Chapter 2
Environmental Biology of Percid Fishes

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Abstract The large percids, including *Perca* and *Sander* species, are economically and ecologically important species that inhabit large temperature regions of the Northern Hemisphere. In this chapter, we provide an overview of the environmental biology of the *Perca* (including yellow perch *P. flavescens* and Eurasian perch *P. fluviatilis*) and *Sander* (including walleye *S. vitreus*, pikeperch *S. lucioperca*, and sauger *S. canadensis*) genera, on which the majority of fisheries and aquaculture practices are focused. Through a comprehensive literature review, we discuss how individual- and population-level vital rates, including growth, foraging, reproduction, recruitment, and mortality, are mediated by biotic (e.g., density dependence, resource availability) and abiotic (e.g., temperature, light) environmental variables. As fisheries exploitation is a major source of size-selective mortality in many percid populations, we also examine the potential impacts of fishing mortality on both population metrics and individual vital rates, and identify several research areas that require further investigation. Through this review we aim to identify the major environmental drivers of variation in percid vital rates and thereby inform management practices for both wild and cultured percid populations.

Keywords *Perca* • *Sander* • Fisheries • Exploitation • Ecology

2.1 Introduction

The large percids (principally *Perca* and *Sander*) constitute ecologically and economically important species throughout large temperate regions of the Northern Hemisphere. Percids have been characterized as cool to warm water fish species, persisting in habitats ranging from warm, highly eutrophied waters to cold, oligotrophic systems. Percids exhibit high levels of phenotypic plasticity and inhabit a broad range of environmental conditions throughout their geographic ranges. While the feeding ecology of these species varies during ontogeny, generally progressing

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from zooplanktivory (e.g., Pycha and Smith 1955) to primarily benthivory and piscivory (e.g., Paradis et al. 2006), percids are opportunistic, euryphagous predators consuming differential prey bases across systems. In many systems, they serve as top predators, exerting influential top-down control on lower trophic levels (Guzzo et al. 2013). Simultaneously, percids may also provide important forage for piscivorous fishes, birds (DeBruyne et al. 2013), and mammals and support a variety of recreational, commercial, and subsistence fisheries.

We review percid environmental biology by considering key processes regulating population abundance and biomass, including individual growth, reproduction, recruitment, and mortality. We focus on both perch, including North American yellow perch (*Perca flavescens*) and Eurasian perch (*P. fluviatilis*), and *Sander*, including North American walleye (*Sander vitreus*), sauger (*S. canadensis*), and Eurasian pikeperch or zander (*S. lucioperca*). However, given our familiarity with lentic North American systems and the multitude of studies on yellow perch and walleye, our examples are likely biased towards these species.

2.2   Individual Growth and Foraging Behavior

Individual growth is one of the most important facets of percid biology, as it may influence mortality, maturation, future growth and reproductive potential, and foraging success of individuals (Madenjian et al. 1996; Quist et al. 2003a; Galarowicz and Wahl 2005; Heibo et al. 2005). Fish growth and foraging behavior can also determine potential yields in aquaculture, commercial, and recreational harvest (Machiels and Wijsman 1996; Isermann et al. 2005). Percids exhibit substantial geographical and sex-related variation in growth both within and among species. *Perca* species tend to grow more slowly and to smaller maximum sizes than *Sander* species (Mehner et al. 1996; Graeb et al. 2005; Ljunggren and Sandström 2007). Growth rates of percids are sexually dimorphic, as females grow more quickly and to larger sizes than males prior to and following maturation, potentially due to higher growth efficiency in females (Mooij et al. 1999; Henderson et al. 2003; Mandiki et al. 2004a; Heibo et al. 2005; Lappalainen et al. 2005; Headly and Lauer 2008; Venturelli et al. 2009; Sect. 19.3.2). Percids also exhibit latitudinal variation in growth rates fairly typical of many fish species; northern populations tend to grow more slowly and live longer than southern populations (Quist et al. 2003a; Sects. 19.3.1 and 19.4.1). Much of this variation between populations and species may be due to genetic differences driven by adaptation to local environmental conditions (Wang and Eckmann 1994; Galarowicz and Wahl 2003; Mandiki et al. 2004b; Zhao et al. 2007; Wang et al. 2009a). In terms of foraging behavior, percid species follow similar ontogenetic patterns in diet throughout life, shifting from zooplankton to benthivory to piscivory as they increase in size (e.g., Graeb et al. 2005; Roswell et al. 2014). However, *Sander* shift to piscivory earlier and are seemingly obligate piscivores, meaning cannibalism can become a regulatory factor on population size in some systems (Frankiewicz et al. 1999). *Perca*, in contrast,

exhibit a more generalist foraging strategy (Knight et al. 1984; Mehner et al. 1996; Campbell 1998; Tyson and Knight 2001; Graeb et al. 2005). Intraspecific variation in growth and foraging behavior is strongly dependent on a suite of environmental variables, including temperature, light, dissolved oxygen, prey availability, and harvest rates. Here, we focus on the responses of percid growth and foraging to these environmental variables, while addressing the implications of changes in growth with respect to aquaculture and fisheries management.

2.2.1 Temperature

Temperature is arguably the most important environmental factor affecting percid growth (Chap. 19) and behavior (Chap. 15). Percids have been described as temperate mesotherms, capable of tolerating a wide range distribution of temperatures (Hokanson 1977; Kitchell et al. 1977; Frisk et al. 2012). Across species and populations, the thermal environment an individual experiences has been consistently and strongly linked to growth rates, often through the use of the growing degree days metric (GDD; Colby and Nepszy 1981; Power and Van Den Heuvel 1999; Zhao et al. 2007; Venturelli et al. 2009; Chezik et al. 2014; Sect. 19.4.1). Thermal optima in fish are dependent on feeding rates (Kitchell et al. 1977), reproductive status (Hokanson 1977), possible pathogen infection (Hockett and Mundahl 1989), and other variables. Among percid adults, pikeperch generally have the warmest thermal optima for growth (27–30 °C; Hokanson 1977; Marshall 1977; Wang et al. 2009b), followed by yellow and Eurasian perch (22–28 °C; Hokanson 1977; Kitchell et al. 1977; Karås and Thoresson 1992; Tidwell et al. 1999; Strand et al. 2011), and walleye (21–23 °C; Huh et al. 1976; Hokanson 1977; Kitchell et al. 1977; Hokanson and Koenst 1986; Kocovsky and Carline 2001; Quist et al. 2003a). There is, however, significant ontogenetic variation in optimal temperatures within species, and juveniles tend to have higher thermal optima (pikeperch, 26–30 °C; perch, 24–29 °C; walleye, 24–28 °C) than adults (Kitchell et al. 1977; Hokanson 1977; Kocovsky and Carline 2001; Rónyai and Csengeri 2008; Frisk et al. 2012). Larval percids tend to exhibit lower thermal optima, ranging from 24 to 29 °C in pikeperch (Lehtonen et al. 1996) to 20–22 °C in perch and walleye (Hokanson 1977; Wang and Eckmann 1994; Jonas and Wahl 1998), although optimal temperatures from 15 to 25 °C have been observed depending on species and habitat (Hokanson 1977; Wang and Eckmann 1994; Lehtonen et al. 1996; Jonas and Wahl 1998). Larval growth is strongly positively influenced by temperature up to thermal optima (Hoxmeier et al. 2006; Irwin et al. 2009). The response of juvenile and adult percid growth to temperature can differ between cool and warm systems (Kitchell et al. 1977; Power and Van Den Heuvel 1999). In cooler systems that do not surpass thermal optima, growth is often positively related to temperature (Colby and Nepszy 1981; Lappalainen et al. 2005; Zhao et al. 2007; Venturelli et al. 2009; Wang et al. 2009b), while the inverse is true in warm systems where high summer temperatures may limit growth (Mehner and Wieser 1994; Hartman and Margraf 1992; Kershner et al.

1999; Tidwell et al. 1999; Quist et al. 2003a; Ložys 2004; Hoxmeier et al. 2006). Due to these mesothermic temperature preferences, adult growth rates may also vary seasonally within intermediate thermal systems, increasing in early summer, slowing in the warmest months, and increasing again as temperatures cool in fall (Kitchell et al. 1977; Mehner et al. 1996; Kocovsky and Carline 2001). There is also evidence of adaptive variation in the thermal tolerances of percids. Southern walleye populations exhibit the highest growth in warmer temperatures (25 °C) than northern populations (22 °C) (Galarowicz and Wahl 2003; Chapter, Fig. 19.5). Thus, the effects of temperature on percid growth are largely non-linear, and may partially depend on an interaction of genetic adaptive variation and developmental stage.

The direct effects of temperature on percid growth can be traced back to bioenergetic responses in metabolic rate and consumption. Conceptually, energy available to fish growth can be described as the difference between consumption and the sum of respiration, metabolism, egestion, and excretion, with each of these rates responding to changes in temperature to determine the potential for individual growth (Kitchell et al. 1977; Karås and Thoresson 1992). In percids, increasing temperatures tend to increase excretion, respiration, and standard metabolic rates assuming a fixed level of consumed energy (Kitchell et al. 1977; Cai and Summerfelt 1992; Karås and Thoresson 1992; Galarowicz and Wahl 2003; Frisk et al. 2012). These responses result in less energy available for growth for percids experiencing increasingly elevated temperatures.

