four main islands

Fig. 2 Salmon rivers in Sapporo, a city of 2 million in Hokkaido prefecture. Top panel: From a bridge over the Kotoni-Hassamu River, a person watches spawning chum salmon (inset). Bottom panel: View of the Toyohira River running through central Sapporo

Fig. 3 Top panel: Aquaculture ponds at a hatchery for white-spotted charr in Shiga prefecture. The sign points to a charr restaurant at the hatchery. Bottom panel: A stream in the mountains of Kyoto prefecture regulated for recreational fishing. Inset is a sign showing fishing rules

Loss of Japanese native freshwater fish species as a result of biological invasions has been a serious problem for biodiversity conservation since about the 1970s, when nonnative largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) began to spread widely into local inland waters because of inter-regional transplantation in Japan (National Federation of Inland water Fisheries Cooperatives 1992). Thirty years after the start of this widespread proliferation of largemouth bass and bluegill, a report by Takami et al. (2002) of the dramatic replacement of native white-spotted charr by nonnative brown trout (*Salmo trutta*) which stocking eyed eggs of unknown provenance by private anglers was suspected as the origin in Monbetsu stream, Hokkaido prefecture alerted scientists and local people to the seriousness of the impact of nonnative salmonids on native biodiversity. Moreover, wild salmonids (defined as those that were spawned in natural environments) are regarded as important fisheries resources (Nakamura and Iida 2009; Morita and Ohkuma 2015). Unlike hatchery-reared or farmed fish with their dented heads and scraped fins, these wild fish are without anomalies in appearance and are preferred by recreational anglers (Nakamura and Iida 2009). More importantly, for the sustainable use of fisheries resources, naturally reproducing wild fish is considered preferable to stocked hatchery-reared fish (Schindler et al. 2010; Morita and Ohkuma 2015). However, wild salmonids are exposed to risks of interactions such as competition and hybridization with stocked hatchery-reared native and nonnative salmonids, and these risks must be considered in the conservation of wild native salmonids (e.g., Rand et al. 2012; O'Sullivan et al. 2020).

In Japan, stocking with nonnative salmonids and hatchery-reared native salmonids has been conducted since the nineteenth century. Initially, stocking programs were publicly operated by the government institutes. And, private anglers have stocked for their own purposes because they have been able to buy hatchery-reared fish for stocking and stocking is not banned by the national or local laws in many regions. In addition, some citizens believe that stocking is beneficial for conservation of the natural environment and native fishes. As a result, Japanese wild native salmonids are becoming threatened because of interactions with nonnative and hatchery-reared salmonids. In this chapter, I review these interactions and propose a perspective on the conservation of wild native salmonids that is based on lessons from the case of Japanese salmonids.

2 Nonnative Salmonids from Outside Japan (Foreign Nonnative Species)

The Japanese government and also private fish farmers actively imported aquatic organisms including fish species from foreign countries in the twentieth century (Maruyama et al. 1987). Some species were stocked directly (e.g., mosquitofish [*Gambusia affinis*]), and others were cultured in hatchery ponds, but some reared individuals escaped into natural waters (e.g., northern snakehead [*Channa argus*]).

These individuals established populations of nonnative species in Japanese waters (foreign nonnative species). In addition, recreational fishing became the major reason for introducing foreign fish species in the late twentieth century (e.g., largemouth bass).

As in other countries, salmonids are favored in Japan for fish farming and recreational fishing. Several species have been introduced from outside Japan; rainbow (*Oncorhynchus mykiss*) and brown trout are the two major foreign nonnative salmonids at present (Hasegawa 2020). As introductions of rainbow trout were initiated by the government, this fish's introduction history has been documented (e.g., Bureau of Fishery, Ministry of Agriculture and Forestry of Japan 1927). Introduction of rainbow trout to Japan started in the late nineteenth century. They were imported to fish hatcheries in Tokyo, Saitama, Fukushima, and Tochigi prefectures from fish hatcheries in the western USA. In contrast, the introduction history of brown trout is unclear. The first introduction of brown trout in Japan is generally considered to be of eyed eggs contaminating the eyed eggs of brook trout (*Salvelinus fontinalis*) imported from a fish hatchery in the USA in about 1900s, and some private companies likely imported the eyed eggs from Europe via their own routes in the late twentieth century (Maruyama et al. 1987). The native range of brown trout encompasses Europe and its surrounding areas. Berrebi et al. (2020) demonstrated that most of the haplotypes found in Japanese brown trout are highly dispersed in Europe, suggesting that it will be difficult to determine the original populations of Japanese brown trout.

Other introduced foreign nonnative salmonids are not widespread in Japan at present. For example, in the late twentieth century there were repeated stockings of coho salmon (*Oncorhynchus kisutch*) in several rivers in Hokkaido prefecture for the purpose of salmon resource enhancement, but the fish could not establish self-sustaining populations (Ishida et al. 1975; Nara et al. 1979; Umeda et al. 1981). Instead, aquaculture of coho salmon has been active in Miyagi and Iwate prefectures since the 1980s (Koseki 2013), and escaped fish are sometimes found in these prefectures (Sasaki et al. 2021). However, population establishment of nonnative coho salmon and their impact on native species have still not been verified. Two *Salvelinus* species, lake trout (*S. namaycush*) and brook trout, were introduced from North America for aquaculture and recreational fishing. Their distributions are very limited in Japan (only Lake Chuzenji for lake trout and five locations for brook trout), likely because they might not have been introduced as frequently as other foreign salmonids (Kitano 2004; Morita 2019).

3 Nonnative Salmonids from Within Japan (Domestic Nonnative Species)

Species introduced to areas outside their native ranges not only from foreign countries but also within the same country can be viewed as nonnative species. However, Senou (2013) inferred that Japanese people are more comfortable with the presence of nonnative species from other regions of Japan because they still see them as "Japanese fish" and do not recognize them as nonnative species. However, the Nature Conservation Committee of the Ichthyological Society of Japan has pointed out that these nonnative fishes, as "domestic nonnative species," still threaten native biodiversity (Senou 2013). Genetically differentiated stocks that are introduced inside their native range are also sometimes regarded as domestic nonnatives (Krueger and May 1991). This point is further discussed in Sect. 4—"*Stocking of hatchery-reared salmonids into waters already inhabited by wild conspecifics*" in this chapter.

Kokanee, the landlocked form of sockeye salmon (*Oncorhynchus nerka*), is the principal domestic nonnative salmonid in Japan (Yamamoto 2015). This species is distributed naturally in some lakes around the north Pacific rim, but native populations in Japan were limited to two lakes (Lake Akan and Lake Chimikeppu) in eastern Hokkaido. The fish were initially consumed by local Hokkaido people called the Ainu. From 1894 to 1896, their eyed eggs were transferred from Lake Akan to a hatchery beside Lake Shikotsu, in western Hokkaido. This lake contained only white-spotted charr and sculpin (*Cottus nozawae*) as native fish species (Akiba 1993). The stocking of chum and masu salmon into the lake were conducted at the same time, but failed. Kokanee were later transferred from Lake Shikotsu to several mountain lakes in Hokkaido and Honshu owing to their high value as an inland fisheries resource (Tokui 1964). They were also introduced from native populations outside Hokkaido and stocked into lakes, including lakes Akan and Chimikeppu. Their genetically native populations in Japan are therefore thought to have disappeared (Yamamoto 2015). In Hokkaido, some rivers have been stocked with hatchery-reared sockeye salmon originating from Japanese Kokanee (Kaeriyama 1993; Ban 2003), but it is hard to know whether they have successfully established populations that contribute to local commercial fisheries. Kunimasu (*Oncorhynchus kawamurae*), which was previously categorized as a subspecies of kokanee (*O. nerka kawamurae*), was extinct in its only original habitat, Lake Tazawa, in Akita prefecture, until the 1940s. However, it was rediscovered in 2010 in Lake Saiko, in Yamanashi prefecture, as a domestic nonnative species. This rediscovery was very big news in Japan (Nakabo et al. 2011).

Owing to their popularity as targets of recreational fishing, masu salmon (e.g., Tsuboi et al. 2006), red-spotted masu salmon (e.g., Yamazaki et al. 2005; Nakao 2008; Kitanishi et al. 2017), and white-spotted charr (e.g., Kondou et al. 1999; Kikuchi and Inoue 2014) have been introduced into many waters outside their native ranges and have become domestic nonnative species. These introductions are carried out by local fisheries managers and sometimes recreational anglers (Sasaki

2005). Unlike the case with kokanee, therefore, records of the introductions of these species are not available for many waters.

4 Stocking of Hatchery-Reared Salmonids into Waters Already Inhabited by Wild Conspecifics

For the purpose of marine (chum, masu, and pink salmon) and inland (white-spotted charr and masu/red-spotted masu salmon) fisheries resource enhancement, hatchery-reared native salmonids have been stocked into rivers already inhabited by their wild conspecifics (Nakamura and Iida 2009; Morita 2014). Also, stockings have been conducted to conserve endangered populations (e.g., Sakhalin taimen *Parahucho perryi* in Shiribetsu river, Hokkaido prefecture: Edo 2016) or to educate the public, especially school children about the environment (e.g., masu/red-spotted masu salmon: Koya and Miyake 2012). Although stockings for fisheries purposes are based on national and local (prefectural) agreements (or both), citizen's groups or private anglers sometimes stock their own fish for conservation attempts or recreational purposes without any consensus built based on the scientific background (such as any genetic differences among populations) (The Ichthyological Society of Japan 2005).

5 Interactions Between Japanese Wild Native Salmonids and Nonnative and Hatchery-Reared Salmonids

Interactions play a key role in the mechanism of the replacements of wild native salmonids by nonnative and/or hatchery-reared salmonids. Native *Salvelinus* species (white-spotted charr and southern Asian Dolly Varden [*S. curilus*]) are especially vulnerable to brown and rainbow trout invasions, and replacements have been reported in some streams (Hasegawa 2020). Masu salmon, another dominant native stream salmonid in Japan, is likely to be more tolerant to nonnative salmonid invasion, although its replacement in several streams has been reported (Shimoda 2012; Hasegawa 2020). Rather, Sahashi et al. (2015) have suggested that wild masu salmon are being replaced by hatchery-reared conspecifics. Although there is a paucity of case studies of wild masu salmon replacement by hatchery-reared conspecifics, the current continued stocking of hatchery-reared masu salmon throughout Japan suggests that replacement may be a serious problem for the conservation of wild masu salmon.

The effects of nonnative and hatchery-reared salmonids spread to the whole recipient ecosystem through interspecific interactions between not only salmonids but also other aquatic organisms. For example, Hasegawa et al. (2017) suggested that the presence of brown trout has decreased fish species richness in the Mamachi

Stream in Hokkaido at the reach scale (i.e., at study sites several tens of meters to 200 m long). Shimoda (2012) found that the number of fish species in the Shizukari River, Hokkaido, increased after the eradication of brown trout. These two studies suggested that brown trout has suppressed fish species richness in rivers. Baxter et al. (2007) demonstrated that nonnative rainbow trout affected benthic invertebrates and algae through rainbow trout monopolization of terrestrial invertebrates as food resources from native southern Asian Dolly Varden, along with a dietary shift in southern Asian Dolly Varden in the Makkari Stream, Hokkaido. They suggested that such alterations in aquatic ecosystems ultimately reach terrestrial ecosystems. In the Mamachi Stream mentioned above, Hasegawa et al. (2018) also demonstrated that stocking with large amounts of hatchery-reared chum salmon fry caused a trophic cascade such as predation upon herbivorous benthic invertebrates by chum salmon fry increased algal biomass.

5.1 Competition

Many studies have focused on interspecific competition as the principal mechanism of the replacement of native salmonids by nonnative salmonids since a long time ago in North America (e.g., Krueger and May 1991) and Europe (Fausch 2007; Korsu et al. 2007). Hasegawa and Maekawa (2009) tested interspecific competition between native white-spotted charr and nonnative brown trout—a replacement species combination actually reported in the stream in Hokkaido by Takami et al. (2002). By using artificial streams, Hasegawa and Maekawa (2009) demonstrated that interference competition, as evaluated by aggression frequency, was more intense between white-spotted charr and brown trout, as brown trout became dominant, than the intraspecific competition among white-spotted charr. Moreover, the foraging efficiency of white-spotted charr decreased in the presence of brown trout. Species replacement occurs when interspecific competition is more intense than intraspecific competition. Although this experiment did not consider density dependence, despite salmonids typically showing density-dependent competition, the results of this simple experiment suggested that interspecific competition caused species replacement in the case of native white-spotted charr and nonnative brown trout. Competitive dominance of nonnative salmonids over native salmonids has been detected in some other combinations, such as white-spotted charr and rainbow trout (Hasegawa et al. 2004). This suggests that interspecific competition may cause the replacement of Japanese native salmonids by nonnative salmonids in these combinations of species.

Competition occurs between wild and hatchery-reared salmonids as well as between native and nonnative salmonids. Hasegawa and Nakashima (2018) suggested that density-dependent competition caused the replacement of wild masu salmon by hatchery-reared masu salmon, which was demonstrated by Sahashi et al. (2015). In general, hatchery-reared fry are grown larger than wild fry to increase their survival after they have been stocked into natural environments. This body size difference is likely to have an impact in determining competitive dominance within conspecifics—more so than the difference in growth environment (i.e., between a hatchery pond and the natural environment). Thus, in an enclosure environment, hatchery-reared masu salmon outcompete wild masu salmon: the growth rate of wild masu salmon decreases in the presence of hatchery-reared conspecifics (Hasegawa and Nakashima 2018). A similar trend has been detected in white-spotted charr as an experimental species stocked for recreational fishing (Yamamoto et al. 2009).

Stocked hatchery-reared salmonids live sympatrically with other wild salmonids in many streams. However, studies testing competition between hatchery-reared and wild salmonids of different species (e.g., hatchery-reared chum salmon vs wild masu salmon described below) are surprisingly rare, even outside Japan. Hasegawa et al. (2014) tested how the presence of hatchery-reared chum salmon fry influenced the outcome of intra- and interspecific density-dependent competition in wild masu fry and wild chum salmon fry in an enclosure environment. The presence of hatchery chum salmon fry negatively affected their wild conspecifics, with both intra- and interspecific competition among the wild fry. Unlike the wild chum salmon fry, the wild masu salmon fry did not show decreased foraging efficiency and growth rates, although the body size of the hatchery-reared chum salmon fry was greater than that of the wild masu salmon fry. This result suggests that the strong competitive ability of masu salmon fry may mask the disadvantage of the smaller body size. These results suggested that the effects of hatchery-reared salmonids varied depending on the species of competing individuals. However, in contrast, in a natural stream stocked with hatchery-reared chum salmon fry, wild masu salmon fry showed a decrease over time in foraging efficiency and growth (Hasegawa et al. 2018). In this situation, the hatchery-reared chum salmon fry vastly outnumbered the wild masu salmon fry, despite the strong competitive ability of the wild masu salmon, because stocking usually creates an abnormally high density of hatchery-reared fish (Fig. 4). Moreover, wild native salmonids are sometimes likely to be outcompeted by their hatchery-reared conspecifics rather than by nonnative salmonids. For example, the enclosure experiment demonstrated that the growth rate decline of wild masu salmon fry in the presence of hatchery-reared conspecifics was greater than that in the presence of nonnative brown trout fry (Hasegawa and Nakashima 2018). This result of the experiment is accountable for phenomena occurred in natural streams that wild masu salmon barely sustain their populations under the presence of nonnative brown trout (Hasegawa et al. 2012), while they are replaced by hatchery-reared conspecifics (Sahashi et al. 2015). Stocking with hatchery-reared fry of native species is sometimes conducted for the purpose of recovering wild populations on the basis of the preconception that the native population has decreased because of nonnative species invasion, but hatchery-reared fry have the potential to be more harmful than nonnative species to wild conspecifics.

Fig. 4 A man stocking chum salmon fry via a hose into the Oyobe River, southern Hokkaido. Inset shows a phalanx of fry just after stocking

5.2 *Reproductive Interference*

Interactions arising at spawning events are also of concern in regard to conserving wild native salmonids. Brook trout, a foreign nonnative *Salvelinus* species, is not widespread in Japan. However, they can hybridize with the native *Salvelinus* species, white-spotted charr (Kitano et al. 2014; Fukui et al. 2016; Kitano 2018) and southern Asian Dolly Varden (Fukui et al. 2021) if they establish populations in streams (Fig. 5). Native *Salvelinus* species can even be exposed to hybridization risk with other genera. White-spotted charr has hybridized with nonnative brown trout, genus *Salmo* (Kitano et al. 2009) (Fig. 5). In some Japanese streams, I have observed that the number of hybrids between white-spotted charr and brown trout was very small compared with the numbers of white-spotted charr or brown trout (Table 1). However, the occurrence of hybrid fish despite high mortality rates of hybrid progeny fry before the start of feeding (about 75%: Suzuki and Fukuda 1971) may imply that large numbers of spawning pairs of the two species exist. Koizumi et al. (2005) reported hybridization between Miyabe charr (*Salvelinus curilus miyabei*), the endemic southern Asian Dolly Varden in Lake Shikaribetsu in Hokkaido, and masu salmon, genus *Oncorhynchus* (a domestic nonnative salmonid). Red-spotted masu salmon have been introduced as domestic nonnative salmonids into the natural ranges of masu salmon (Nakao 2008; Kitanishi et al. 2017). In these areas,

Fig. 5 Top to bottom: White-spotted charr, brown trout, brook trout, a hybrid of white-spotted charr and brown trout, and a hybrid of white-spotted charr and brook trout. Photo credits: brown trout, K Hasegawa; others, S Fukui

Table 1 Numbers of fish captured by electrofishing in each stream in each surveyed year. "Location" indicates the geographic coordinates of each survey site. BT: brown trout; WC: white-spotted charr; SADV: southern Asian Dolly Varden; MS: masu salmon; RT: rainbow trout; Hybrid: BT × WC

			Location (°)		Number captured					
Prefecture	Stream	Year	N	E	Hybrid	BT	WC	SA DV	MS[a]	RT
Yamanashi	Kane[b]	2012	35.593	138.725	3	183	274	0	723	1
		2013			28	230	327	0	1210	0
Gifu	Odori	2012	36.307	137.108	0	223	105	0	57	60
Tochigi	Yanagisawa	2013	36.747	139.419	4	182	80	0	261	0
	Toyamasawa	2013	36.750	139.406	0	197	27	0	3	0
Hokkaido	Koronai	2013	41.588	140.404	2	95	58	0	92	0
	Hekirichi	2013	41.879	140.583	0	97	15	0	0	12
	Torizaki	2013	42.046	140.489	0	113	0	3[c]	0	Rare[d]
	Toyohata	2013	42.366	142.426	0	115	8	0	115	0
	Konbu	2012	42.798	140.602	0	75	20	0	862	12
	Mamachi	2009	42.803	141.614	2	1411	97	0	2727	20
	Monbetsu	2014	42.817	141.419	0	467	102	0	0	0
	Sousuke	2012	42.883	140.746	1[e]	69	35	84	98	279

[a] Masu salmon and red-spotted masu salmon are native subspecies in the Kane and Odori streams, respectively. However, nonnative subspecies were introduced into both streams. A hybrid of the Japanese masu salmon group called Honmasu inhabits the Yanagisawa and Toyamasawa streams

[b] The original data are shown by Tanizawa et al. (2016)

[c] SADV in Torizaki Stream is a domestic nonnative species

[d] The actual number of rainbow trout captured was not recorded

[e] DNA analysis confirmed that this specimen was a BT×WC hybrid, not BT×SADV

hybridization has become a problem in terms of native masu salmon conservation and a reduction in body size of anadromous masu salmon as a coastal fisheries resource.

Hybridization between wild and stocked hatchery-reared conspecifics is also a serious problem for conserving wild native salmonids. These hybrid fish appear almost indistinguishable from wild fish, so it is hard to make citizens understand the seriousness of the hybridization. However, hybridization with stocked hatchery-reared fish—especially those transplanted from other populations—presents problems. Each salmonid population has a genetic uniqueness adapted to its local habitat. This is disturbed by the transplantation of hatchery-reared fish originating from different regions, and the hybridization causes disruption of the adapted genes and loss of fitness (Grant 2012). Interpopulation transplantation of hatchery-reared salmonids was broadly conducted in Japan before the genetic problems became known. For chum, masu, and pink salmon as commercial marine fisheries resources, official records of interpopulation transplantation were kept by national and prefectural governments, and the results of some experimental transplantations have been published in the scientific literature (e.g., for chum salmon, Tezuka and Nakamura 1996; masu salmon, Mayama et al. 1989; pink salmon, Mayama 1985). In a similar way, white-spotted charr and masu or red-spotted masu salmon for recreational fishing in inland waters were transplanted between populations under government initiatives; they were also transplanted by personal anglers (Nakamura 2007; National Salmon Resources Center 2011).

Recent studies have pointed out that hybridization between wild and hatchery-reared conspecifics has the potential to alter the life history traits of salmonid populations. In Japan, stocking of masu salmon obtained from fluvial populations into anadromous masu salmon populations is considered problematic, because hybridization between such populations decreases the proportion of anadromous individuals (e.g., Suzuki and Ohkawa 2011; Ohkuma et al. 2016). The concern with this type of hybridization is not only loss of native genetic diversity but also this decrease in the proportion of anadromous individuals, which are an important target of marine fisheries.

If the spawning season of nonnative or hatchery-reared salmonids is later than that of wild native salmonids, redd superimposition is likely to damage populations of wild native salmonids (Taniguchi et al. 2000). For example, the redds of Sakhalin taimen, which are endangered in Japan and are spring spawners, are dug into by nonnative rainbow trout, another spring spawner species (Nomoto et al. 2010). Nomoto et al. (2010) demonstrated that about 30% of the Sakhalin taimen's redds in the Furen River, Hokkaido, were superimposed upon by rainbow trout redds; they predicted that this would lead to a decrease in taimen populations.

5.3 Predator–Prey Interaction

Predator–prey interactions occur among salmonids regardless of whether they are native, nonnative, or hatchery-reared. In Japan, the nonnative brown trout is a piscivorous salmonid that is likely to be of serious concern for the conservation of native salmonids and the management of salmonids as fisheries resources. Although the ways in which predation influences the population dynamics of prey salmonids have not been studied well, previous studies have reported predation by nonnative brown trout on wild and hatchery-reared masu salmon (Mayama 1999; Hasegawa et al. 2012) and domestic nonnative kokanee (Shiraishi and Tanaka 1967; Misawa et al. 2001).

Hasegawa et al. (2021) observed that the diets of white-spotted charr, masu salmon, and brown trout were dramatically biased toward newly stocked hatchery-reared chum and masu salmon. The ways in which hatchery-reared fry influence higher trophic levels need to be clarified if we are to understand predator–prey interactions in relation to hatchery-reared fry (e.g., Hasegawa and Fukui 2022; Hasegawa et al. 2023).

6 Attitudes Toward Wild Native Salmonid Conservation in the Face of Nonnative and Hatchery-Reared Salmonid Releases

In the twentieth century, the government of Japan prioritized the transplantation of foreign and domestic aquatic organisms, including salmonids, for fisheries promotion through stocking and aquaculture, with very little regard for the invasiveness of these organisms (Maruyama et al. 1987; Senou 2013). Also, interpopulation transplantation of hatchery-reared salmonids of the same species was actively conducted. These activities under the initiative of governments have now gradually been restrained as we have become increasingly aware of the outcomes of interactions among wild native, nonnative, and hatchery-reared salmonids, although problems remain with interactions between wild and hatchery-reared fish inhabiting release locations. Today, stocking (sometimes illegal) by personal anglers and stocking by the public as part of environmental education projects have become more serious causes of the widespread distribution of nonnative and hatchery-reared salmonids than stocking initiated by governments. Japanese thinking is largely influenced by Buddhism, and allowing animals to escape from cages is praised as a goodwill gesture in Buddhist teachings. In addition, as described above, the presence of domestic nonnative fishes is permitted on an emotional level because the Japanese public view them as Japanese fishes. This is even more so for stocked hatchery-reared fishes, if they are conspecific to wild native fishes. Watanabe (2016) suggested that these Japanese psyche is a deep motivator for the stocking of natural streams with fish for environmental education purposes. To solve the problems associated with the stocking of nonnative and hatchery-reared salmonids, we need to develop not only government systems but also public education campaigns based on biological knowledge.

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Demographic and Genetic Attributes of Small, Isolated Populations of Gila Trout: Prospects for Persistence Under a Shifting Climate Regime

Thomas F. Turner, David L. Propst, and James E. Brooks

Abstract By the time Gila trout *Oncorhynchus gilae* was described in the mid-twentieth century, it persisted only in a few disconnected small headwater streams in the upper Gila River catchment of southwest USA. Isolation of remnant populations eliminated the possibility of recolonization after local population extirpation following catastrophic disturbance. Small population size and demographic isolation suggested that Gila trout should be sensitive to press disturbances associated with lowered precipitation and increased drought, together with catastrophic disturbances like wildfire and associated debris flows. Using data collected over a 35-year period, we explored the relationships between population abundance and age-structure (remnant and replicated), population fitness (estimated as relative condition factor), and genetic diversity measured as allelic richness and heterozygosity. Of particular interest were temporal trends in population response to pulse (wildfire) and press disturbances (extended drought) over the time series. There was little evidence that within-population genetic diversity was related to population fitness. Despite being genetically depauperate, we found that Gila trout populations were resilient to the pressures of extended decreasing precipitation and drought, but not to multiple mega wildfires that the upper Gila River catchment experienced over the past 35 years. Gila trout has survived with human assistance, but it is a fragile persistence made additionally so because of its reduced genetic diversity. A robust

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wildfire rescue plan, repatriation to historic habitat, restoration of gene flow across extant populations in dendritically complex drainages, and genetic rescue are necessary actions to ensure the demographic and genetic survival of the species.

Keywords Climate change · Conservation strategies · Disturbance · Fitness · Inbreeding · Genetic rescue

1 Introduction

Gila trout *Oncorhynchus gilae* historically occurred in cold-water habitats throughout the Gila River system of southwest New Mexico and central Arizona, USA (Behnke 2002) but with European settlement of the region in the nineteenth century its range was reduced to remote and largely inaccessible upland streams. Reasons for its rapid and extensive range contraction were similar to those experienced by other inland North American salmonids—resource extraction, habitat loss and degradation, and widespread introduction of nonnative trout species (Hepworth et al. 1997; Gresswell 2011; Penaluna et al. 2016; Budy et al. 2019). Restriction to small, disconnected streams made Gila trout populations especially vulnerable to the vicissitudes of stochastic natural stressors such as extended drought, wildfire, and elevated debris flows (Propst et al. 1992; Brown et al. 2001; Kennedy et al. 2008; Wick et al. 2014). Populations that survived natural catastrophic events experienced demographic bottlenecks. When described in 1950 Gila trout was known to occur in two small streams (Miller 1950). Since then, only three additional populations have been found. Each population was physically isolated by impassable waterfalls and extensive dry stream channels. Whether via founder effects, demographic disconnection, or other factors, demographic isolation contributed to each being genetically distinct (Loudenslager et al. 1986; Riddle et al. 1998; Camak et al. 2021).

Early recognition of the genetic distinctiveness of each remnant population was an important consideration in the design and implementation of conservation strategies for Gila trout. Given the limited number and restricted range size of populations and the precarious security of each, an initial conservation objective was to replicate each remnant population (= lineage) in at least one other stream (USFWS 1979). From the outset, replication was achieved by capturing individuals from a donor population and releasing them in a suitable stream devoid of nonnative trout. Each stocking consisted of multiple size classes (= age classes) of fish but never more than about 200 individuals and often fewer than 100. Critical uncertainties were whether a comparatively small number of fish could establish a viable population of Gila trout and if these stocked fish collectively represented the full genetic complement of the donor population.

An essential element to understanding the dynamics and viability of Gila trout populations is the relative role of extrinsic abiotic and biotic drivers versus its intrinsic biological and genetic characters. In its primeval environment, primary biotic influences included species interactions (e.g., inter-specific competition and predation), food availability, riparian community integrity (Baxter et al. 2005), and intra-specific interactions (e.g., density dependence). Inter-specific interactions were limited in most streams, especially higher elevation reaches, because Gila trout was the sole fish species present and as the apex predator it had neither vertebrate aquatic predators nor competitors in the adult life stage. Food availability and quality were probably not limiting, unless fish densities were high (Hart et al. 2013). Abiotic factors were likely more influential drivers of population persistence and individual fitness (Sievers et al. 2017). In unaltered, pristine environments abiotic factors included a stream's physical attributes such as length of suitable habitat, habitat heterogeneity (e.g., pools, riffles, and runs), thermal regime, flow regime, underlying geochemical features, and water quality. For example, periodic drought and elevated water temperature or seasonal flooding could cause elevated mortality of recently hatched fish. Reduced or failed recruitment might therefore reduce population vitality and persistence, especially if recruitment failed across several consecutive years. In addition, resistance to, or recovery from, disturbance likely depended partly on genetic diversity of affected populations (Frankham et al. 2010). It is generally expected that population vitality and genetic diversity are positively correlated (Reed and Frankham 2003; but see Yates et al. 2019; Teixeira and Huber 2021).

Effects of negative abiotic drivers such as wildfire and drought generally were experienced at a regional scale, but severity of the effect likely varied among populations with some being eliminated and others persisting at reduced levels. The likelihood that a lost population was restored depended upon accessibility of the affected stream to persistent neighboring populations capable of providing colonists. Diminished populations recovered *in situ* or were aided by colonists from adjoining populations. Presumably, this mixing of individuals among streams contributed to maintenance of genetic diversity and ultimately population and species viability. By the mid-twentieth century, demographic isolation of surviving Gila trout populations yielded two general outcomes for genetic diversity. First, Gila trout populations became increasingly genetically differentiated from one another over time through random fixation of alleles in local populations and coincident differences of allele frequencies across populations (Peters and Turner 2008; Camak et al. 2021). Second, genetic diversity was lost in each local population as alternative alleles were fixed. Both processes were caused by genetic drift that drove the process of differentiation and fixation at a rate that was indirectly proportional to the effective population size, N_e, of each population (Wright 1969). At present, effective population size is ≤ 100 in all remnant and replicate populations of Gila Trout, and <50 in some (Camak et al. 2021). Conservation geneticists consider $N_e < 50$ as a critical threshold where a local population is expected to experience declines in mean fitness due to inbreeding (Franklin 1980). Critically low genetic diversity is also expected to severely reduce a population's capacity to respond to potential biotic and abiotic stressors detailed above.

Thus, by the late 1970s, when conservation of Gila trout began in earnest (Propst et al. 2020), the species was demographically isolated into small populations with lowered genetic diversity. Yet despite this precarious circumstance, Gila trout has, with some human assistance, survived. Because remnant and replicate populations vary in standing levels of genetic diversity, we sought to explore the relationship of within-population diversity and vitality over time. Does low genetic diversity negatively affect viability of Gila trout populations in the wild? If so, then metrics of population abundance, health, or fitness should be positively related with genetic diversity in local populations (Reed and Frankham 2003; Willi et al. 2006; Markert et al. 2010). Alternatively, if genetic diversity was not a strong predictor of population persistence or fitness, what were the primary drivers of population persistence and health (Yates et al. 2019; Teixeira and Huber 2021)? To address these questions, we used data compiled since 1985 to estimate genetic diversity and demographic health of Gila trout populations and evaluate their relationships with specific environmental factors. Although a 35-year dataset seems sufficient to document effects of an array of naturally occurring environmental drivers of population viability, it might be temporally insufficient to fully capture negative effects of severely reduced genetic diversity on viability. Nonetheless, our aim was to provide perspective on conservation approaches taken in the past and those that might be implemented as the landscape shifts to a warmer and drier environment.

2 Methods

2.1 Study Area

Gila trout populations considered in this study occupied streams of the upper Gila River catchment of southwest New Mexico; except the McKnight Creek population that was in the Mimbres River catchment (Fig. 1). Occupied reaches ranged from about 2 to 26 km in length (Big Dry and Mogollon Creeks, respectively) and occurred mainly at elevations between 2000 and 2500 m (Table 1, Fig. 2). Base flows (June–July) varied from about 10 to 50 L/s. Precipitation occurred mainly in winter (December–February) and during the monsoon season (July–September). Rain on snowpack and intense convectional monsoon storms occasionally caused substantial scouring floods. Since about 2000, the region has experienced extended drought (Gutzler 2013; Garfin et al. 2014; Williams et al. 2020) with historically perennial stream reaches becoming intermittent (Overpeck and Udall 2020), including several considered in this study. Although wildfires are a natural feature on the landscape, their frequency and intensity has increased considerably in the past 30 years (Singleton et al. 2019; Gila National Forest 2020) and all drainages having Gila trout populations were affected by wildfire during this time. Total annual precipitation (snow and rain) and Palmer Drought Severity Index (PDSI, Palmer 1965) were used to characterize and illustrate climatic changes experienced in southwest New Mexico during the study (1985–2020). Over the course of this study, total annual precipitation declined significantly (Fig. 3a). This decline was reflected in mean annual PDSI values (Fig. 3b); between 1985 and 1999, PDSI indicated comparatively wet conditions (Index values greater than 1.0) but from 2000 through 2020 the region underwent a severe drought, with annual PDSI less than −1.0 in 11 of 21 years.

