Salmonids in New Zealand: Old Ways in New Lands

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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 kōkopu (*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 coexistence 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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