Temperature also drives development, behavior, activity, and habitat selection in percids. In pikeperch, larval development is optimized at 24–29 °C, while temperatures above 20 °C promote feeding activity in walleye and perch (Wang and Eckmann 1994; Lehtonen et al. 1996). Temperatures below 14–15 °C appear to decrease larval walleye feeding activity (Koenst and Smith 1976). In addition, foraging activity, exhibited in traits such as attack rate, swimming performance, and consumption, have all been positively related to temperature in larval percids, while searching and handling time is negatively related (Bergman 1987; Johnston and Mathias 1994; Jonas and Wahl 1998). At particularly high temperatures, juvenile and adult percids tend to have opposite behavioral responses. Adult percids will attempt to compensate for decreased energy efficiency at high temperatures by decreasing activity levels. However, this decrease in activity may not be sufficient to completely compensate for increased metabolic rates and may also decrease consumption through reduced foraging activity, thereby reducing individual growth (Mehner and Wieser 1994; Kocovsky and Carline 2001; Quist et al. 2002). If alternative habitats are available, many percids will migrate to areas with more preferable temperatures (Kocovsky and Carline 2001; Quist et al. 2002), moving either laterally (e.g., among lake basins or lagoon and sea habitats; Kershner et al. 1999; Ložys 2004) or vertically (e.g., from nearshore or epilimnetic areas to the meta- and hypolimnion in stratified lakes; Lester et al. 2004; Jones et al. 2006).

2.2.2 Light and Vision

Sander and *Perca* species exhibit unique adaptations and habitat preferences with regard to light intensity, visibility, and photoperiod that differentially influence their foraging behavior and growth. Much of this variation is driven by differences in eye structure among species. *Sander* species possess the *tapetum lucidum*, a highly reflective layer of the retina that greatly increases the sensitivity of the eye to light, enabling the use of dimmer habitats, while *Perca* species lack such a structure (Ali et al. 1977). As a result, the species strongly diverge in photic habitat preferences. Larvae of all percids begin life exhibiting positive phototaxis, but *Sander* larvae switch to negative phototaxis as their eyes develop, at approximately 8 weeks of age (Schumann 1963; Bulkowski and Meade 1983; Luchiari et al. 2006; Wang and Appenzeller 2006). Juvenile and adult walleye and pikeperch prefer low light conditions, exhibit nocturnal and crepuscular activity peaks, and feed more efficiently in turbid, low light, and nighttime conditions (Scherer 1971; Ali et al. 1977; Mathias and Li 1982; Lester et al. 2004; Luchiari et al. 2006). In contrast, juvenile and adult yellow and Eurasian perch prefer high light conditions and exhibit diurnal feeding behavior, although they may also be most active during crepuscular periods to balance foraging success with predation risk (Huh et al. 1976; Ali et al. 1977; Huusko et al. 1996; Gardeur et al. 2007; Sects. 15.2 and 15.3). Photoperiod also differentially affects growth of percids. In experiments examining the relative importance of temperature and photoperiod to percid growth, the growth of *Perca* species was highly sensitive to photoperiod, decreasing when individuals are exposed to extended or unnatural lighting conditions, while the growth of *Sander* species was driven more by temperature (Huh et al. 1976; Gardeur et al. 2007; Shewmon et al. 2007).

Differences in eye structure may also partially explain variation in the response of *Perca* and *Sander* species to eutrophication and turbidity. Growth, predation success, and consumption are strongly negatively affected by increasing turbidity in Eurasian and yellow perch while their foraging activity increases, potentially in an attempt to increase the probability of encountering prey or in response to decreased predation risk in high turbidity environments (Radke and Gaupisch 2005; Ljunggren and Sandström 2007; Irwin et al. 2009; Reichert et al. 2010; Wellington et al. 2010). The contrast of prey to the environment is also extremely important, especially in larval *Perca* species, where high contrast environments promote larval survival and growth and low light or contrast may delay onset of feeding, slow growth, and increase mortality (Hinshaw 1985; Tamazouzt et al. 2000). Interestingly, there is a difference between responses to sedimentary and phytoplanktonic turbidity in *Perca*. Phytoplankton has a much stronger negative effect on *Perca* growth and foraging than sediment, which may imply that algal blooms are particularly detrimental to larval and juvenile growth (Radke and Gaupisch 2005; Wellington et al. 2010). *Sander* species, on the other hand, do not appear to be affected by turbidity until it reaches extremely high levels, up to an order of magnitude higher than levels that affect *Perca* (Vandenbyllaardt et al. 1991; Ljunggren and Sandström

2007). Even then, their growth is not as strongly affected, although their prey selection may change toward larger items (e.g., large zooplankton in juvenile pikeperch), which may affect the ontogenetic switch to piscivory (Vandenbyllaardt et al. 1991; Ljunggren and Sandström 2007; Zingel and Paaver 2010). In the wild, *Sander* species may even prefer more eutrophic, stained, or turbid systems than *Perca* species, as pikeperch have been observed to forage more efficiently in eutrophic systems with higher levels of water color (Lehtonen et al. 1996; Keskinen and Marjomäki 2003).

2.2.3   Dissolved Oxygen

Percid species appear to be fairly tolerant of low dissolved oxygen (DO) concentrations (Petrosky and Magnuson 1973; Suthers and Gee 1986). In terms of direct effects of DO on growth, percids exhibit ontogenetic differences in DO tolerance. Small individuals can tolerate lower DO than larger fish, which may play an important role in predator-prey dynamics, potentially allowing small fish to use low DO habitats as refugia from larger predators (Robb and Abrahams 2003). In general, percids appear to suffer negative effects on growth when DO concentrations decline below 2 mg/L (Suthers and Gee 1986; Arend et al. 2011; Brandt et al. 2011; Roberts et al. 2011), although feeding rates and consumption may begin to decline at DO levels as high as 3.5 mg/L without significant changes in growth (Carlson et al. 1980).

   Most effects of DO are observed as sub-lethal effects on percid habitat selection and behavior (Chap. 15). Percids have been shown to avoid areas below 1.5–3 mg/L DO (Suthers and Gee 1986; Roberts et al. 2009, 2012). In lakes with hypolimnetic hypoxia, fish move upward to the metalimnion, thereby reducing benthivory and increasing zooplanktivory, which may lead to reduced growth rates (Roberts et al. 2009; Arend et al. 2011; Brandt et al. 2011). However, diet and hydroacoustic observations in Lake Erie, North America, have revealed that yellow perch make foraging "dives" through the hypolimnetic hypoxic zone in summer and therefore are able to consume benthic invertebrates (Roberts et al. 2012). Interestingly, the potential effects of these short-term exposures to hypoxic habitats appear to be minimal (Roberts et al. 2009, 2011). In walleye, DO may moderate thermo- and phototactic responses, forcing fish to reduce their residence time in or entirely abandon preferred habitats when DO falls below 2–3 mg/L (Scherer 1971; Brandt et al. 2011). Because preferred temperatures and light levels for walleye often spatially overlap with hypoxic zones in lakes, they may be forced into habitats above thermal and photic optima. However, hypoxia may not be entirely negative for large predators such as walleye, as many forage fish species may also aggregate at the metalimnion due to tradeoffs between thermal and oxygen preferences, thereby condensing prey and increasing walleye consumption (Brandt et al. 2011). Thus, while hypoxia may be an important moderator of behavior and habitat selection, its effects on percid biology may be mixed.

2.2.4   Ontogeny and Prey Availability

Sander and *Perca* species follow fairly similar trends in their diet ontogeny, but differ substantially in the timing of ontogenetic diet shifts (especially to piscivory) and foraging behavior (Sect. 15.2). *Sander* species are specialist piscivores with large gape sizes and canine teeth, actively selecting preferred prey types (Campbell 1998; Graeb et al. 2005). In contrast, *Perca* species lack canine teeth, exhibit slower increases in gape size with growth, and exhibit more generalist, passive prey selection behavior dependent on prey availability and foraging efficiency (Knight et al. 1984; Mehner et al. 1996; Graeb et al. 2005). *Perca* species also tend to exhibit higher foraging and attack rates than *Sander* species (Graeb et al. 2005; Ljunggren and Sandström 2007).

Perca and *Sander* larvae begin to feed roughly 4–5 days post hatch, at about 9 mm in length for walleye and 6 mm for pikeperch, yellow perch, and Eurasian perch (Johnston and Mathias 1994; Wang and Eckmann 1994; Peterka et al. 2002; Fulford et al. 2006). Newly hatched larvae begin feeding on small planktonic items such as algae, rotifers, molluscan veligers, and copepod nauplii, eventually graduating to larger prey items like adult copepods, *Ceriodaphnia*, and larger daphnid species as they increase in length to around 20–35 mm (Fox and Flowers 1990; Wang and Eckmann 1994; Specziár and Biró 2003; Graeb et al. 2004; Specziár 2005; Galarowicz et al. 2006; Withers 2012). Depending on availability, percid juveniles larger than 35–40 mm will subsequently switch to larger benthic prey, consisting of organisms such as chironomid larvae, mayfly nymphs, amphipods, and *Mysis* (Fox and Flowers 1990; Johnston and Mathias 1994; Specziár and Biró 2003; Galarowicz and Wahl 2005; Specziár 2005; Roswell et al. 2013). The ontogenies of *Perca* and *Sander* diverge at this point; the faster growing walleye and pikeperch will switch to almost exclusive piscivory at sizes from 35 to 100 mm depending on the abundance and size of available fish prey, preferring fish from one fifth to one tenth their own length (Turesson et al. 2002; Persson and Brönmark 2002; Specziár and Biró 2003; Galarowicz and Wahl 2005; Graeb et al. 2005; Specziár 2005; Galarowicz et al. 2006; Hoxmeier et al. 2006), while yellow and Eurasian perch continue to eat a mixture of zooplankton and benthic invertebrates (Diehl 1993; Schaeffer et al. 2000; Svänback and Eklöv 2001; Tyson and Knight 2001; Roswell et al. 2013). Some *Perca* populations eventually switch to piscivory at sizes larger than 150 mm, often around 3–5 years of age, eating young-of-year cyprinid and clupeid species when abundant (Knight et al. 1984; Tyson and Knight 2001; Svanbäck and Eklöv 2001; Headly and Lauer 2008). However, *Perca* species are especially plastic in their dietary preferences, and there are examples of *Perca* populations greatly delaying ontogenetic shifts or never switching to benthivory or piscivory throughout life (e.g., Quevedo et al. 2009; Roswell et al. 2014).