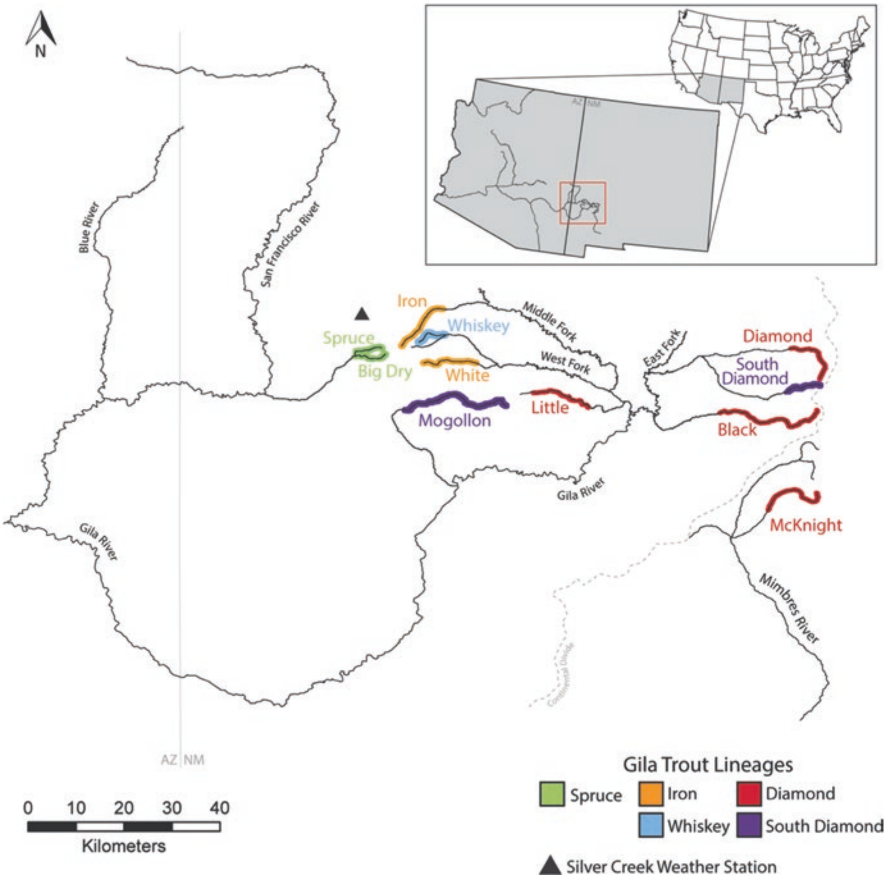


Fig. 1 Upper Gila River drainage, New Mexico, USA. Each of the five remnant Gila trout lineages located on map with replicates highlighted in same color. Map by A.C. Cameron

2.2 Population Data

Demographic and genetic data used herein were gathered during various activities associated with Gila trout research, monitoring, and conservation over the past 35 years (1985–2020). For this study, 11 Gila trout populations were considered; all remnant populations and six replicate populations (Table 1). Frequency of population samples used varied from one (Whiskey) to 13 (McKnight). Samples were collected pre- and post-founding in Black, South Diamond, and Mogollon Creeks; wildfire interrupted Gila trout presence in Black and South Diamond Creeks and a piscicide application interrupted occurrence in Mogollon Creek. Otherwise, samples were composed of descendants of initial founding (human or natural).

Restriction of Gila trout to remote streams with limited access posed limitations on sampling methods, frequency, and thoroughness. Although data were collected

Table 1 Gila trout populations considered in this study. Remnant populations in **bold.** Population status (Period of occupancy) as of 2020

Population	Elevation (m)	Occupied habitat (km)	Period of occupancy	# Demographic samples	# Genetic samples
Diamond	2335–2425	6.1	–1989, 1995–present	12	3
McKnight	2155–2460	8.6	1970–2013	13	1
Black	2085–2630	17.0	1996–2013, 2013–present	9	1
Little	1850–1970	5.2	1995–present	3	1
South Diamond	2335–2425	6.7	–1995, 1997–present	9	3
Mogollon	1955–2240	27.1	1989–1997, 1997–present	11	1
Iron	2580–2700	4.3	–present	11	2
White	2280–2655	8.8	1993–2000	2	0
Whiskey	2395–2445	1.3	–2012	1	3
Spruce	2135–2420	3.5	–2012	5	3
Big Dry	2140–2350	1.9	1986–present	6	1

Fig. 2 Gila trout habitat, Black Canyon, upper Gila River catchment, New Mexico, USA, illustrating the comparatively small streams typically occupied by the species. Photo by D.L. Propst

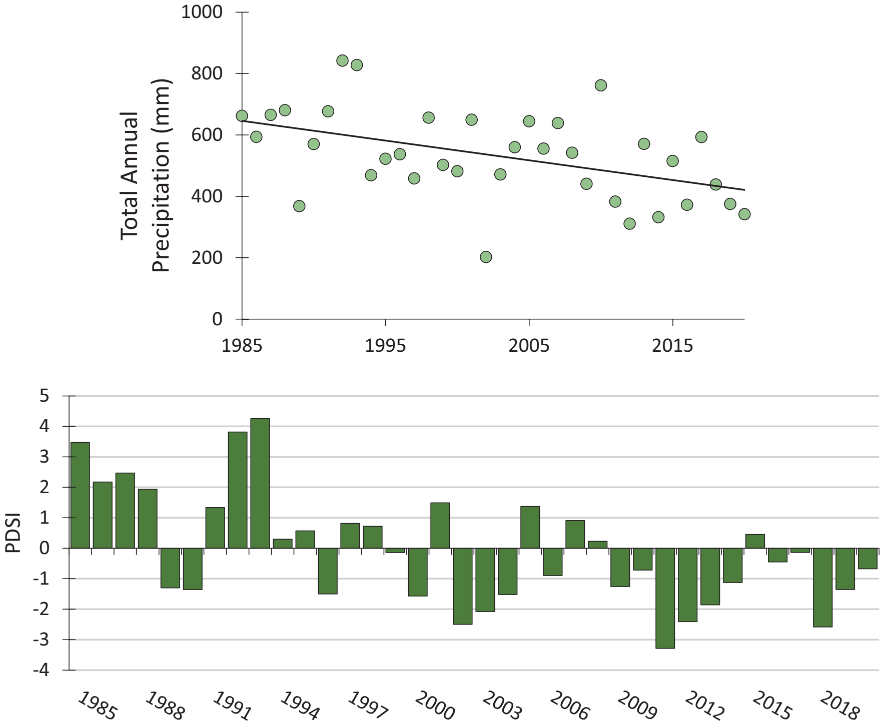


Fig. 3 Total annual precipitation in upper Gila River catchment, New Mexico, USA (Silver Creek Station; https://www.ncdc.noaa.gov/cdo-web/search) (upper panel) and Palmer Drought Severity Index (https://app.climateengine.com/climateEngine) (lower panel). Positive PDSI values indicate moist conditions and negative values indicate dry conditions

by various individuals for different projects and objectives, sampling methods were consistent across efforts. Fish were stunned using backpack electrofishers and netted, held briefly, mass (g) and length (mm, total length [TL]) determined and recorded, and released near the area of capture. Specimens were captured in a single pass of the sample site in which all available habitats (e.g., pools, riffles, runs, and eddies) were sampled; no effort was made to "hunt" fish not immediately netted. Sampling typically began at downstream terminus of Gila trout occurrence and proceeded to upstream extent of occurrence. In some instances, the occupied reach was sampled continuously from bottom to top, but in others discrete sites were sampled. Number of sample sites, and their lengths, depended on length of occupied reach but collectively encompassed at least 10% of occupied reach. Gila trout populations were sampled to document demographic status (monitoring), obtain gametes (spawning), repatriation (donors), and evacuation (extirpation risk), but most collections were monitoring events. Although sampling methods were consistent, month of collection varied among projects. March and April collections occurred during spawning, June–July collections were during base-flow periods, August–September during monsoon season, and October–November collections were after most storm-induced flow spikes. Upon emergence from redds, age-0 fish were <30 mm TL and by late October–early November some age-0 individuals were 90+ mm TL. Collections made soon after emergence (June–July) under-sampled age-0 Gila trout, whereas collections later in the year likely yielded roughly accurate estimates of age-0 abundance.

Because abiotic environmental data (e.g., water temperature, stream discharge, and water quality) were not available for each stream, we used regional total annual precipitation as an inclusive metric to ascertain response of Gila trout populations to abiotic environmental influences. Three metrics were considered demographic response variables: Gila trout abundance, population size structure, and fish condition. Abundance (CPUE = catch per unit effort) was calculated as the number of individuals collected/elapsed electrofishing time (s). Specimens were grouped in 10-mm length classes to characterize size structure (length–frequency) of each sample (Neumann and Allen 2007). Condition was calculated for each specimen ≥100 mm TL using Fulton's formula of $K_{TL} = (TL^3/mass)*10^5$ (Fulton 1904; Pope and Kruse 2007). Catch-per-unit-effort estimates were a comparatively crude measure of fish abundance as several factors influenced its accuracy; a key factor was probability of capture, which was influenced by skill of personnel, size of fish, and conditions under which collections were made. Despite this limitation, CPUE is commonly used to depict fish abundance in situations where population estimates are not practical nor feasible (Hubert and Fabrizio 2007); such was the case in most Gila trout collections. Length–frequency characterization of each sample provided a snapshot of the spread and strength of size classes in a sample and thus an indication of annual recruitment and survival within a population. Condition (K_{TL}) served as a comprehensive index of a fish's physiological well-being. For a species that grows isometrically, values <1.00 are indicative of some stressor or paucity of resources, and values >1.00 suggest it has adequate resources, such as food, and stressors are absent or minimal (Hammock et al. 2021). Because March and April samples included pre-spawning gravid females, these samples were not considered in assessments of condition (K_{TL}) of populations. Mean condition of all specimens 100–149 mm TL (sub-adults), all specimens ≥150 mm TL (adults), and size groups combined in a sample were used for inter- and intra-population comparisons.

We tested for density dependence by plotting mean condition (K_{TL}) and adult (individuals ≥150 mm TL) CPUE across all Gila trout samples within each population, except those having fewer than four collections (Little, White, and Whiskey). Pearson's correlation coefficient (*r*) was calculated to assess the relationship of CPUE and condition (K_{TL}), where a significantly negative value of *r* is expected if density-dependent factors are operating.

2.3 Genetic Data

Three genetic datasets were used to compare and rank genetic diversity across Gila trout populations. The first included genetic samples collected in 2002 as part of a broad-scale study of native trout in the southwestern US (Gila trout and Apache trout *O. g. apache*; Wares et al. 2004), where 146 Gila trout from 10 populations (four remnant and six replicate) were genotyped at six microsatellite DNA loci (Peters and Turner 2008). The second included genetic samples collected in 2012 following airlift rescue of Gila trout from the Whitewater-Baldy megafire, except Iron Creek that was sampled 1 year after the fire to locate survivors. A total of 639 samples from 6 populations (5 remnant and 1 replicate) were genotyped at 13 DNA microsatellite loci (Turner et al. 2014) including one locus examined by Peters and Turner (2008). The third dataset also focused on samples from Gila trout rescue and relocation efforts in 2012 but was limited to the five remnant populations. In this case, 156 Gila trout were genotyped at 2381 single-nucleotide polymorphism (SNP) loci distributed across the genome (Camak et al. 2021). Some populations were represented in all three datasets, some in only one. No genetic data were obtained from the Iron Creek replicate, White Creek.

Methodological and analytical details are presented in the original papers and reports. For each dataset, we computed allelic richness (A_R) and observed heterozygosity (H_O), averaged across loci for each population, as metrics that reflected standing levels of genetic diversity within a local population. A_R and H_O are strongly positively correlated under idealized theoretical conditions, but in real populations both measures deviate from one-to-one correspondence due to independent fluctuations in population size, local selection, and other factors. For example, Luikart and Cornuet (1998) showed that a recent demographic bottleneck can temporarily increase heterozygosity due to stochastic effects associated with severe reduction in population numbers. This effect persists at most for a few generations after the bottleneck event. Thus, for real datasets, these two metrics give complementary, but different insights into diversity.

2.4 Ecological and Genetic Comparisons

Fulton fish condition (K_{TL}) was averaged across individuals collected during distinct sampling events and then averaged across events to yield grand mean K_{TL} for each Gila trout population. Grand K_{TL} means were ranked in descending order from most (1) to least (10). Similarly, Gila trout populations were ranked in descending order from most (1) to least (10) genetically diverse. To estimate genetic diversity ranks, Z-scores were calculated separately for A_R and H_O for each dataset, summed as a composite measure of diversity, and then ranked across summed scores. This procedure ensured that A_R and H_O were equally weighted in the ranking procedure. Ranks for grand mean condition and composite genetic diversity were compared using

Kendall's non-parametric rank correlation procedure to test the null hypothesis of no association of fish condition and standing levels of genetic diversity.

3 Results

3.1 *Demographic Attributes*

Abundance (CPUE) of each remnant population and its replicate(s) varied from year to year, but none evidenced a distinct trend (Fig. 4). Abundance (based on individuals ≥100 mm TL) was typically less than 0.04 fish captured/s and rarely greater than 0.08 fish captured/s. Nor was there a relationship between total annual precipitation and abundance ($R^2 = 0.038$, $p = 0.110$).

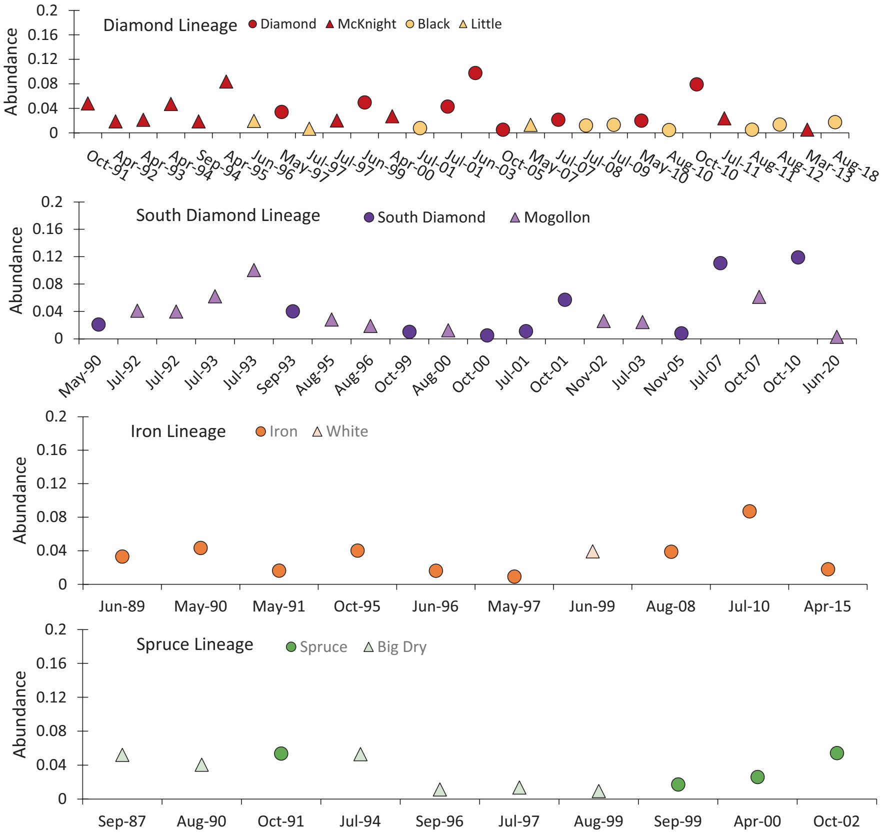


Fig. 4 Abundance (# specimens/s elapsed electrofishing time) of Gila trout in remnant and replicate populations, upper Gila River catchment, New Mexico, USA

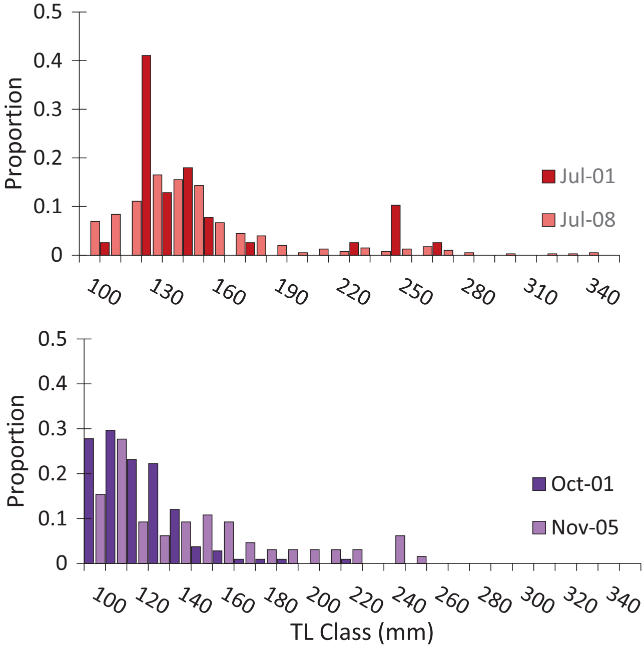


Fig. 5 Size structure of Black (Jul 01 & Jul 08) and South Diamond (Oct 01 & Nov 05) populations illustrating significant and marginally significant intra-population differences (D = 0.574, $p < 0.001$ and D = 0.398, $p = 0.098$, respectively)

Size structure of Gila trout populations (specimens ≥100 mm TL) was similar across years within a stream; among all intra-stream comparisons only four had significantly different size structures (Fig. 5). Much more common were the similar size structures illustrated by Iron (Oct 1993–Oct 1995) and Big Dry (Jul 1994–Sep 1996) populations (Fig. 6). Most Gila trout collections were composed mainly of individuals between 100- and 200-mm TL; individuals greater than 300 mm TL were extremely rare (Supplemental Table 1).

Mean condition (K_{TL}) for remnant and replicate samples (sub-adults and adults) of each lineage varied little from year to year (Table 2, Fig. 7). The grand mean for each lineage (mean of remnant sample mean K_{TL}s) was slightly greater than 1.00 for all lineages (except Whiskey, for which there was only a single mean annual K_{TL} of 1.2218). Aside from Whiskey, grand mean K_{TL} (excluding March and April samples) ranged from a maximum at Spruce to a minimum at Iron (Table 3).

In addition to there being no evident trend in Gila trout condition over time (Fig. 7), there was no relationship between sample condition and total annual precipitation (11 months prior to sample and month of sample) for sub-adults or adults (Fig. 8). Likewise, there was little evidence for negative density-dependent regulation in all but 1 of 11 Gila trout populations examined. When CPUE was plotted against K_{TL}, negative values of the Pearson correlation coefficient, r, were observed in Diamond, McKnight, South Diamond, Mogollon, and Iron populations. Positive

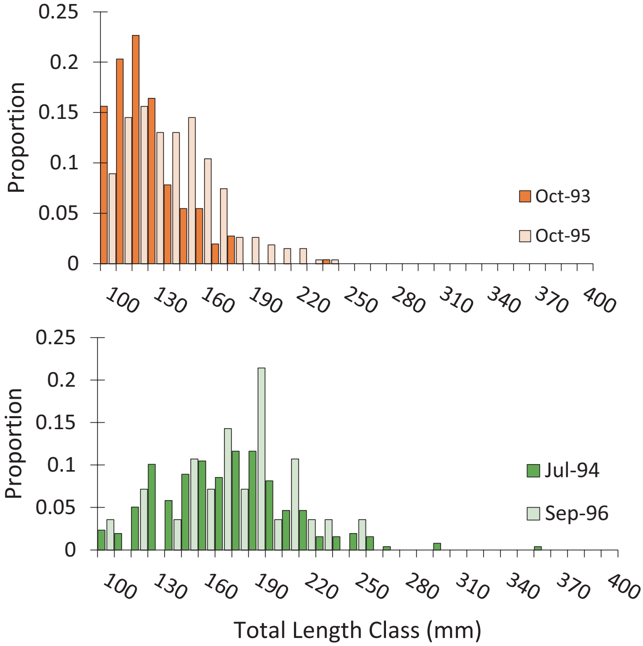


Fig. 6 Size structure of Iron (Oct 93 & Oct 95) and Big Dry (Jul 94 & Sep 96) Gila trout populations illustrating non-significant intra-population differences ($D = 0.192$, $p = 0.527$ and $D = 0.226$, $p = 0.267$, respectively)

values of r were observed in Black, Spruce, and Big Dry populations. No values of r were significantly different from zero, although the value for South Diamond was marginal ($r = -0.39$, $p = 0.074$).

3.2 *Genetic Diversity*

Standing levels of genetic diversity differed in a consistent fashion among Gila trout populations across three genetic studies based on genomic DNA markers (i.e., microsatellites and SNPs). Diamond Creek and its replicates were nearly always the most diverse, and Spruce Creek and its replicate were always the least diverse across three genetic studies (Fig. 9a–c). Whiskey Creek exhibited higher diversity in the 2002 dataset but less in the 2012 sample, resulting in a change in rank from second to fourth, respectively, across datasets (Fig. 10). Biplots of A_R and H_O showed increased heterozygosity in Iron Creek at SNP loci that may have resulted from a recent bottleneck (Camak et al. 2021). Increased heterozygosity in Iron relative to Diamond led to swapping diversity ranks in the SNP dataset.

Table 2 Gila trout sub-adult (100–149 mm TL), adult (>150 mm TL), and sub-adult & adult combined mean condition (K_{TL})

Lineage	Replicate	Sub and adult mean K_{TL}	Sub mean K_{TL}	Adult K_{TL}
Diamond (all)		1.0548	1.0511	1.0704
Diamond (w/o Apr)		1.0505	1.0487	1.0645
	McKnight (all)	1.1101	1.1050	1.1283
	McKnight (w/o Apr & Mar)	1.1036	1.1070	1.1054
	McKnight (Apr & Mar)	1.1158	1.1033	1.1747
	Black	1.0344	1.0355	1.0296
	Little	1.0669	1.0118	1.0688
South Diamond		1.0479	1.0306	1.0488
	Mogollon	1.0335	1.0334	1.0436
Iron (all)		1.0538	1.0595	1.0651
Iron (w/o Apr)		1.0320	1.0373	1.0460
Iron (Apr)		1.2498	1.2590	1.2365
	White	1.0813	1.1089	1.0300
Whiskey		1.2218	1.2522	1.1004
Spruce (all)		1.0608	0.9659	1.090
Spruce (w/o Apr)		1.1034	1.0404	1.1357
Spruce (Apr)		0.9331	0.7425	0.9513
	Big Dry	1.1040	1.1464	1.0819

3.3 *Fish Condition and Genetic Diversity*

There was no relationship between adult fish (specimens ≥150 mm TL) condition and genetic diversity composite ranks across Gila trout populations (Table 3; Kendall's rank correlation sample estimate $\tau = -0.29$, T-statistic = 16, $p = 0.29$). Composite ranks were adjusted to account for differences in rank across studies by swapping ranks of Diamond and Iron Creeks (Kendall's rank correlation sample estimate $\tau = -0.33$, T-statistic = 15, $p = 0.22$). Similarly, Whiskey and South Diamond (and replicates) were swapped, yielding no correlation (Kendall's rank correlation sample estimate $\tau = -0.24$, T-statistic = 17, $p = 0.38$).

4 Implications and Conclusions

Despite a decline in precipitation and periods of prolonged drought, we found little evidence of temporal trends or patterns in the abundance (measured as CPUE) of fish (individuals ≥100 mm TL) in any Gila trout population during the 35-year study period. Within Diamond and South Diamond lineages, there was variation in

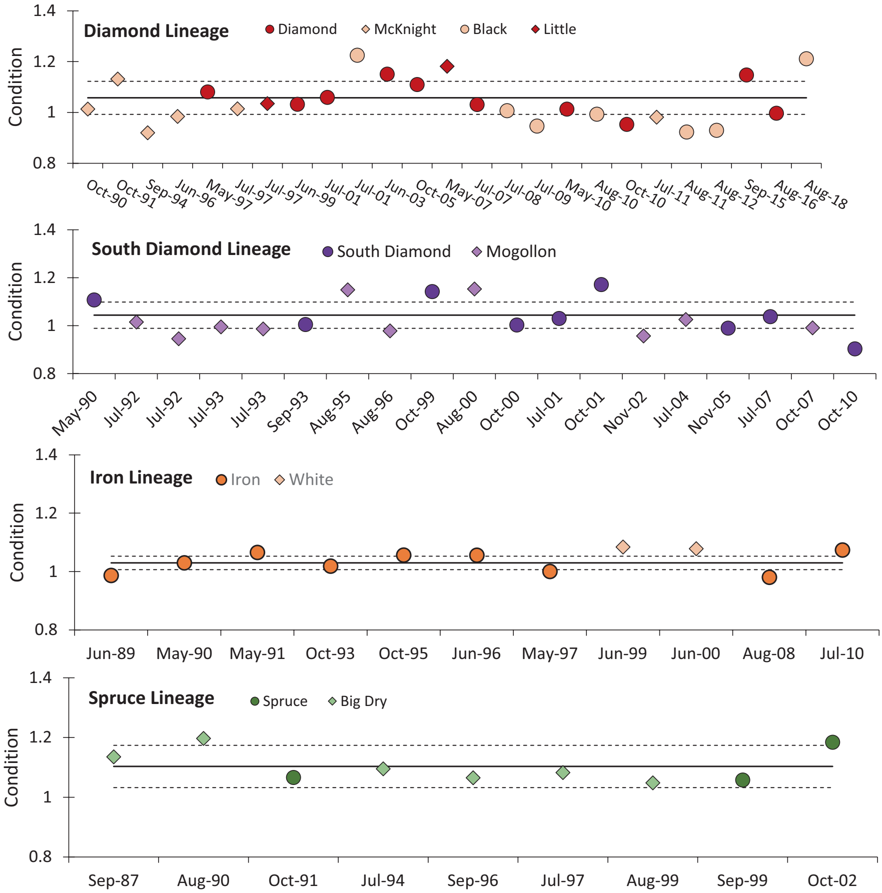


Fig. 7 Condition (K_{TL}) of Gila trout samples (only specimens ≥100 mm TL) from four lineages. Solid horizonal line = grand mean K_{TL} of each remnant population and dashed lines = 95% Confidence Interval for that lineage. Whiskey lineage had a single collection and is therefore not depicted

abundance from one sample to the next, but less variation was noted for Iron and Spruce lineages. Among all populations, abundance was usually less than 0.08 individuals/s, but in several instances exceeded 0.1 individuals/s. As estimated, abundance was a crude measure of population size at a point in time and was not informative in revealing temporal population trends or patterns if such existed. Failure to identify trends in abundance was somewhat surprising given patterns of environmental change that are known to negatively influence other inland salmonid species (Bell et al. 2021a). We expected we would detect a relationship between precipitation and Gila trout abundance but did not. If Gila trout populations suffered declines in abundance in response to drying conditions, then they recovered in the time elapsed between sampling events. Moreover, because there is no natural

Table 3 Population grand mean condition (K_{TL}), number of sample means used to calculate mean population condition, rank K_{TL}, and genetic diversity rank. Ranks are in descending order. Only specimens ≥150 mm TL (adults) used to calculate grand mean K_{TL}. Genetic diversity rank is based on the sum of Z-scores of mean allelic richness and observed heterozygosity. Genetic data were not available for the White Creek population

Population	Grand mean K_{TL}	# samples	K_{TL} Rank	Genetic diversity Rank
Spruce	1.1357	3	1	9
Whiskey	1.1004	1	2	8
Big Dry	1.0819	6	3	10
Little	1.0688	3	4	5
Diamond	1.0645	10	5	1
McKnight	1.0539	5	6	2
South Diamond	1.0488	9	7	6
Iron	1.0460	9	8	3
Mogollon	1.0436	11	9	7
White	1.0300	2	10	–
Black	1.0296	7	11	4

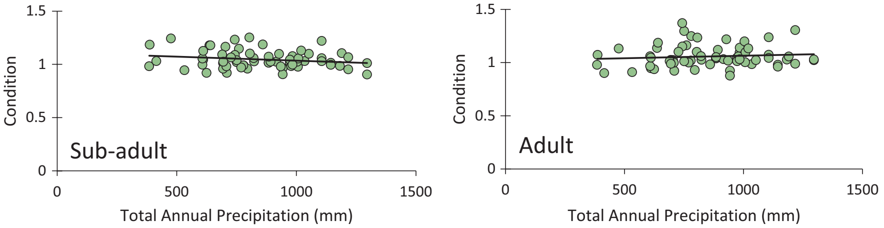


Fig. 8 Total annual precipitation and condition (K_{TL}) of sub-adult and adult Gila trout populations from upper Gila River catchment, New Mexico, USA. Each dot represents mean K_{TL} (sub-adult or adult) of a single collection on a single sampling event. Neither sub-adult nor adult condition was related to total annual precipitation

migration among populations, recovery of local population abundance was achieved solely through local reproduction unless bolstered by human-assisted translocation (e.g., Black Canyon). Overall, these data suggest Gila trout populations were remarkably resilient to decreased precipitation and increased drought over the last 35 years.

Within-population size structure comparisons yielded few differences in length–frequency of compared samples. General lack of difference between size structure of samples was due, in part, to exclusion of individuals ≤100 mm TL from comparisons. Proportion of individuals (≥100 mm TL) per length class were normally distributed in most collections and most individuals were between 100- and 200-mm TL; most collections had several individuals greater than 200 mm TL, but few had individuals greater than 300 mm TL. The compressed TL distribution was consistent across streams and was, in part, a consequence of the comparatively small size

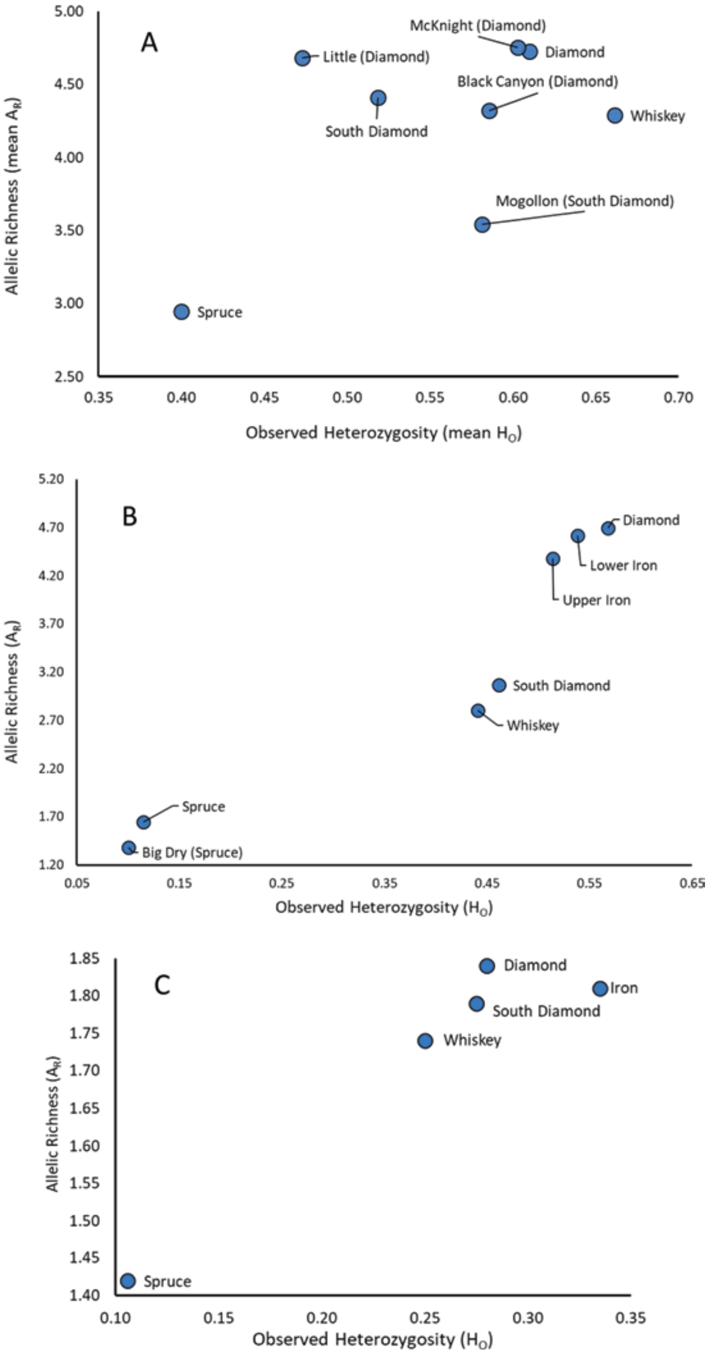
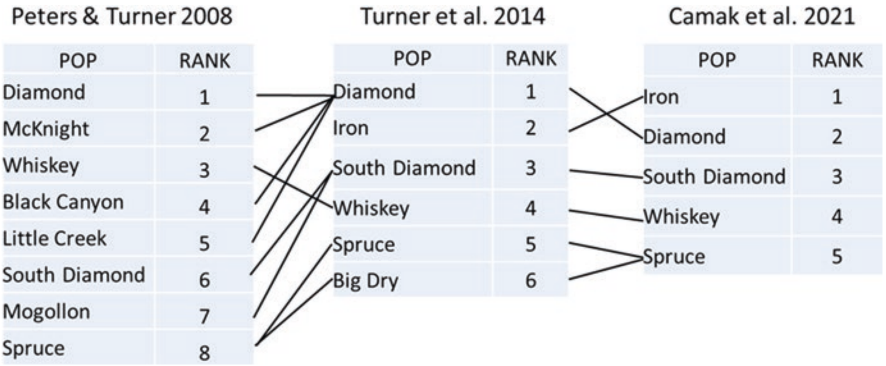


Fig. 9 (**a**–**c**) Biplots of mean observed heterozygosity (H_O, x-axis) and mean allelic richness (A_R, y-axis) derived from: (**a**) microsatellite data from Peters and Turner (2008); (**b**) Microsatellite data from Turner et al. (2014); and (**c**) 2381 putatively neutral SNPs (Camak et al. 2021). Points in the upper right side of graphs are more genetically diverse, those in the lower left more depauperate



Peters & Turner 2008

POP	RANK
Diamond	1
McKnight	2
Whiskey	3
Black Canyon	4
Little Creek	5
South Diamond	6
Mogollon	7
Spruce	8

Turner et al. 2014

POP	RANK
Diamond	1
Iron	2
South Diamond	3
Whiskey	4
Spruce	5
Big Dry	6

Camak et al. 2021

POP	RANK
Iron	1
Diamond	2
South Diamond	3
Whiskey	4
Spruce	5

Fig. 10 Comparison of ranks, in descending order, of genetic diversity across three genetic studies of Gila trout based on mean allelic richness and mean observed heterozygosity combined. Line crossovers indicate changes in rank across datasets. Whiskey exhibited a decline in diversity from 2002 to 2012 associated with a drought-induced population bottleneck. Iron Creek exhibited higher observed heterozygosity in the SNP study which increased its rank in the Camak et al. (2021) dataset. Otherwise, genetic diversity ranks are consistent across studies

of most streams occupied by Gila trout. Similarity in size structure across populations suggests that similar population processes act upon local populations even though they are demographically isolated. Populations are geographically proximal and so it is possible that regional environmental variation acts in a way that is fairly uniform across populations.

