

Predation of Atlantic salmon across ontogenetic stages and impacts on populations

Morten Falkegård ^{1a}, Robert J. Lennox ^{1b}, Eva B. Thorstad ^{1b}, Sigurd Einum ^{1c}, Peder Fiske ^{1b}, Øyvind A. Garmo ^{1d}, Åse H. Garseth ^{1e}, Helge Skoglund ^{1f}, Monica F. Solberg ^{1g}, Kjell R. Utne ^{1g}, Knut W. Vollset ^{1f}, Leif Asbjørn Vøllestad ^{1h}, Vidar Wennevik ^{1g}, and Torbjørn Forseth ^{1b}

^aNorwegian Institute for Nature Research, Fram Centre, PO Box 6606 Langnes, NO-9296 Tromsø, Norway; ^bNorwegian Institute for Nature Research, PO Box 5685 Torgarden, NO-7485 Trondheim, Norway; ^cCentre for Biodiversity Dynamics, Norwegian Institute for Science and Technology, PO Box 8900 Torgarden, NO-7491 Trondheim, Norway; ^dNorwegian Institute for Water Research, Økernveien 94, NO-0579 Oslo, Norway; ^eNorwegian Veterinary Institute, PO Box 4024 Angelltrøa, NO-7457 Trondheim, Norway; ^fLaboratory for Freshwater Ecology and Inland (LFI), NORCE Norwegian Research Centre, PO Box 22 Nygårdstangen, NO-5838 Bergen, Norway; ^gInstitute of Marine Research, PO Box 1870 Nordnes, NO-5817 Bergen, Norway; ^hCentre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, PO Box 1066 Blindern, NO-0316 Oslo, Norway

Corresponding author: Morten Falkegård (email: morten.falkegard@nina.no)

Abstract

Managers and stakeholders increasingly ask whether predation is a driving force behind the poor status of many species, and whether predator control is likely to be a successful management action to intervene. We review existing literature on Atlantic salmon *Salmo salar* predation and predator control, as well as general ecological theory on the role of predation in the life cycle of this iconic fish. Many bird, mammal, and fish predators target salmon at different life stages. In healthy salmon populations, predation is likely compensated for by reduced intraspecific competition during the freshwater stage. There is little evidence that predation alone has been an underlying mechanism for driving salmon populations below conservation limits. However, depending on the predator's response to salmon abundance, predation may keep decimated populations from recovering, even when the actual causes of decline have been removed. Under such a scenario, predation control may contribute to recovery, but there are no strong examples that clearly demonstrate the efficacy of managing predators to recover threatened salmon populations, challenging further applications.

Key words: predators, predation impact, predator species, *Salmo salar*, stock recovery

Introduction

Few species on the planet inspire as much fascination and sympathy as the Atlantic salmon *Salmo salar*. Salmon is a symbol of the native ecosystems in the North Atlantic and of healthy, free-flowing rivers. Indeed, the salmon has an important ecosystem role connecting the distant Arctic and subarctic oceans with oligotrophic coastal waters (Nislow et al. 2004; Williams et al. 2009; Guyette et al. 2013; Auer et al. 2018). Historical overfishing of salmon resulted in the reduction of many salmon populations, and habitat modification, river damming, aquaculture, pollution, disease, biological invasions, and climate change have led to abundance reductions, local extinctions, and range consolidation (Parrish et al. 1998; Forseth et al. 2017). Many contemporary salmon populations in Scandinavia, the Baltics, western Europe, the British Isles, and North America persist at a fraction of their historical abundance, and few salmon populations are performing at peak productivity (Chaput 2012). Consequently, there is a strong need for restoration action that can provide meaningful progress towards

improving the status of the wild salmon (Lennox et al. 2021).

Coincident with the reductions of many wild salmon populations, there has been increasing focus on the potential role that predators may exert on reducing salmon populations (e.g., Harris et al. 2008; Lacroix 2014). Salmon life histories have evolved in the presence of the predation pressure that they experience, from the egg to the adult stage (Table 1), and predation remains a significant part of their life cycle. This is illustrated by co-evolution of complex life cycle parasites, for instance, *Anisakis* sp. and *Diplostomum* sp. that are trophically transmitted from salmon and other fish to fish-eating mammals and birds, respectively (Auld and Tinsley 2015). Predation can also be a highly visible cause of mortality that generates sympathy, and in some cases leave the impression of a simple cause–effect relationship that can be modified with interventions against predators. Salmon predators represent a major conflict point for people, which has inspired a variety of studies seeking to identify mechanistic relationships between salmon populations and their predators to determine

Table 1. Overview of Atlantic salmon predators and a general description of the life stages, habitats, and preferences that they exhibit for Atlantic salmon.