Prey size and availability have important implications for growth throughout ontogeny. Percids exhibit a type II functional response to increasing prey densities (Hoxmeier et al. 2004, 2006; Galarowicz and Wahl 2005), and growth rates of diverse ages of percids have been positively related to prey density (Hartman and

Margraf 1992; Diehl 1993; Wang and Eckmann 1994; Hoxmeier et al. 2004; but see Hoxmeier et al. 2006). However, growth is driven not simply by prey density, but also the availability and capture efficiency of appropriately sized and energy-rich prey throughout ontogeny. Early in life, the lack of large zooplankton, such as *Daphnia*, may restrict growth and delay switching to either benthic invertebrates or fish (Mills et al. 1989; Graeb et al. 2004; Fulford et al. 2006; Lappalainen et al. 2005; Vinni et al. 2009). The absence of large benthic invertebrates during the juvenile stage may negatively impact growth and condition, which could delay the final switch to piscivory (Hayward and Margraf 1987; Diehl 1993; van Densen et al. 1996; Schaeffer et al. 2000; Tyson and Knight 2001; Vinni et al. 2009). Finally, the switch to piscivory appears to be largely driven by the size and density of forage fish, creating a potential growth bottleneck if small forage fish (e.g., young of year clupeids or cyprinids) are not available (Knight et al. 1984; Hartman and Margraf 1992; Persson and Brönmark 2002; Sherwood et al. 2002; Kolar et al. 2003; Keskinen and Marjomäki 2004; Galarowicz and Wahl 2005; Headly and Lauer 2008; Sect. 15.2.1). This heavy reliance of growth on consumption based upon prey size and availability likely drives the strong compensatory density dependent growth effects commonly observed in yellow perch (e.g., Post et al. 1997; Headly and Lauer 2008; Irwin et al. 2009; Ivan et al. 2011), Eurasian perch (e.g., Diehl 1993; Byström and Garcia-Berthou 1999; Heibo et al. 2005), walleye (e.g., Knight et al. 1984; Muth and Wolfert 1986; Fox and Flowers 1990; Schueller et al. 2005; Venturelli et al. 2009), and pikeperch (e.g., Lehtonen et al. 1996; Lappalainen et al. 2005; Sect. 19.4.3).

Prey densities may also affect population behavior and size distributions. Eurasian perch and yellow perch exhibit rapid, plastic niche partitioning in lakes based on foraging success, diverging into littoral and pelagic sub-populations with distinct habitats, morphologies, diet preferences, and growth patterns (Post et al. 1997; Svanbäck and Eklöv 2001, 2006; Quevedo et al. 2009; Roswell et al. 2013; Sects. 15.2 and 15.5). Varied growth rates and limited forage fish may result in populations with bimodal size distributions, with faster growing individuals able to switch to piscivory and reap the associated energetic benefits of fish prey, while slower growing individuals continue to eat invertebrates and suffer reduced growth (Post and Evans 1989; van Densen et al. 1996; Post et al. 1997; Svanbäck and Eklöv 2001; Specziár 2005; Johnston et al. 2012a). In extreme cases, lack of appropriately-sized prey may even result in stunted populations (Heath and Roff 1996; Heibo et al. 2005; Persson and Brönmark 2002; Vinni et al. 2009).

At an individual level, growth is strongly related to prey consumption rate (Kitchell et al. 1977; Karås and Thoresson 1992), and the implications of food limitation or starvation are severe. Larvae may be able to resist starvation for 11–19 days depending on water temperature (Jonas and Wahl 1998; Olin et al. 2012; Andree et al. 2014), but their energy densities decline rapidly in the first 5 days without food, reaching a "point of no return" after 6–8 days where their activity levels, prey capture and handling efficiencies, and predation avoidance abilities decline precipitously (Jonas and Wahl 1998). Juveniles can withstand starvation for a longer time period (16–21 days), but ultimately follow the same patterns of

decreasing activity and increasing predation susceptibility as larvae (Jonas and Wahl 1998). Percids may attempt to compensate for lack of food by decreasing respiration rates and activity (Cai and Summerfelt 1992; Mehner and Wieser 1994) and increasing consumption when food is available (Mattila et al. 2009). However, these measures are often not sufficient to avoid decreases in growth (Mehner and Wieser 1994; Mattila et al. 2009). As a result, prey availability and consumption can have wide-ranging effects at both the population and individual levels.

2.2.5 *Exploitation*

All of the percid species discussed in this chapter are highly important economic resources, and many populations are subject to high rates of fishing mortality that may affect both population size structures and individual growth patterns. Size selective harvest has the potential to reduce mean age and size in percid populations through selective removal of older, larger individuals, as seen in walleye (Colby and Baccante 1996) and yellow perch (Heyer et al. 2001; Lauer et al. 2008; Collingsworth and Marschall 2011a). Reductions in abundance may also release the population from intraspecific competition and other density-dependent effects, leading to faster growth (Paukert and Willis 2001; Lauer et al. 2008). Alternatively, size selective fishing that removes the largest individuals may also remove the fastest growing fish, leaving individuals that suffer from poor growth, thus reducing the average individual growth potential in the population (Machiels and Wijsman 1996). This can lead to differential mortality rates between growth trajectories; in one Eurasian perch population, the smallest fish in a given year class suffered highest mortality from ages 0 to 1 from natural causes, while mortality of larger fish from the same year class peaked from ages 2 to 4 due to fishing (Machiels and Wijsman 1996). Changing population growth patterns and size structure may also affect the potential value of the stock, either by reducing commercial yields (as seen in Lake Michigan yellow perch; Marsden and Robillard 2004; Lauer et al. 2008) or decreasing popularity to recreational anglers, who generally prefer relatively fewer but larger fish over many small ones (Isermann et al. 2005). Because of the economic and intrinsic value of these fisheries and the strong influence growth may have on their production, a clear understanding of the potential ramifications of fishing pressure is needed to properly manage and maintain percid populations.

2.3 Reproductive Ecology

Life history traits of large percid species, namely maturation, gonad development, fecundity, spawning behavior, and offspring traits, exhibit a wide range of variation both within (e.g., Colby and Nepszy 1981) and across percid species (e.g., Marshall 1977). In general, all *Perca* and *Sander* species are iteroparous, periodic spawners

that typically spawn in spring (Johnston and Leggett 2002; Lappalainen et al. 2003; Heibo et al. 2005). Each species exhibits a capital spawning strategy, with gonad development taking place throughout the fall and winter months prior to spawning (Malison et al. 1994; Henderson et al. 2000). Within species, variation in life history traits appears to be driven by a combination of plastic responses to environmental conditions (Jansen 1996; Johnston et al. 2012a) and adaptation to local environmental conditions (Hokanson 1977; Wang et al. 2012; Collingsworth and Marschall 2011a). Because variation in reproductive characteristics can have strong effects on population traits such as individual and population growth, mortality, and recruitment (Lester et al. 2000; Collingsworth and Marschall 2011a), understanding the environmental mechanisms controlling observed reproductive life history trait variation can provide vital information for both management of wild populations and improved aquaculture practices.

In this section, we present an overview of the general reproductive ecology and life history patterns exhibited by *Perca* and *Sander* species. We also describe environmental factors, including temperature, light, dissolved oxygen, spawning habitat, and food resources, that appear to drive variation in many aspects of percid reproductive biology. In addition, we examine recent evidence that maternal effects (i.e., correlations between the traits of an individual female and her offspring) may be an important factor in determining the size and fitness of percid eggs and larvae. Finally, because all of our focal species support highly valuable recreational and commercial fisheries world-wide (Baccante and Reid 1988; Lappalainen et al. 2003; Lauer et al. 2008; Vainikka et al. 2012) we discuss the potential implications of fishing exploitation with regard to variation in percid reproductive life history traits.

2.3.1 Maturation

Maturation, i.e., the initial development of gonads in preparation for spawning and subsequent allocation of energy to gonadal development and spawning behavior, can affect future growth, reproductive potential, and mortality (Hayes and Taylor 1990; Bronte et al. 1993; Lester et al. 2000; Roff et al. 2006). In general, percid maturation schedules are typical of a periodic life history strategy (Winemiller and Rose 1992). Maturation is sexually dimorphic among species, wherein males mature at ages 1 or 2 and females mature at ages 3–4 (Muth and Wolfert 1986; Diana and Salz 1990; Jansen 1996; Henderson and Morgan 2002; Lappalainen et al. 2003; Wang et al. 2009c). However, all species exhibit broad variation in maturation schedules among populations, with estimates of age at maturity ranging from as early as age 1 (Muth and Wolfert 1986; Houthuijzen et al. 1993; Madenjian et al. 1996) to as late as age 10 (Colby and Nepszy 1981; Raikova-Petrova and Živkov 1998; Lester et al. 2000; Lappalainen et al. 2003). Length at maturation also varies considerably depending on sex and species (Lester et al. 2000; Heibo et al. 2005; Purchase et al. 2005). Across several populations, males tend to mature around 80–150 and 300–350 mm TL in *Perca* and *Sander* (Diana and Salz 1990; Purchase

et al. 2005; Wang et al. 2009c; Venturelli et al. 2010a), while females mature between 150–200 and 350–450 mm TL (Diana and Salz 1990; Heibo et al. 2005; Wang et al. 2009c; Venturelli et al. 2010a), respectively.