Grand mean condition (mean of all sample means over time for each population) of each remnant population was greater than 1.0 in all Gila trout populations. Over the course of the study, mean condition of replicate population samples varied about the grand mean of that lineage with no evident pattern or trend. A minority of replicate samples of three lineages were within the 95% CI of their respective remnant population grand mean: 4 of 15 Diamond, 4 of 10 South Diamond, and 0 of 2 Iron. Only one Spruce replicate was outside the 95% CI of the Spruce grand mean. Mean condition of most samples (remnant and replicate) of each lineage exceeded 1.0, generally indicating physiologically healthy populations. The comparatively high condition of the Whiskey population was due in part to there being only a single collection of comparatively few specimens from this population. There was little evidence of negative density dependence in any Gila trout population, as we failed to observe the predicted significant negative relationship of CPUE (as a proxy of density) and condition in any Gila trout remnant or replicate population analyzed. A marginal negative relationship was observed in South Diamond Creek that is a small and relatively homogeneous stream with potentially limiting resources at densities observed in this study. Instances of positive density dependence, as suggested in relationships observed in Spruce and Iron Creeks, are sometimes observed in very small populations (Courchamp et al. 1999; Willi et al. 2022) subject to Allee effects, but this remains to be tested in Gila trout.

Finally, we observed no relationship of grand mean K_{TL} and genetic diversity ranks across Gila trout populations. This result was also somewhat surprising because a positive relationship of population “health” or “fitness” and standing levels of genetic diversity is generally expected (Frankham et al. 2010). Standing levels of genetic diversity in Spruce and Whiskey lineages and their replicates are remarkably low, yet these populations persisted in the wild at relatively high mean condition over the study period. It is important to note that Fulton condition is a quantitative trait with a strong genetic basis in inland trout [i.e., heritability was 0.50 in Lahontan cutthroat trout (Robinson et al. 2008) and 0.52 in Rainbow trout (Perry et al. 2005)]. It is expected that loss of genome-wide diversity (as measured by neutral markers like microsatellites and SNPs) should correlate to loss of variability unless strong directional selection had already reduced genetic variance in K_{TL}. While failure to detect a significant relationship is not proof that a relationship does not exist, it appears that Gila trout populations are resilient to press abiotic disturbances like drought (*sensu* Lake 2000), biotic factors such as density dependence, and lack of genetic variability, at least in the short term. At best, these factors appear to be weak drivers of population health in Gila trout over the time span of this study. Yet, if that is true, then what factors pose the greatest risk to persistence, especially under future climate-change scenarios (e.g., Kennedy et al. 2008)? Are there potential interactions among risk factors that should inform future conservation planning and management?

5 Resilience and the Future of Gila Trout

Catastrophic pulse disturbances pose the single greatest risk of extirpation of local Gila trout populations (Brown et al. 2001). In other words, density-independent, abiotic pulses of wildfire and debris-laden flows are the most important proximal causes of local extirpation (Brown et al. 2001; Burton 2005; Bixby et al. 2015; Rust et al. 2019; for more detail on press vs. pulse disturbance, see Lake 2000). An extreme example is the Whitewater-Baldy Fire and post-fire debris flows that negatively affected seven Gila trout populations, eliminated four, and likely would have eliminated others from the wild without intervention. Because wildfires are expected to increase in frequency, magnitude, and severity as climate change continues (Waring and Coops 2016; Singleton et al. 2019; Brown et al. 2021), this will be a persistent and acute extinction risk for Gila trout. Our results suggest rescue, temporary relocation to a hatchery or preferably a refuge stream, and post-disturbance repatriation are components of a viable and necessary conservation strategy. This is because repatriated populations (e.g., McKnight, Mogollon, and Little Creeks) did not differ appreciably in condition or abundance from populations with no history of repatriation (e.g., Iron Creek). Likewise, repatriated populations showed little evidence of density-dependent effects on mean condition of sub-adult and adult fishes.

This is not to say that press disturbances, like the extended and persistent drought of the 2000s, did not have important negative demographic and genetic impacts on aquatic species, including Gila trout (Ault et al. 2016). Although we did not observe strong declines in abundance related to drought, comparisons of genetic diversity of samples obtained in 2002–2012 showed dramatic reductions of observed heterozygosity for Spruce and Whiskey Creek populations (Fig. 10). Although time-series data were not available for Iron Creek, whole-genome SNP data showed evidence of a recent bottleneck that occurred after the Whitewater-Baldy Fire (Camak et al. 2021). Diamond and South Diamond lineages did not show appreciable changes in heterozygosity at microsatellite DNA loci over time, but Diamond lost allelic diversity at the MHC Class II locus, which is involved in the adaptive immune response to pathogens (Turner et al. 2014). Thus, all populations of Gila trout show some evidence of loss of genetic diversity over the study period, probably due to bottlenecks and random drift within small and isolated populations.

For a genetic bottleneck to occur and be detected in time-series or in whole-genome data, the focal population must have been reduced to a fraction of its pre-disturbance adult population size during the disturbance. Although post-fire population surveys are few, those for Iron Creek indicated that Gila trout persisted, and density had recovered to near pre-fire levels by 2018. Recovery to pre-disturbance abundance levels in the absence of stocking or colonization by another population indicated that Iron Creek is a resilient yet genetically depauperate population.

How do genetically depauperate populations maintain resilience and persist at relatively high condition and abundance without supplementation of individuals from donor populations and/or hatcheries? This is an important, but largely unanswered question. Possible explanations involve compensatory effects, purging of deleterious mutations, different modes of selection (e.g., Bell et al. 2021b), and/or evolutionary robustness and plasticity arising as emergent properties of metabolic gene networks (Wagner 2012). First, resources for fish that survived are likely to be abundant following disturbance because aquatic insects rebound quickly (Jager et al. 2021) and achieve high abundance when fish predators are in low density. Resource abundance enhances reproductive success, leads to lower variance in reproductive success among individuals, and enhances recruitment. These ecological conditions, when paired with reproductive output of Gila trout, increase capacity for rapid demographic recovery, but as noted above, Allee effects may limit potential for demographic recovery if the number of survivors is too low (Courchamp et al. 1999). In any event, demographic recovery from a bottleneck does not alleviate low genetic diversity because genetic variation recovers as new mutations accumulate over evolutionary, not ecological, time. Severe genetic bottlenecks can lead to purging of deleterious alleles and a temporary increase in population fitness and health (Swindell and Bouzat 2006), although the degree to which purging is effective can be difficult to predict (Leberg and Firmin 2008). The genomics revolution offers new insight into the function of gene networks, duplicated genes, epigenetics, and other mechanisms that could enhance capacity for robust and/or plastic physiological response to fluctuating or novel environmental stressors, even when allelic variation at neutrally evolving genes is very low (Turner et al. 2020). This is an area of ongoing research that could be fruitful in organisms such as Gila trout.

A widely held paradigm that has extensive theoretical as well as empirical support among ecologists and conservation geneticists is that genetic diversity within a species or its constituent populations is positively correlated with its overall well-being whether determined by its abundance or some measure of fitness (Reed and Frankham 2003; Markert et al. 2010; DeWoody et al. 2021). The longstanding idea that diversity at neutrally evolving genes is linked to fitness and extinction risk, however, has recently been challenged (Yates et al. 2019; Teixeira and Huber 2021). Our results suggest weak, if any, relationships of standing levels of diversity at neutral genes and population fitness as measured by condition over the short term. Over longer time periods, mechanisms like those described above that protect a population from deleterious effects of inbreeding in the short term are expected to break down, leading to diminished fitness in the long run (Willi et al. 2022). Perhaps more importantly, the capacity to withstand novel challenges, like a new pathogen or sustained drought, may already be substantially diminished in Gila trout. Thus, the combination of population survey and genetic data presented here implies that Gila trout are resilient but not resistant to drought. Resilience is defined as demographic bottlenecking followed by *in situ* recovery to pre-disturbance abundance levels (Bogan et al. 2015), excepting individuals from a donor population (including the hatchery) introduced via human assistance. Without periodic introduction of migrants, however, a repetitious cycle of drought and wildfire will further erode neutral genetic diversity of Gila trout thereby diminishing its adaptive potential or evolvability with climate change (Willi et al. 2006).

6 Genetic Diversity Management

There are ongoing and proposed management actions aimed at maintaining and enhancing genetic diversity in Gila trout (USFWS 2021). In principle, these actions seek to balance sometimes opposing goals that include maintaining lineage identity, increasing within-lineage genetic diversity through gene flow, and limiting opportunities for hybridization with nonnative trout. First, the recovery plan calls for replication of each remnant population in at least three geographically distant areas to minimize the probability of lineage extirpation from large-scale catastrophic fires. Establishment of replicates for each lineage also provides potential donors to repopulate extirpated streams should the need arise. Second, the plan prescribes re-establishment of natural gene flow among remnant populations where one or more lineages are stocked into unoccupied dendritic stream networks capable of supporting Gila trout. This strategy allows for natural interactions among individuals and genotypes to potentially restore metapopulation dynamics among repatriated populations. However, all remnant, replicate, and metapopulations are, or will be, isolated from interactions with nonnative rainbow trout, with which Gila trout readily hybridizes. Isolation is achieved by natural and constructed barriers to upstream dispersal, thus limiting opportunities for within-species gene flow at a broad spatial scale (Propst et al. 2020).

A potential solution to the problem of limited natural gene flow is to implement a protocol of human-assisted gene flow, referred to as genetic rescue (Whiteley et al. 2015). In genetic rescue, a proportion of individuals from a genetically distinct population are translocated to introduce genetic variation into the recipient population. The number of individuals translocated is estimated as a function of local effective population size to maintain genetic identity (by not swamping the local gene pool) but to allow for enhanced diversity of the recipient population (see Kovach et al. 2021). Surviving remnant populations within the upper Gila River catchment, namely Iron, Whiskey, Diamond, and South Diamond appear to have exchanged individuals and genes naturally in the recent past (Camak et al. 2021). Based on a gene-tree topology reconstructed from this dataset (Propst et al. 2020), we surmise that natural gene flow followed an isolation-by-distance model, where geographically proximal populations exchanged genes at higher rate than the more distal populations. This information, along with information on local gene diversity and effective population size can be incorporated into a plan for genetic rescue of these now completely isolated populations.

The remnant Spruce and its replicate Big Dry populations occur in the San Francisco River watershed and are more deeply evolutionary divergent from the upper Gila populations (Riddle et al. 1998; Camak et al. 2021). Spruce and Big Dry also have the lowest levels of genetic diversity compared to all other remnant Gila trout populations, and as such, are prime candidates for genetic rescue. However, it is not clear which population should serve as donor, or whether outbreeding depression (a possible outcome of genetic rescue) may be an issue. In this case, the Gila Trout recovery team has advocated genetic rescue using carefully controlled crosses and backcrosses, likely in a hatchery environment (Wade Wilson, USFWS, pers. comm.). All of these measures should enhance genetic robustness of Gila trout and increase its probability of persistence as long as a well-crafted fire evacuation plan is in place and is executed appropriately.

7 Persist in Place, or Shift in Space?

Gila trout is resilient to many disturbances on the landscape, including drought, but is sensitive to wildfire and associated debris flows. Strongholds for Gila trout remain in watersheds that are protected from land-use transformation and water extraction because they occur on officially designated wilderness or National Forest lands, where destructive anthropogenic activities are banned or strictly regulated. These same watersheds, however, are increasingly likely to burn under the new fire regime imposed by climate change (Gergel et al. 2017; Coop et al. 2020). Because of the isolated nature of these streams, and the presence of constructed barriers to upstream fish movement to protect against hybridization with nonnative species, downstream expansion of habitat within the watershed is unlikely. Furthermore, downstream and lower elevation habitats are likely to exceed maximum thermal tolerances of Gila trout under some climate-change scenarios (Kennedy et al. 2008; Schultz et al. 2017; but see Armstrong et al. 2021). Upstream movement, if possible, may locally ameliorate this, but the severity of fire impacts on local populations is expected to increase in upstream reaches (Gido et al. 2019). Establishment of populations in watersheds outside the historical range of Gila trout is not a viable option as these regions would likely experience similar fire and drought risk as the Gila watershed. Moreover, these watersheds already support diminished populations of other native salmonid species and introduction of Gila trout into them would impose additional, and unacceptable, stressors on them, including increased risk of introgression with Gila trout. It thus appears that the only option is to expand Gila trout habitat within its historical range. Many available and suitable streams for Gila trout repatriation have been restored or are in the process of being readied for Gila trout occupancy. Restoration of remaining suitable streams will require considerable physical effort as well as political resolve to make these streams available to Gila trout. For this to succeed, however, requires focused attention on strategies to protect and enhance genetic diversity in Gila trout, coupled with extensive and intensive continuous genetic and demographic monitoring of extant Gila trout populations and their habitats. Finally, directed research is needed on the demographics of local Gila trout populations and how they respond to biotic, abiotic, and intrinsic factors associated with long-term environmental change.

This chapter compiled extensive, yet incomplete, demographic and genetic data and illustrated the demographic resilience of Gila trout to extended drought as well as its heightened risk to population extinction by catastrophic natural events such as wildfire when it persists only as scattered small populations on the landscape. The decline of Gila trout over the past 150 years is visibly measured by the km of stream habitat no longer occupied (USFWS 2021). The two populations known when the species was described in 1950 (Miller 1950) occupied about 12 km of stream, less than 5% of that occupied by Gila trout when Europeans first arrived in the American Southwest. This loss can and is being partially repaired by repatriation to historic habitat. Genetic management of Gila trout must be implemented in the context of strong abiotic controls (fire) on population persistence, where catastrophic loss is anticipated and planned for. The approach most likely to yield positive results is restoration of Gila trout lineages to large dendritically complex drainages, such as upper West Fork Gila River, where lineages are released to tributary streams and fish randomly move, mix, and spawn without direct human manipulation. This, together with genetic rescue protocols to maintain genetically diverse populations to serve as donors to restore populations lost to fire or other causes, will thereby help to ensure long-term persistence of this iconic species.

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Ecological Traits and Fishery of the Upper Limay River: A Key System for Salmonids in the Andean North Patagonia

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Abstract The Limay River is one of the most relevant fluvial systems of the northern Andean Patagonia, being the only effluent of Lake Nahuel Huapi. Since the last third of the twentieth century, its course has been fragmented by the construction of dams. These human-induced alterations have modified the dynamics of the fish populations. Herein, we describe the ecological and functional characteristics of the upper Limay that rises from Nahuel Huapi Lake and mouths into the Alicurá Reservoir. The fish fauna is composed of four introduced salmonids and four native species. The distribution patterns of these species are not homogeneous along the river. The fish assemblage is dominated by *Oncorhynchus mykiss* and *Salmo trutta* showing different life tactics from strictly resident to migratory forms entering the lentic environments for reproduction and show very different abundances. Native species are locally restricted. Only salmonids are found in the tributaries. The river, its tributaries and secondary habitats, activated in high water periods, constitute an excellent spawning and breeding habitat for salmonids, which, added to the connectivity between lakes suggest the potential occurrence of meta-populations. The river system supports an important sport fishery, focused on *O. mykiss* and *S. trutta*, which attracts national and international anglers who make a fundamental contribution to the regional economy.

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1 Introduction

The Upper Limay River basin constitutes one of the most important fluvial systems in the northern Andean Patagonia. This river drains the large Nahuel Huapi Lake and receives water from several permanent and temporal streams. It mouths into the Alicura Reservoir. The course of the river marks the boundary between Río Negro and Neuquén provinces and lies within Nahuel Huapi National Park. Many different economically productive activities are developed along its drainage basin, such as extensive livestock farming, conifer forestation and urban developments. Moreover, the river is utilized for recreational fisheries and canoeing, and for the commercial breeding of *Oncorhynchus mykiss* (Walbaum 1792), rainbow trout.

The Upper Limay River has been studied widely over the last 20 years, focused on fish ecology and their conservation/exploitation dilemma. Information has been obtained through sampling by electrofishing and volunteer sport anglers, campaigns during which fishing guides and local anglers have recorded catch data, surveys, and analysis of historical catch data from fishing tournaments.

This river system is inhabited by four introduced salmonids and four native fish species, with species-specific spatial and temporal distributions across different aquatic habitats. For the purposes of this study, we focus on salmonids.

The Limay and its tributaries are used for spawning and nursery by both resident and migratory salmonids coming into the river from neighbouring lakes. Habitat use is not temporally or spatially homogeneous. We observed different species distribution patterns along the main stem and a diversity of interspecific interactions among salmonids and between salmonids and native species, and even more, possible effects of escaped *O. mykiss* from Alicura fish farms. Given that the Limay also represents the limit of the Nahuel Huapi National Park, protection and conservation of native fauna is mandatory. Conservation efforts not only include the fish fauna but also mammals, such as the “huillin”, *Lontra provocax* (Thomas 1908), birds, and amphibians. The Upper Limay is a worldwide reference for national and international anglers due to the fishing quality, the landscape characteristics, and its proximity to San Carlos de Bariloche City and its local services.

Apparently, the climate change may affect this region through an increase in the average annual air temperature, and consequently in river water temperature, in the annual precipitation regime and volume, and modifications in the land use. Due to these alterations, the physicochemical and environmental characteristics of the river could change dramatically, resulting in a reduction of the habitat quality underlying the fish population dynamics.

This study summarizes the major characteristics of this hydrological system, its fish fauna, and the use of the river and its tributaries by salmonids and the fishery that generates considerable economic activity in the region.

2 The Limay River: General Description

The Limay River is located at the border between Neuquén and Río Negro provinces (Fig. 1) and flows towards the Atlantic Ocean covering an area of 58,500 km^2. Its waters originate in the Andean Cordillera and drain through a vast network of rivers and glacial lakes to converge with large rivers such as Collón Cura (Fig. 1). There is a steep gradient of decreasing precipitation from west to east, with forested zones mainly in the west and more arid areas in the east. The major collector of the basin is the Limay River, which originates in Nahuel Huapi Lake and flows 430 km in a southwest–northeast direction, with an average flow volume of 650 m^3/s. It converges with the Neuquén River, thus forming Negro River.

The Limay River flows down through the Patagonian steppe as a single large waterway, with very few permanent and temporary watercourses. The main affluent,

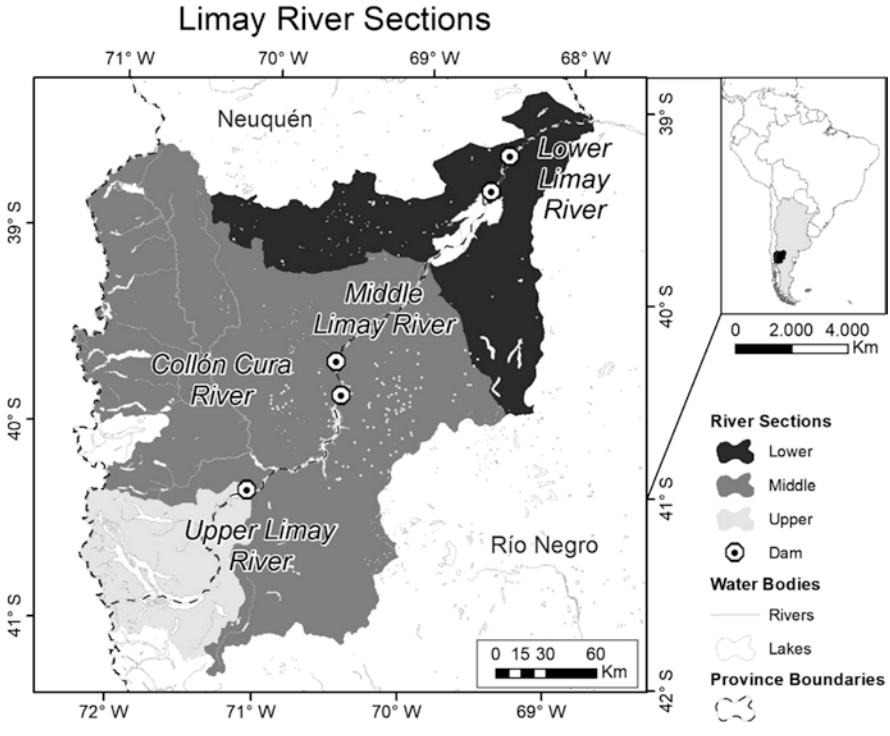


Fig. 1 Location, principal channels of the system, dams, and sections of the Limay River

the Collón Cura River, collects the waters of a large part of the eastern Neuquén Province. From the uppermost reaches to its confluence with Neuquén River, there is some 530 m difference in altitude. Its hydrological regime is a mixture of rain + snow regulated by numerous headwater lakes in the western region. The main rain falls in winter, enhance the accumulation of snowmelt on the high mountains and a period of high waters. Snowmelts at the beginning of the spring lead to a second period of high waters. The lowest water level occurs at the end of summer, lasting until the onset of the autumn rains (Sosnovsky et al. 2020).

Five dams for electrical purposes have been built along the length of the Limay River—from west to east: Alicurá, Piedra del Águila, Pichi Picún Leufú, Exequiel Ramos Mexía, and Arroyito—all together represent 25% of the electrical resource of Argentina. These dams split the Limay River into three sections. The lower Limay drains 13,700 km^2, stretching from the tail end of the Exequiel Ramos Mexía Reservoir to the confluence with Neuquén River. The middle Limay drains 37,700 km^2; beginning downstream of the Alicurá Reservoir, receives water from the Collón Cura sub-basin and ends at the tail end of the Ramos Mexía Reservoir. The upper Limay (Fig. 2) drains 7100 km^2 from the origin of the river in Nahuel Huapi Lake to Alicurá Dam, receiving water mainly from the Traful River. This section is 55 km in length and flows down over a wide valley with south–north orientation and 70 m difference in altitude with an average daily flow of 175 m^3/s. Although the upper section is the shortest, it is one of the main yields of all the water of the

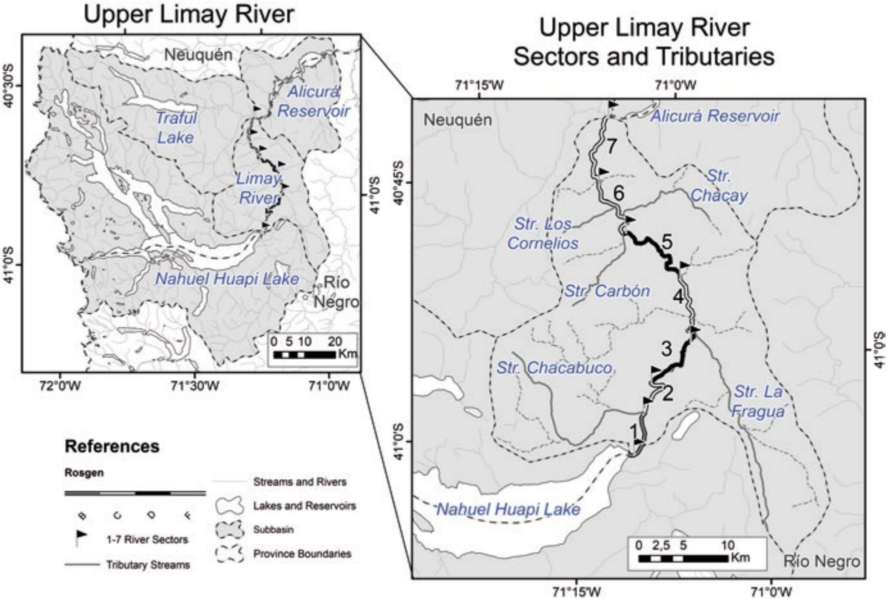


Fig. 2 Tributary streams and river sectors 1–7 on the Upper Limay River. Characterization of the sectors according to Level 1 of the fluvial channel classification based on the morphology of the valley and the channel (Rosgen 1994)

basin (Pessacg et al. 2018) and is the only unregulated section of the Limay River and maintains its natural hydrological regime and its connectivity with the subbasins of Nahuel Huapi and Traful (Fig. 2).

3 The Upper Limay: Functional Characteristics

The Upper Limay crosses a steppe-wide region, dominated by *Mulinum spinosum* (Cav.) Pers. and *Stipa* spp. The riparian vegetation includes shrubby species like *Berberis* spp. and *Discaria* spp., although an exotic tree, *Salix fragilis* L., has colonized the river banks (Serra et al. 2012). The river receives both permanent and temporary tributaries with medium or low flows, which do not change the current physicochemical properties of the main stem. The Alicurá Reservoir has an important influence on the final reaches of the river (sector 7 in Fig. 2), with waters flowing very slowly and large bank flooded areas, regulated by the delivery or retention of flows from the Alicurá Dam. Close to the uppermost sources, the substrate is composed of boulders and cobbles decreasing in size downstream where fine material and sand predominate near the reservoir. Along the river, scattered patches of aquatic vegetation include *Myriophyllum quitense* Kunth 1823, *Juncus* sp., and a noteworthy invasive alga, *Didymosphenia geminata* [(Lyngbye) M. Schmidt 1899, Lamaro et al. 2019]. Heterogeneity of habitats quality together with seasonal variations in discharge provides an opportunity for the development of different life stages of salmonids.

4 Introduction and Stocking of Salmonids into the Limay River: Causes of Its Success?

According to Macchi et al. (2008) the introduction of salmonids into the Limay River has a long history characterized by successive stocking, from 1904 onward, of *Coregonus clupeaformis* (Mitchill 1818), *Salvelinus namaycush* (Walbaum 1792), *Oncorhynchus mykiss, Salvelinus fontinalis* (Mitchill 1814), *Salmo salar* Linnaeus, 1758, and *S. trutta* Linnaeus, 1758 (Tulian 1908). Only the last four naturalized successfully, probably due to occurrence and abundance of suitable spawning habitats and their ability to spread along the river courses together with successful management strategies.

From 1904, year of the earliest introductions (Marini 1936) to the end of the 1920s, *Sa. fontinalis* and *S. salar* were the only salmonids spawning in the Limay River basin. Although the former was more abundant, both species adapted rapidly and initially spread along the entire length of the Limay River and its tributaries (Marini 1942). However, *Sa. fontinalis* was the dominant species until around 1945. The introduction of *O. mykiss* and *S. trutta* (around the end of the 1920s and beginning of the 1930s; Macchi et al. 2008) was associated with a dramatic change in the composition of the salmonids populations. From 1939 onward, *O. mykiss* and *S. trutta* dominated the catch records from Collón Cura and its basin, and the middle and lower sections of the Limay River (González Regalado 1941). Three years later, these two species apparently displaced *Sa. fontinalis* in the upper Limay (Bruno Videla 1944), and around 1947, *O. mykiss* became the dominant species all along this river section (Macchi et al. 2007).

The displacement of *Sa. fontinalis* to the headwaters of the Limay River (Fernández et al. 2018) and the decline in population numbers of *S. salar* (Rechencq et al. 2017) are currently under study. Macchi et al. (2008) suggested that the number of spawners and the number of spawning events of each single species have been an important factor of this replacement. These authors found that the number of *S. trutta* introduced into the Limay River between 1931 and 1986 was one order of magnitude less that the number of *Sa. fontinalis*. Several characteristics of the habitats also appear to have conferred a competitive advantage to *S. trutta* and *O. mykiss* over *Sa. fontinalis* and *S. salar.* This involves a combination of physical, chemical, and/or biological factors that may affect different life stages and their competitive ability during ontogeny (Lallement et al. 2020). In addition, salmonids could have modified the physical, chemical, and biological characteristics of the habitats in which their populations developed (Pascual et al. 2009; Habit et al. 2015). Thus, the scenarios where the initial colonization processes have undergone significant changes over time (Macchi et al. 2008).

5 Current Status of the Fish Populations Along the Limay River

Two fishing techniques were used to assess fish composition of the Upper Limay: angling (fly and spinning modalities) for larger fish individuals and electric fishing for smaller fish. Rod & line sampling included 50 volunteer sport anglers, using a sampling design that distributed the fishing effort along the entire river with a monthly periodicity including the open and closed fishing seasons, repeating the scheme over 3 successive years (Rechencq 2003). Sampling with electric fishing was conducted in 10 sampling sites selected along the river with a climatic seasonal periodicity over 2 years.

Like in most lakes and rivers, salmonids dominate the fish assemblages (Fernández et al. 2018; Lallement et al. 2020). In particular, in the upper Limay and its tributaries the fish assemblage is composed of *O. mykiss*, *S. trutta*, *Sa. Fontinalis*, and *S. salar* and four native species *Percichthys trucha* (Valenciennes 1833), *Olivaichthys viedmensis* (MacDonagh 1931), *Hatcheria macraei* (Girard 1855), and *Galaxias maculatus* (Jenyns 1842). The most abundant are *O. mykiss* and *S. trutta,* that maintain an important recreational fishery during the spring and summer. The relative abundance and size of these two species vary widely over the year and along the length of the river (Fig. 3). Overall, *O. mykiss* shows higher catch numbers and average sizes during the autumn, winter, and spring, that is, during the spawning period (Rechencq 2003; Wegrzyn and Ortubay 2009). Catches during this period include 2–8 years old individuals with average size around 42 cm (Table 1). During the summer, the catches include 1–5 years of age and an average size of 30 cm individuals. *S. trutta* is more abundant during the autumn months, coinciding with its reproductive migration and the beginning of the spawning season. The largest sizes are found during the autumn and winter (Fig. 2, Table 1). During the closed season, which is slightly longer than the reproductive period, the age distribution includes

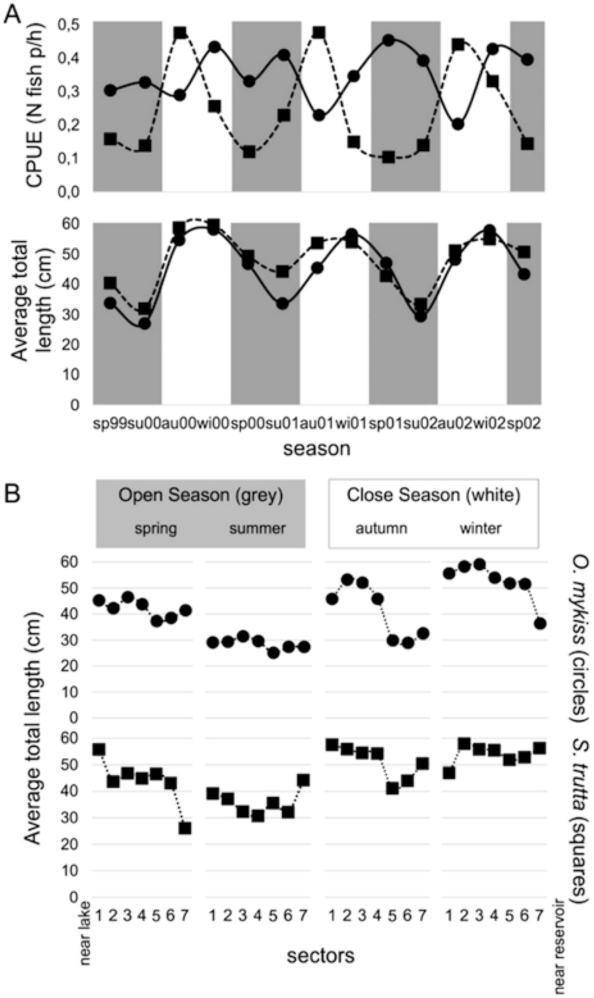


Fig. 3 Panel **a**: Temporal distribution of the relative abundance (Capture Per Unit Effort—CPUE) and average total length (cm) of *O. mykiss* (circles) and *S. trutta* (squares). Panel **b**: Spatial distribution of the average sizes (cm) of *O. mykiss* (circles) and *S. trutta* (squares)

Table 1 Number of fish captured (N) and average total length (TL) with standard deviations (±SD), average age (years), and [age range] (years) of *O. mykiss* and *S. trutta* adults for each season, for the Upper Limay

	O. mykiss			*S. trutta*		
Season	N	TL (cm)	Age (years) [min–max]	N	TL (cm)	Age (years) [min–max]
Spring	257	43.33 ± 14.73	3.2 (1–5)	88	43.97 ± 15.92	3.4 (1–7)
Summer	205	30.03 ± 10.80	2.6 (1–5)	87	37.15 ± 18.12	3.1 (1–6)
Autumn	324	49.93 ± 16.27	4.6 (2–7)	649	54.05 ± 13.49	5.0 (2–8)
Winter	614	57.48 ± 10.70	4.7 (2–8)	340	56.89 ± 12.56	4.9 (2–8)

2–8 years old individuals of an average size =55 cm. The open season of recreational fishing includes individuals with 1–7 years and an average size =46 cm in spring and 37 cm in the summer (Table 1).