Predator	Description	Key References
Crayfish (Decapoda)	Crayfish are a diverse group of benthic freshwater crustaceans that are occasionally salmon predators. Signal crayfish (<i>Pacifastacus leniusculus</i>) is an invasive species in Europe that can prey on salmon eggs. Large signal crayfish may pose a particularly large threat to salmon by excavating and consuming eggs over winter	Findlay et al. 2015
Sharks (Elasmobranchs)	Sharks can target salmon in the marine environment, predominantly as post-smolts or kelts. Spiny dogfish (<i>Squalus acanthias</i>) are regionally abundant in some areas overlapping with salmon but at least one survey failed to identify any Atlantic salmon smolt predation despite observations that they are predators of Pacific salmon smolts. In the Bay of Fundy, tagged kelts are strongly presumed to be eaten by porbeagle sharks. Shortfin mako and other sharks may also be salmon predators; however, identifying the identity of salmon predators far out at sea is challenging based only on depth and temperature profiles	Morgan et al. 1986; Beamish et al. 1992; Lacroix 2014; Strøm et al. 2019
Lamprey (<i>Petromyzon marinus</i> and <i>Lampetra fluviatilis</i>)	River lamprey has been observed to parasitize Atlantic salmon smolt in Ireland. Sea lamprey may attack salmon in the ocean, but this is little studied	Swink and Hansen 1986; Beamish and Neville 1995; Kennedy et al. 2020
Eel (<i>Anguilla anguilla</i> and <i>Anguilla rostrata</i>)	Eel migrate into rivers throughout the North Atlantic where they feed on invertebrates, fish, and other animal prey, and grow before returning to spawn at sea. There is little known about eel predation on salmon except some observations that they eat salmon fry in Ireland	Piggins 1958; Thomas 1962
Atlantic salmon	Like many other species, salmon can be cannibalistic. Parr can cannibalize fry when they emerge from gravel, and parr will eat eggs deposited by females onto spawning grounds. Adults eat injured parr or mature male parr on spawning grounds	Symons and Heland 1978; Pepper et al. 1985; Cunjak and Therrien 1998; Armstrong et al. 2001; Henderson and Letcher 2003; Johansen et al. 2010; Näslund et al. 2015
Brown trout (<i>Salmo trutta</i>)	Trout are opportunistic predators that feed on salmon eggs, fry, parr, and smolts. Trout are observed on spawning grounds of salmon consuming eggs, and there are multiple lines of evidence that trout are a significant predator of smolts as they migrate to sea. Freshwater resident and migratory trout overwintering in lakes during the spring can consume a large number of smolts, and sea trout may also target post-smolts in estuaries or at sea during their marine phase	Solås et al. 2019; Hanssen et al. 2022; Nash et al. 2022
Charr (<i>Salvelinus fontinalis</i> and <i>Salvelinus alpinus</i>)	Although charr are frequently co-occurring with salmon in northern watercourses, there is little evidence of direct predation by charr on salmon. Charr in Alaska, however, have been observed to be relevant predators of Pacific salmon (<i>Oncorhynchus</i> sp.) smolts. Brook charr (<i>Salvelinus fontinalis</i>) overlap with Atlantic salmon in Canada and the United States and are observed to consume salmon eggs and fry where they overlap in the wild as well as where they have been stocked as non-native species	Ruggerone and Rogers 1984; Legault and Lalancette 1987; Henderson and Letcher 2003
Northern pike, muskellunge, and chain pickerel (<i>Esox lucius</i> , <i>Esox masquinongy</i> , and <i>Esox niger</i>)	The northern pike is a significant piscivorous predator that is native in some salmon rivers and introduced in others. Pike are ambush predators that wait for passing fish and are known to consume large amounts of salmon fry, parr, and smolts, particularly in lakes. Muskellunge are a larger relative of pike native to the eastern part of North America, which was introduced to at least one salmon river in New Brunswick where it is not considered a major threat to the salmon smolts. However, another pike species, the chain pickerel, native to the Atlantic slope and introduced in eastern Canada, are a major predator on salmon and considered to have an important impact on the populations	Larsson 1985; Jepsen et al. 1998; Curry et al. 2007; Nilsson and Eklöv 2018; Svenning et al. 2020
Burbot (<i>Lota lota</i>)	Burbot are benthic predators in rivers and lakes. Burbot predation is thought to be significant in some watercourses, with a general preference for smaller smolts	Larsson and Larsson 1975; Larsson 1977; Larsson 1985
Cods (Gadidae)	Gadiforme fishes include Atlantic cod (<i>Gadus morhua</i>), pollock/saithe (<i>Pollachius virens</i>), and haddock (<i>Melanogrammus aeglefinus</i>) that are known to consume salmon smolts in many estuaries. Where there is alternative prey available, these fish may switch prey and focus less on salmon	Hvidsten and Møkkelgjerd 1987; Hvidsten and Lund 1988; Svenning et al. 2005a
Striped bass (<i>Morone saxatilis</i>)	Striped bass is an amphidromous predator native to North America. Striped bass have extended their range northward in recent years in concert with climate change to areas like Labrador, increasing their numbers in many important Atlantic salmon rivers and estuaries in Nova Scotia and New Brunswick. Striped bass are a well-documented predator of Atlantic salmon smolts as they migrate through the tail of rivers and estuaries where striped bass are effective predators. Striped bass may particularly benefit from salmon passing through dams, including injured individuals compromised by the infrastructure	Blackwell and Juanes 1998; Beland et al. 2001; Gibson et al. 2015; Andrews et al. 2018; van Leeuwen et al. 2021

Table 1. (concluded).