Variation of percid maturation schedules is related to differences in growth and mortality rates, especially in juveniles (Colby and Nepszy 1981; Lappalainen et al. 2003; Heibo et al. 2005). Populations with faster individual growth rates tend to mature at younger ages than populations with slower growing individuals (Madenjian et al. 1996; Heibo et al. 2005; Schueller et al. 2005). Individual growth and mortality rates are strongly linked with maturation of percids (Chap. 19); therefore, any environmental variable that affects growth or mortality rates (Sects. 2.2, 2.5, and 19.4) may also impact maturation. For instance, temperature has a negative effect on age at maturation in many populations, mainly through its positive effects on growth (Raikova-Petrova and Živkov 1998; Venturelli et al. 2009). This trend contributes to latitudinal variation in maturation schedules among percid populations, where colder, slower growing northern populations tend to mature at older ages and larger sizes and warmer, faster growing southern populations tend toward maturation at younger ages and smaller sizes (Lappalainen et al. 2003; Heibo et al. 2005). Variation in annual temperatures may also influence short-term patterns in maturation schedules, and Venturelli et al. (2009) found that maturation in walleye was better described as a function of growing degree days (GDD) than either age or length. Percids may require an extended cooling period less than 10–12 °C during winter for proper gonad development (discussed below); extension of this period may allow a larger proportion of smaller females to develop their gonads and mature than during a relatively warm year (Hokanson 1977; Hermelink et al. 2011).

In addition to temperature, maturation may also be dependent on fish condition, often driven by food availability and population density. Maturation of female walleyes has been found to be positively related to body lipid stores, especially the initial maturation of females age 2–5 in the transition period from juveniles to adults (Henderson et al. 2000; Henderson and Morgan 2002). This is thought to be due to tradeoffs in present and future reproductive success, where small females in poor condition would delay maturation in favor of increasing size, and thus reproductive output, the following year (Henderson and Morgan 2002). There are also several examples of compensatory density-dependent shifts in maturation schedules in percids following changes in population abundance (Schueller et al. 2005; Sect. 19.4.3). For example, following rehabilitation of the walleye fishery in Lake Erie, population abundance increased, leading to decreased condition and growth, which resulted in increased age and length at maturity (Muth and Wolfert 1986). In the opposite case, abundant food resources in a newly freshened reservoir led to rapid growth and early maturity in Eurasian perch (Houthuijzen et al. 1993). Therefore, availability of food resources, mediated through intraspecific competition or changes in the environment, may have important effects on percid maturation schedules.

In many percid populations it remains unclear whether observed variation in maturation schedules is primarily reflective of phenotypic plasticity (Purchase et al. 2005) or evidence of adaptation to local environmental regimes (Wang et al. 2009b; Collingsworth and Marschall 2011a). Evidence from the literature suggests both

processes may play a role in shaping maturation schedules of percids. Johnston et al. (2012a) suggested that older age and larger size at maturation in walleye than sauger may allow for more plasticity in those traits, which would enable walleye to respond to short-term changes in the environment. However, Wang et al. (2009b) found significant adaptive variation in the maturation schedules of Laurentian Great Lakes walleye populations, suggesting each had adapted to their local environment and incumbent selection pressures. Unfortunately, quantitative assessment of plastic and adaptive variation in maturation is lacking for most percid species, despite the wide range of literature documenting differences in these traits (e.g., Lappalainen et al. 2003 for pikeperch). Disentangling plastic and adaptive variation can be difficult, but may provide important information into the underlying differences among species and populations and can also indicate important changes in the selection pressures on populations, whether through fisheries exploitation (e.g., Barot et al. 2004) or other ecosystem changes (e.g., Wang et al. 2008).

2.3.2 Fecundity

Fecundity varies significantly among percid species due to differences in body and egg size. Pikeperch, with their small eggs but relatively large body size, have by far the highest fecundity, with estimates ranging from 24,000 to over 2.5 million eggs per female (Lehtonen et al. 1996; Kosior and Wandzel 2001). Pikeperch are followed by walleye, which produce 24,000–614,000 eggs per female (Wolfert 1969; Serns 1982; Muth and Ickes 1993; Colby and Baccante 1996). Finally, yellow and Eurasian perch have been estimated to produce 1,910–157,594 eggs per female (Jansen 1996; Lauer et al. 2005; Pedicillo et al. 2008). Much of this observed variation is due to the positive correlations between fecundity and maternal length, age, and, most strongly, mass (Serns 1982; Muth and Ickes 1993; Jansen 1996; Lauer et al. 2005; Johnston et al. 2012a, b). Large, old females can produce orders of magnitude more eggs than small, young females, drastically increasing their reproductive output in a given year (Venturelli et al. 2009; Collingsworth and Marschall 2011b).

Variation in fecundity has been linked to the thermal environment, photoperiod, and food supply (Colby and Nepszy 1981). Compensatory density dependent responses in walleye fecundity have been attributed to changes in food supply, fish growth, and condition through intraspecific competition (Colby and Nepszy 1981; Baccante and Reid 1988; Rose et al. 1999; Moles et al. 2008; Collingsworth and Marschall 2011b; Johnston et al. 2012a). Differences in fecundity among populations may also be related to adaptation of egg size to local environments (Johnston and Leggett 2002); given equal reproductive investment, populations adapted to produce smaller eggs would be assumed to exhibit higher fecundity. This trend was observed across several northern Ontario lakes in walleye, where fecundity increased with increasing lake-specific GDD (>5 °C), potentially through adaptive mechanisms to decrease egg size (and thus increase fecundity) in more benign environments (Baccante and Colby 1996).

2.3.3 Gonad Development and Egg Size

All percids can be described as capital spawners, meaning gonad development takes place throughout the year preceding spawning in spring (Malison et al. 1994; Henderson et al. 2000). *Perca* and *Sander* species follow very similar trajectories of gonad development following a short, 1–3 month quiescent period after spawning (Hokanson 1977; Ciereszko et al. 1997; Henderson et al. 2000). Male gonads generally start to develop in fall and are fully developed by the mid-winter months, able to sustain spermiation for up to 6 months until spawning in early spring (Malison and Held 1995; Shewmon et al. 2007). In females, ovary growth begins from August to October, and continues throughout the winter (Diana and Salz 1990; Malison et al. 1994; Malison and Held 1995; Ciereszko et al. 1997; Henderson et al. 2000; Lappalainen et al. 2003). Vitellogenesis begins in oocytes in November and continues until just before spawning (Hokanson 1977; Malison et al. 1994; Henderson et al. 2000; Hermelink et al. 2011). Final hydration and maturation of the oocytes occurs just before spawning (Malison et al. 1994; Sandström et al. 1995). It is also at this time that the gelatinous, ribbon-like skein forms around the eggs of *Perca* species, linking them in a single long strand (Sandström et al. 1995, 1997). Oocyte number and energy content are generally determined by December or January; although the ovary will roughly double in size between January and spawning, additional gains are of little energetic value (Sandström et al. 1995, 1997; Henderson et al. 2000). Oocyte size is determined by January in *Perca* (Sandström et al. 1997; Henderson et al. 2000) but may continue to develop until just before spawning in *Sander* (Malison et al. 1994). Among percids, walleyes produce the largest eggs (1.4–2.1 mm in diameter; Wolfert 1969; Muth and Ickes 1993; Wang et al. 2012), followed by *Perca* spp. (0.94–2.0 mm; Ciereszko et al. 1997; Lauer et al. 2005; Pedicillo et al. 2008) and pikeperch (0.5–1.5 mm; Marshall 1977; Lappalainen et al. 2003).

In mature percids, the annual onset and quality of gonad development is driven by both endogenous mechanisms and exogenous inputs, the most important of which are temperature and photoperiod (Ciereszko et al. 1997). Percids require an extended winter period of 3–5 months with temperatures below 10 °C (perch and walleye) or 15 °C (pikeperch) for proper gonad development to occur (Hokanson 1977; Sandström et al. 1997; Hermelink et al. 2011). Winters that are either characterized by a short cold period (i.e., less than 3 months) or warm (i.e., mean temperatures above 15 °C) can lead to suboptimal ovary development, decreased egg size, and atresia of oocytes (Ciereszko et al. 1997; Sandström et al. 1997; Migaud et al. 2002; Shewmon et al. 2007; Hermelink et al. 2011). In *Perca* species, warm winter and spring temperatures may also lead to poor development of the skein, which can break down and cause high egg mortality during incubation (Sandström et al. 1997). Thus, poor thermal conditions may significantly affect reproductive success in some populations of percids (e.g., Schlumberger and Proteau 1996).

Photoperiod appears to control the onset of gonad development in percids (Malison et al. 1994; Migaud et al. 2004), as a natural decline in photoperiod has

initiated gonad development in perch even without a concomitant decrease in temperature (Wang et al. 2006; Shewmon et al. 2007). In experimental treatments, photoperiod also plays a role in proper gonad development, as perch exposed to unnaturally long or constant photoperiod regimes either failed to mature or exhibited low gonadosomatic indices and poor oocyte quality (Migaud et al. 2004, 2006; Wang et al. 2006). Thus, it appears that an interaction of photoperiod and temperature is vitally important to the proper maturation and reproduction of percid species, where photoperiod initiates the process and optimal temperatures are needed for later development and maturation.