These variations in catches and average sizes may indicate the occurrence of two types of life history tactics (sensu Kendall et al. 2015) in the two species. Phenotypes can be recognized by colour and body shape. One phenotype, named ‘resident’ is composed of fish that live their entire lives in the river, or move between the tributaries and the main stem. The second phenotype, named ‘migrant’ applies to fish entering the river from the headwater lakes to spawn. During parts of the year, both phenotypes of these two species apparently co-occur in the river. The migrant phenotype of *S. trutta* is present for a short time period (Rechencq 2003), whereas *O. mykiss* behaves differently, with a larger resident component and fewer differences in abundance year-round. Unlike other salmonids the seasonal variations in the relative abundance of this species are less pronounced over the year, with no marked peaks. The largest sizes are observed in winter, coinciding with those of *S. trutta*. Valiente et al. (2010) reported individuals of the same life history tactic for *S. trutta* in the middle Limay, and proposed that the co-occurrence of resident populations is due to a higher productivity of some watercourses.

N. Jodar (2019) reported the occurrence of *O. mykiss* escaped from the Alicurá Reservoir fish farms (recognizable by peculiar characteristics, such as erosion of the fins and body shape); always being captured near the reservoir and representing around 2% of the total catches. These frequent escapements have greatly changed the fish assemblage composition of the reservoir (Alonso 2003), where they are present in large numbers in the shallower strata and close to the farms (Cussac et al. 2014). Although the captures from the river are low, we do not know how these individuals may affect the naturalized *O. mykiss* populations. *P. trucha*, a native species captured with rod & line also presents seasonal peaks in numbers, although much less marked, coinciding with its spring reproductive season (Fernández et al. 2019; Rechencq 2003).

6 The Upper Limay, an Important Nursery

The river provides habitats for salmonids spawning along its length. Given the habitat heterogeneity, the spawning area is distributed in patches along the river with some specific sites providing better conditions for redds construction. In the uppermost length of the river the substrate is composed of large elements (sector 1, Fig. 1), making this section less suitable for spawning. The lowermost reaches (sector 7, Fig. 1) are influenced by the Alicurá Reservoir, so the substrate is largely dominated by fine sediments and the water flows very slowly, hence most unfavourable for reproduction. The most suitable sections for spawning are located from Chacabuco and La Fragua streams (sectors 2 and 3, Fig. 1). This sector is also the most frequented by recreational anglers at the beginning and the end of the fishing season, since the large spawners of *O. mykiss* and *S. trutta* are present on these dates.

Suitable reproduction areas may represent a limiting factor due to the requirements of these species for redds construction (Keeley and Slaney 1996). The overlapping of spawning substrates between spawners of *S. trutta* and *O. mykiss* has been reported in rivers of other parts of the world (Scott and Irvine 2000). A similar phenomenon apparently occurs in these rivers, being one of the limiting factors for the relative abundance of the earlier life stages. *O. mykiss,* whose reproductive season begins slightly later than that of *S. trutta* and lasts till the spring, may construct their redds in substrate previously used by *S. trutta,* whose eggs or alevins may still be present in the site. This situation would lead to detrimental mortality of *S. trutta*.

7 Juvenile Distribution in the Upper Limay: Life After Hatching

Electrofishing sampling conducted along the Limay River banks supported the occurrence of six native and introduced species. *O. mykiss* and *S. trutta* juveniles persisted year-round whereas the occurrence of *P. trucha* was seasonal. Fry of *O. mykiss* and *S. trutta* occurred in the spring samples (Table 2), indicating that the emergence occurs between the end of winter and the spring, when the water level is high and relatively stable. This period activates the secondary streams that enable fry to encounter microhabitats suitable for growth and development, given that at

Table 2 Number (N), average total length (TL), and average weight (TW), with standard deviations, of *O. mykiss* and *S. trutta* juveniles for each season in the Upper Limay

	O. mykiss			*S. trutta*		
Season	N	TL (mm)	TW (g)	N	TL (mm)	TW (g)
Spring	309	31.37 ± 6.51	0.36 ± 0.30	51	34.67 ± 8.91	0.53 ± 0.56
Summer	100	54.28 ± 19.39	2.42 ± 5.18	126	58.92 ± 10.64	2.34 ± 1.34
Autumn	120	59.86 ± 17.39	3.08 ± 3.11	109	57.11 ± 10.60	2.34 ± 1.64
Winter	59	64.34 ± 30.49	5.06 ± 9.16	36	68.25 ± 20.24	4.43 ± 4.01

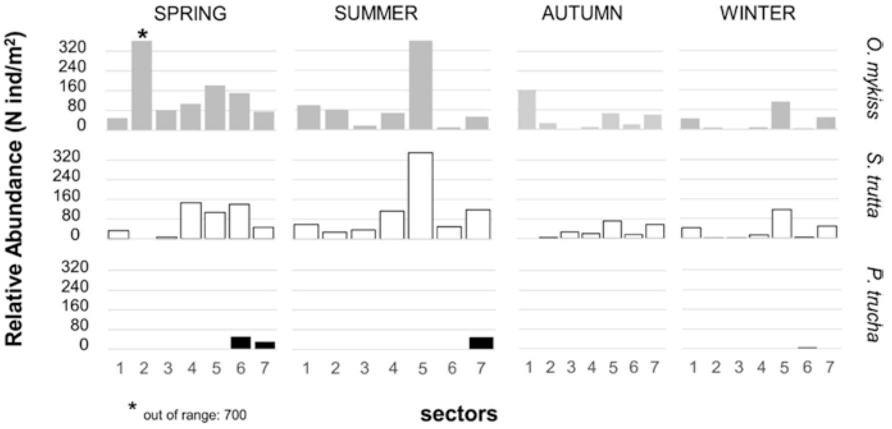


Fig. 4 Seasonal distribution by river sector of juvenile relative abundance: *O. mykiss* (grey), *S. trutta* (white), and *P. trucha* (black)

the fry stage, individuals cannot move far from their hatching sites (Stradmeyer et al. 2003), Fig. 4 suggests that *O. mykiss* spawns in a large section of the river course, whereas *S. trutta* uses a more limited range. In the summer, when the *S. trutta* individuals have attained larger sizes and are able to move larger distances in search of suitable areas for shelter and growth, occupy new reaches along the main stem. *P. trucha* was present in high numbers in sites close to the reservoir. The highest catch of juveniles of this species (length 29–87 mm) was recorded in spring and summer, whereas in autumn and winter they occurred only occasionally (Fig. 4). These individuals were recorded in vegetated banks where the river is shallow and flows slowly.

8 Tributary Streams: Suitable Habitats for Salmonids Reproduction

Fish species found in the tributary streams were *O. mykiss*, *S. trutta*, and *S. fontinalis*, the latter only in the upper reaches of La Fragua stream. *O. mykiss* was the dominant species in Chacay and La Fragua streams and was dominant together with *S. trutta* in Carbón and Los Cornelios streams (Fig. 5). Only fish individuals up to 2 years of age were found. Therefore, we can infer that there are no resident individuals in these water courses, with the exception of the Chacabuco stream. However, we found male parrs with gonadal development indicating that they would mature sexually in the following reproductive season. This was observed only in the sampling sites of the headwaters what appears to be a common reproductive tactic in several salmonids (Wootton 1998). *S. trutta* was dominant in the Chacabuco stream, showing variable abundance in all other streams. Like *O. mykiss*, this species does

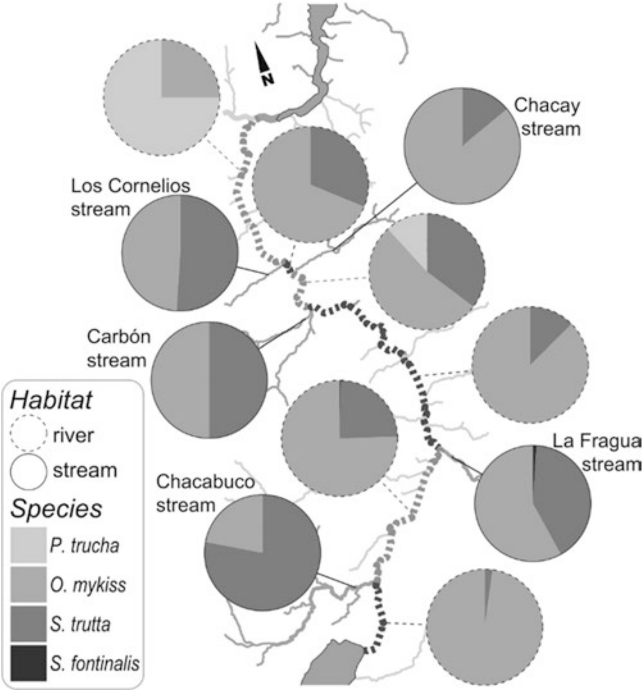


Fig. 5 Relative abundance of juveniles captured in five affluent streams and in the sectors of the Upper Limay located between the river source, the mouth of each stream, and the tail end of the reservoir

not seem to live permanently in the streams, although it is possible to find individuals of both sexes with advanced gonadal development and no more than 2 years of age. An exception is Chacabuco stream, where a resident population of *S. trutta* was found with individuals up to 8 years of age (Lippolt 2004).

9 Salmonids Diet in the Limay River

Apparently, the wide dispersion of salmonids in Patagonia was favoured by their ability to adapt their feeding tactics to prey availability (Macchi et al. 1999). This trophic behaviour enabled their rapid spread throughout the water basins, and their current dominance as apex predators (Fernández et al. 2018).

In the upper Limay, salmonids select the most abundant prey, shift prey as they grow and are basically the same as in all water bodies of the region, although the prey type may differ (Macchi et al. 1999). *O. mykiss* and *S. trutta* have a similar diet, but the former is more diverse. For both species, individuals less than 200 mm in length feed on insect larvae (mainly *Diptera, Trichoptera*, and *Ephemeroptera*), terrestrial insects, amphipods, and a gastropod of the genus *Chilina*. Individuals >200 mm in length feed almost exclusively upon the decapod *Aegla* sp.

These diets differ in lentic waters (Macchi et al. 1999; Rechencq et al. 2017; Fernández et al. 2018). In headwater lakes, *S. trutta* presents a pronounced piscivorous behaviour, feeding mainly upon larvae and adults of the fish 'puyen', *Galaxias maculatus*, (Macchi et al. 2007), whereas the diet of *O. mykiss* includes *G. maculatus* and the decapod *Samastacus* as the main items (Rechencq et al. 2017).

In tributary streams inhabited by individuals up to 2 years of age, *O. mykiss* and *S. trutta* feed almost exclusively on insect larvae (mainly *Diptera* and *Trichoptera*) and terrestrial insects, and to a lesser extent, *Chilina* sp. A particular case is Chacabuco stream, which sustains a resident population of *S. trutta*. Here, individuals <200 mm feed mainly on terrestrial insects and insect larvae, mainly of *Trichoptera*, *Amphipoda*, and *Chilina* sp., whereas individuals >200 mm feed almost exclusively upon the decapods *Samastacus,* and occasionally *Chilina* sp. and fish. In this stream, *O. mykiss* rarely grows >200 mm, feeding on insect larvae, terrestrial insects, and *Amphipoda.*

10 Patterns of Fish Distribution

The multiple life history tactics exhibited by salmonids in Limay River are apparently the result of compromises between cost and benefit in the adaptation process to habitat templates (Southwood et al. 1974). In the upper Limay there is a large diversity of water bodies associated with a west–east environmental gradient, the result of differences in topography, climate, and vegetation, such that both native and introduced fish species find extensive areas that provide food, shelter, and suitable reproductive habitats.

Salmonids dominate the fish assemblages in the upper Limay, but the spatial use varies between species in the main channel and tributaries. Native species are poorly represented near the lentic habitats (Rechencq 2003; Nabaes Jodar 2019), or in low abundance related to plants abundance, lime deposits, and slow-flowing waters (Lallement et al. 2020). Two possible reasons could explain this pattern. The habitat preferences of native species may not be present in the tributaries of the upper Limay, which respond to an irregular natural regime with sudden changes in water flow and velocity after rainfall episodes. These changes are better tolerated by salmonids, which probably determines their current predominance, especially *O. mykiss*. On the other hand, negative interactions between native species and salmonids could be stronger in lotic systems than in lakes, resulting in an almost total exclusion of the former in most tributaries (Habit et al. 2010).

Lallement et al. (2020) reported that in the rivers and streams of the upper Limay, *O. mykiss* is the most abundant species and exhibits the widest distribution, probably for the environmental similarities with the region where they originally evolved (Fausch 2008). On the contrary, due to the scarcity of regulated streams in the Upper Limay (streams with stable flow regimes year round), *S. trutta* dominates over

O. mykiss only in a small number of streams. The abundance of *Sa. fontinalis* is low and according to Macchi et al. (2008), its presence appears limited by negative interactions with other salmonids.

In the upper Limay and its tributaries, *O. mykiss* and *S. trutta* are the dominant species and *Sa. fontinalis* is restricted to the uppermost reaches of some streams. Fry of *O. mykiss* occur in most of the river, whereas *S. trutta* fry are more abundant in the middle reaches (Fig. 5). This heterogeneous distribution may be due to (1) differences between the species in the optimum spawning and rearing sites and/or (2) competitive interactions between these species whereby one becomes predominant over the other depending on the habitat quality or the prevailing environmental conditions.

The tributary streams differ in their flow regimes. The first type is irregular, with sudden changes and rapid responses to rainfall events (a ‘flashy’ stream *sensu* Baker et al. 2004), whereas the second type presents a more stable flow regime with moderate changes in flow following precipitation. Sosnovsky et al. (2020) suggested that these patterns may explain differences in terms of characteristics of the drainage basins and the origin of the watercourse. We observed that all tributaries are suitable for reproduction and rearing, although their differences may explain the presence and predominance of certain life history tactics (Perkin et al. 2017).

11 Connectivity of the Upper Limay: Does It Sustain Salmonids Meta-populations?

If we consider the connectivity among watercourses of the Upper Limay and the salmonids dynamics, the occurrence of a meta-population structure seems a viable hypothesis. According to Ruxton and Doebeli (1996) and Copper and Mangel (1999), a meta-population is a group of local populations linked by dispersal and interbreeding of individuals at short ecological time scales. Dispersal could affect both the genetics of every local population as well as their abundance and dynamics. Despite the fact that no specific studies have elucidated the occurrence of salmonid meta-population dynamics, the structure in the Upper Limay and its tributaries offers a broad habitat selection where different life stages can develop. The main stem of the river connects large waterbodies such as Nahuel Huapi Lake, Traful Lake, and Alicurá Reservoir (Fig. 2), where salmonids can move over long distances for both feeding and reproduction. This process has been well documented by mark-and-recapture methods (Vigliano et al. 2000), and monthly samples by anglers (Rechencq 2003). Both life tactics and trophic migrations for reproduction imply a diversity of movements that involve the headwaters, the main river, the secondary branches, and the tributary water courses (Lippolt 2004) that rises a longitudinal and lateral connection dynamics across habitats.

Moreover, studies by Vigliano et al. (2000) on several Patagonian rivers have shown that there is no fidelity of spawners to their original hatching streams. The spawners of both species either residents or migrants come from the lentic headwaters. Both components seem to participate in common reproductive events, sharing reproductive time and space.

We too have considered that the geographical scale previously mentioned and the complexity and hydrological connectivity of the system ensure a diversity of heterogeneous habitats underlying sets of habitat patches with different levels of suitability for specific life stages. Thus, it is likely that in the Upper Limay there are local populations each with a specific probability of extinction inhabiting discrete patches, separated spatially by other patches of lower or different quality. Nevertheless, the fact that they are connected by a network of water courses of different hydrological topology implies that in the case of a local extinctions it will then become recolonized through dispersal from another sub-population. This finds support by the extinction–recolonization process observed after the eruption of the Puyehue-Cordon Caulle volcano in 2011. The volcanic ash over various water bodies caused the disappearance or displacement of fish species but all these habitats were recolonized naturally from other unaffected habitats (Lallement et al. 2016).

The validation of the hypothesis of the existence of a metapopulation in the upper Limay is of utmost importance for the design of fishery management strategies. This is due to the consequences of such strategies for other associated local populations, beyond the upper Limay, whose effects may be difficult, if not impossible, to predict.

12 The Upper Limay, a First-Class Recreational Fishery

In general, recreational fisheries generate a considerable economic activity. In Patagonia, this aspect has been assessed by several authors (Vigliano et al. 2000; Vigliano and Alonso 2007) along the characterization of the human component of fisheries. Nataine et al. (2018) evaluated the relative importance of the recreational fisheries in the economic and social dynamics of San Carlos de Bariloche and its influence area.

Several studies concur to emphasize that the Limay is chosen by anglers because of the quality and quantity of fish that can be caught in a typical outing, the beauty of the landscapes, the relatively easy access and its proximity to Bariloche City. Most users are domestic tourists (Nataine et al. 2018), soliciting local fishing guides and related services whereas a small percent of foreign anglers, from USA and Europe, visit the river as part of fishing trips. Considering the highly positive evaluation of the river given by local, national, and international tourists, and taking into consideration the economic resources generated from the sale of fishing permits (>12,000 per season in Bariloche area), and the expenses associated with fishing equipment and supplies, the river in its current condition is of enormous value for the local economy.

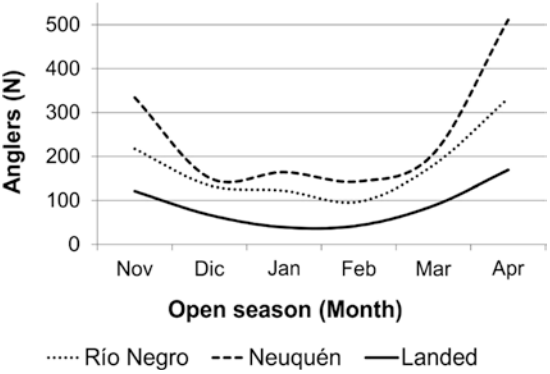
13 Fishery Management

This fishery is managed through regulation of fishing modalities, the number of fish individuals that can be kept, and the period during which the activity can be carried out. These rules are aim at a set of regulations which are valid for the entire Patagonia; checks are carried out by the authorities to ensure that anglers have a fishing license during the season, and to prevent poaching, particularly during the closed season.

The fishing season starts on 1st November (spring in the southern hemisphere) and lasts until the end of April. During the last 2 years, the fishing season of the Limay has been extended until the end of May (autumn in the southern hemisphere). On the first 20 km of the river only fly-fishing is permitted, underlying a catch-and-release strategy. On the rest of the river, spinning is also permitted and one specimen per outing can be kept. From 1st April, catch and release is obligatory. Both fishing techniques are carried out from the shore or from boats or rafts. There are many points where anglers can reach the river freely. Fishing licenses may sometimes be required at some of these access points, although in general anglers can access the river without impediment from rural roads. The official agencies responsible for management are the Nahuel Huapi National Park administration, their park guards on the west coast, and the *Mesa Honoraria Directiva de Pesca Deportiva* (a delegation of the fishing authority of Rio Negro Province) and their guards team over the east coast.

The fishery focuses on *O. mykiss* and *S. trutta,* although, occasionally, *Sa. fontinalis*, *S. salar*, and *P. trucha* can also be caught. The differential distribution of these species throughout the fishing season is accompanied by the heterogeneous arrival of anglers along the length of the watercourse. Figure 6 shows the number of anglers registered during a typical fishing season in the Limay River. The greatest fishing pressure occurs in the first months and at the end of the season, and the Neuquén coast (under Nahuel Huapi National Park jurisdiction) is the most visited. The number of anglers using boats or rafts is also important. This method enables anglers to access more distant river sections and also means that they can fish in different sites

Fig. 6 Number of anglers registered over an entire fishing season, observed fishing from the coasts of Neuquén and Río Negro provinces or from a boat or raft



during a single fishing outing, distributing the fishing pressure along the length of the river course. Based on surveys carried out at the fishing sites, Nataine et al. (2018) reported that the most common duration of a fishing outing is 5 h. One more important issue is the fish capture in terms of the fishing effort applied. Our unpublished results suggest that the average capture per unit effort (CPUE) is 0.48 *O. mykiss* individuals/fishing hour and 0.34 *S. trutta* individuals/fishing hour.

Currently, the management of the fishery does not include the most important population dynamics aspects of the target species in the Limay River. The fishing season lasts 6 months, aimed at the protection of the reproductive season. Nevertheless, part of the *S. trutta* populations already begin to move to the Limay River towards the end of the season, showing a pre-reproductive behaviour in May. Also, it has been reported that it is not unusual to detect *O. mykiss* individuals in November recovering from their recent spawning, at a starting time of the fishing season and the fishing pressure is higher. In order to preserve the quality of these populations, it is important to take into account migratory patterns, reproduction areas, target sizes and resident and/or migratory components, measures that can only be implemented effectively through a systematic monitoring of their population dynamics.

Since we are dealing with a worldwide important habitat in terms of fishing value, it is essential to design a strict management programme, with consistent objectives and monitoring indicators on the environmental quality. An example of this was the implementation, several years ago, of the mandatory practice of catch and release of salmonids in an important stretch of the Superior Limay River, but no monitoring was implemented to evaluate the effectiveness of this measure. The lack of monitoring procedures for the implemented strategies is one of the major problems in fishery management. However, no monitoring was implemented to evaluate the effectiveness of this measure. The lack of monitoring procedures of the strategies implemented is one of the major problems in the management of the fishery.

14 To Sum Up, Key Reasons for the Importance of the Upper Limay, with Emphasis on Salmonids

The movement and translocation of species due to human activities bring about numerous consequences. Although these are usually negative, they can also have positive effects associated with the possibilities of exploitation or profitable use of the introduced species. In Patagonia, several salmonids have been introduced that had not previously coexisted even in their original ranges, and have prospered coexisting with native fish that, in turn, had not been studied either. The evaluation of the environmental impact of these introductions, the study of the different adaptive responses of the other components of the ichthyofauna and the knowledge of the effects on the diversity of species and the quality of the habitat are essential for the design of global management strategies. ecosystems and to minimize the potential negative impacts of these practices, widely disseminated and developed by enforcement authorities, fishermen's associations and government agencies.

The case of the salmonids introduced in the Upper Limay is illustrative after the introduction of four salmonid species: *Sa. fontinalis* and *S. salar*, followed by *O. mykiss* and *S. trutta*, and the successful settlement of spatially structured populations. The species show marked differences of abundance and distribution, but for the most they all are self-sustaining. Within the Upper Limay, *O. mykiss* and *S. trutta* predominate and often reach sizes that are uncommon in other aquatic systems of northern Patagonia, making this river of special interest for sport fishing with the aforementioned economic benefits.

What factors have made the upper Limay such an ideal habitat for introduced salmonids? We describe several ecological and functional characteristics of this river, its tributaries, and the current basin. Also, we briefly described the river fish assemblage, particularly the salmonid meta-populations and the fishery they form a part of. Available data indicate the presence of two main groups of fish, which follow different tactics: residents that live their entire lives in the river or its tributaries, and migrants that come into the river from Nahuel Huapi Lake and/or other related habitats for reproduction. The incorporation of migrants coming in from habitats with higher trophic diversity, together with the availability of big sized prey in the Upper Limay, could explain the abundance of specimens of a size far above the expected capacity of the river. The habitats of the Upper Limay present a great abundance of sites suitable for spawning—unlike many other sites in the river basin—which might attract these migrants. The spawning of residents and migrants increases the abundance of fry and juveniles, some of which remain in the river or its tributaries, while others migrate upstream towards the lake or downstream towards other parts of the basin. Whether juveniles inherit the parental strategies has not been documented, it seems however that the combination of the river's hydrological characteristics and its connectivity with other water bodies are key factors in the establishment and dynamics of these salmonids and in the generation of a fishery. One key factor yet to be assessed is whether a meta-population structure actually occurs. According to Copper and Mangel (1999), undetected meta-population structure in salmonid populations may obscure signals such as abundance trends that managers use to establish conservation strategies. This is brought about because they tend to consider closed populations for which both immigration and emigration are insignificant, variations in reproductive success are not taken into account, and the relationship between abundance and habitat quality is not included in the analysis, which may hamper management efforts.

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Dynamics of a Warmwater-Coldwater Fish Assemblage in a Wildfire-Prone Landscape

David L. Propst, Dustin J. Myers, Jill M. Wick, and Ryder J. Paggen

Abstract Gila trout *Oncorhynchus gilae* historically occupied high-elevation (>2000 m) headwater streams of the Gila River in southwest New Mexico and central Arizona, USA. By the mid-twentieth century, human activities such as resource extraction and nonnative species introductions caused habitat degradation and loss, thereby restricting the trout to a few small remote streams in the upper Gila River catchment in New Mexico. Since 1989, conservation efforts have been hampered by numerous wildfires that caused elimination of some populations and greatly reduced others. But wildfires also eliminated nonnative fishes from streams thereby making them available for Gila trout repatriation. Elimination of all fishes, including nonnative trout, from upper Black Canyon (ca. 17 km), an East Fork Gila River tributary, by wildfire and associated sediment-laden flows in 1995 and subsequent colonization by native warmwater species (longfin dace *Agosia chrysogaster*, speckled dace *Rhinichthys osculus*, Sonora sucker *Catostomus insignis*, and desert sucker *Pantosteus clarkii)* provided the opportunity to study the dynamics of a mixed warm-coldwater fish assemblage. Although upper Black Canyon was thermally compromised (summer maxima >25 °C), age-0 hatchery-produced Gila trout (≈1000–2000) were released annually from 1998 through 2012. Establishment of a nonnative piscivore, brown trout *Salmo trutta*, added complexity to the study. By 2012, native warmwater species had thriving populations but despite limited reproduction annual stocking of Gila trout likely enabled it to persist in the stream. It was not possible to determine the effects of brown trout predation on the Gila trout

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population or negative interactions, if any, between native warmwater fishes and Gila trout. Regardless, warmwater fish and brown trout abundance was greatest in downstream reaches and that of Gila trout was greatest in the most upstream reach. Inter-annual differences in somatic metrics (condition and size structure) of the Black Canyon Gila trout population were as great as it were between it and reference populations. Unassisted re-population of upper Black Canyon by native warmwater species succinctly illustrated the importance connectivity within a drainage and the rapidity in which this was accomplished is testimony to the resilience of each species to major disturbance. In 2013, wildfire again eliminated all fishes from upper Black Canyon. Hatchery-produced Gila trout were annually stocked from 2013 through 2018 and sampling in 2018 yielded a large number of age-0 fish, suggesting that a Gila trout population might be established in upper Black Canyon, but in the absence of native warmwater fishes and piscivorous brown trout.

Keywords Mixed fish assemblages · *Oncorhynchus gilae* · Condition factor · Size structure · Catastrophic disturbance · Wildfire · Nonnative trout · Assisted repatriation · Conservation

1 Introduction

Gila trout *Oncorhynchus gilae* historically inhabited high elevation tributaries of the Gila River in southwestern New Mexico and central Arizona, USA (Fig. 1). By the late nineteenth century, extensive European settlement and accompanying habitat alteration caused by widespread domestic livestock overgrazing, timber harvest, and mineral extraction had rapidly reduced its occurrence to remote, small, upland streams. Its persistence was additionally challenged by extensive introduction of nonnative salmonids, especially rainbow trout *O. mykiss* and brown trout *Salmo trutta*. When concerted conservation efforts for the species began in the last quarter of the twentieth century, Gila trout occurred in only five small, isolated streams, all within federally managed lands (Propst et al. 2020).

Initially, the overarching conservation strategy for Gila trout was to secure occupied habitats and replicate each remnant population in other suitable streams. Securing a population typically involved ensuring it was not exposed to nonnative trout invasion by constructed or natural fish movement barriers and closing it to recreational angling. Because each remnant population was genetically distinct (Turner et al. this volume), multiple replicates of each strain were deemed essential to achieve genetic as well as demographic security. Initially, this approach appeared successful in that within about 10 years, each remnant population had at least one replicate. The efficacy of this approach was tested with the elimination of Gila trout from Diamond Creek, the species type locality, by wildfire in 1989 (Propst et al. 1992). Subsequent fires in the mid-1990s and elimination of several Gila trout populations further challenged the merits of Gila trout conservation in small

Fig. 1 Gila Trout, *Oncorhynchus gilae. Photo by DJ Myers*

single-strand headwater streams (Brown et al. 2001). Consequently, conservation strategies shifted to establishing Gila trout populations in large, dendritically complex drainages in the belief that such systems would be sufficiently large that if wildfire burned in the catchment Gila trout would have refuge in unburned portions and individuals from unaffected reaches could colonize reaches depopulated by the effects of wildfire.

As conservation strategies for Gila trout were evolving in the 1990s to ameliorate the risk posed by wildfires, empirical and theoretical evidence for climate change, in particular global warming, was rapidly accumulating and model projections for the American Southwest, and the entire Gila River drainage, were particularly dire (Williams et al. 2020). Collectively, these models projected increasing temperatures, increasing aridity, shifting precipitation patterns (including increased frequency of extreme events), diminishment and loss of snowpack, and altered stream flow regimes (Gutzler 2013; Dettinger et al. 2015; Udall and Overpeck 2017). The net effect of climate change would be substantially less optimal habitat for trout, but also an increase in wildfire frequency, extent, intensity, and severity (Westerling et al. 2006).

In a region having comparatively few perennial streams, even at higher elevations, and these are generally disconnected, persistence of robust trout populations is problematic even under current climatic conditions. Optimal habitat for Gila trout is limited and generally occurs ≥2000 m. Under conditions projected by climate models, the lower elevational limits of optimal habitat will increase (Kennedy et al. 2008). The contraction of optimal habitat will be driven mainly by elevated thermal regimes and diminished and altered flow regimes. With these changes, lower reaches of traditional Gila trout habitat will become inhabitable by warmwater species. Survival of Gila trout might therefore ultimately depend on whether it can coexist with warmwater species in thermally sub-optimal trout habitat.