Maternal size, condition, and adaptation to local environments also appear to play a role in gonad development and egg size in percids. Many studies have linked increases in egg size and quality to increases in maternal length, mass, and age (Johnston and Leggett 2002; Lauer et al. 2005; Johnston et al. 2012b; Olin et al. 2012; Andree et al. 2014). Larger, older females tend to exhibit increased GSI and invest relatively more in reproduction than smaller or younger females (Diana and Salz 1990; Heyer et al. 2001; Olin et al. 2012). Female body condition, driven through acquisition of resources throughout the summer and fall preceding ovary development, may also determine the amount of energy available to invest in reproduction (Johnston and Leggett 2002; Lappalainen et al. 2003; Wang et al. 2006; Collingsworth and Marschall 2011b; Johnston et al. 2012b). Therefore, food intake and lipid availability in females may be an important factor determining egg size and quality, with potential ramifications for recruitment the following year (Madenjian et al. 1996; Tyson and Knight 2001).

Interestingly, these maternal effects appear to vary among populations, and there does not appear to be a single optimum egg size for any species (Johnston and Leggett 2002; Collingsworth and Marschall 2011b). Rather, the relative strength of maternal effects and egg size appear to be highly conserved within populations and highly varied among populations (Wang and Eckmann 1994; Venturelli et al. 2010b; Wang et al. 2012). For instance, Moodie et al. (1989) showed that larval survival in walleye was related to relative larval size differences within populations rather than size variation among populations (i.e., the smallest larvae from a single population suffered high mortality rates, but larval size differences among populations did not explain patterns in larval survival). System productivity often has a negative relationship with egg size, likely because more productive systems offer more food resources, reducing the strength of size-dependent mortality on larvae (Johnston and Leggett 2002; Heibo et al. 2005; Wang et al. 2012). Egg size in walleye and Eurasian perch has also been shown to decrease with increasing latitude, potentially because longer lived northern populations invest less in annual reproduction. However, maternal effects appear to be strongest at the northern and southern edges of a species' distribution, where environmental conditions are usually marginal and contribute a greater benefit to the production of relatively larger offspring by larger females (Johnston and Leggett 2002; Heibo et al. 2005). Thus, some of the variation in maternal effects, reproductive investment, and egg size in percids may be largely determined through adaptive mechanisms responding to long term environmental conditions to optimize reproductive success.

2.3.4 Spawning Behavior

Percids exhibit a strikingly wide array of spawning strategies, behaviors, and habitats among species (Sect. 15.6). A common theme among percid species is that spring spawning bouts are prompted primarily by temperature and photoperiod (Hokanson 1977; Ciereszko et al. 1997; Rinchard et al. 2011), although the optimum temperatures range widely among species. Walleye spawning takes place at temperatures from 2 to 15 °C, with peak spawning often occurring at temperatures between 4 and 10 °C (Hokanson 1977; Roseman et al. 1996; Ivan et al. 2010; Martin et al. 2012). Walleye undergo spawning migrations to rivers, streams, and reefs within lakes, and exhibit high levels of spawning site fidelity, which may be strong enough to cause genetic differences among stocks (Rinchard et al. 2011; Stepien et al. 2012). Males are usually first to the spawning areas, followed initially by older females and later by younger females, which may prolong the spawning season in populations with extended age structures (Casselman et al. 2006; Venturelli et al. 2010a). Slightly adhesive, demersal eggs are broadcast onto preferred substrates at depths less than 5 m, usually gravel and cobble in river beds and exposed shorelines and reefs in lakes (Roseman et al. 1996; Rinchard et al. 2011; Raabe and Bozek 2012). Fertilization is external, and fertilization success in the wild may be fairly low (Heidinger et al. 1997), potentially because walleye sperm activity decreases by up to 70 % in the 30–40 s following activation, which is a trait common among all percids (Casselman et al. 2006). While pikeperch are similar to walleye in that they undergo spawning migrations and exhibit strong site fidelity (Lappalainen et al. 2003), the remainder of their spawning behaviors differ significantly from those of their congener (Sect. 15.6). Pikeperch prefer warmer temperatures but have highly plastic thermal preferences, spawning between 4.5 and 26 °C throughout their range (Hokanson 1977), although preferred temperatures range from 8 to 18 °C (Lappalainen et al. 2003; Hermelink et al. 2011). Males appear first on the spawning grounds and will excavate nests in a variety of substrates, including mud, vegetation, sand, and gravel (Hokanson 1977; Lappalainen et al. 2003). Nesting sites can be as deep as 16 m, taking into account preferences for cool temperatures and low light intensity (Schlumberger and Proteau 1996). Females deposit a clutch of highly adhesive eggs in the nest and leave soon after. Males will aggressively defend the clutch until hatching and swim up of fry (Schlumberger and Proteau 1996; Hermelink et al. 2011). The additional parental care provided by pikeperch appears to yield higher fertilization rates and egg survival than found in walleye (Marshall 1977).

The *Perca* species exhibit yet another set of spawning traits that dissociates them from either pikeperch or walleye. Like those species, spawning in perch is triggered by increases in temperature and photoperiod (Migaud et al. 2002; Collingsworth and Marschall 2011b). Spawning occurs at temperatures intermediate to those of the *Sander* species, ranging from 4 to 19 °C with an optimum around 8–10 °C (Forney 1971; Collingsworth and Marschall 2011b). Perch in warmer areas spawn earlier in the year and may experience a protracted spawning period compared to those in

cooler systems (Sandström et al. 1997). Alternatively, very cold temperatures (2–3 °C) have also been observed to suspend spawning in perch (Sandström et al. 1997). Spawning aggregations of perch concentrate on preferred substrates, namely dead vegetation, coarse woody debris, and large cobble (Robillard and Marsden 2001; Pedicillo et al. 2008; Čech et al. 2009; Sect. 15.6). Spawning depth can range from 2 to 20 m, and is influenced by a number of factors that may influence egg survival, including temperature, dissolved oxygen, wind, and ultraviolet radiation (Huff et al. 2004; Williamson et al. 1997; Čech et al. 2009). In a unique adaptation, both yellow and Eurasian perch lay their eggs as part of a gelatinous, accordion-like skein that may reach up to 2 m in length (Scott and Crossman 1973). The skein is draped over woody debris and vegetation, and is believed to deter predators, hold the egg mass in place, promote fertilization, and aid in oxygenating the eggs (Treasurer 1983; Newsome and Tompkins 1985; Reyes et al. 1992).

2.3.5   Incubation and Offspring Survival

Despite the striking diversity in their spawning strategies and behaviors, perch, pikeperch, and walleye eggs exhibit similar trends in their responses to temperature, light, and dissolved oxygen. Optimal temperatures for incubation of perch and walleye eggs range from 9 to 20 °C (Koenst and Smith 1976; Hokanson 1977; Guma'a 1978; Wang and Eckmann 1994; Huff et al. 2004), while pikeperch incubation is optimized at 11.5–20 °C (Muntyan 1977; Lappalainen et al. 2003). Percid eggs appear fairly resistant to fluctuations in temperature during incubation, although very large perturbations (20 °C or more) have been shown to decrease hatching success and swim up rates in walleye (Schneider et al. 2002). Warm temperatures may also promote bacterial and fungal infection of eggs and cause perch skeins to deteriorate, which can greatly increase egg mortality (Sandström et al. 1997). On average, percid eggs will hatch in 9–13 days at preferred temperatures, although hatch times are negatively related to temperature and may vary from 3–4 days at warmer temperatures (15–21 °C) to 19–35 days at colder temperatures (7–11 °C) (Oseid and Smith 1971; Malison et al. 1994; Huff et al. 2004). Incubation of eggs at or near optimal temperatures has also been shown to result in increased larval length at hatch, which may increase larval survival (Wang and Eckmann 1994). Extension of the incubation period by low temperatures can leave eggs more vulnerable to mortality through wave displacement and predation (Johnson 1961; Clady 1976; Roseman et al. 1996; Lappalainen et al. 2003; Huff et al. 2004; Ivan et al. 2010). Percid eggs are also relatively tolerant to low dissolved oxygen (DO) conditions. However, higher DO may shorten the incubation period and increase larval size at hatch, which may promote early life survival (Oseid and Smith 1971). Average larval length at hatch varies among species. Walleye larvae are among the largest of any percid species at hatch, ranging from 6 to 8.6 mm (Houde and Forney 1970; Marshall 1977). Yellow and Eurasian perch produce intermediately sized larvae (4.6–6.0 mm; Thorpe 1977; Weber et al. 2011), and pikeperch larvae are smallest at hatch (4.5–5.5 mm; Lappalainen et al. 2003).

Egg and larval mortality can be extremely high (up to 80 %) in the first 5 days after fertilization (Moodie et al. 1989; Latif et al. 1999), and parental effects may contribute to variability in egg and larval survival following spawning (Wang and Eckmann 1994; Andree et al. 2015). In walleye, Moodie et al. (1989) found that smaller females produced smaller eggs and higher proportions of deformed larvae that failed to survive. In addition, larval size at hatch and survival have each been shown to increase with maternal age, ova lipid provisioning, and fatty acid content of eggs (Wiegand et al. 2004, 2007; Johnston et al. 2012b). For yellow perch, Heyer et al. (2001) found that larger females produced shorter larvae with larger yolk sacs that could potentially lead to improved survival during the pelagic stage. Similarly, in Eurasian perch Olin et al. (2012) demonstrated that larger females produced larger, heavier larvae that better survived starvation. In contrast, Andree et al. (2014) found negative relationships between maternal size and age and larval survival in yellow perch during the first 5 days post-hatch using older and larger yellow perch females than Olin et al. (2012), but no significant relationship during days 6–14, which suggests that maternal effects may vary with both maternal and larval ontogeny. Finally, the added parental care provided by pikeperch may increase egg and larval survival relative to that of walleye, despite their relatively small eggs and larvae (Marshall 1977; Lappalainen et al. 2003). Therefore, parental effects may not only influence egg size (as discussed above) but also larval survival, which can potentially affect recruitment of these species (Roseman et al. 1996; Venturelli et al. 2009).

2.3.6 Fishery-Dependent Selection

As described above, percid species support highly valuable commercial and recreational fisheries throughout their respective ranges (Lehtonen et al. 1996; Lester et al. 2000; Lappalainen et al. 2003; Lauer et al. 2008). Therefore, fishing mortality may very well be an evolutionarily recent and important factor influencing life history trait expression in these species. Harvest of percids has been shown to decrease population abundance in many areas (e.g., Marsden and Robillard 2004; Lauer et al. 2008), which may lead to increased growth and fecundity due to release from intraspecific competition for resources (Baccante and Reid 1988; Colby and Baccante 1996). However, size selective harvest can also cause truncation of size and age distributions, skewed sex ratios, and reduction of the spawning stock, which in turn may result in a shortened spawning period (due to the lack of old, large females) and increase variability in recruitment (Colby and Nepszy 1981; Lauer et al. 2008; Collingsworth and Marschall 2011b). Harvest of older, larger individuals coupled with faster growth can also drive maturation schedules toward maturity at younger ages through both phenotypically plastic responses to growth and contemporary evolution in response to harvest (Muth and Wolfert 1986; Jansen 1996; Heibo et al. 2005; Sharpe and Hendry 2009; Wang et al. 2009c). Finally, maternal effects, coupled with maturation at younger ages and smaller sizes, can result in the production of

fewer eggs of poorer quality, reducing offspring fitness and further depressing recruitment (Heyer et al. 2001; Venturelli et al. 2009; Olin et al. 2012). Thus, exploitation can have major effects on the life histories of percid populations, which in turn may determine sensitivity to fisheries exploitation (Lester et al. 2000). Because reproductive characteristics of percids are highly variable, as we have demonstrated in this section, it is crucial that information on specific populations of interest are collected in order to determine proper management actions and gauge population-wide responses to changing conditions (Purchase et al. 2005).

2.4 Early Life Survival and Recruitment

2.4.1 Patterns of Percid Early Life Survival and Recruitment

For most fish populations, recruitment success is the key determinant of future population size. While the precise definition of recruitment will vary across fish stocks depending upon life histories, available data, and stage-specific survival rates, we generally define recruitment as annual population-level reproductive success, i.e., the number of young fish which survive through early life to contribute to adult or harvestable components of a population. For many fish populations, annual recruitment success may be set during very early life and the number of individuals which survive through a very early life stage (e.g., larval stage) may be strongly correlated with the number of individuals which ultimately recruit to the adult population. In such cases, biotic and abiotic factors affecting survival through these very early life stages will determine recruitment success. In contrast, recruitment of other fish populations may not be set until later in life, and factors affecting survival of later life stages may have stronger influence on recruitment.

Similar to most fish species, percid populations display high inter-annual recruitment variation. In fact, year-class strength of several percid populations exhibit particularly strong *boom-and-bust* patterns. As mentioned above, percids may be characterized as periodic species based on Winemiller and Rose's (1992) life-history continuum (i.e., they produce relatively large clutches of small to medium sized offspring; Sect. 2.2). Moreover, excepting nest-guarding behavior in pikeperch, they provide low parental care for offspring, although active selection of spawning location and packaging of eggs in skeins by perch could be viewed as pre-hatching parental care. In turn, these reproductive traits result in large clutches of larvae with small to medium sized yolk sacs and low survival rates. Due to their high abundance, small changes in survival rates of larval percids have the potential to lead to large responses in the number of individuals that survive to subsequent life-stages and ultimately recruit to adult populations.

Houde (1994) compared recruitment patterns of marine and freshwater fishes and suggested that recruitment of marine fishes is often set during early larval stages, while recruitment of fish in small freshwater systems is set during later juvenile stages. In general, marine larvae are small, making them susceptible to drift and

spatio-temporally variable physical, chemical, and lower trophic level processes which affect their survival through both density-dependent and -independent processes. In comparison, freshwater larvae tend to be larger and their recruitment may be more influenced by biological interactions and density-dependent processes acting on later life stages. Percids inhabit a diversity of environments, from small ponds and streams to huge lacustrine, brackish, and riverine systems. Thus, not surprisingly, the age when recruitment is set varies among percid populations. While recruitment success of many percid populations appears to be dependent on processes affecting early life stages (e.g., Anderson et al. 1998; Kjellman et al. 2003), other populations respond to later life processes (e.g., Hansen et al. 1998; Ivan et al. 2011). The age when recruitment is set may even vary among species within a single system. Ivan et al. (2011) examined when recruitment was set for yellow perch and walleye in Saginaw Bay, Lake Huron, USA (1970–2008) and found that the catch of age-0 walleye in the fall was strongly correlated to the catch of age-1 walleye in the following year and the catch of age-2 walleye 2 years later; indicating that walleye recruitment was set by fall of age-0. However, Ivan et al. (2011) also demonstrated that in Saginaw Bay catch of age-0 yellow perch in the fall was not related to catch of yellow perch 2 years later. Rather, catch of age-1 yellow perch in the fall was strongly related to catch of age-2 yellow perch the following year, indicating that yellow perch recruitment was set by fall of age-1.

Across most fish species, survival during early life is strongly related to size and hence feeding opportunities and growth rates. While some studies have pointed out mechanisms (e.g., Marshall et al. 2010) and specific cases (e.g., Litvak and Leggett 1992; Dibattista et al. 2007) whereby the *bigger-is-better* axiom may not hold, as a general rule larger larval fish are less susceptible to both starvation and predation mortality (Miller et al. 1988). Obviously, high feeding rates increase growth rates and decrease the likelihood of starvation mortality. Moreover, as fish increase in size (a) swimming speeds and gape sizes tend to increase, allowing for consumption of additional larger and more active prey and (b) mass-specific metabolic rates decrease, allowing a greater proportion of consumed energy to be directed towards growth, while minimizing energy depletion and starvation risk. For example, as larval yellow perch increase in size their swimming speeds increase (Houde 1969) and they expand their diets (e.g., Fulford et al. 2006). Similarly, Graham and Sprules (1992) found that the size of zooplankton prey consumed by larval walleye increased with size, and Johnston and Mathias (1994) demonstrated that prey consumption increased exponentially with larval walleye length. In addition, metabolic energy utilization decreases as size of larval walleye increases (Madon and Culver 1993), suggesting that larger larval walleye can tolerate a longer period without food compared to smaller larvae. Jonas and Wahl (1998) estimated that larval walleye reach a "point-of-no-return" after a 6 day starvation period and that after 5–6 days of starvation larval walleye were less successful at capturing prey and more vulnerable to predators, and Letcher et al. (1996) found that larger larval yellow perch can survive longer without feeding than smaller larval perch. Thus, increased growth of young fish tends to facilitate further growth and minimizes the probability of starvation. Further, as swimming speeds increase, larger larval fish are able to both

actively avoid predators and overcome predators' gape limitations. Thereby, risk of predation mortality also generally decreases as larval fish increase in size. Consistent with these expectations, Brandt et al. (1987) found that alewife (*Alosa pseudo-harengus*) predators in Lake Ontario selectively fed on smaller larval yellow perch, and Brooking et al. (1998) revealed that larger walleye larvae were better able to escape alewife predation. Collectively, these studies demonstrate that generalized cross-taxa positive linkages among larval fish size, feeding success, swimming speeds, growth, and survival hold for larval percids.

The effects of growth and size on survival rates may extend beyond very early life stages and also influence survival during later young-of-year and yearling life stages. Similar to larval stages, as later stage juvenile fish increase in size they may be better able to actively avoid large piscivores, and their larger body size coupled with development of larger, more rigid spines may deter potential gape-limited predators. Post and Evans (1989) experimentally demonstrated that the risk of predation for young-of-year yellow perch may decrease with total length. Similarly, Roswell et al. (2014) found that during July–November piscivorous walleye in Saginaw Bay, Lake Huron selectively consumed small young-of-year yellow perch. However, predation risk may also indirectly influence growth and activity, and therefore mortality, rates of juvenile percids. In yellow perch, Rennie et al. (2010) observed positive relationships between an index of predation and metrics of growth such as maximum size, specific growth rates, and growth efficiencies. However, these effects traded off with negative relationships between predation and specific consumption and activity rates, suggesting predation-induced shifts in behavior can modify percid life history patterns (Sect. 15.3).

In addition to predation mortality during the growing season, size may also mediate overwinter mortality of juvenile fishes. Winter represents a time of resource scarcity, and young percids, both *Perca* (Griffiths and Kirkwood 1995; Huss et al. 2008; Heerman et al. 2009; Pothoven et al. 2014; Roswell et al. 2014) and *Sander* (Post and Evans 1989; Rennert et al. 2005; Pothoven et al. 2014) species, may lose significant energy stores over winter, which could leave them vulnerable to starvation mortality. Such mortality may be size dependent; larger fish are less likely to experience starvation during winter, as their larger size allows for greater energy storage and lower mass-specific metabolic rates. Several authors have indicated that size-dependent overwinter mortality could be important for young percids (e.g., Post and Evans 1989; Fitzgerald et al. 2006; Heerman et al. 2009) and poor growth before winter or very long, severe winter conditions could lead to poor population-level recruitment (e.g., Post and Evans 1989). In contrast, other studies have revealed that size-dependent overwinter mortality may be minimal for young percids (Johnson and Evans 1991; Pratt and Fox 2002). Thus, in many cases young percids may obtain sufficient size and energy content prior to winter or may be able to readily feed during winter, such that starvation mortality is minimal. However, even if young fish do not directly starve to death during winter, the threat of starvation may lead to risky foraging behavior, increasing predation mortality of young fish and compromised physiological condition, potentially enhancing prevalence of disease-related mortality (Garvey et al. 2004; Sect. 4.4.5). Shuter and Post (1990) suggested

that overwinter mortality may strongly mediate the northerly latitudinal distributions of yellow perch in Canada; in more northerly systems the growing season may be too short for young perch to reach a sufficient size to survive winter. Further, they speculated that with climate warming this interaction between growing season and overwinter survival could be relaxed, allowing yellow perch populations to persist in more northern lakes (Shuter and Post 1990). In short, the importance of overwinter mortality is likely system-specific and has the strongest influence in colder, less productive systems. In addition, overwinter mortality is more likely to affect perch rather than sander species; because, despite their physiological similarities, perch tend to hatch later and obtain a much smaller size by winter relative to sander (Pothoven et al. 2014; Sects. 2.1 and 2.2).