2 Setting

In 1995, wildfire induced ash- and sediment-laden flows eliminated nonnative trout and native fishes (cyprinids and catostomids) from upper reaches of Black Canyon, a Gila River tributary in southwest New Mexico (Fig. 2). Over the next 2 years, native cyprinids and catostomids from downstream refugia colonized depopulated stream reaches but nonnative trout did not. In June 1998, a fish movement barrier was constructed to preclude return of nonnative salmonids to the upper-most 17 km of Black Canyon and release of hatchery-reared native Gila trout was planned for that autumn. After barrier construction, a final check of Black Canyon was made to ensure absence of nonnative trout; four brown trout and one rainbow trout were found at a single location. Because rainbow trout hybridize with Gila trout and brown trout prey upon and compete with Gila trout their presence was untenable. Surrendering Black Canyon to nonnative trout was not an option. The presence of

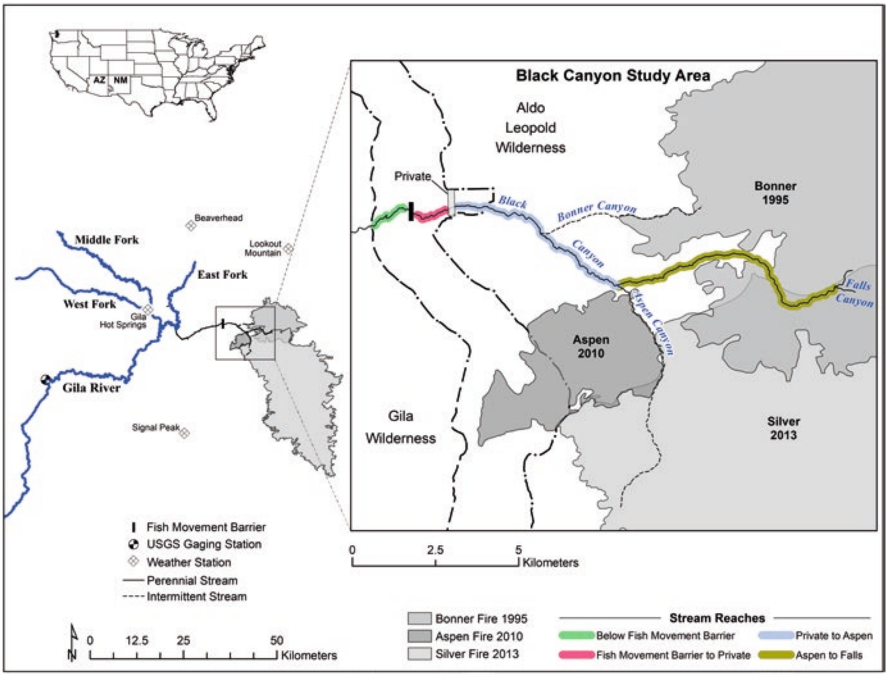


Fig. 2 Black Canyon, New Mexico study area

viable populations of four native warmwater species (longfin dace *Agosia chrysogaster*, speckled dace *Rhinichthys osculus*, Sonora sucker *Catostomus insignis*, and desert sucker *Pantosteus clarkii*) precluded use of piscicides to eliminate nonnative trout. The alternative was mechanical removal of nonnative trout with electrofishing gear. From June through October 1998, Black Canyon was electro-fished on multiple occasions with multiple crews to capture nonnative trout (Brooks and Propst 1999). In addition to brown trout and rainbow trout, seven cutthroat trout *Oncorhynchus clarkii* individuals were collected. All brown trout collected (n = 345) were of a single cohort (age 1) and evidently of hatchery origin as scale circuli were evenly spaced, all rainbow trout (n = 24) were sub-adults or adults (>170 mm total length), and cutthroat trout were all adults (>250 mm total length). The likely provenance of brown trout, absence of age-0 rainbow trout, and first record of cutthroat trout strongly suggested their illegal release rather than their invasion from downstream reaches. Based on October sampling, it was likely all rainbow trout and cutthroat trout were removed but possible that some brown trout might remain. Nonetheless, hatchery-produced age-0 (≈100 mm total length) Gila trout were released throughout upper Black Canyon in November 1998.

Black Canyon was next sampled in July 2001 and only native fishes were captured. Gila trout was most common in the upper-most reach (Aspen-Falls) and represented by several size classes, including age-0 individuals (<90 mm TL). Speckled dace was the most common fish in both sampled reaches (Barrier-Private reach not sampled in 2001).

The absence of nonnative trout in Black Canyon in 2001 indicated the 1998 removal effort had been successful. In addition, the presence of Gila trout <90 mm TL confirmed in-stream reproduction. At this point, it appeared that Black Canyon could support a mixed warmwater-coldwater assemblage, and the decision was made to not sample Black Canyon for several years. When next sampled in 2008, multiple size classes of brown trout were found throughout Black Canyon upstream of the fish movement barrier. These fish were either progeny of individuals that survived the 1998 mechanical removal effort or individuals and progeny of brown trout that traversed the gabion basket barrier, or both. In 2009, the gabion fish movement barrier was replaced with a concrete structure that presumably was more effective in precluding fish passage to upper reaches.

Beginning in 2008, the paramount management imperative was to suppress or eliminate brown trout so that a viable Gila trout population could be maintained in Black Canyon. A second objective was to document the dynamics of a mixed native warmwater-coldwater fish assemblage. Our expectation was that in time Gila trout would occur primarily, if not exclusively, in upstream, colder reaches (i.e., Aspen-Falls), that reproduction and recruitment by Gila trout would be limited, and that reference Gila trout populations would be demonstrably more robust (e.g., abundance, condition, and size structure) than the population in Black Canyon. Among native warmwater species, we anticipated that speckled dace and desert sucker would be the most successful (e.g., distribution, abundance, and size structure) and that longfin dace and Sonora sucker might maintain smaller populations in upper Black Canyon. The presence of brown trout would provide an opportunity to characterize, if not quantify, the impact of a nonnative predator and competitor on native fishes.

In addition to the presence of a nonnative predator, global warming (Kennedy et al. 2008) was expected to present another challenge to maintenance of a viable Gila trout population in Black Canyon. Regional metrics indicate that the upper Gila River drainage climate is warming, that total annual precipitation is declining, and river flow regimes have been altered. While regional metrics do not reflect exactly the climatic and hydrologic conditions in Black Canyon over this period, they do indicate the changes that have likely occurred—increasing air temperatures, diminished summer flows, altered flow regimes, and elevated water temperatures.

Our purpose herein is to use information obtained on an assemblage of native warmwater fishes and Gila trout to determine if such communities have long-term viability. Specifically, we wished to determine if somatic and demographic attributes of Gila trout in such a mixed assemblage were demonstrably different from those attributes in solely Gila trout populations. In addition, we wished to characterize somatic and demographic attributes of the native warmwater species in the presence of Gila trout. And finally, to evaluate efficacy of mechanical removal of a nonnative salmonid.

3 Approach

Study Area—Black Canyon lies entirely within the Gila National Forest of southwestern New Mexico, USA and almost its entire course is within designated wilderness (Aldo Leopold and Gila Wildernesses). From its origins in the Black Range (elevation ca. 2450 m), Black Canyon flows east to join East Fork Gila River (elevation 1770 m) a short distance upstream of the latter's confluence with the Gila River (Fig. 2). The study area was in the upper 17 km of Black Canyon, extending from the fish movement barrier (elevation 2074 m) upstream to the confluence of Falls Canyon (elevation 2440 m). In upper reaches, the stream was canyon-bound and bordered by mixed conifers (white fir *Abies concolor* and Douglas fir *Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). Near Aspen Canyon confluence, the stream entered a broad valley with scattered ponderosa pine stands and Gamble oak (*Quercus gambellii*) (Fig. 3). Downstream of Bonner Canyon, the stream progressed through more constricted terrain to the fish movement barrier. Riparian vegetation consisted of ponderosa pine, narrow leaf cottonwood (*Populus angustifolia*), and willow (*Salix* sp) was scattered among ponderosa pines along the stream. Three tributaries joined Black Canyon in its course within the study area; Falls Canyon was perennial, and Aspen and Bonner canyons were intermittent. Fish did not occur above the waterfalls a short distance (ca. 50 m) upstream of the confluence of Black and Falls canyons.

Methods—The study area was divided into four sampling reaches. The most upstream and canyon-bound reach extended from Aspen Canyon to Falls Canyon confluence (8.7 km). The middle valley reach was from the upstream boundary of a

Fig. 3 Black Canyon near confluence of Aspen Canyon, New Mexico

small private inholding to Aspen Canyon (5.8 km). The penultimate downstream reach was from the fish movement barrier to the downstream boundary of the private property (1.3 km). The stream was not sampled in the 1.1 km private property reach. And the lowest was a 3-km reach downstream of the fish movement barrier. Nonnative salmonids were not removed from this reach, and it was accessible to fishes from downstream reaches and tributaries (Whitney et al. 2017; Hedden et al. 2022). Species codes (first three letters of genus and species, e.g., AGOCHR = *Agosia chrysogaster* longfin dace and ONCGIL = *Oncorhynchus gilae* Gila trout) were used on graphs and tables to conserve space.

Following release of Gila trout in 1998, Black Canyon was not sampled until 2001. After a 7-year hiatus, it was again sampled in 2008. Thence, the stream was sampled annually in July or August through 2012. The extent of the study area sampled in a year was dependent upon personnel availability and weather; the Barrier-Private reach was sampled in all years (June in 2008), Private-Aspen reach in all years, and Aspen-Falls reach in 2008, 2011, and 2012. The fish assemblage downstream of the barrier was sampled multiple times prior to, during, and after the 2008–2012 sampling period. The Below Barrier reach data are presented to provide a contrast to above barrier data. Two or three crews, each composed of 3-5 individuals and sampling in different stream sections, used battery-powered backpack shockers to stun fish. Stunned fish were netted and mass (±1 g) and total length (±1 mm, TL) of large-bodied individuals (≥100 mm TL) determined. Small-bodied individuals were typically only counted, but in several years, TL was measured for subsamples of small-bodied fishes. In 2011, small-bodied fishes were not counted; elevated water temperatures and handling stress necessitated rapid processing of fish to reduce mortality. All fish, except nonnative brown trout, were returned to stream near point of capture. Abundance was the number of individuals captured/elapsed time electrofishing (#/min).

Water temperature data were obtained from temperature loggers deployed by New Mexico Surface Water Quality Bureau (NM Environment Department). Regional precipitation and temperature data 1980 through 2020 were obtained from four weather stations in the upper Gila River drainage (USGS HUC # 15040001) NOAA website (www.ncdc.noaa.gov/cdo-web). Two stations (Lookout Mountain and Signal Peak) were at high elevations (2591 m and 2548 m, respectively) and the remaining two (Beaverhead and Gila Hot Springs) were somewhat lower (2033 m and 1718 m, respectively). Gila River discharge data were obtained from the USGS Gila River near Gila gage (# 09430500).

Three metrics were used to characterize the well-being of Gila trout, brown trout, Sonora sucker, and desert sucker: condition, size structure, and abundance (catch-per-unit-effort: #/min elapsed electrofishing time). Because Gila trout have near isometric growth (i.e., $W = aL^3$) throughout their lives, Fulton's Condition Factor was used to estimate general physiological condition of Gila and brown trout (Pope and Kruse 2007). The factor is determined by $K_{TL} = (\text{Mass}/\text{Total Length}^3) * 10^5$. Because condition was normally distributed for each year and reach, ANOVA was used to compare mean condition between years, reaches, and populations. The Kolmogorov–Smirnov Goodness of Fit two-sample test was used to compare annual intra-reach, inter-reach, and population size structure (Neumann and Allen 2007). Specimens were grouped in 10-mm TL classes for K-S analysis. Gila trout specimens <70 mm TL (age 0) and brown trout specimens <100 mm TL were excluded from analyses. All statistical procedures were done with XLSTAT (Addinsoft 2021).

Reference Gila trout populations were in McKnight and Diamond creeks. Diamond Creek (elevation ca. 2430 m) was about 14 air km north of Black Canyon while McKnight Creek (elevation ca. 2340 m) was about 14 air km south of Black Canyon. Both streams were roughly comparable to Black Canyon in habitat dimensions (stream width, depth, and discharge) but upper Black Canyon was substantially longer (≈18 km) than Diamond Creek (≈6 km) and McKnight Creek (≈8 km). There was no stream unaffected by wildfire and drought within the current range of Gila trout that also had a mixed warmwater-coldwater assemblage that might serve as a reference for mixed assemblage or warmwater species comparisons. Black Canyon downstream of the fish movement barrier was sampled (nonnative salmonids not removed) relatively frequently from 1996 through 2021 and thus provided some perspective on the changes in the fish assemblage in upstream reaches.

Following an initial stocking of age-0 (70–115 mm TL, number not recorded) hatchery-produced Gila trout in Black Canyon upstream of the barrier in late 1998, it was stocked annually thereafter in autumn. Numbers released annually ranged from several hundred to several thousand. Most releases were of age-0 fishes (80–115 mm TL), but two releases were of larger and older fish (105 individuals averaging about 300 mm TL in 2009 and about 1000 individuals averaging 150 mm TL in 2016). Individuals <100 mm TL were considered juveniles, those between 101 and 150 sub-adults, and >150 adults (Propst and Stefferud 1997).

4 Results

Regional Climatic, Discharge, and Water Temperature Patterns (1980–2020)—Total annual precipitation over the past 40 years has declined significantly at four upper Gila River catchment weather stations (Fig. 4). Although total annual precipitation declined, mean daily discharge at the Gila River near Gila gage did not (Fig. 5). However, extreme flow events (floods and minimum flows) increased. Since 1980, there have been 10 annual peak flows exceeding 283 m^3/s (=10^4 ft^3/s), whereas in the preceding 51 years there were only 4 years with peak flows greater than 283 m^3/s. Annual minimum daily discharge and summer (June and July) mean daily discharge decreased over the 1980–2020 period. At the two weather stations that recorded mean daily air temperature, mean annual temperature increased significantly (Fig. 6). Temperature loggers deployed upstream of Aspen Canyon confluence and at Aldo Leopold Wilderness boundary recorded mean daily water temperatures in 2012 approaching 20 °C, but maximum daily water temperatures exceeded 25 °C frequently in June at both locations and less frequently in July and August (Fig. 7).

Temporal Changes in Fish Assemblage—Although the upper Black Canyon fish assemblage was greatly reduced, if not eliminated, by ash- and sediment-laden flows associated with the 1995 Bonner Fire, native cyprinids and catostomids were comparatively common in the Below Barrier reach a year after the fire and

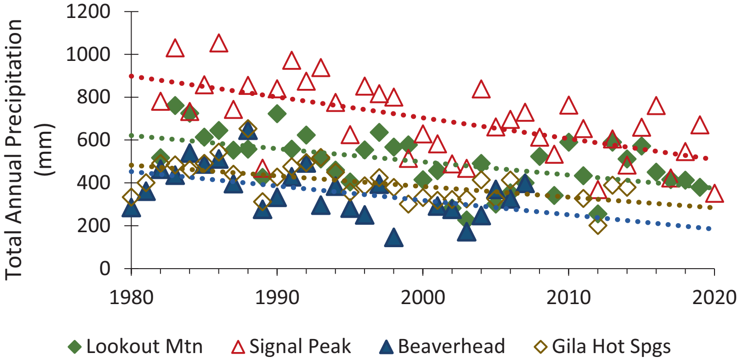
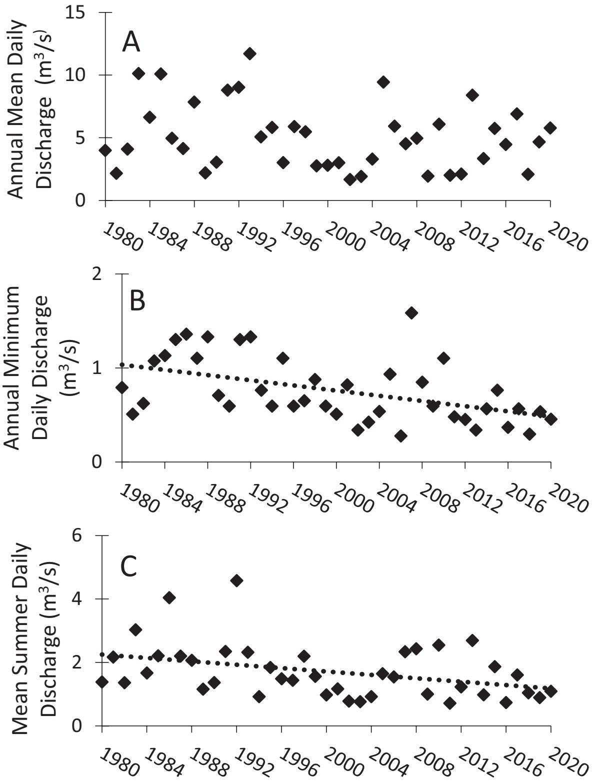


Fig. 4 Total annual precipitation at four weather stations in the upper Gila River catchment. Dashed lines indicate significant ($\alpha = 0.05$) relationship

Fig. 5 Discharge attributes of Gila River at USGS Gila River near Gila gage (09430500), New Mexico. Dashed lines indicate significant (α = 0.05) relationship



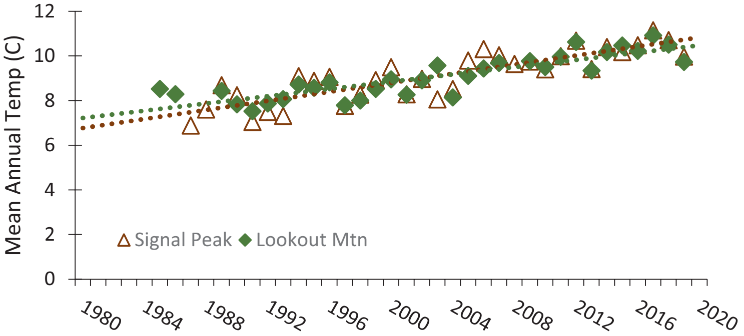


Fig. 6 Mean annual air temperature at two weather stations in upper Gila River catchment, New Mexico. Dashed lines indicate significant (α = 0.05) relationship

especially in 1998 (Fig. 8). Speckled dace was the most common species in all collections and nonnative salmonids were rare. Although abundance was variable across collections, fish numbers, especially speckled dace, increased substantially in 2012 and 2013, crashed following ash and sediment flows caused by the 2013 Silver Fire, and no fish was collected in this reach until October 2014 when 12

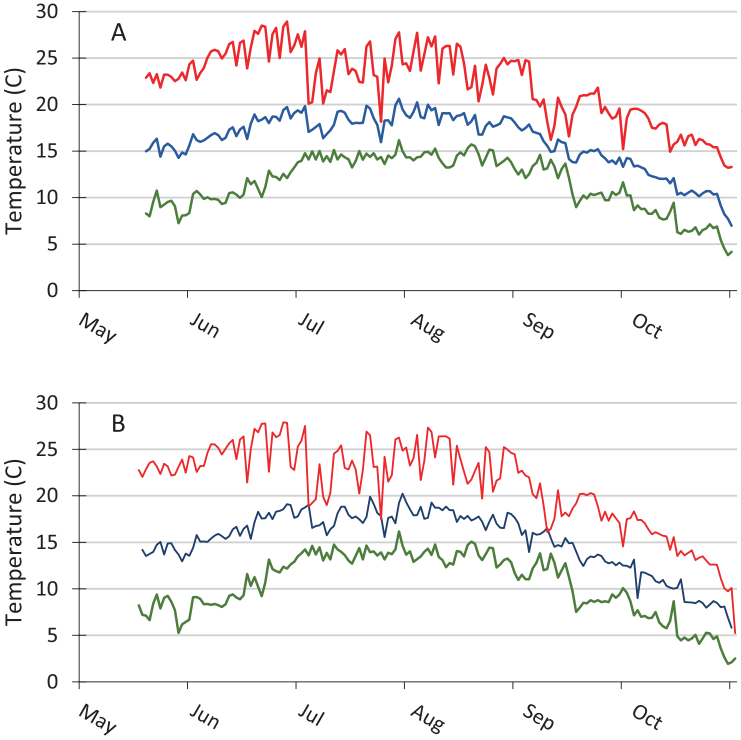


Fig. 7 Mean, maximum, and minimum daily water temperature in Black Canyon at Aldo Leopold Wilderness boundary (**a**) and just upstream of Aspen Canyon confluence (**b**), New Mexico, May–October 2012

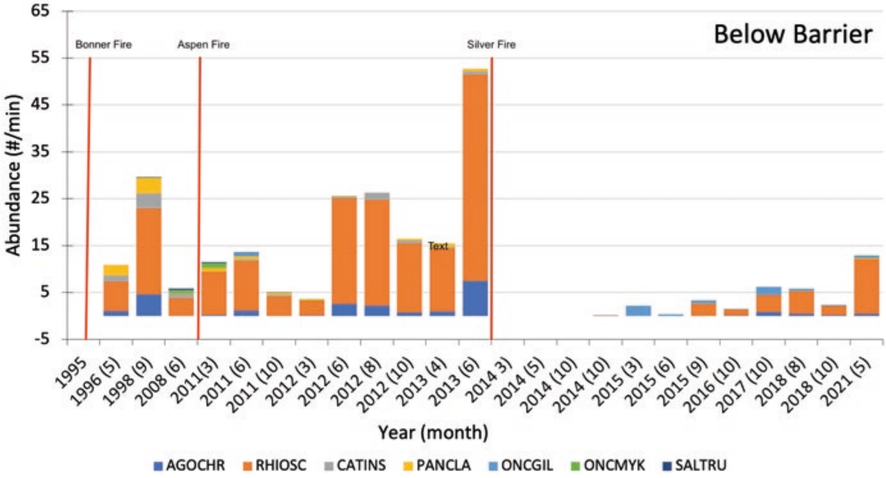


Fig. 8 Abundance (#/min) of fishes in Black Canyon Below Barrier reach, New Mexico, 1996–2021. Month of sampling in parentheses

speckled dace and a single Gila trout were collected. Thereafter, fish abundance increased slightly through 2021 but remained considerably less than in the collections preceding the Silver Fire.

Within a year of the Bonner Fire, native fishes moved from downstream refugia to the upper reaches of Black Canyon. Thereafter, fish abundance in the reaches upstream of the barrier generally increased through 2012 (Fig. 9). Ash and sediment flows associated with the Aspen Fire contributed to the comparatively low abundance of fishes in the Barrier-Private and Private-Aspen reaches in 2010. Speckled dace was typically the most common fish in all reaches in all years; low abundance of fishes in 2011 was largely a reflection of partially counting small-bodied fishes in the Barrier-Private reach and not counting them in the Private-Aspen and Aspen-Falls reaches. Neither brown nor Gila trout was common in any reach in 2011 but desert sucker was moderately common in the Aspen-Falls reach. In 2012, fishes attained their greatest abundance in the Barrier-Private and Private-Aspen reaches while that in the Aspen-Falls reach was moderately high. The 2013 Silver Fire eliminated fishes from all reaches (Fig. 10). In 2013 and subsequent years, hatchery-reared Gila trout were released in autumn at several locations in the above-barrier reaches. Most, if not all, Gila trout captured in the Aspen-Falls reach in 2016 were hatchery-produced fish. But in August 2018, a large portion of the sample in the Private-Aspen reach was age-0 fish (<90 mm TL), which were almost certainly spawned in the stream. The fish movement barrier precluded the natural colonization of the upper reaches of Black Canyon by native warmwater species.

Longitudinal Abundance of Fishes—Although variable from year to year, abundance of warmwater species generally declined from down- to upstream (Fig. 11). In average, longfin dace and speckled dace were roughly equally abundant in the Barrier-Private and Private-Aspen reaches and rare or uncommon in the most upstream reach. Sonora sucker was most common in the Barrier-Private reach and absent in the most upstream. Desert sucker abundance was greatest in the Barrier-Private reach, and it was more common in the most upstream reach than other warmwater species. Gila trout abundance increased from lowest to most upstream reach. In contrast, brown trout abundance was greatest in the middle reaches, and there its abundance was low compared to Gila trout. Since the 2013 Silver Fire only Gila trout occupy the reaches upstream of the fish movement barrier.

Size structure of Black Canyon Gila Trout Population and Reference Populations—During 2008–2012, the number of Gila trout captured varied considerably across reaches and years within each reach (Table 1). Age-0 individuals (≤90 mm TL) were rarely collected in any reach in any year (Fig. 12). An unknown portion of the fishes collected each year in each reach in July–August were hatchery-produced fish. When stocked (typically October or November) most releases were comprised of age-0 (<130 mm TL) but in 3 years larger fish (157–196 mm TL) were

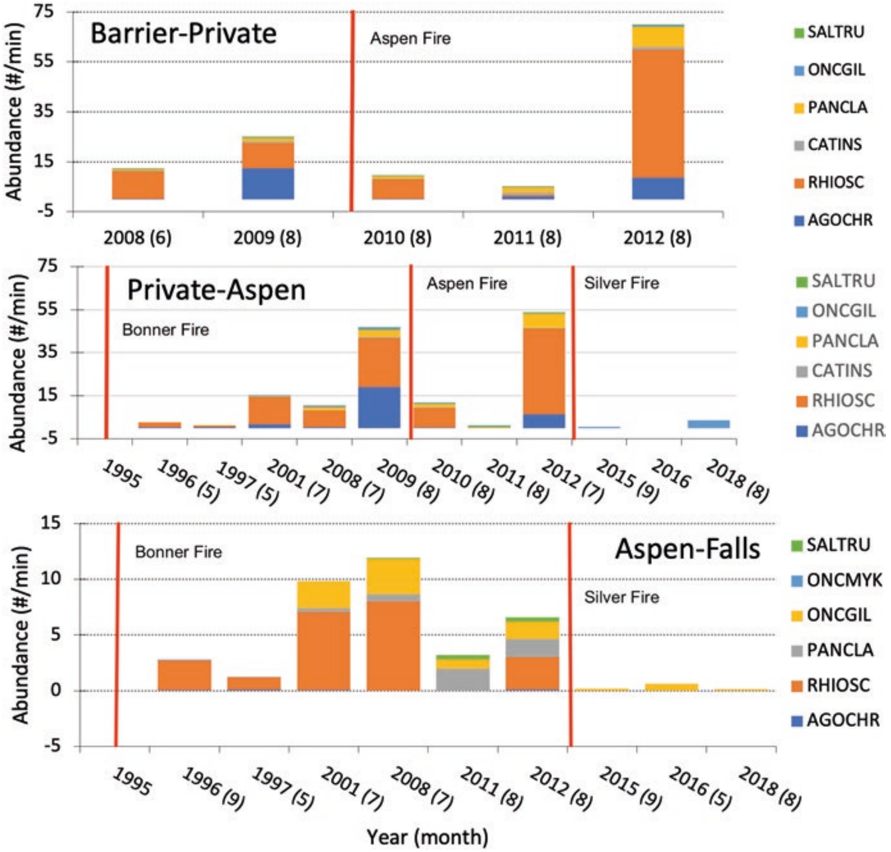


Fig. 9 Abundance (#/min) of fishes in Black Canyon reaches upstream of fish movement barrier, 1996–2018. Aspen Fire not indicated on Aspen-Falls reach because it did not burn in Aspen-Falls catchment. Note different abundance axes

released and in 2009 about 100 >275 mm TL were released (Table 2). Some stocked fish likely survived to be collected the following year as age-1 individuals between 100- and 150-mm TL. And some stocked fish survived for multiple years. Most collections were comprised largely of fish <200 mm TL, but in several years fish >200 mm was a substantial portion of the collection (e.g., 2010 and 2011 in Private-Aspen reach).

Size structure of Gila trout in each reach across years was generally similar. Between year differences in size structure were different for only two comparisons:

Fig. 10 Debris and fine sediment deposits in Black Canyon in Barrier-Private reach following the 2013 Silver Fire

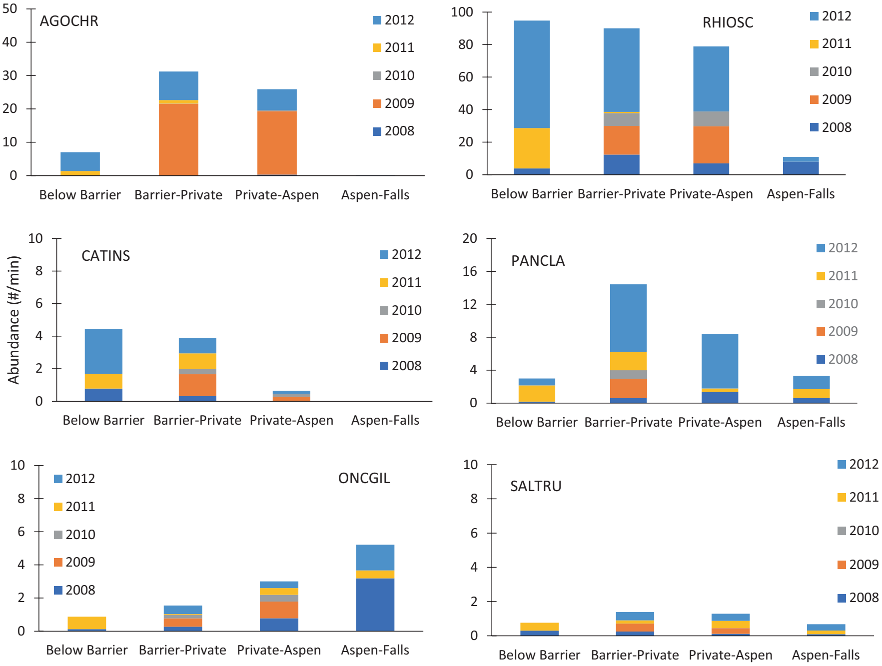


Fig. 11 Abundance of fishes from most downstream reach to most upstream. The Below Barrier and Aspen-Falls reaches were not sampled in 2009 and 2010. The Below Barrier reach was sampled one (2008), three (2011), and four (2012) times. In 2011, small-bodied fishes in Private-Aspen and Aspen-Falls reaches were not counted. Note different scales on Abundance axis

Table 1 Black Canyon Gila trout population and reference population statistics, 2001 and 2008–2012

Population		Year	Month	N (TL)	TL range (mm)	TL mean (mm)	N (mass)	Mass mean (g)
Black	Barrier-Private	2008	Jun	12	126–340	159.0	11	55.8
		2009	Aug	27	110–233	149.3	27	29.5
		2010	Aug	19	105–233	151.1	19	39.1
		2011	Aug	7	101–300	205.9	7	126.0
		2012	Aug	58	106–300	169.5	57	54.9
	Private-Aspen	2001	Jul	13	40–223	90.5	8	31.0
		2008	Jun	82	105–215	134.6	65	26.2
		2008	Jul	257	40–335	149.9	248	46.1
		2009	Aug	246	55–290	149.0	234	41.3
		2010	Aug	149	95–340	176.8	148	70.5
		2011	Aug	98	81–327	157.7	97	49.0
		2012	Jul	53	106–300	172.8	51	59.1
	Aspen-Falls	2001	Jul	100	24–270	76.46	33	52.1
		2008	Jul	103	70–231	116.5	100	20.8
		2011	Aug	67	99–239	162.1	67	43.6
		2012	Aug	219	41–300	154.3	204	49.3
Diamond		2001	Jul	138	70–203	115.8	138	18.8
		2008	Apr	83	42–241	129.4	65	37.4
		2010	Oct	386	47–240	117.8	294	24.6
McKnight		2011	Jul	235	64–185	122.8	235	21.1

Barrier-Private 2011–2012 and Aspen-Falls 2011–2012 samples (Table 3). Size structure was different for all Barrier-Private/Private-Aspen comparisons, except 2012 (Table 4). The size structure of the 2012 Private-Aspen/Aspen-Falls samples was different.

The size structure of the Black Canyon Gila trout population was different from that of the Diamond population in 2008 and McKnight population in 2011 (Table 5). Figure 13 illustrates the differences in size structure of the populations. In both Diamond and McKnight creeks maximum specimen TL rarely exceeded 220 mm whereas in Black Canyon several individuals in most years exceeded >300 mm TL.

Post-Silver Fire monitoring of the above barrier Gila trout population was initiated in 2015. Most, if not all fish, collected in 2015 and 2016 were hatchery-produced individuals (Fig. 14). In 2018, however, a substantial number of age-0 (<90 mm TL) individuals were collected.

Condition (K_{TL}) of Black Canyon Gila Trout and Reference Populations—Mean Gila trout condition was >0.9000 in all years in all Black Canyon reaches, except Barrier-Private in 2009 when it was 0.8341 (Table 6). Most variation in mean annual

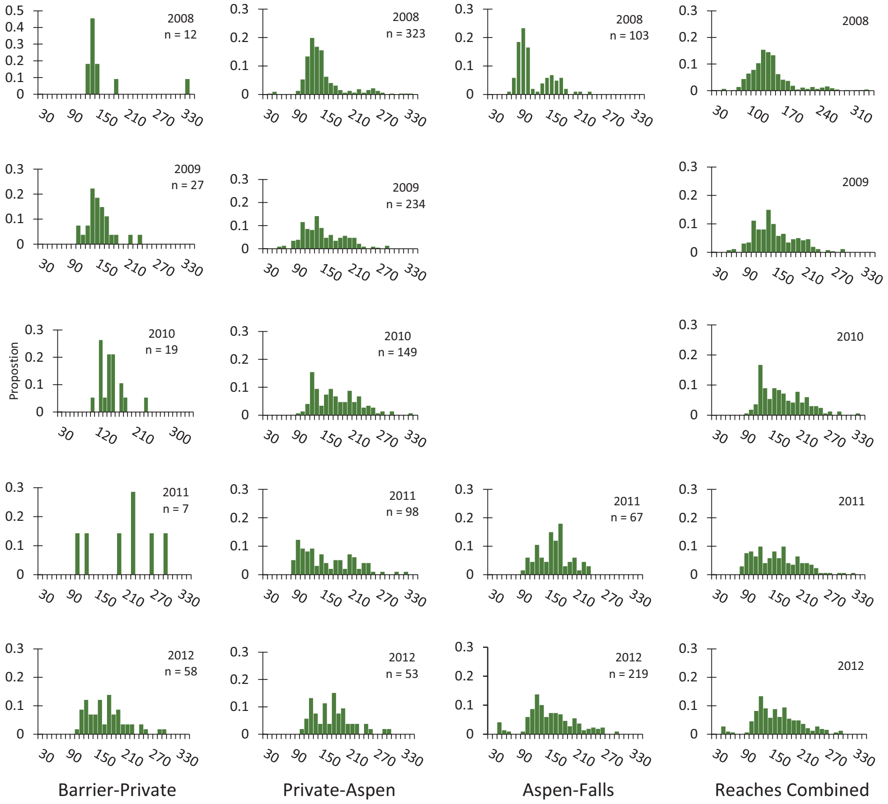


Fig. 12 Size structure of Black Canyon Gila trout population, 2008–2012

condition was in the Barrier-Private reach. Mean condition of Gila trout in the Barrier-Private reach in 2009 was significantly less than that in 2008 and 2010 (Table 7). In 2011, mean condition in the reach was greater than that in 2012 but not 2010. In the Private-Aspen reach, annual mean condition differences from 2008–2009 through 2010–2011 were significant but that of 2011–2012 was not. Only two Barrier-Private/Private-Aspen condition comparisons were different; condition was less in Barrier-Private reach in 2009, but greater in 2011 (Table 8). All Private-Aspen/Aspen-Falls comparisons were non-significant; mean condition of the 2011 Private-Aspen/Aspen-Falls samples was virtually identical. In two of four population condition comparisons, K_{TL} of the Black Canyon population was greater than that of the reference population and less in the other two (Table 9). All population comparisons yielded significant differences.

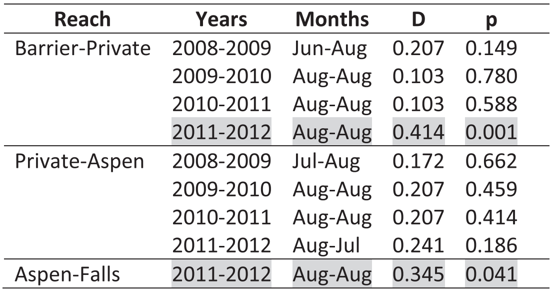
Brown Trout Population Attributes—Although absent in 2001, brown trout occurred throughout the upper reaches of Black Canyon in 2008. Despite annual efforts (2008–2012) to suppress their numbers by removing all individuals captured, the number captured generally increased over time (Table 10). The size

Table 2 Hatchery-reared GT stocked in Black Canyon, New Mexico. Numbers released in 1998 and 1999 not recorded

Year	Date	Number	Mean TL (mm)[a]
1998	Nov		
1999	20 Oct		
2000	1 Nov	1872	80
2001	31 Oct	2000	
2002	–	2000	–
2004	–	2160	190
2005	–	445	91
2006	–	2815	81
2007	–	288	196
2009	22 Dec	900	107
2009	22 Dec	105	297
2011	21 Nov	1045	130
2012	31 Oct	1022	102
2013	23 Oct	1007	114
2013	4 Dec	2169	119
2014	23 Oct	3167	109
2015	22 Sep	3514	89
2016	29 Mar	1015	157
2017	25 Sep	4112	104

[a] Converted from English units

Table 3 Black Canyon intra-reach Kolmogorov–Smirnov Goodness of Fit Test results comparing Gila trout size structure (10-mm size classes) year-to-year in each reach (specimens <70 mm TL excluded). Shaded cells indicate significant ($\alpha = 0.05$) differences in size structure



Reach	Years	Months	D	p
Barrier-Private	2008-2009	Jun-Aug	0.207	0.149
	2009-2010	Aug-Aug	0.103	0.780
	2010-2011	Aug-Aug	0.103	0.588
	2011-2012	Aug-Aug	0.414	0.001
Private-Aspen	2008-2009	Jul-Aug	0.172	0.662
	2009-2010	Aug-Aug	0.207	0.459
	2010-2011	Aug-Aug	0.207	0.414
	2011-2012	Aug-Jul	0.241	0.186
Aspen-Falls	2011-2012	Aug-Aug	0.345	0.041

Table 4 Black Canyon inter-reach Kolmogorov–Smirnov Goodness of Fit Test results comparing annual Gila trout size structure (10-mm size classes) between reaches (specimens <70 mm TL excluded). Shaded cells indicate significant (α = 0.05) difference in size structure

	Barrier-Private/Private-Aspen		Private-Aspen/Aspen-Falls	
Year	**D**	***p***	**D**	***p***
2008	0.621	<0.0001	0.276	0.132
2009	0.483	0.001		
2010	0.483	0.001		
2011	0.552	<0.0001	0.207	0.396
2012	0.069	0.996	0.345	0.042

Table 5 Kolmogorov–Smirnov Goodness of Fit Test results for Black Canyon population and reference populations size-structure comparisons (10-mm TL size classes). Shaded cells indicate significant (α = 0.05) differences in size structure

Populations	Months	Blk TL	Blk TL range	Ref TL	Ref TL range	D	*p*
Black-Diamond 2001	Jul-Jul	125	70-227	116	70-203	0.241	0.118
Black-Diamond 2008	Jul-Apr	141	70-340	146	91-241	0.483	0.001
Black-Diamond 2010	Aug-Oct	174	95-340	119	71-226	0.207	0.408
Black-McKnight 2011	Jul-Jul	161	81-327	123	72-185	0.379	0.021

structure of the population (reaches combined) indicated that reproduction and recruitment occurred each year from 2007 through 2011, except 2008 (Fig. 15). Most individuals collected were <300 mm TL, but larger individuals were found each year. No between year size-structure differences were detected (Table 11). Mean condition of brown trout each year >1.0000 in all years (Table 12). Between year condition was different in 2009–2010 and 2010–2011 (Table 13).

Mass of Gila and Brown Trouts—Total mass of collected Gila trout (excluding individuals <70 mm TL) was variable across years and reaches (Table 14). It generally increased in Barrier-Private and Aspen-Falls reaches from 2008 through 2012. In Private-Aspen reach, total mass was greatest in 2008 and steadily declined to its lowest in 2012. In years all reaches were sampled, total Gila trout mass was least in 2011 and greatest in 2012. Brown trout total mass (excluding individuals <70 mm TL) was likewise variable among reaches and year to year. It was greatest in Barrier-Private and Aspen-Falls in 2012. Total brown trout mass increased from 2008 through 2012. Brown trout mass exceeded that of Gila trout in all years in Barrier-Private, all but one in Private-Aspen, and never in Aspen-Falls.

Warmwater Species Population Attributes—Because large numbers of desert sucker were often collected, TL and mass were obtained from a representative subsample of desert suckers collected in each reach each year. For example, in the Private-Aspen reach in 2008, 595 desert suckers were captured, TL was obtained from 131 and mass determined for 126. Desert sucker abundance generally increased from 2008 through 2012 (Table 15). Although the range of TL was similar across years, mean TL was more variable (Fig. 16). Size structure of the Black Canyon desert sucker population, however, did not differ from one year to the next (Table 16). Mean annual condition of desert suckers exceeded 1.1 in all years and was greatest

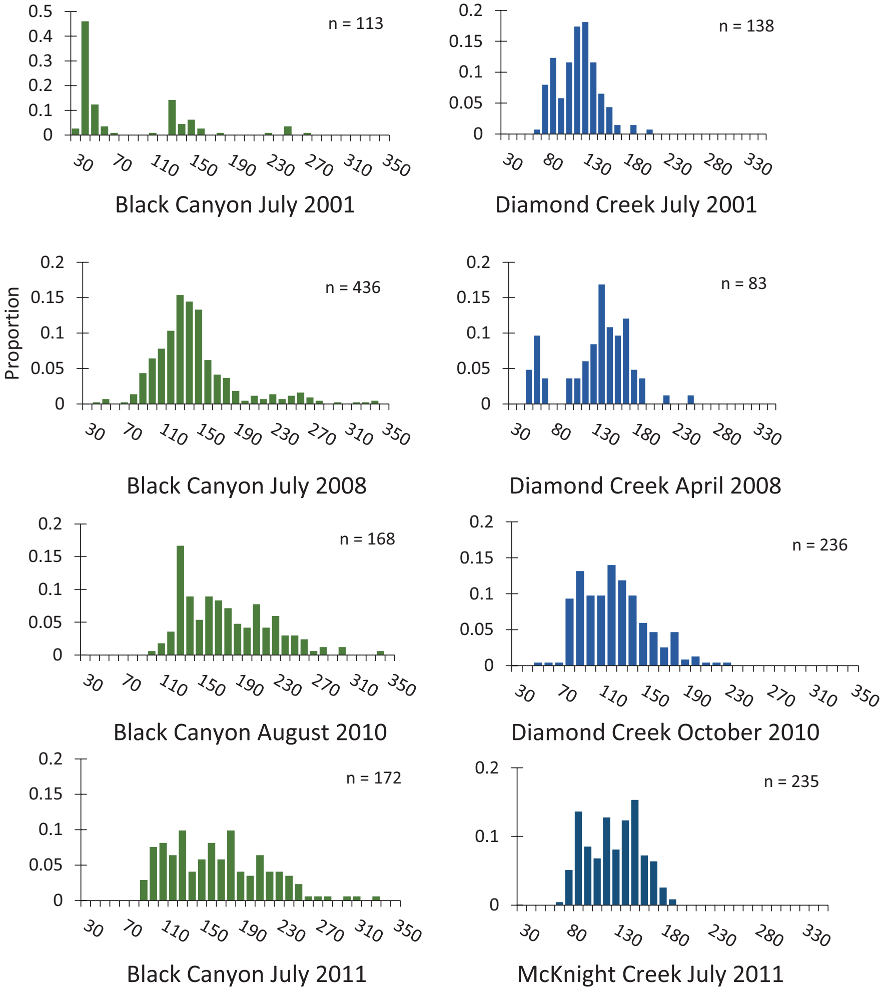


Fig. 13 Size structure of Black Canyon Gila trout population and that of its reference populations. 2008 Black Canyon—Diamond Creek and 2011 Black Canyon—McKnight Creek were significantly different (see Table 5). Note different proportion axis scale on Black Canyon July 2001 graph

in 2010 (Table 17). Between year mean condition differences were different for all years (Table 18).

The TL range of Sonora suckers captured each year indicated multiple age classes and annual reproduction (Table 19). Most individuals were between 100- and 250-mm TL but several larger fish were captured in all years (Fig. 17). Size structure of the population did not differ from year to year (Table 20). Mean condition of the population exceeded 1.2 in all years but 2009 when it was slightly less (Table 21). Mean condition was different only between 2009 and 2010 (Table 22).

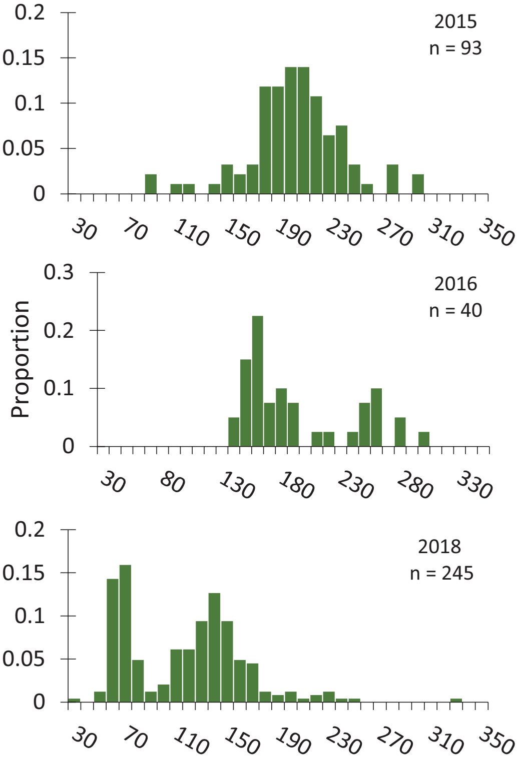


Fig. 14 Post-Silver Fire size structure of Gila trout population in Black Canyon upstream of fish movement barrier. The September 2015 and August 2018 samples were taken in Private-Aspen and Aspen-Falls reaches whereas the May 2016 sample was from the Aspen-Falls reach. Note the different proportion axis scale for the 2016 collection

Table 6 Fulton's Condition Index (K_{TL}) of Gila trout in Black Canyon. Individuals <70 mm excluded

Reach	Year	Month	n	K_{TL} range	K_{TL} mean
Barrier-Private	2008	Jun	11	0.8396–1.0734	0.9638
	2009	Aug	27	0.5788–1.1285	0.8341
	2010	Aug	19	0.9060–1.2649	0.9878
	2011	Aug	7	0.8392–1.7326	1.0672
	2012	Aug	56	0.6818–0.9149	0.9149
Private-Aspen	2008	Jul	245	0.6575–1.3994	1.0206
	2009	Aug	232	0.6164–1.5313	0.9621
	2010	Aug	110	0.8017–1.3432	0.9937
	2011	Aug	87	0.6420–1.2298	0.9133
	2012	Aug	51	0.6818–1.2301	0.9206
Aspen-Falls	2008	Jul	97	0.7073–1.2644	0.9735
	2011	Aug	67	0.6717–1.2288	0.9366
	2012	Aug	204	0.6575–1.2660	0.9377

Table 7 Black Canyon intra-reach condition annual comparisons ANOVA results. Shaded cells indicate significant differences in mean K_{TL}

Reach	Years	Months	F	*p*	d.f
Barrier-Private	2008-2009	Jun-Aug	7.796	0.008	1,36
	2009-2010	Aug-Aug	17.133	<0.0001	1,44
	2010-2011	Aug-Aug	1.114	0.302	1,24
	2011-2012	Aug-Aug	5.479	0.022	1,62
Private-Aspen	2008-2009	Jul-Aug	13.326	<0.0001	1,545
	2009-2010	Aug-Aug	3.930	0.048	1,342
	2010-2011	Aug-Aug	32.376	<0.0001	1,195
	2011-2012	Aug-Jul	0.036	0.849	1,134
Aspen-Falls	2011-2012	Aug-Aug	0.084	0.772	1,136

Table 8 Black Canyon annual inter-reach condition comparison ANOVA results. Shaded cells indicate significant differences in mean K_{TL}

	Barrier-Private/Private-Aspen			Private-Aspen/Aspen-Falls		
Year	F	*p*	d.f.	F	*p*	d.f.
2008	0.764	0.383	1,321	2.644	0.105	1,411
2009	14.769	<0.0001	1,259			
2010	0.067	0.796	1,127			
2011	9.946	0.002	1,92	0.000	1.000	1,172
2012	0.218	0.641	1,104	0.161	0.689	1,98

Table 9 Black Canyon Gila trout and reference populations condition (K_{TL}) comparisons ANOVA results. Shaded cells indicate significant differences in mean K_{TL}

Populations	Year	Months	Mean BLK K_{TL}	Mean REF K_{TL}	F	*p*	d.f.
Black-Diamond	2001	Jul-Jul	1.2224	1.0540	77.321	<0.0001	1,178
Black-Diamond	2008	Jun-Apr	1.0034	1.1010	25.023	<0.0001	1,487
Black-Diamond	2010	Aug-Oct	0.9934	0.9534	11.499	0.001	1,270
Black-McKnight	2011	Aug-Jul	0.9247	0.9822	27.123	<0.001	1,390

In 2008 and 2011, small subsamples of speckled dace were measured, and a larger subsample was measured in 2012 (Fig. 18a). Several individuals >100 mm TL were captured in 2008 and 2012. The size range of individuals collected indicated successful reproduction and recruitment each year. The abundance of speckled dace varied considerably from year to year but was greatest in 2012 (Fig. 18b).

A subsample of longfin dace in the 2011 and 2012 collections was measured. Most specimens were <65 mm TL (Fig. 18c). The presence of longfin dace <40 mm TL indicated successful reproduction in both years. Like speckled dace, longfin dace abundance varied considerably from year to year.

Table 10 Black Canyon brown trout population statistics, 2008–2012

Reach	Year	Month	n	TL range (mm)	TL mean (mm)	Mass mean (g)
Barrier-Private	2008	Jun	11	154–472	271	343.2
	2009	Aug	25	152–247	213	97.7
	2010	Aug	11	70–360	134	87.8
	2011	Aug	32	126–371	178	74.1
	2012	Aug	55	55–403	189	128.6
Private-Aspen	2008	Jun	8	74–316	137	69.9
	2008	Jul	43	50–426	184	115.6
	2009	Aug	80	134–410	228	128.2
	2010	Aug	73	70–431	193	171
	2011	Aug	102	72–365	168	63.1
	2012	Jul	54	55–403	191	130.4
Aspen-Falls	2008	Jul	3	143–165	153	36.0
	2011	Aug	30	85–346	189	94.9
	2012	Aug	52	60–416	170	76.8

5 Implications and Conclusions

For species restricted to high elevation cool-coldwater habitats, climate change presents multiple challenges to their persistence. For Gila trout that naturally had a comparatively limited distribution in headwater reaches of streams draining the Mogollon Rim of central Arizona and southwest New Mexico (Behnke 2002), the contraction (within stream shrinkage of habitat) and reduction (loss of perennial streams) of suitable habitat imposes an additional layer of difficulty to its survival. Over past 20 years or so, climate models have predicted altered flow regimes and more extreme flow events (Stewart et al. 2005; Hamlet and Lettenmaier 2007; Wenger et al. 2011), increasing aridity (Seager et al. 2007; Seager and Vecchi 2010; Udall and Overpeck 2017; Overpeck and Udall 2020), elevated stream thermal regimes (Schultz et al. 2017), and more large and intense wildfires (Chikamoto et al. 2017; Brown et al. 2021). Exacerbating the changes wrought by extended drought (Cook et al. 2015; Ault 2020) is the increasing frequency and intensity of wildfire (Dennison et al. 2014; Abatzoglou and Williams 2016; Singleton et al. 2019). These projections and events are playing out over the upper Gila River catchment as illustrated by regional temperature, precipitation, stream flow records, and multiple large wildfires. Since 2000, 21 wildfires have each burned over 4050 ha on the Gila National Forest, including the 56,175 ha Silver Fire (Gila National Forest 2021). Over the past 40 years, total annual precipitation has decreased and mean annual ambient temperature has increased in the Gila River catchment. Both contribute to warming of streams that historically provided habitat for Gila trout. For a sibling species, Apache trout *Oncorhynchus apache*, median temperature for optimal growth must be below 19 °C and lower if daily fluctuations are >12 °C (Recsetar et al. 2014). Median 2012 summer (June–July) water temperatures in Black Canyon were 17.2 and 16.8 °C at Aldo Leopold Wilderness boundary and above Aspen

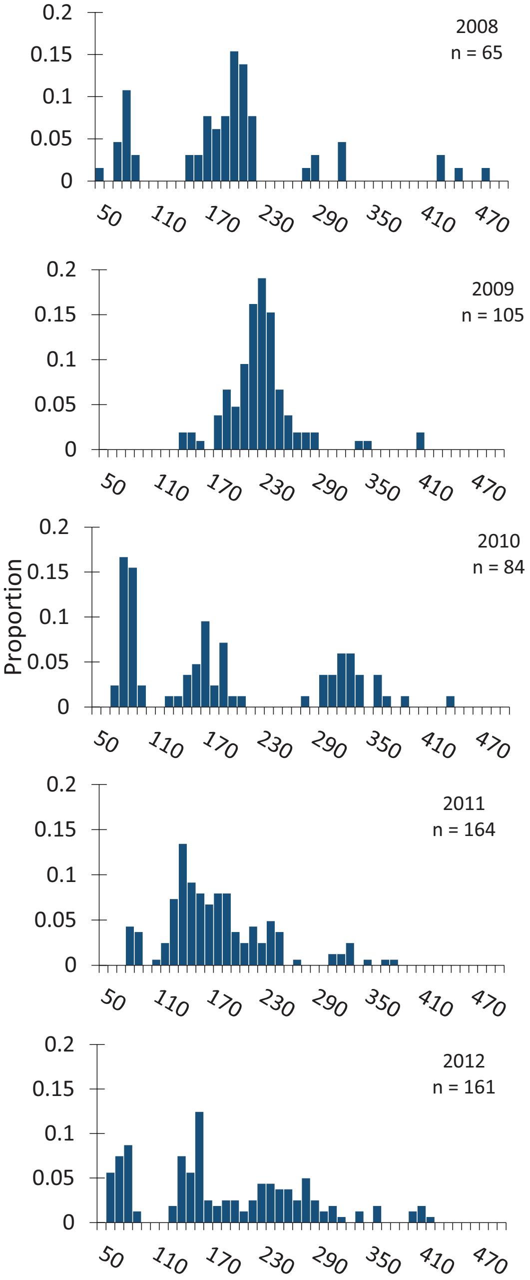


Fig. 15 Size structure of the Black Canyon brown trout population upstream of fish movement barrier (reaches combined), 2008–2012. Aspen-Falls reach not sampled in 2009 and 2010

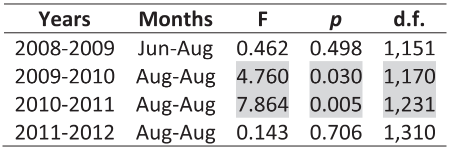
Table 11 Black Canyon Kolmogorov–Smirnov Goodness of Fit Test results comparing brown trout inter-annual size structure (10 mm TL size classes). Reaches combined.

Years	Months	D	*p*
2008–2009	Jun–Aug	0.109	0.650
2009–2010	Aug–Aug	0.174	0.250
2010–2011	Aug–Aug	0.130	0.565
2011–2012	Aug–Jul	0.217	0.141

Table 12 Fulton's Condition Index (K_{TL}) of brown trout in Black Canyon (reaches combined)

Year	Month	n	K_{TL} range	K_{TL} mean
2008	Jun	54	0.7148–1.8264	1.0535
2009	Aug	99	0.6886–1.4486	1.0339
2010	Aug	73	0.7527–1.7493	1.0842
2011	Aug	160	0.7111–2.1048	1.0239
2012	Aug	148	0.7148–1.8264	1.0294

Table 13 Brown trout annual mean condition comparison ANOVA (reaches combined) results. Shaded cells indicate significant (α = 0.05) differences in mean condition



Years	Months	F	*p*	d.f.
2008-2009	Jun-Aug	0.462	0.498	1,151
2009-2010	Aug-Aug	4.760	0.030	1,170
2010-2011	Aug-Aug	7.864	0.005	1,231
2011-2012	Aug-Aug	0.143	0.706	1,310

Table 14 Mass of Gila and brown trouts in upper Black Canyon (reaches combined), 2008–2012

Reach	Year	n	ONCGIL Total mass (kg)	n	SALTRU Total mass (kg)
Barrier-Private	2008	11	0.640	10	3.532
	2009	27	0.797	25	2.442
	2010	19	0.743	11	0.996
	2011	7	0.882	32	2.371
	2012	57	3.131	54	6.945
Private-Aspen	2008	313	13.129	51	5.529
	2009	234	9.667	76	9.743
	2010	148	7.753	62	10.603
	2011	97	4.755	102	6.435
	2012	51	3.015	53	6.910
Aspen-Falls	2008	100	2.083	3	0.108
	2011	67	2.921	30	2.848
	2012	204	10.050	51	3.917

Table 15 Black Canyon desert sucker population statistics (reaches combined), 2008–2012

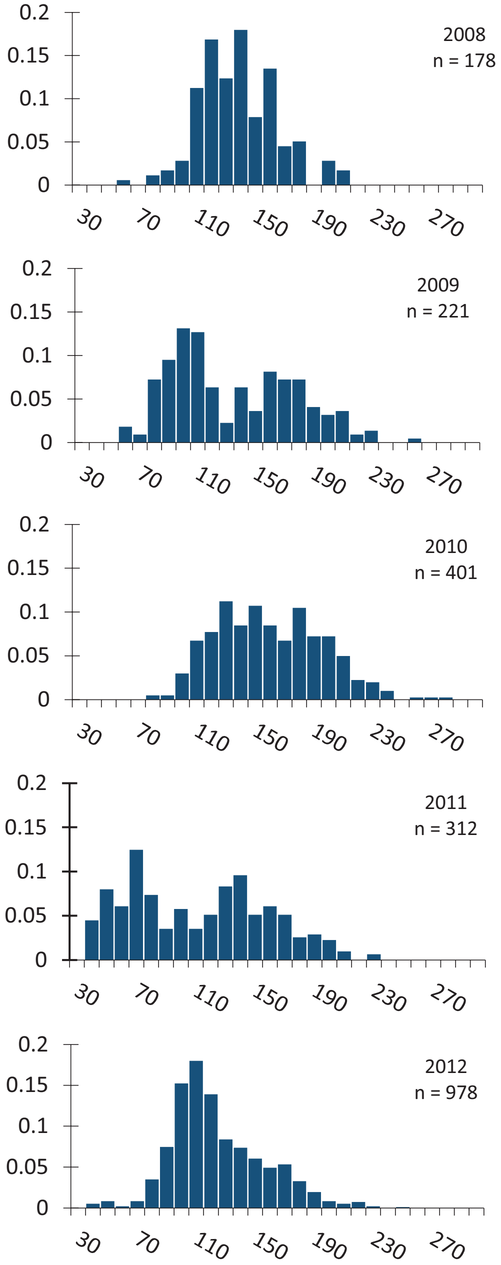
Year	Month	TL n	TL range (mm)	TL mean (mm)	Mass n	Mass mean (g)
2008	Jun	178	53–210	134.6	164	135.0
2009	Aug	221	53–259	130.0	219	190.0
2010	Aug	401	71–271	154.9	387	57.5
2011	Aug	312	32–225	107.1	134	32.2
2012	Jul & Aug	978	38–245	119.6	839	25.8

Canyon confluence, respectively, but daily fluctuations at both locations were >12° almost every day in June 2012. Mean annual daily discharge in the Gila River has not declined since 1980, but frequency of days with extremely low mean discharge has increased substantially. Collectively, these metrics (wildfire frequency, declining annual precipitation, increasing ambient temperature, and altered flow regimes) indicate that many, if not all, streams within the upper Gila River catchment are becoming less suitable for maintaining Gila trout populations.

The elimination of fishes from upper Black Canyon by the 1995 Bonner Fire provided an opportunity to determine the potential for Gila trout to persist in a thermally compromised stream. And the movement of native warmwater species into upper Black Canyon added another dimension to evaluate: the potential for coexistence in a mixed warmwater-coldwater fish assemblage. An additional challenge for Gila trout and fellow native fishes was the return of nonnative piscivorous brown trout, especially individuals >175 mm TL (Jonsson et al. 1999; Budy and Gaeta 2018), to upper Black Canyon.

The rapidity with which the four native warmwater species recolonized upper Black Canyon was impressive. Although the specific location of the refugia they survived ash and sediment flows in is uncertain, it is likely colonizers moved from perennial tributaries (Squaw and Apache creeks) about 12 river km downstream of the fish movement barrier and not affected by recent wildfires. Small-scale movement (≈2 km) of Sonora sucker and desert sucker was documented by Booth and Shipley (2012) and Booth et al. (2013). Based on otolith microchemistry, Whitney et al. (2017) provided information indicating that speckled dace colonizers were likely from downstream Black Canyon tributaries or survived in the most downstream reaches of Black Canyon near the East Fork Gila River confluence. Although Whitney et al. (2017) did not have data to support longfin dace, Sonora sucker, or desert sucker movement from downstream tributaries, it is likely these refugia were the source of upstream colonizers. Presence of each native warmwater species in Squaw and Apache creeks and lower Black Canyon was confirmed in 2020 (Paggen, unpubl. data). If Squaw and Apache creeks were the source of colonizers, speckled dace moved over 20 km to the mid-reach of upper Black Canyon (about confluence of Aspen Canyon) in a year or less (July 1995–May 1996). The other species were all present in upper Black Canyon by 2001. By 2008, each species had substantial populations composed of multiple size classes in the lower two study reaches (Barrier-Private and Private-Aspen) and desert sucker regularly occurred in the upper-most reach (Aspen-Falls). Both speckled dace and desert sucker met our

Fig. 16 Black Canyon desert sucker population size structure (reaches combined), 2008–2012



expectations that each would establish populations in the study reach but we did not expect that both longfin dace and Sonora sucker would also have multiple size-class populations in upper Black Canyon. Abundance of longfin dace was quite variable from year-to-year, indicating its status in upper Black Canyon was more tenuous than that of other native warmwater species.

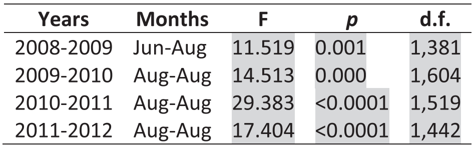
Table 16 Black Canyon desert sucker population inter-annual size structure Kolmogorov–Smirnov Goodness of Fit Test results

Years	Months	D	*p*
2008–2009	Jun–Aug	0.179	0.650
2009–2010	Aug–Aug	0.107	0.990
2010–2011	Aug–Aug	0.179	0.698
2011–2012	Aug–Aug	0.214	0.472

Table 17 Black Canyon desert sucker annual condition (reaches combined), 2008–2012

Year	n	K_{TL} range	K_{TL} mean
2008	164	0.6982–2.4231	1.3299
2009	219	0.7124–3.3175	1.2459
2010	387	0.7154–2.5185	1.3073
2011	134	0.6361–1.9073	1.2162
2012	310	0.4158–1.5259	1.1482

Table 18 Black Canyon desert sucker inter-year condition ANOVA results. Shaded cells indicate significance



Years	Months	F	*p*	d.f.
2008-2009	Jun-Aug	11.519	0.001	1,381
2009-2010	Aug-Aug	14.513	0.000	1,604
2010-2011	Aug-Aug	29.383	<0.0001	1,519
2011-2012	Aug-Aug	17.404	<0.0001	1,442

Table 19 Black Canyon Sonora sucker population statistics, 2008–2012 (reaches combined)

Year	Month	TL n	TL range (mm)	TL mean (mm)	Mass n	Mass mean (g)
2008	Jun	25	51–285	191.0	23	117.4
2009	Aug	67	72–290	151.2	67	58.9
2010	Aug	82	62–334	175.5	79	90.4
2011	Aug	162	40–319	145.6	124	71.2
2012	Aug	75	28–317	190.2	73	106.6

Gila trout lacked a pathway for a natural return to Black Canyon. The nearest Gila trout population, Diamond, was over 70 river km distant and where streams were perennial provided habitat for only warmwater species, including piscivorous smallmouth bass *Micropterus dolomieu* (Johnson et al. 2008). Thus, the annual release of hatchery-produced Gila trout in upper Black Canyon from 1998 through 2012 was necessary to establish and potentially maintain a population. Population augmentation, however, made determination of whether Black Canyon could sustain a naturally recruiting Gila trout population problematic. Using the presence of individuals <100 mm TL in August (i.e., Fig. 12) as an indicator of successful in-stream reproduction, there was limited survival of age-0 individuals in 3 years between 2008 and 2012. Nonetheless, from 2008 through 2012, multiple size classes were present in each above-barrier reach. When compared to reference populations, the size structure of Black Canyon was different in two comparisons

Fig. 17 Black Canyon Sonora sucker population size structure (reaches combined), 2008–2012

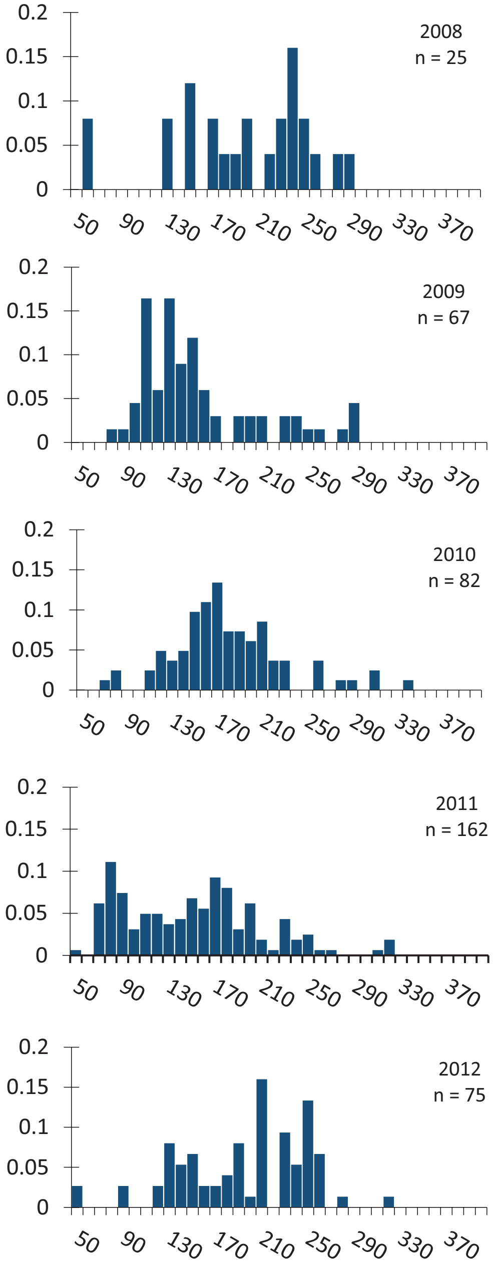


Table 20 Black Canyon Sonora sucker population inter-annual size-structure Kolmogorov–Smirnov Goodness of Fit Test results (reaches combined and individuals <100 mm TL excluded)

Years	Months	D	*p*
2008–2009	Jun–Aug	0.161	0.544
2009–2010	Aug–Aug	0.161	0.652
2010–2011	Aug–Aug	0.129	0.876
2011–2012	Aug–Aug	0.129	0.871

Table 21 Black Canyon Sonora sucker population mean annual condition (reaches combined), 2008–2012

Year	n	K_{TL} range	K_{TL} mean
2008	23	1.0601–1.5411	1.2530
2009	67	0.7063–1.6789	1.1834
2010	79	1.0982–1.7403	1.2606
2011	124	0.7337–1.9877	1.2419
2012	73	0.7404–1.8441	1.2123

(Black-Diamond 2008 and Black-McKnight 2011), which was likely due to the number of large Gila trout (>250 mm TL) in Black Canyon and absence of any fish >250 mm TL in Diamond or McKnight creeks. Abundance of Gila trout in each Black Canyon reach was <1.0/min and varied considerably across years, especially in the Barrier-Private reach. Mean annual condition (K_{TL}) exceeded 1.0 only once in each Barrier-Private and Private-Aspen. Comparisons of the Black Canyon population to reference populations did not yield consistent differences. For example, mean K_{TL} of Black Canyon fishes was greater than reference population in two comparisons, but in two others the reference population K_{TL} was greater. In 2012, the longitudinal distribution of Gila trout indicated that if Black Canyon was to support a viable Gila trout population it would be centered in the most upstream reaches.