2.4.2 Influence of Environmental Variables on Percid Recruitment

Annual percid year-class success appears to be influenced by both abiotic and biotic factors, with recruitment of some populations responding most strongly to abiotic conditions (e.g., temperatures, water levels, structural habitats), some populations controlled by biotic interactions (e.g., prey availability, predation pressure, competition, intra-population compensatory density-dependent effects) and some influenced by the interaction of abiotic and biotic processes. The breadth of factors controlling percid recruitment partially reflects the diversity of systems occupied by percids and the premise that abiotic factors may have strong effects on year-strength in large systems, while biotic interactions dominate in small systems. However, various studies of percid early life survival have also demonstrated the strong influence of biotic interactions in large systems (e.g., Brandt et al. 1987; Ljunggren et al. 2010; Redman et al. 2011) and the effect of abiotic factors in small systems (e.g., Kallemeyn 1987; Pope et al. 1996; Quist et al. 2003b).

Abiotic influences: Myers (1998) suggested that annual recruitment success of fish populations at the edge of their latitudinal ranges are most likely to be affected by inter-annual variation in weather and climatic conditions. For example, recruitment rates of some percid populations towards the northern extreme of their range are positively associated with growing season (spring, summer, and autumn) water temperatures (e.g., Tolonen et al. 2003). However, such positive associations between growing season temperatures and year-class strength are also evident for percid populations located far south of such northern distributional extremes (e.g., Koonce et al. 1977; Kallemeyn 1987; Sarvala and Helminen 1996; Nyberg et al. 2001; Pitlo 2002; Wysujack et al. 2002; Kjellman et al. 2003; Quist et al. 2003b, 2004; Paxton et al. 2004; Redman et al. 2011). While most studies demonstrating a positive association between growing season temperatures and year-class strength are not able to robustly evaluate the mechanisms underlying such relationships, growing season temperatures likely act both directly and indirectly. For example, water temperatures may directly (a) influence the production of eggs by adults, (b) development

rates of eggs once deposited onto substrates, and (c) affect growth rates of both larvae and later stage young percids. Further, water temperatures may act indirectly by (a) affecting production of prey and (b) perhaps more importantly, by influencing the phenology of young percids and their potential prey, predators, and competitors (see below). Rapid warming in the spring may in particular favor strong year-classes as such conditions may (a) allow for rapid egg development and short duration of the egg stage when storm events could dislodge eggs from suitable substrates and (b) maximize the likelihood that percid larvae will emerge just prior to spring peaks in zooplankton prey (Busch et al. 1975; Pitlo 2002). In contrast, associations between year-class strength and late summer and fall temperatures (e.g., Henderson and Nepszy 1988; Sarvala and Helminen 1996) likely reflect the positive effect of water temperatures on young-of-year growth, allowing young fish to grow large enough to avoid size-selective predators and minimize size-based overwinter mortality.

Climatic influences on percid recruitment extend beyond the effects of water temperature. Beard et al. (2003) found a strong year effect on walleye recruitment success across lakes in Wisconsin, USA, likely reflecting some regional climatic process. Similarly, Schupp (2002) demonstrated that walleye recruitment in Minnesota, USA, lakes was negatively influenced by the 1991 Mt. Pinatubo eruption in the Philippines, which may have influenced both water temperatures and light penetration, thereby affecting system productivities. Pope et al. (1996) found that in a South Dakota, USA, lake, yellow perch year-class strength was greatest during years with high precipitation and fairly stable conditions (low wind and minimal daily temperature deviation). Precipitation patterns structure stream discharge and flow dynamics and may influence percids spawning in fluvial systems. Moreover, discharge of riverine waters may strongly influence environmental conditions in receiving basins. High seasonal precipitation may lead to large sediment and nutrient-rich discharge plumes. Such plumes may support phytoplankton production and lead to high densities of zooplankton prey (thereby facilitating growth of larval percids), while simultaneously providing a poor visibility environment, where young percids may be less conspicuous to visual predators (Reichert et al. 2010).

Water currents may rapidly transport larval fish into or out of favorable nursery habitats, and thereby affect growth and survival. As such, annual differences in regional water circulation and local water currents have the potential to shape recruitment patterns. The role of water currents in structuring recruitment of marine fishes was initially suggested by Hjort (1914) and has subsequently been evaluated for a plethora of marine fish species. In contrast, the role of water currents in influencing recruitment success of freshwater fishes has received relatively limited attention. However, several relatively recent studies of walleye and yellow perch in the Laurentian Great Lakes have demonstrated the potential for water currents to affect percid early life survival in large freshwater systems (e.g., Dettmers et al. 2005; Beletsky et al. 2007; Zhao et al. 2009). Both eggs and larval percids are susceptible to transport by water currents (e.g., Roseman et al. 2001, 2005; Höök et al. 2006). Intense storm events and resulting strong water currents have the potential to

push eggs off of suitable incubation reefs, leading to very low recruitment success during some years (Roseman et al. 2001; Zhao et al. 2009). Similarly, transport of larval percids to suitable nearshore or offshore nursery areas has been linked to annual recruitment success of both yellow perch and walleye (Dettmers et al. 2005; Beletsky et al. 2007; Zhao et al. 2009).

Biotic influences: In addition to abiotic effects, young percid survival and recruitment success may be influenced by a variety of biotic factors. However, it is difficult to draw generalities regarding biotic controls on percid recruitment, as biotic controls (a) have been identified in both small (e.g., Nielsen 1980; Quist et al. 2004) and large (e.g., Ljunggren et al. 2010; Forsythe et al. 2012) systems, (b) have been proposed to affect both larval (Brandt et al. 1987; Kjellman et al. 2003) and later juvenile life-stages (Nielsen 1980; Ritchie and Colby 1988; Hartman and Margraf 1993), and (c) may include a variety of biotic interactions, such as, predation (Hartman and Margraf 1993; Quist et al. 2003b), prey availability (Ritchie and Colby 1988; Ljunggren et al. 2010), disease (Paxton et al. 2004), and inter-specific competition (Quist et al. 2004; Forsythe et al. 2012). Further, biotic controls on young percid survival may be mediated by abiotic processes (e.g., turbidity affecting vulnerability to predation or foraging success; water currents influencing overlap with prey) and a variety of biotic processes may interactively affect early life survival.

Intra-population density-dependence is a common line of evidence for biotic controls on percid recruitment. Several researchers have developed Ricker-type stock-recruitment models to describe annual variation of percid year-class strength (e.g., Craig and Kipling 1983; Paxton et al. 2004; Forsythe et al. 2012), and such models are based on the assumption of compensatory density-dependent effects (i.e., reduced per capita recruitment success with increasing spawning stock size). While such models do not specify the mechanisms of compensatory density-dependent controls, percids may be limited by spawning habitat, leading to reduced per capita reproductive success at high spawner densities, or high densities of young percids may compete for limited prey or lead to concentrated cannibalism. Similar to most ecological systems, studies to identify density-dependent effects for percids have focused on compensatory effects (Sect. 19.4.3). Nonetheless, while less prominent, depensatory effects may also influence recruitment success. Forney (1971) suggested that survival of young yellow perch in Oneida Lake, New York, USA was influenced by depensatory density-dependence. Specifically, Forney (1971) found that during the 1960s large numbers of young yellow perch were able to swamp predation pressure by walleye, thereby leading to higher per capita survival for young yellow perch. However, when subsequently examining this pattern over a longer time series (40 years), Irwin et al. (2009) found that depensatory controls were replaced by compensatory controls on yellow perch survival and growth.

Young percids are selective foragers, initially selecting small-bodied zooplankton prey and then transitioning to feed on larger zooplankton, benthic invertebrates and fish (Sect. 2.1). Thus, their early life growth and survival may be dependent on availability of suitable prey for specific ontogenetic stanza. If larval hatching and exogenous feeding does not overlap spatially and temporally with available small prey, their survival may be compromised. Such overlap may be strongly mediated

by physical processes, e.g., spring warming affecting temporal overlap and water currents affecting spatial overlap. Moreover, consumption of zooplankton or other preferred prey by competitors may lead to dramatic reductions in small-bodied prey and lead to very low percid recruitment success. For example, Ljunggren et al. (2010) found that in coastal areas of the Baltic Sea, intense planktivory by sprat (*Sprattus sprattus*) led to severe reductions in zooplankton densities and almost complete recruitment failure of Eurasian perch. Similarly, Quist et al. (2004) suggested that in cool years walleye hatch later and grow more slowly in Kansas, USA, reservoirs and therefore compete directly with abundant gizzard shad (*Dorosoma cepedianum*) larvae for zooplankton prey. In contrast, early hatching and rapid growth in warm years allowed walleye to gain a size advantage and prey directly on gizzard shad larvae, rather than compete with them (Quist et al. 2004).