The long-term potential for native warmwater species and Gila trout coexistence appeared possible based on the longitudinal distribution of native fishes in upper Black Canyon and the robust warmwater species populations. But could the Gila trout population persist without frequent augmentation and the continued suppression of nonnative piscivorous brown trout? The low numbers and irregular collection of age-0 Gila trout might reflect brown trout predation and the need for continued Gila trout augmentation. Brown trout tended to be more common in Barrier-Private and Private-Aspen reaches and Gila trout was more common in the Aspen-Falls reach. Whether this pattern was a consequence of brown trout occurring where there was abundant warmwater fish prey or other factor(s) is impossible to discern. Regardless of the specific reason(s) for the observed distribution pattern of brown trout, it was apparent that suppression efforts had to continue and likely be more frequent and intensive, similar to successful suppression efforts elsewhere (Healy et al. 2020), to enable a mixed warm-coldwater assemblage to coexist in Black Canyon.

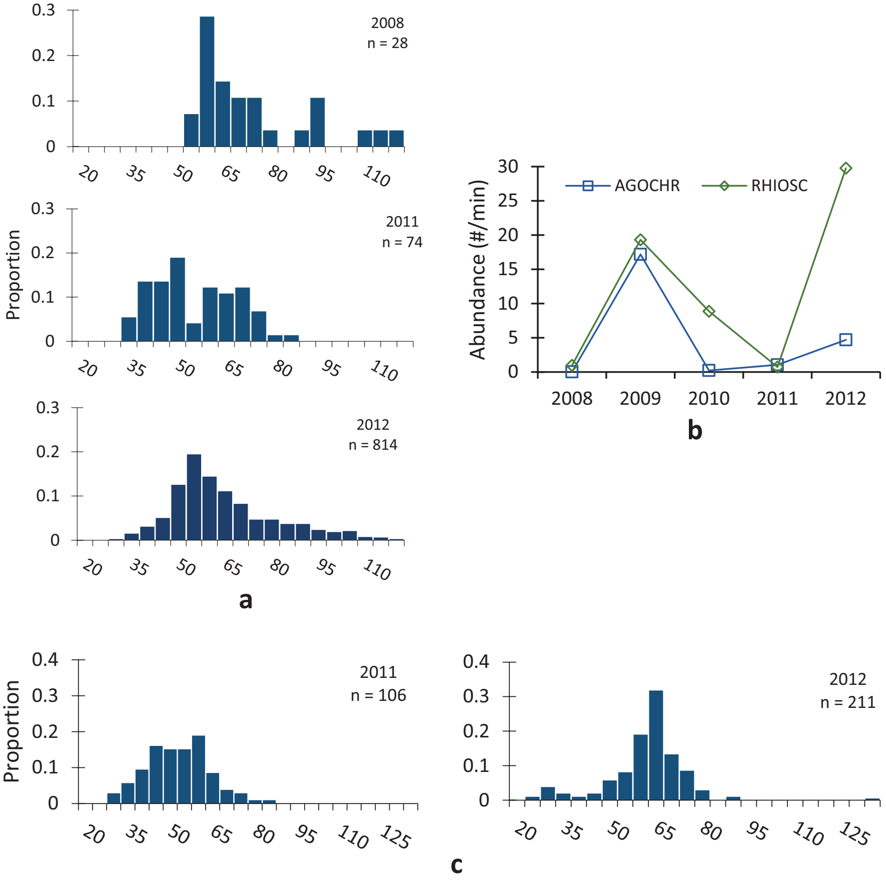


Fig. 18 (**a**) Black Canyon speckled dace population size structure (reaches combined), 2008, 2011, and 2012. (**b**) Abundance of speckled dace and longfin dace in Black Canyon, 2008–2012. A subsample of specimens of each species was tallied only in Barrier-Private reach in 2011. (**c**) Black Canyon longfin dace population size structure in Black Canyon (reaches combined), 2011 and 2012

Table 22 Black Canyon Sonora sucker population inter-year condition comparison ANOVA results (reaches combined). Shaded cells indicate significant difference ($\alpha = 0.05$)

Years	Months	F	*p*	d.f.
2008-2009	Jun-Aug	0.274	0.602	1,90
2009-2010	Aug-Aug	9.234	0.003	1,144
2010-2011	Aug-Aug	0.635	0.426	1,201
2011-2012	Aug-Aug	1.069	0.302	1,195

Our study ended abruptly in early summer 2013 when monsoon rains following the Silver Fire washed ash and fine sediments into Black Canyon eliminating all fishes upstream of the fish movement barrier. Although a number of physical and chemical factors, including displacement by elevated flows, might have contributed to elimination of fishes (Gresswell 1999), it is likely a combination of scoured stream channel in upper-most reaches and deposition of large volumes of fine sediments in middle and lower reaches were major contributors to elimination of fishes, similar to what Rust et al. (2019) reported for upper Rio Grande streams following wildfire and late summer storms.

Following the Silver Fire hatchery-produced Gila trout were released annually in upper Black Canyon and in August 2018 the collection of large numbers of individuals <90 mm TL indicated successful *in situ* spawning and recruitment. In the absence of brown trout, and native warmwater species, it appears Gila trout might establish a viable population in upper Black Canyon. Clearly, native speckled dace, desert sucker, and Sonora sucker could thrive in upper Black Canyon, and it is likely the fourth, longfin dace, could also. What is less certain is whether Gila trout could in the presence of native warmwater fishes. Nonetheless, the results of our study are encouraging in that native warmwater species maintained robust populations and Gila trout maintained mixed size classes, albeit with annual augmentation, in Black Canyon despite the presence of piscivorous brown trout. With brown trout eliminated, we believe that a coexisting warm-coldwater fish assemblage in upper Black Canyon is possible. Other studies (e.g., Dunham et al. 2003; Gido et al. 2019; Jager et al. 2021) have reported the resilience of native fishes to catastrophic wildfire and this study provides yet another example of the resilience of native warmwater species to such events. But this resilience cannot be manifested without connectivity among refugia and depopulated streams, as demonstrated by native warmwater fishes rapidly colonizing depopulated reaches of Black Canyon and the inability of Gila trout to populate Black Canyon without human assistance.

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The Future of Salmonids in a Rapidly Changing World

Jack E. Williams, Jeffrey L. Kershner, and John A. Zablocki

Abstract Salmonid fishes are among the most adaptable and resilient to change of any fish group but also among the most threatened. The pace of change in today's world and the ever-increasing human footprint are limiting the ability of these remarkable fish to successfully adapt. Land use modifications, the introduction of non-native salmonids, aquaculture, pollution, and diminishing water supply all threaten salmonid populations across the globe. Climate change adds significant threats to populations that may already on the brink. We ask "How do we ensure the future of salmonids in this rapidly changing world?" and provide a three-part strategy for stream conservation consisting of (1) protecting and restoring important habitats and populations, (2) building resistance and resilience to disturbance, and (3) forming alliances with diverse interests to solve common problems. Conservation in the twenty-first century is challenged by twin complications of climate change and demands of an ever-growing human population. As we look into the future of salmonid and stream conservation, novel approaches such as World Heritage Site designations and the growing Rights of Nature movement should receive more attention. Ultimately, conservation success will be driven as much or more by societal perceptions and desires than by scientific principles.

Keywords Climate change · Conservation · Protection strategy · Resilience · Restoration · Threatened species

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1 Introduction to a Brave New World

Early in the summer of 2021, we witnessed the highest temperatures ever recorded in a number of countries representing a large component of the remaining salmonid habitat. Record temperatures in the western USA coupled with years-long drought threatened habitat for native salmonids. The Colorado River USA reservoirs are now at their lowest point since the reservoirs filled after the dams were built in the 1930s. Temperatures exceeding 45 °C occurred in British Columbia, Canada, reaching thresholds resembling the deserts of Mexico or the USA. Numerous weather records were broken. At the same time, temperature records in Lapland, Norway, and Siberian Russia also were broken, areas that rarely if ever have seen temperatures above 40 °C in the early summer.

In 2021, large wildfires burned across many parts of North America, Europe, and Siberia. Fires greater than 200,000 ha now occur almost every year in some part of the world and future projections indicate the high likelihood of a fire-prone environment driven by increasing temperatures (Pechony and Shindell 2010). Smoke filled summers in the USA and Canada as well as in southern Europe and Russia are now a new normal. Catastrophic flooding in Germany, other parts of Europe as well as in China and the USA has devastated human communities and ecosystems alike.

Record breaking heat and drought have unfortunately become a new normal in today's world. The top ten hottest years on record have all occurred during this century with 2016 and 2020 virtually tied for the hottest years on record (NASA 2021). It is clear that our weather and climate are now changing in a dramatic and threatening fashion.

Worldwide, drought conditions and wildfires have severely impacted streams and waterways, causing conflicts between water users, municipalities, and environmentalists. As we attempt to conserve salmonids in an uncertain future, we face the harsh reality that clean water is in increasingly short supply in many regions, pitting the needs of human society against the needs of aquatic ecosystems. Ultimately, both human and natural systems will require sustainable water use, but in many parts of the world, human demands for water outpace our ability to plan for sustainable resource allocation.

While the uncertainty of climate change has brought many of these issues to the forefront, traditional threats to salmonids and freshwater ecosystems such as pollution, land use change, and the presence of non-native species continue to be significant threats worldwide. Meanwhile, the growing human population in many countries compounds both traditional and novel threats.

One might argue that salmonids have learned to live with change as a constant theme over millions of years (Montgomery 2003). They are among the most successful and adaptable of fishes and are native to a myriad of habitats across the Northern Hemisphere, including small and large freshwater lakes, streams of all shapes and sizes, large rivers, estuaries, and oceans. As a group, salmonid fishes are remarkable in their diversity of life history patterns among the species, including their long migrations between oceans and freshwaters (anadromy) and migrations within freshwaters (fluvial, adfluvial), allowing them to fully exploit available habitats and express great variation in longevity, breeding seasons, and growth rates (Quinn 2005). Salmonids also distinguish themselves from other fishes in their ability to colonize new habitats and to re-colonize habitats that have recovered from disturbances such as floods or wildfires (Rieman and Clayton 1997; Pess et al. 2014).

While their ability to adapt and change is significant, the ever-growing human footprint on their ecosystems has severely restricted their ability to react to changing environmental conditions. In this chapter, we ask "What are the most serious threats to salmonid populations worldwide and how do we design future conservation efforts to ensure the long-term persistence of this remarkable group of fishes?"

2 The Changing Landscape and Evolving Threats to Salmonids in the Anthropocene

Native salmonids face rapidly changing environments as a result of the interaction of climate change with other stressors (Kovach et al. 2017). The impacts of these stressors have resulted in significant worldwide declines in many species and caused others to be threatened with extinction or in some cases to become extinct (IUCN 2018). Muhlfeld et al. (2018) reported that approximately 54% of the 124 recognized species and subspecies of trout and char worldwide have been assessed for conservation status by the IUCN and of those, 73% are threatened with extinction and four are now extinct.

2.1 The Multiple Effects of Non-native Fishes

Climate change has emerged as a significant global factor in the decline of coldwater-dependent salmonid fishes, but most salmonids face multiple risk factors (Fig. 1). Historically, perhaps the most significant threat to native salmonids has been the introduction of non-native species. Ironically, two of the most damaging introduced species to native salmonids are salmonids themselves, Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta*, which are native to North America and Europe, respectively, but have been widely introduced beyond their native ranges (IUCN 2018). The introductions of these species have in many cases led to replacement of native salmonids, reduced the abundance and diversity of other native species, resulted in introduced diseases in native trout populations, and through hybridization, reduced the genetic diversity of native stocks (Muhlfeld et al. 2019; Borgwardt et al. 2020).

Fish culture and the introduction of hatchery salmonids have had significant impacts on many native salmonid populations. For example, a recent study estimates that the costs to wild salmon from ocean farming of Atlantic Salmon *S. salar*

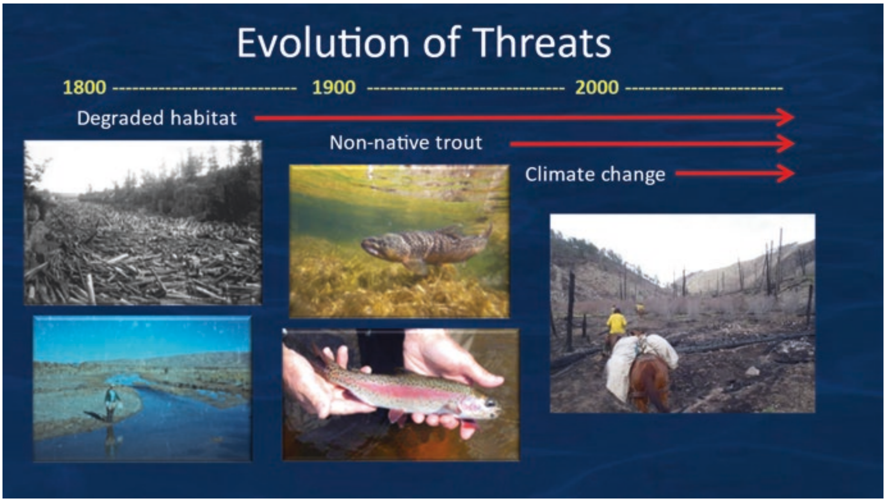

Fig. 1 Evolution of threats to stream salmonids. Starting in 1800s: overfishing and overgrazing; followed by pollution, non-native species introductions, and hatchery impacts in the 1900s; then combined with climate change in more recent decades. Figure modified from Trout Unlimited State of the Trout report; additional photo credit Jim Brooks (lower right, Gila trout habitat)

may exceed US$300 million due to introduced diseases, loss of forage fish, and introgression between farmed salmon and wild fish (Just Economics 2021). Sea lice associated with salmon farming have been shown to impact native Atlantic Salmon and sea-run Brown Trout (Thorstad and Finstad 2018) and to migrating smolts of Pacific Salmon in Canadian waters (Krkosek et al. 2007). The presence of elevated levels of disease pathogens also increased in areas around fish farms in proximity to local native salmon waters (Shea et al. 2020).

Culture of non-native Brown Trout and their introduction into waters where native Marble Trout *Salmo marmoratus* or other subspecies of Brown Trout may occur has led to hybridization with native fish and in some cases local extinctions (Schöfmann et al. 2019). Introduction of Rainbow Trout, Brown Trout, and Brook Trout *S. fontinalis* into native Cutthroat Trout *O. clarkii* waters in North America has led to widespread replacement of native fish in many waters and hybridization with native cutthroat in others (Leary et al. 1984; Henderson et al. 2000).

2.2 Overfishing and Fisheries Management

Overfishing of native freshwater salmonids has resulted in the decline and in some cases local extirpation of life history forms and species (Lobón Cerviá et al. 2019; Markevich and Esin 2019). Overfishing can result from both intensive commercial harvest of salmonids and/or harvest from sport anglers, or for food. Where salmonids are important food sources, non-native salmonids are often viewed as desirable fish to introduce into waters which have been over-harvested. Overfishing of freshwater forms occurs by local anglers harvesting fish for food or commercial fishing, particularly in lake fisheries where there may be large-bodied life history forms (Markevich and Esin 2019). Evolutionary consequences of overfishing may include not only the loss of larger life history forms, but also change in life history patterns such as feeding, habitat use, and spawning (Markevich and Esin 2019).

Anadromous salmonids show similar patterns of overfishing in many parts of the world. Overfishing can occur at almost any stage of their life history, but often occurs when fish stage to spawn. These fish are most vulnerable in the estuaries of rivers or in the rivers themselves as they ascend to their spawning grounds. Salmon are highly prized as food sources by many cultures and as a source of income from the sale of these fish. Angling for anadromous salmonids has become a multimillion dollar industry in many parts of the world and while angling harvest is strictly regulated in many areas, other parts of the world have less restrictive angling regulations or regulations that are poorly enforced (World Wildlife Fund 2001). Many countries have enacted strict catch and release requirements for anadromous salmonids, but there have been concerns over the long-term effects of catching, playing, and releasing a fish that still must travel long distances to spawn (Hume 2021).

2.3 Habitat Loss and Degradation

One of the most pressing threats to salmonids worldwide is loss of habitat. Habitat degradation can affect both the amount of habitat available to salmonids and the quality of remaining habitat. Loss of habitat can be linked to changes in population size as well as limiting the expression of life history attributes (migration, spawning) that may influence the persistence of a population. For example, populations of native trout in western North American deserts may be limited to headwater streams where access is precluded from larger fluvial habitats (Hendrickson and Tomelleri 2019; Propst et al. 2020). Similar issues have been noted for native Cutthroat Trout, Brook Trout, and Bull Trout *S. confluentus* in Canada and the USA, native Brown Trout in Europe, and native Char in Japan (Dunham et al. 1997; Rieman et al. 1997; Colyer et al. 2005; Hudy et al. 2008; Morita 2019). Populations of trout and char that lose access to larger river systems and lakes may no longer express the large-bodied life history forms that migrate between these habitats, but also represent founders of other populations that may have been extirpated through human or natural caused disturbances such as wildfires or severe floods (Rieman et al. 1997).

In some cases, the loss of habitat may not represent the loss of a physical connection but represent a change in water quality. In western North America, extreme summer temperatures may limit the ability of salmonids to move to downstream habitats that may provide important rearing areas (Armstrong et al. 2021). Identifying suitable temperature gradients for salmonids that exist across the landscape during these critical periods may provide one strategy for conserving remaining resident salmonids and identifying possible strongholds (Isaak et al. 2014), but habitats that may not be suitable during one part of the year may provide important connectivity to feeding habitat or migratory corridors during other times (Colyer et al. 2005, Armstrong et al. 2021).

Traditional land use practices such as logging, livestock grazing, and the increased development of human communities continue to influence ecosystems across the globe (Foley et al. 2005). While forest practices have been modified to protect salmonid habitat in parts of the world, effects from logging in riparian areas and sediment inputs from logging roads continue to be an issue in many countries. The consequences of poorly designed and implemented timber harvest may influence the types and amounts of woody debris that provide important stream habitat and increase channel complexity (Bisson et al. 1997). The results of these changes can include the amount and depth of large pools in streams (Woodsmith and Buffington 1996; McIntosh et al. 2000) and may increase the amount of fine sediment in pools (Lisle and Hilton 1992).

Livestock grazing is a dominant land use worldwide and occurs on almost one quarter of the land surface (Ramankutty et al. 2008). Riparian corridors along streams are relatively small areas of land that make up less than 1% of the landscape but provide water and enhanced forage opportunities for livestock (Armour et al. 1994). This increased livestock use can have direct effects on stream habitat where stream banks are trampled, causing increased sediment inputs and a loss of riparian cover along the stream (Platts 1981; Knapp and Matthews 1996; Belsky et al. 1999). This loss of cover may increase stream temperature during the summer and decrease the amount of terrestrial food inputs that are available to salmonids (Saunders and Fausch 2012).

2.4 Water Supply Degradation

The demand for water to supply industrial, agricultural, and domestic uses increases worldwide as the climate warms and water availability declines in many areas (UNESCO 2019). The alteration of stream habitat by the creation of dams and diversions has had a significant impact on riverine fish populations worldwide (World Wildlife Fund 2004). In combination with the alteration of spawning and rearing habitat, anadromous salmonids have exhibited significant reductions in historically available habitats. In the western USA, almost half of the formerly available habitat for anadromous salmonids is now blocked or unavailable (McClure et al. 2008). Blockages of migratory habitat may lead to a truncation of life history forms where only resident, non-migratory forms remain. Similar trends exist for almost all salmonids worldwide. In Japan, low head dams and diversions threaten Southern Asian Char populations by altering stream habitat and restricting access to migratory habitat (Morita 2019). As the demand for water increases, the potential impact on salmonid populations will increase as well.

As the climate changes, effects that were associated with current management may be amplified (Jonsson and Jonsson 2009; Smialek et al. 2021). Summer stream temperatures in many areas have been increasing and as temperatures have warmed, physiological effects such as decreased growth, cardiac stress, and an increase in the occurrence of disease outbreaks have occurred (Borgwardt et al. 2020). As stream flows decline and temperatures rise during critical summer months, the competition for scarce water may limit available water for stream-dwelling salmonids.

Sidebar—*Upper Klamath Lake and River USA*—The Klamath River was once one of the most important anadromous salmonid fisheries in the western USA. Originating in the mountains of Oregon, tributaries of the Klamath River flow into Upper Klamath Lake, an important stronghold for native fishes such as Redband Trout and Lost River *Deltistes luxatus* and Shortnose Suckers *Chasmistes brevirostris*. Downstream of Upper Klamath Lake, the river acquires flows from tributaries in California and supports populations of Chinook *O. tshawytscha* and Coho Salmon *O. kisutch* as well as Steelhead (anadromous Rainbow Trout). These fish are important to indigenous peoples who live along the Klamath River as well as in the area of Upper Klamath Lake. Four dams were built along the river near the Oregon-California border in the early twentieth century to provide hydroelectric power and irrigation water. The Bureau of Reclamation encouraged settlement of lands around the Upper Klamath Lake and river to develop irrigated agriculture. Unfortunately, the dams also blocked fish migrations and impounded water that warmed and produced toxic algal blooms. In the early 2000s, competition for water to protect endangered salmonids and native suckers and agricultural interests became intense as a changing climate was providing less water into the system over a period of a decade. In 2008, state water managers in Oregon and California found that removal of the dams would reduce energy costs by US$100 million compared to needed upgrades of the structures. Removal of the four dams began in 2023 and will restore nearly 500 km of salmonid habitat and improve water quality for people and fish.

In recent years, scientists have warned that the combination of hotter temperatures, increased wildfires, earlier snowmelt, and flooding due to rain on snow events will significantly impact salmonid habitat and increase population loss (Keleher and Rahel 1996; Haak and Williams 2012). Similar predictions for various parts of the world were made in the recent volume "Trout and Char of the World" (Kershner et al. 2019; Kovach et al. 2019). As the climate warms and conditions change for native salmonids worldwide, additional threats from hydropower, irrigation, land use, overfishing, and non-native species introductions make the future of salmonids problematic. Against this backdrop, we propose the following actions to help ensure the future of salmonids in this rapidly changing world.

3 A Blueprint for Stream Salmonid Conservation

As conservation scientists, we've operated under the basic tenant of protecting the best and restoring the rest where possible (Rieman and Allendorf 2001; Williams et al. 2011). The meaning of this is clear. Where we can, protect large interconnected landscapes to maintain the best habitat for native salmonids. Watersheds containing strong populations should be protected by regulation or special designation to the greatest extent possible. Protected landscapes with interconnected populations will be critical to the long-term success of salmonids worldwide. How to achieve these principles is less clear, especially as human populations continue to expand, exotic species proliferate, and the problems of a rapidly changing climate manifest themselves across a warming planet. Furthermore, within the current range of many salmonids, large landscapes of high-quality habitat are becoming increasingly rare. Restoration is necessary but difficult in many areas as competition for land and water is intense. So, how best to proceed with conservation in this era of competing uses and rapidly changing environment?

We describe the following three-part strategy for stream salmonid conservation that can work across the vast regions where salmonids are native.

1. Protect and restore important habitats and populations
2. Build resistance and resilience to degradation and disturbance
3. Form alliances and work with diverse interests to solve common problems

3.1 Protecting and Restoring Important Habitats and Populations

High-quality stream habitat for salmonids is characterized by natural or near natural flow regimes, rivers that are connected with and not isolated from their floodplains, vibrant and diverse riparian habitat along streams, and complex, sometimes braided stream channels with abundant structure in the form of large wood, boulders, or rock ledges. In wetter environments, high-quality stream habitat is part of an interconnected stream network where salmonid populations have access to various headwater and downstream channels. But in more arid zones, high-quality habitats may consist of single isolated streams. Such is the case in Mexico, Northern Africa, and elsewhere where remaining native trout populations occur in small streams that may themselves be subject to drying during summer months (Hendrickson and Tomelleri 2019; Lóbon-Cervía et al. 2019).

Examples of high-quality river systems in North America include the upper Flathead River (Canada, USA), upper Snake River (USA), and rivers such as the Alagnak, Kvichak, and Nushagak in Bristol Bay (Alaska). Russia's Kamchatka Peninsula and the Zhupanova River are widely known for major salmon and rainbow fisheries in near-pristine conditions. The Neretva River (Bosnia, Herzegovina) is one of the largest and most diverse rivers in the eastern part of the Adriatic Basin.

Of course, few rivers in today's world are as pristine as Alaska's Alagnak or Russia's Zhupanova. Identifying the best remaining habitat can be challenging, especially in regions where knowledge of historical conditions prior to modern human intervention is limited. In many parts of the world, the fish themselves may be among the best indicators of habitat conditions. Diverse native fish communities that include native salmonid populations are likely indicative of quality streams and healthy watersheds (Dauwalter et al. 2011, 2019).

Protecting large, diverse populations, often known as "strongholds," is a proactive approach to conservation. Most existing conservation efforts focus on threatened populations and degraded habitats, which are important to recover but are expensive and complex undertakings. As a result, some scientists and organizations encourage increasing efforts to protect remaining high-quality populations and habitats in river systems before they become degraded (Williams et al. 2011; Garrett et al. 2019). The Wild Salmon Center has mapped a network of "salmon strongholds" in countries across the Pacific Rim where salmonid diversity is highest and populations are robust, which provides good targets for protection efforts (wildsalmoncenter.org/stronghold-approach/).

While large, connected metapopulations are generally desirable, threats from land use and non-native introductions are cause for concern in many areas. How do we conserve populations and species in areas where large, high-quality landscapes no longer exist? Restoration efforts that focus on securing and expanding remaining populations may provide the best conservation option. Expanding existing habitat patches by removing barriers (dams, roads, culverts, water diversions) or rewatering stream reaches should produce larger salmonid populations with a greater chance of long-term persistence. In the arid American Southwest, conservation efforts for native trout usually focus on rebuilding large populations by reconnecting streams and improving riparian habitats in areas where increasingly large wildfires threaten remaining populations (Propst et al. 2020).

Climate change poses increasing threats to cold-water dependent fishes and freshwater stream habitats. Increasing stream temperatures may decrease habitat availability for salmonid fishes, especially in lower-elevation valley bottom habitats that were historically some of the most productive habitats available to these fishes. At the same time, higher stream temperatures increase the potential for invasion and spread of native and non-native warm-water fishes (Rahel and Olden 2008). Parasite and pathogen problems also increase with these changing conditions.

Climate change is responsible for a myriad of problems beyond temperature, including reduced late-season stream flows, drought, wildfires, and paradoxically, increasing storm severity and intense flooding. Existing stressors for stream systems often are made worse as climate change increases. For instance, elevated rates of erosion and sedimentation that are common in many developed watersheds, typically increase with more intense storms and flooding. Fortunately, there are many restorative and adaptation opportunities that can improve habitat conditions in areas where climate-driven disturbances such as drought, wildfires, and floods occur (Table 1; Isaak et al. 2012; Williams et al. 2015).

Some salmonid streams may be naturally resistant to temperature increases as ambient conditions warm because of their high elevation, heavily forested watershed, or inflow from cold-water springs (Isaak et al. 2014). Such cold-water refuge streams should be identified and protected. Most streams, however, warm as air temperatures increase. Many natural stream restoration actions can improve local habitats for cool-water and, at least in theory, reduce stream warming more broadly. These include improvements in riparian habitats and replanting native trees, developing narrower and deeper channels (rather than wide shallow channels that expose more surface water to ambient temperatures), increasing channel complexity (braided channels and sinuosity), adding structure (large wood, boulders) that can facilitate development of deeper, cool-water pools, and restoring instream flows (Williams et al. 2015). These actions, if applied broadly to headwaters, may provide cumulative cooling for downstream rivers. As with most restorative actions, project monitoring is essential to demonstrate effectiveness of actions and to encourage additional funding for future efforts.

In many areas, stream channels have been relocated or simply pushed to the edge of meadows and valleys to make way for farms or other human development. This typically results in a straighter channel, and subsequent loss of sinuosity and pool habitats. Restoring the channel to its original location reverses these problems and increases cool-water habitat as pools reform and hyporheic flows are recreated between pool habitats. In one example from Idaho (USA), stream channel restoration resulted in increased stream length (from 1007 m to 1973 m) as sinuosity increased and the number of pools increased (from 9 to 86), greatly improving cold-water habitat availability for native Yellowstone Cutthroat Trout *O. clarkii bouvieri* (Williams et al. 2015; Fig. 2).

Table 1 Comparisons of common climate impacts, corresponding adaptation strategies, and restoration response for stream and river ecosystems

Climate impacts	Strategic response	Restoration actions
Heat: Warmer summer temperatures; reduced snowpack	Increase shading and cold-water refuge habitats	Restore riparian vegetation; add instream structure to create deep pools
Drought: Earlier peak flows; reduced late season flows	Improve watershed function to improve flows	Restore headwater meadows and wetlands; restore channel meanders and complexity
Wildfires: Widespread burns of increasing intensity; debris flows; ash flows	Increase resistance to fire within stream and riparian areas by increasing their width and depth	Restore width and vigor of riparian habitats; reintroduce beavers; construct beaver analog dams
Floods: Higher peak flows; increased stream erosion and sedimentation	Increase capacity of streamside zones to absorb and dissipate flood energy; increase flow capacity at road-stream crossings	Reconnect rivers to floodplains; restore floodplain habitats; replace small culverts with large culverts or bridges

Fig. 2 Photo of Crow Creek, Idaho (USA) as the former stream channel was being restored. Water remains in the straightened channel (adjacent to the road near the bottom of the photo), and the restored, more sinuous channel (now flowing across the middle of the meadow near the top of the photo). Figure from Williams et al. (2015)

3.2 Building Resistance and Resilience to Degradation and Disturbance

Much of the success of salmonids over time can be attributed to their wide diversity of life history strategies, including short and long migrations, variation in timing of migrations, seasonal spawning variation, spawning habitat variation, differences in size and age at maturity, variation in feeding habitats, and changes in habitat preferences among juvenile and adult fish (Quinn 2005; Jonsson et al. 2019). Restoring the full expression of life histories in populations will increase their resistance to loss (resistance) and increase their ability to recover following disturbance (resilience).

Life history diversity exhibited by salmonid fishes is a product of their evolutionary history combined with habitat diversity. The diversity of lotic and lentic habitats, the complexity of these habitats, and diversity of estuarine habitats act as templates for life history strategies (Southwood 1977). Hence, many habitat restoration efforts should be aimed at increasing habitat complexity and reconnecting stream and stream-lake networks in an effort to increase life history diversity within populations.

The ability of diverse natural systems to persist over time in the face of changing environmental conditions has been attributed to the "portfolio effect" (Figge 2004) or to their "biocomplexity" (Hilborn et al. 2003). The large number of separate stocks of Sockeye Salmon supporting the Bristol Bay (Alaska, USA) fishery has been credited with the long-term success of that fishery (Hilborn et al. 2003; Schindler et al. 2010); whereas the "weak portfolio" of Fall Chinook Salmon in California's (USA) Central Valley appears to have contributed to the collapse in 2008 of that fishery, which was supported by a single run of Chinook in the Sacramento River (Carlson and Satterwaite 2011).

Haak and Williams (2012, 2013) stress the importance of developing a diverse portfolio of habitats and populations in salmonid conservation efforts. They emphasize the need to restore and protect life history diversity within stream salmonid populations because this component of diversity is among the first lost as habitats are degraded and migratory pathways become fragmented. For instance, salmonids that are isolated in a lake or stream will often display the ability to migrate once habitats are reconnected and barriers to movement are eliminated. In trout and char populations, reconnection of larger rivers with their tributary streams can result in development of fluvial and adfluvial life histories in addition to resident populations (Dunham et al. 1997; Colyer et al. 2005).

The value of developing and protecting a diverse portfolio in conservation is similar to goals of financial managers to develop a diverse investment portfolio as a hedge against future financial uncertainty (Fig. 3). If multiple populations exist in a target area or could be restored, portfolio theory can help managers understand the role of each population to future conservation and how to manage for a "strong portfolio" and long-term persistence (Haak and Williams 2012).

Salmonid populations that exist in isolated streams will be more susceptible to disturbances than will populations that occur more broadly across multiple interconnected streams where the chances of escaping lethal conditions are increased

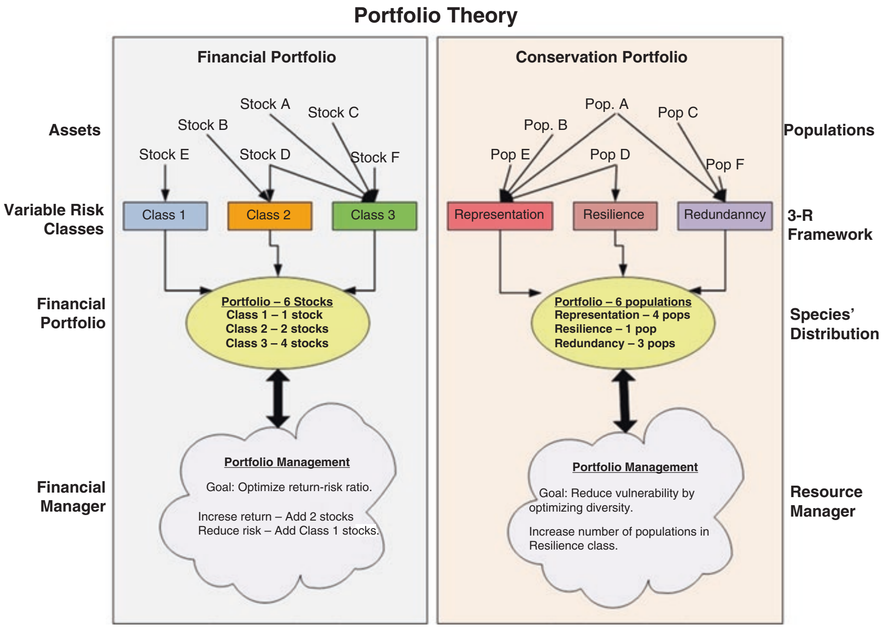

Fig. 3 Comparison of portfolio theories in the financial and ecological realms. In this hypothetical comparison, fish populations are the assets to be managed in the portfolio. The 3-R framework is a way to classify populations for their conservation value. In this example, the conservation portfolio lacks assets in the Resilience category, indicating the need to develop larger populations that can recover from major disturbances. Figure from Haak and Williams (2012)

(Haak and Williams 2012). Isaak et al. (2012) describe the value of large, interconnected trout populations in western USA as a hedge against climate change uncertainty and population loss by large-scale disturbances such as wildfires.

Despite the benefits of interconnected stream networks, stream reconnection projects also may have the inadvertent effect of facilitating invasion by warm-water fishes (Fausch et al. 2009). Such fish passage projects must proceed with caution and include adequate fisheries surveys of habitats that will be reconnected. Developing replicate populations in additional stream systems can achieve some of the same benefits of stream reconnection projects in terms of protecting scarce resources from loss from drought, wildfire, or flood (Vincenzi et al. 2012; Propst et al. 2020).

Sidebar—*Disturbance and Trout Persistence*—Wildfires are becoming an increasing cause of population declines in stream salmonids, especially as populations are progressively more isolated in small stream segments and wildfires are larger in size and intensity. In the American Southwest, isolated populations of Gila Trout *O. gilae*, Apache Trout *O. apache*, and Cutthroat Trout have been increasingly susceptible to population losses (Neville et al. 2006; Propst et al. 2020). Large and intense wildfires during 2012 and 2013 eliminated populations of the rare Gila Trout, which not only reduced the number of extant populations but also decreased remaining species-level genetic diversity and heterozygosity (Propst et al. 2020). In reaction to increased wildfire intensity, beavers have been introduced into small stream systems to improve watershed function and to create wide and deep pool habitats that are more resistant to wildfire impacts (Fig. 4). Decreased heterozygosity and allelic richness have also been observed in a population of Marble Trout in Slovenia subjected to repeated catastrophic flood events (Pujolar et al. 2016). The long-term implications of such genetic degradation cannot be good even if populations persist in the short term.

It is difficult to quantify the size of populations necessary to provide resistance or resilience to disturbance. Researchers have attempted to answer this question and have developed varied answers that are dependent on the density of the stream network, the species in question, and habitat availability, among other factors. Nonetheless, in studies of western USA trout populations, Hilderbrand and Kershner (2000) determined that occupied habitat of 27.8 km or more in length is adequate for long-term persistence. Dunham et al. (2002) found that stream salmonid populations occupying large habitat patch sizes (≥10,000 ha) have a greater likelihood of withstanding environmental change over time. Such studies help quantify the size of smaller populations that may be at risk and in need of habitat supplementation.

The science of adapting streams for climate change is relatively new and much remains to be learned not only about the effectiveness of stream restoration actions on climate change resistance and resilience, but how adaptation efforts may impact non-target ecosystem dynamics. Studies examining the results of planting riparian woodland species along upland UK streams found increased levels of coarse particulate matter and corresponding increases in the shredder components of macroinvertebrate communities (Thomas et al. 2016). In this case, resilience to climate change impacts may occur not only through desired changes in the riparian

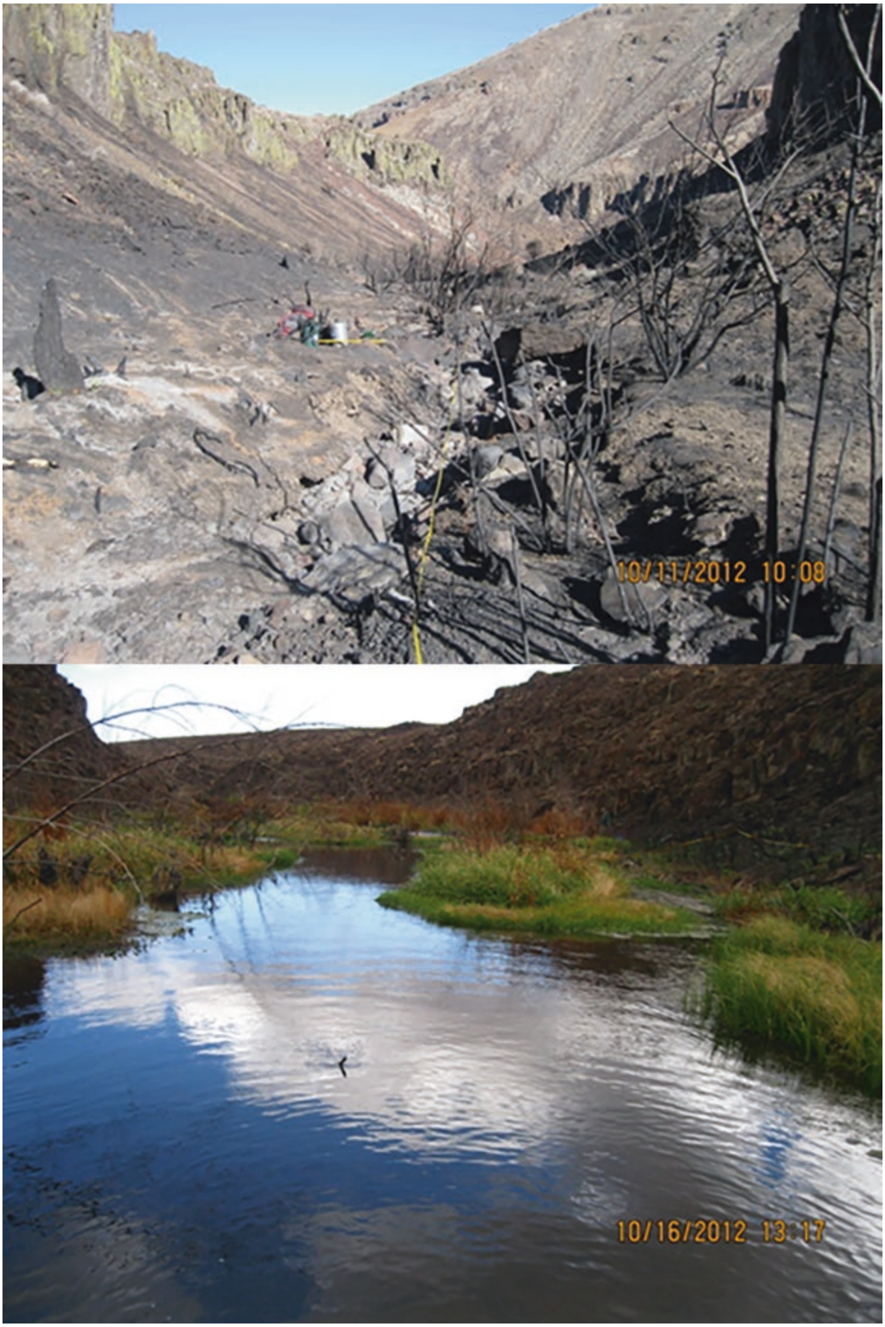

Fig. 4 Lahontan Cutthroat Trout *O. clarkii henshawi* habitat in southeastern Oregon, USA, following Halloway wildfire that burned 99,350 ha in 2012. Top: Stream segment without beavers showing thorough burn through narrow stream channel. Bottom: Stream segment with beavers showing unburned wetland area surrounding beaver pond

community but also through increased diversity in macroinvertebrate taxa. The study illustrates the complexity inherent in stream-riparian dynamics and caused Thomas et al. (2016) to advocate for additional efforts to understand ecosystem consequences of adaptation projects. We concur with that admonition and encourage project monitoring and additional studies to improve our understanding of adaptation opportunities and impacts.

3.3 Forming Alliances to Solve Common Problems

Science provides important information to society on the health of ecosystems and often describes threats and needed changes to natural resource management. Unfortunately, science alone is seldom sufficient to move society in the necessary direction of conservation and sustainability. Additional forces are needed to gain the social and political will to implement the changes described by scientists as necessary.

For conservation to succeed, especially at the time scales of decades and human generations, novel and powerful coalitions and partnerships must be formed with societal factions that, more often than not, have proved detrimental to conservation goals in the past. Finding common ground and identifying common problems is key.

Anglers and conservationists are natural allies in the pursuit of salmonid conservation. Non-governmental organizations like Trout Unlimited (USA), Wild Salmon Center (Pacific Rim Countries), Salmon and Trout Conservation (UK) Save the Blue Heart of Europe (Balkan Region), and The Nature Conservancy (worldwide) are good initial partners for scientists seeking help and increased capabilities to achieve conservation goals. These organizations and their memberships can help drive progressive policies with government managers and can greatly expand the capacity for monitoring and restoration work.

Citizen science programs and opportunities are rapidly expanding in many regions and will not only increase the capability of conservationists to achieve their goals but will help build scientific literacy among the participating public. Although anglers have been assisting in stream monitoring for decades, the recent proliferation of iPhone apps and other data recording devices has simplified stream monitoring for the interested public and facilitated the rapid expansion of angler-based monitoring programs beyond water quality and into fish distribution studies, spawner surveys, and the monitoring of threats from energy development to climate change (Williams et al. 2016).

Indigenous peoples often depend on abundant fish and wildlife populations for subsistence as well as cultural enlightenment. Although individual tribes and indigenous governments may approach fish and wildlife management from their own differing perspectives, many advocate for policies that favor robust fish populations and are natural allies in stream and river restoration projects. Similarly, partnerships between private conservation groups and indigenous people have proven critical to protect the headwaters of Bristol Bay and its Sockeye Salmon *O. nerka* fishery in Alaska from large-scale mining proposals (www.savebristolbay.org).

Dwindling water supplies are a serious problem for many stream salmonids and also are a concern to society more broadly. Cities and local governments are increasingly worried about maintaining the quality and quantity of municipal water supplies as human populations grow and droughts become more severe. Those working to restore streams in upper parts of watersheds may find allies with those dependent on water supplies further downstream. Many municipal water supplies originate in native forests and rangelands that also provide habitat for remaining stream salmonid populations.

Farmers and water irrigation districts are potential partners in conservation. As water supplies become scarce, improvements in irrigation efficiency and delivery can benefit both farmers and fish. Installing drip irrigation systems or lining canals to prevent subsurface losses may allow for more water to remain in streams. Alternate crop choices may require less water or chemical applications, which would benefit stream integrity.

As climates warm, drought and heat are driving large wildfires across many regions. Streams and rivers can provide natural fire breaks. Improving riparian habitats and expanding the width of wet zones along streams by introducing beavers, constructing beaver analog dams, or restoring riverine floodplains increase the ability of farms and forests to resist large-scale wildfires by providing a network of natural firebreaks across the land. In the western USA, the reintroduction of beavers has increased habitat quality for Cutthroat Trout in small rangeland streams and provided ponds that increase the survival of fish and amphibians during wildfires while increasing the resistance of the landscape to rapid wildfire spread (Talabere 2002; Williams et al. 2015).

Finding common ground with other organizations and working to solve common problems will create conservation opportunities that would otherwise go unrecognized. Developing conservation partnerships with anglers, non-governmental organizations, indigenous peoples, local governments, foresters, or local irrigation districts provides important weight for science to influence politicians and policymakers. When properly designed, stream and water conservation should benefit a wide audience of collaborators, be broadly supported by the public, and promote societal engagement (Higgins et al. 2021).

4 Looking Toward the Future

Conservation of streams and rivers in the twenty-first century is a complex yet urgent task. On the one hand, conservationists need to understand what has been lost, how much damage has occurred, what stressors are impacting our streams, and how they might be alleviated or mitigated. But at the same time, we must be able to envision a sustainable future. The public must be engaged and understand the commonality among risks to human systems and nature. What remains possible and how can it be achieved? Our environment and human-built systems are changing rapidly and challenge us not only to make the right decisions but to make them quickly.

As the natural world degrades, there is much at risk. Not only are native species and biodiversity threatened with extinction, but watersheds that support biodiversity also are the source of clean and abundant water for agriculture, industries, and human consumption. Streams and rivers also are part of our spirit; a source of enlightenment and a place to relax and recreate. This then is what makes the task of conservationists so urgent. Future generations risk not only a loss of diversity, but also the capacity for experience and wonder that inspire people to hold on to what they have. People are part of nature, and in the end, we all share a common fate.

In the western USA, the native Lahontan Cutthroat Trout *Oncorhynchus clarkii henshawi* has been extinguished from somewhere on the order of 90% of its historic stream habitat, and close to 99% of its historic lake habitat. Historically, native Americans witnessed runs of thousands of large Cutthroat Trout from Pyramid Lake, Nevada, into Lake Tahoe on the California border and its tributaries. These fish provided an important food source to native Americans and early white settlers who moved into that area. Within a period of decades, this fishery declined due to water diversion, land use, non-native fish introductions, and overfishing.

Today, there are some 15 million people a year that visit Lake Tahoe. This great glacial lake in the Sierra Nevada is among the 99% of lake habitat that is now gone. Probably more consequential than large Cutthroat Trout vanishing from the lake is their vanishing from memory and human experience. Imagine the imprint on the human psyche that a giant run of 10 kg trout coursing up through the Truckee River to Lake Tahoe today. Imagine the inspiration that has been lost. Oscar Wilde described a cynic as a person who knows the “price of everything and the value of nothing.” To be successful, conservationists must be the quintessential anti-cynic. It is incumbent upon us to remind the world of the value of something. Conservation is not an exercise in being right about things, it is an exercise in doing right about things.

The example of the Lahontan Cutthroat Trout is representative of the fate of many native salmonids worldwide. Today, freshwater biodiversity is declining at a rate more than twice as fast as terrestrial and marine biodiversity (Tickner et al. 2020). And yet despite being lost at a far greater rate, the proportion of freshwater protection has lagged far behind terrestrial and marine protection. To the extent that freshwater systems do still provide suitable habitat for stream-dwelling salmonids, in the vast majority of cases, the native salmonid has been supplanted by introduced species.

Across Europe, seven nations (Iceland, Finland, France, Norway, Slovenia, Spain, Sweden) have legislation aimed at preserving the remaining free-flowing rivers within their borders (Schäfer 2021). These protections are similar to those of the Wild and Scenic Rivers Act in the USA that seeks to protect the free-flowing nature of rivers with outstanding natural, cultural, or recreational value. Some of the European laws were enacted during recent decades in reaction to large-scale and controversial hydroelectric projects. The potential for a European network of protected rivers clearly exists if development of river protection laws could be enacted in remaining countries. Without specific legislation to protect rivers and their headwaters, aquatic conservation goals will be increasingly hard to achieve. River conservationists have realized that most existing schemes for habitat protection focus on terrestrial boundaries and are inadequate for large river systems that may flow in and out of protected areas and across political boundaries (Higgins et al. 2021).

Science must inform and guide efforts to restore what has been damaged and to protect what is threatened with loss. But at the same time, scientists must reach beyond technical knowledge to share with the public their values and concerns in order to achieve common goals. Efforts like "Save the Blue Heart of Europe" combine scientific expertise with citizen science to highlight the importance of restoring and protecting the critically important rivers of central Europe. Over 3000 new hydroelectric projects are planned in addition to the 100 plus plants under construction. Combining scientific expertise that highlights the important aquatic and riparian values of these rivers with public advocacy for the protection of these systems has increased public and governmental awareness of their importance, as well as highlighting the social impacts of riverine development on local communities.

In 2019, salmonid ecologists gathered in Granada, Spain, argued for adding outstanding cold-water rivers around the world to the United Nation's World Heritage List in order to gain international recognition of their values and increase the likelihood of their protection (Dauwalter et al. 2020). The Nakama River on Iriomote Island is part of a four-island chain in Japan on the World Heritage List. In the USA, several National Parks that include iconic salmonid rivers are included in the World Heritage List. While many countries include a mix of cultural and natural sites on their World Heritage Lists, there are many high-quality rivers with high biological diversity that need recognition and protection and could conceivably be added as World Heritage Sites.

In recent years, the "Rights of Nature" movement has provided a small but growing number of rivers with legal rights against harm, opening up a new opportunity for river protection. The movement claims that certain ecosystems have the right to exist, flourish, to naturally evolve without human-caused disruption, and to be represented by a guardian in a court of law (Challe 2021). Since Ecuador became the first country to formally recognize the Rights of Pachamama (Mother Earth) in 2008, notable rivers around the world have been granted legal rights. In the USA, the Yurok First Nation granted the Klamath River legal personhood in order to address habitat threats through legal action. Rights of Nature protection also has been provided to the Riviére Magpie (Canada), Río Salado (Mexico), and Yarra River (Australia), among others (http://riverresourcehub.org/resources/rights-of-rivers-global-map/). Of course, time will tell as to how effective the Rights of Nature movement becomes in actually protecting nature but the potential is intriguing.

Scientists with a strong ethical concern for the natural world often puzzle as to our seeming inability to live in harmony with nature. Aldo Leopold (1949) wrote that "*We shall never achieve harmony with land, any more than we shall achieve justice or liberty for people. In these higher aspirations, the important thing is not to achieve, but to strive*." Kurt Fausch (2015), a fisheries scientist and ethicist, argues that humans will always treat land and rivers poorly if we believe we own them, and therefore have the right to degrade them. Although perhaps difficult to explain, we think that a growing number of scientists who have studied nature over the course of their lives would agree that natural, free-flowing rivers have some innate value to humans in their natural state and should have some sort of right to protection. As others grow to understand and appreciate these same values of a natural river, our ability to provide for their protection increases accordingly.

So "What is the Future of Salmonids in a Rapidly, Changing World?" Conservation and protection of rivers and their species will depend not only on laws and regulations, but also on the will of the people. So, it becomes part of the duty of scientists and conservationists generally to inform the broader human community about what is at risk and the importance of protecting rivers and aquatic systems that support not only aquatic biodiversity but human communities as well. Our future will not only be defined by science, but also by our emotions, our collective imagination, and our collective actions or inactions.

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A Short Reflection on Protecting the Remaining Biodiversity of Salmonid Fishes

John J. Piccolo

Abstract Earth is faced with an anthropogenic biodiversity crisis. The Sixth Mass Extinction is the first mass extinction to be driven by a single species, *Homo sapiens*. In this brief essay, I briefly recount salmonid biodiversity, concluding that a vast portion of historic biodiversity has already been lost, mirroring global biodiversity loss in general. I then recount the concepts of instrumental and intrinsic value, anthropocentrism and ecocentrism, in relation to biodiversity conservation. I conclude that intrinsic natural value is an incontrovertible aspect of biodiversity conservation, and that ecocentrism is one key aspect of a truly sustainable transformation of the relationship among human and nonhuman beings. A sound rationale for protecting the world's remaining salmonid biodiversity must rest in part upon the recognition of, and respect for, intrinsic natural value.

Keywords Ethics · Values · Conservation · Intrinsic · Instrumental · Ecocentrism · Anthropocentrism

> So much must be done in so short a time to protect the remaining genetic diversity of these fishes that I cannot responsibly suspend judgments…in the hope that irrefutable data might one day be collected.
>
> Robert J. Behnke (1992), "Native Trout of Western North America."

1 Introduction

The world's salmonid biodiversity is found in five genera in the family Salmonidae, including the salmon, trout, charr, grayling, whitefish, taimen, and lenok. The known number of species is in the range of 100–200, depending upon how these are defined—there is considerable debate over which groups should be lumped or split.

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Behnke (2007), for example, listed some 30 species of salmon, trout, and charr (excluding grayling and whitefish), which many would consider a conservative estimate. In any case, in most salmonid species, reproductive isolation due to a strong homing instinct leads to many distinct populations occurring within river drainages, i.e. great intraspecific biodiversity (Taylor 1991). The sum biodiversity of salmonid fishes, therefore, if one includes all adaptive diversity, is practically immeasurable (Behnke 2002, 2007). Hence, a project aiming to protect the world's salmonid biodiversity is indeed a daunting task, enveloping diverse ecological and social knowledge. When faced with a monumental task, it is sometimes wise to focus on a goal that might be achievable, that which Sir Peter Medawar (1967) called "the art of the soluble"; a scientist, realizing that there are more questions than one might ever hope to answer, should focus on the most difficult problem that in fact *might* be answered. Before we set out to answer the question "*How* are we to protect the world's salmonid biodiversity?", perhaps it is worthwhile to reflect upon the question "W*hy ought we* to protect salmonid biodiversity?".

1.1 The Status of the World's Salmonid Biodiversity: A Dwindling Natural Legacy

The fact that I just wrote that salmonid biodiversity is practically immeasurable makes it seem paradoxical to state that we have already lost a vast majority of salmonid biodiversity worldwide. It would be pointless to try to put a figure of the number of unique populations that have been extirpated worldwide, particularly due to river regulation, habitat destruction, and overfishing since the industrial revolution. Before we can make educated guesses based upon historic declines which we have witnessed, such as the Columbia and Sacramento River basins in western North America, where wild salmon runs have declined by some 80% since the arrival of European settlers in the 1800s (Lichatowich 2001) or the Atlantic salmon runs of eastern North America, which have declined some 95% since settlement in the 1600s (Behnke 2002). Comparing these systems to those in Alaska or the Russian far east, one can guess that in developed regions, roughly 10% or less remains today of the post-glacial biodiversity that existed some 5000–10,000 years ago; the cutthroat (*Oncorhynchus clarkii*) and rainbow (*O. mykiss*) species complexes in western North America provide a well-documented example (Behnke 1992). Across the pond, the landlocked Atlantic salmon in Lake Vänern, Sweden, a stone's throw from my office door, have suffered a decline of at least 90% since the earliest reliable catch records from the 1700s (Piccolo et al. 2012).

The drivers of salmonid biodiversity loss are well documented and need not be reviewed here—overfishing, habitat destruction, invasive species, and others, coupled with the looming effects of climate change, have been the subject of countless articles and books. My question here is why we should strive to protect the remaining salmon biodiversity. Although this may seem self-evident, the reader may find it profitable to reflect more deeply on this question, and how the answer to this question may help to solve the problem.

2 The Values of Salmonid Biodiversity

In the early days of fishery management, the answer as to why salmonids should be protected was usually because they could be fished for either food, sport, or income. Bill Ricker (1954), for example, developed his famous stock-recruit models in part to ensure sustainable salmon populations. Of importance for this reflection, Ricker understood stock-recruit in relation to local adaptation of salmonid populations (i.e., intraspecific diversity), which plays a key role in biodiversity conservation (Behnke 2002; Piccolo 2011). Of course, for populations that are commercially valuable, for either food or sport fisheries, it is relatively easy to justify a conservation program because the financial costs may be less than the gains, or at least the costs may not greatly exceed the benefits (perverse subsidies notwithstanding). The stock-specific salmon fisheries management in Alaska, USA, provides one such example (Piccolo et al. 2009).

With the global awareness of the environmental crises in the 1960s–1970s, conservation focus began to shift away from simply economically valuable species to unique and threatened species in general—whales, pandas, and whooping cranes became icons of threatened nature, and societal values led to environmental legislation in many countries, such as the US Endangered Species Act. Species conservation could be justified because the species had a right to exist and flourish (Taylor et al. 2020); such arguments led to the birth of the Society for Conservation Biology by leading ecologists of the time, such as Jared Diamond, Paul Ehrlich, and Michael Soulé (Soulé 1985).

Times rolled on, and by the date of the release of the UN Millenium Ecosystem Assessment (2005) conservation focus began to shift to the “ecosystem services” returning to a broadly similar argument as that of early fisheries management, i.e., protection can be justified largely by “services” to people, either supporting, regulating, provisioning, or cultural. In practice, most ecosystem services assessments originally focused on economic valuations (Costanza et al. 2017). More recently, the concept of “nature’s contributions to people” a concept that is also largely about benefits for people (Piccolo et al. 2022).

This back-and-forth of the justifications for conservation can be roughly termed as being based upon either instrumental (utilitarian) or intrinsic (inherent) value, i.e. should nature be protected for solely for the sake of humans to use, or also for its own sake (Chan et al. 2016; Piccolo 2017). For those salmonid populations that are of economic or subsistence value for commercial, sport, or household fisheries, protecting them for sustainable use might easily appeal to their instrumental value (Watz et al. 2022). For the many populations of salmonids that have no fisheries value, however, arguing that they should be protected for the sake of humans seems futile. Perhaps they have some cultural value, or some future option value, but these alone hardly seem viable, and they might easily change if, for some reason peoples' opinions change. If we wish to have lasting protection for the world's salmonid biodiversity, scientists and managers should be prepared to argue for the intrinsic values of nature and the rights of fish populations to persist and flourish. In the section below, I summarize the elegant rationale for biodiversity protection known as an eco-evolutionary conservation ethic, one that should intuitively appeal to ecologists and evolutionary biologist.

2.1 Intrinsic Natural Value: "What Good Is It Anyway?"

To illustrate the practical aspects of intrinsic natural value, Piccolo et al. (2022) retell philosopher J. Baird Callicott's (2017) story of Edwin (Phil) Pister, a fish biologist for over 50 years at California Fish and Game (Pister 2010). Pister was the founder of The Desert Fishes Council (DFC 2021), and he led efforts to protect the native golden trout (*Oncorhynchus mykiss aguabonita*) of California, as well and many other desert fishes. Pister was a student of Starker Leopold (Aldo's son), from whom he seemed to have developed a land ethic (Behnke 2002). Pister's efforts culminated with a successful legal case before US Supreme Court to protect the desert pupfish (*Cyprinodon macularius*) under the Endangered Species Act. Later, he saved another pupfish species by transferring the entire population in a bucket when its desert spring habitat was being dewatered (Pister 1993). Pister got a lot criticism from fellow California Fish and Game employees during the "hook and bullet" era of game management (Callicott 2017): "*The concern and care lavished by Pister on these tiny non-game species of fish baffled his colleagues… Of each such species rising to the attention of a judge, instead of a fly, they would ask him, what good is it, anyway? For years Pister struggled to answer that question. For example, some of these fish thrived in salt-saturated brine; so maybe research on their remarkable kidneys could provide information applicable in medicine. But would such speculative option value—to put the issue in economistic terms—outweigh the value of drinking water for thirsty LA and agricultural, commercial, and residential development in western Nevada? Hardly. His quest for an effective answer to the what-good-is-it-anyway question led Pister to Environmental Ethics (the journal). And there, in the concept of intrinsic value, he found the answer that had eluded him. That answer—species of desert fish have intrinsic value—certainly satisfied Phil Pister, who now had a term and a body of academic literature to justify his own intuitive application of the concept to endangered species.. Pister finally found a rejoinder that has provided us environmental philosophers with as much insight and rhetorical leverage as we ever provided him. He answered the question, what good is it, anyway? with a question of his own: what good are you?*"

Pister's point, of course, was that these fishes had some inherent good of their own, an intrinsic value, that could justify their continued existence. The existence of such intrinsic natural value has been the subject of debate in western philosophy since the Enlightenment (Rolston 2020), but many scholars have concluded that such value can no longer rationally be denied (see Piccolo et al. 2022). Philosopher Holmes Rolston III has delved deeply into the "origins of value in human and natural history" (Rolston 1999, 2010); he finds that, ultimately "Earth is value-able, able to create value"; that there can be no firm dividing line between life forms that hold intrinsic value and those that do not. In the simplest terms, an eco-evolutionary worldview, i.e., the belief in the descent of species through natural selection, makes it difficult to see how an arbitrary dividing line can be drawn between human and nonhuman life, wherein intrinsic value suddenly appears within humans. "*Natural selection picks out whatever traits an organism has that are valuable to it, relative to its survival. When natural selection has been at work gathering these traits into an organism, that organism is able to value on the basis of those traits. It is a valuing organism, even if the organism is not a sentient valuer, much less a vertebrate, much less a human evaluator. And those traits, though picked out by natural selection, are innate in the organism. It is difficult to dissociate the idea of value from natural selection.*"

The naïve philosophical argument that only rational beings can value has long since broken down under the weight of the evidence provided by the scientific understanding of evolution by natural selection (Callicott 2013). The recognition of the intrinsic values of nature shifts human worldviews from *anthro*pocentric to *eco*centric. Or, as American ecologist Aldo Leopold (1949) wrote: "*a land ethic changes the role of Homo sapiens from conqueror of the land-community to plain member and citizen of it*."

3 Ecocentrism: The "Key-Log" for Breaking Our Anthropocentric Logjam

> The "key-log" which must be moved to release the evolutionary process for an ethic is simply this: quit thinking about decent land-use as solely an economic problem. Examine each question in terms of what is ethically and esthetically right, as well as what is economical expedient. <u>A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise.</u>
>
> Aldo Leopold (1949) "The land ethic" *in* "A Sand County Almanac"

There are many arguments as to why we should strive to protect biological diversity, in our case the biodiversity of the world's remaining salmonids. Most of these arguments will naturally rely on why the fish are valuable to people, i.e., upon their instrumental value. Like all animals, humans often care most for our own—Darwin (1872) himself recognized that ethics begin with family and tribe, before they can extend to nations; but he also recognized extending ethics to nonhumans as the noblest of moral achievements. Many argue that a conservation ethic founded *wholly* upon instrumental value, however, is ultimately doomed to failure (Taylor et al. 2020). As soon as expediency dictates that a species is no longer of instrumental valuable to anyone, it is no longer worth protecting. Much of the world's salmonid biodiversity cannot be caught, sold, or eaten (Fig. 1); if we can't recognize and

Fig. 1 A wild, endemic landlocked Atlantic salmon smolt from River Klarälven, Sweden. Nearly extirpated by overfishing, pollution, and dam-building, comprehensive conservation efforts have brought this unique population back from the brink of extinction. Today over 1000 wild spawners return annually to the river, less than 10% of historic pre-industrial levels, but a large increase from some 100 spawners in the 1960s–1970s (Piccolo et al. 2012). The wild salmon cannot currently support a fishery, so they are of little instrumental value for people. The main conservation argument for such populations is often their intrinsic value, i.e. their right to exist and flourish

respect its intrinsic value there will be little reason to protect it. Rare species are paradoxically often of least instrumental value to people. It has been argued that, in the "Anthropocene," conservation must be about peoples' needs first (Kareiva and Marvier 2012). But is such a world really the most just of which we can conceive with the great intellect which nature has endowed upon us?

If we wish to progress with protecting the remaining biodiversity of salmonid fishes, we must work toward the expression of ecocentric values, even while recognizing the legitimate instrumental values that people gain from nature. Ecologists must learn to be comfortable speaking about peoples' moral obligations to nature, in equal measure as we speak about nature's contributions to people (Piccolo et al. 2022). The eco-evolutionary worldviews of most ecologists can and ought to foster an ethic of principled responsibility for protecting biodiversity for its own sake, as well as for humans' sake.

We are well underway with Earth's six mass extinction, the first of which has been driven by the unrestrained greed of a single species. In the past few hundred years, humans have driven to extinction a large fraction of the historic biodiversity of salmonid fishes; best estimates are that only ca. 10% of historic salmonid biodiversity remains in most developed regions. If we are to protect what remains of the wonderful diversity of these fishes, *now* is the time to speak openly and loudly about their unique value and their right to continue to flourish.

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