Both larval and juvenile percid survival may be strongly controlled by predation by piscivores, and studies have demonstrated the possible influence of predators targeting young percids during both larval and later life stages. For example, Brandt et al. (1987) highlighted the potential for alewife to consume huge numbers of larval yellow perch in Lake Ontario, North America, and Quist et al. (2003b) pointed to the importance of predation by white crappie on walleye in reservoirs. In contrast, predation by walleye on post-larval young-of-year yellow perch may strongly limit year-class strength in Lake Erie and Saginaw Bay, Lake Huron (Hartman and Margraf 1993; Fielder and Thomas 2006; Roswell 2011). Given the potential high abundance and local concentration of larval percids, we suggest that intense, short-term predation on larval percids has the potential to strongly compromise cohort success. However, such an effect may be under-appreciated because larval percids are difficult to document in stomachs of potential piscivores due to rapid digestion rates.

The effect of predation on recruitment success may be mediated by other biotic interactions. As described above, predation mortality may be strongly size-selective (e.g., Post and Evans 1989; Roswell et al. 2014). Therefore, high prey availability and conditions that favor rapid growth by young percids should minimize predation mortality. Moreover, potential predators on young percids do not rely solely on percids as prey. For example, Ritchie and Colby (1988) found that alternating years of high production of burrowing mayflies, *Hexagenia*, corresponded to walleye recruitment success, leading to the hypothesis that *Hexagenia* served as a preferred prey for potential walleye predators. In addition, Fitzgerald et al. (2006) found that overwinter survival of young yellow perch was inversely related to abundances of alternative prey in gizzard shad and white perch (*Morone americana*). Thus, the presence of alternative prey may serve as important buffers for predation and thereby enhance young percid survival.

In many cases, researchers have documented negative associations between percid year-class strength and abundance of potential predators without demonstrating the exact mechanism underlying such negative associations. For example, Redman et al. (2011) and Forsythe et al. (2012) demonstrated negative associations between alewife densities and yellow perch year-class strength in southern Lake Michigan, USA. Fielder et al. (2007) demonstrated a strong negative effect of

alewives on walleye recruitment in Saginaw Bay, Lake Huron; after the alewife population crashed, walleye recruitment increased dramatically. Mercado-Silva et al. (2007) suggested a negative association by rainbow smelt (*Osmerus mordax*) on young walleye in lakes in Wisconsin, USA, may limit walleye recruitment. While alewife and rainbow smelt are known to consume larval percids, they also consume zooplankton and small benthic invertebrates. Thus, such negative associations may develop through both predatory and competitive effects.

2.5   Adult Mortality

As compared to larval and juvenile fish, adult fish experience much lower mortality rates. Similar to many other moderate- to long-lived fish species, percids display highly variable mortality rates across populations and over time within individual systems. This variability is likely related to the broad set of natural and anthropogenic-induced phenomena that can contribute to mortality of adult percids.

Mortality rates of fishes are often divided into mortality from fisheries harvest and natural mortality. The latter can encapsulate a variety of phenomena, including mortality related to starvation, predation, disease, parasitism, severe temperatures, low oxygen, and responses to biotic and abiotic chemicals. A number of studies suggest that adult mortality rates are size-dependent; e.g., through a cross-taxa analysis of marine fish, Pauly (1980) demonstrated that natural mortality declined with asymptotic length. Similarly, Lorenzen (1996) analyzed annual instantaneous natural mortality rates (M) across a broad set of marine, freshwater, and cultured fish species and demonstrated that natural mortality is size-dependent: $\ln(M)$ scales negatively and linearly with $\ln$(mean mass), such that $\ln(M) = \ln(a) + b \times \ln(\text{mass})$ where b represents a dimensionless scaling parameter. After accounting for mass, Lorenzen's (1996) analysis suggested that mortality rates did not differ significantly among natural environments (lakes, rivers, oceans); however, natural mortality rates were significantly higher in natural systems than in cultured ponds, cages, and tanks. Moreover, Lorenzen (1996) found that the mass-mortality scaling parameter was significantly more negative in culture systems than in natural systems. Lorenzen (1996) attributed this latter finding to the presence of predation in natural systems and argued that non-predation natural mortality must scale more negatively with body size than predation mortality. Specific to percids, Lorenzen (1996) (a) estimated a mass-mortality scaling parameter (b) of roughly-0.4 (which is more negative than the −0.29 value estimated across species and natural systems) and (b) estimated a significantly higher mortality at unit mass compared to natural populations of other similarly-sized species (see Fig. 4 in Lorenzen 1996).

While a variety of phenomena may contribute to individual mortality events, various studies have attempted to describe broad, across-system variation of intra-specific mortality rates in fishes. Blanck and Lamouroux (2007) examined such broad patterns in life-history traits (including longevity and mortality) of European freshwater fishes, and found that latitude had a stronger effect on life-history traits

than habitat type: specifically, higher latitude populations tended to live longer (i.e., lower adult mortality). While Blanck and Lamouroux (2007) included pikeperch (n = 38 populations) in their analysis, they did not appear to find a significant effect of latitude for this percid species. In contrast, Heibo et al. (2005) explored how life-history traits of Eurasian perch varied across latitude and found the expected patterns: mortality decreased with latitude and life-span increased with latitude.

A number of specific natural sources of mortality have been identified for adult percids, despite their relatively low mortality rates. They are susceptible to a variety of diseases and parasites (e.g., Szalai and Dick 1991; Kane-Sutton et al. 2010; Jensen et al. 2011), and disease outbreaks have led to large die-offs of certain populations, e.g., a large die-off of yellow perch in Lake Erie, North America, was associated with viral hemorrhagic septicemia virus (Kane-Sutton et al. 2010). In addition, percids are susceptible to a large number of both piscine and terrestrial predators. Szalai and Dick (1991) estimated a natural mortality rate for yellow perch in Dauphin Lake, Manitoba, Canada as 61 %, with predation by northern pike (*Esox lucius*) accounting for 19 % and 45 % for females and males, respectively. Over the past three to four decades, double-crested cormorants (*Phalacrocorax auritus*) have expanded dramatically throughout North America and high local abundances of these piscivorous birds have been blamed for percid population declines in many systems (e.g., Burnett et al. 2002; VanDeValk et al. 2002; Rudstam et al. 2004; Fielder 2010).

Percids can persist in a fairly broad range of temperatures (Sect. 2.1). Lethal temperatures are dependent on acclimation temperature, but according to Hokanson (1977) the ultimate upper incipient lethal temperature for percids is between 28 and 35 °C. Similarly, percids can tolerate fairly low dissolved oxygen levels. For example, Roberts et al. (2011, 2012) demonstrated that yellow perch can survive and even grow at dissolved oxygen concentrations as low as 2 mg/l. And, percids can tolerate a relatively broad range of pH. Walleye may tolerate a range of 6.0–9.0, while yellow perch may persist in water with pH as low as 4.2 (Schneider et al. 2002). Moreover, Heibo and Vøllestad (2002) did not find a difference in mortality rates of European perch in highly acidic (pH ≤5.0) versus non-acidic (pH ≥6.0) lakes.

While non-fisheries-related mortality is often grouped into a *natural mortality* category, several non-fisheries sources of mortality may be heavily mediated by anthropogenic activities (i.e., they may not truly be *natural* phenomena). For example, humans have contributed to the spread of several pathogens, including ones that target percids and various intentional and unintentional introduced species prey upon and/or parasitize percids. Further, anthropogenic chemical contamination, thermal pollution, and both point-source and non-point-source loading of nutrients can cause oxygen concentration and thermal conditions leading to lethality.

Mortality through fisheries harvest can greatly exceed natural mortality. In fact, collapses of some percid populations have been partially attributed to fisheries harvest (e.g., Marsden and Robillard 2004). In many systems, percids are simultaneously targeted by both commercial and recreational fisheries. While commercial fisheries have historically been blamed for crashes of many fish stocks, declines of some percid populations are undoubtedly related to intense recreational harvest

(Post et al. 2002). Moreover, while direct fisheries harvest may be a major component of total mortality, indirect effects of fisheries practices may also be responsible for high mortality. For instance, by-catch of percids by fisheries targeting other species may lead to high percid mortality (e.g., MacMillan and Roth 2012). Additionally, both recreational and commercial fishing practices which capture percids and then release them back into the environment may nonetheless result in high indirect mortality, as capture and handling may lead to various physiological costs and compromise the short-term and long-term survival of adult percids (e.g., Hyvarinen et al. 2008).

2.6 Conclusions

As we have reviewed in this chapter, percid species represent a suite of highly plastic species capable of thriving in systems ranging from small streams to large lakes and bays. As such, the mechanisms controlling the important vital rates discussed in this chapter (i.e., growth, reproduction, recruitment, and mortality) likely vary both spatially and temporally across different species, populations, and environments. In many systems, percid populations have strong influences on local ecosystem dynamics through predatory and competitive interactions with other species while also supporting valuable recreational and commercial fisheries harvest. Because of their economic and ecological importance, a large body of research, partially reviewed here, exists on many aspects of percid biology and ecology. However, important gaps remain in many areas of percid biology, including, for example, the roles of biotic and abiotic factors in influencing recruitment of populations, the importance of harvest rates on the life history ecology of percid species, and the respective contribution of different sources of mortality to adult longevity and population abundance. Some of these questions remain unanswered partially because percids are such a diverse and widespread group and local environmental conditions, adaptation, and plasticity all likely play a role in population- and individual-level variation. Thus, future research should focus on the level of and causes of observed variation in population traits, and may lead to a clearer understanding of percid biology and its responses to local environmental phenomena. Such information should aid in developing management practices and promoting the persistence of percid populations throughout the globe.

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