Predator	Description	Key References
Smallmouth bass (<i>Micropterus dolomieu</i>)	Smallmouth bass are an important sportfish in central North America that has been stocked into coastal rivers in the United States and Canada. Smallmouth bass live in both lakes and rivers and are predators that readily consume small fish including Atlantic salmon	Ramberg-Pihl et al. 2023
Zander (<i>Sander lucioperca</i>)	Zander is a large lake-dwelling percid in some rivers of eastern Norway and Denmark. Where present, zander is a significant smolt predator	Jepsen et al. 2000; Koed et al. 2002
Sculpins (Cottidae)	Sculpins are small, benthic fish that specialize in running water, often overlapping with salmon spawning and fry-rearing areas. There are observations of fry predation by sculpins but mixed results as to whether they consume salmon eggs	Gabler and Amundsen 1999; Gaudin and Caillere 2000; Palm et al. 2009
Bluefin tuna (<i>Thunnus thynnus</i>)	Bluefin tuna is a large, marine fish predator, which dive to deep depths and typically hunts small fish, squid, and crustaceans. They may opportunistically take Atlantic salmon during their ocean migration	Strøm et al. 2019
Mergansers (<i>Mergus merganser</i> and <i>M. serrator</i>)	Mergansers search for fish on the surface or dive and chase juvenile salmon in rivers and lakes. Mergansers seem to prefer small salmon that are pre-smolts. Mergansers are frequently found in estuaries during the smolt migration; these are productive areas with abundant alternative prey, which significantly reduce the smolt predation risk	Lindroth 1955; Wood and Hand 1985; Sjöberg 1988; Feltham 1990; Kålås et al. 1993; Feltham 1995; Næsje et al. 2005; Svenning et al. 2005b
Gannet (<i>Morus bassanus</i>)	Gannets plunge-dive into surface waters to capture pelagic prey and they are shown to eat many different marine fish species, including post-smolt Atlantic salmon off the coast of Newfoundland, Canada	Montevecchi et al. (2002)
Cormorants (Phalacrocoracidae)	Cormorants are opportunistic predators that eat a wide variety of fish. Like mergansers, cormorants seem to preferentially predate the smaller smolts. Cormorants have received attention as salmon predators due to dramatic increases in their populations in several locations. In surveys from Denmark and Ireland, estimated cormorant predation on salmon varied from 8% to 79%	Kennedy and Greek 1988; Magath et al. 2016; Bregnballe and Nitschke 2017; Jepsen et al. 2019; Källo et al. 2020
Hérons (Ardeidae)	Hérons are large wading birds that spear fish. In Europe, grey heron (<i>Ardea cinerea</i>) is the most common species, and in North America, it is the great blue heron (<i>Ardea herodias</i>). There is little known about the impacts of heron predation on Atlantic salmon, but blue herons in North America have been observed to consume large numbers of juvenile Pacific salmon (<i>Oncorhynchus</i> sp.)	Miyamoto and Araki 2020; Sherker et al. 2021
Otter (<i>Lutra lutra</i> and <i>Lutra canadensis</i>)	Two species of otters are native around Atlantic salmon rivers, one in North America and one in Europe. Otters in Europe have been greatly depleted, and in Norway, they were locally extinct for many years. Otters are territorial but may be nomadic as well. Otters are fish eaters and therefore directly remove some salmon from rivers, but also eat salmon predators, such as pike and trout and will exclude mink, a potential benefit to the salmon. Otters may eat juvenile salmon, but the major impact is predation of adults, which have few other natural predators	Erlinge 1968; Erlinge 1972; Carss et al. 1990; Ludwig et al. 2002; van Dijk et al. 2020; Sortland et al. 2023
Mink (<i>Neovison vison</i>)	American mink is native to North American rivers and invasive in Europe after escaping from fur farm operations. This is a generalist predator that will readily eat fish, especially in winter time. Mink prefer smaller fish but are generalist foragers. Mink are most effective in smaller rivers and at low flows when salmon are more easily accessible	Gerrell 1967; Gerrell 1970; Heggenes and Borgstrøm 1988
Seal (Phocidae)	Grey seals (<i>Halichoerus grypus</i>) and harbour seals (<i>Phoca vitulina</i>) are predators of salmon post-smolts, adults, and kelts. Both species are generalists, and neither is specifically focused on salmon. Only a part of the population may specialize on catching salmon in short time periods, and a few individuals may move into rivers to catch salmon; however, some populations may not target salmon at all, and studies have not consistently found salmonids to be part of the seal diet	Carter et al. 2001; Wright et al. 2007; Graham et al. 2011; Granqvist et al. 2018; Scharff-Olsen et al. 2019; Leach et al. 2022
Toothed whales (Odontocetes)	Toothed whales are predatory cetaceans, including dolphins. Toothed whales are salmon predators throughout their distribution, especially orca in Canada that specialize on Pacific salmon. Evidence from pop-up satellite archival tag demonstrates predation of salmon kelts by toothed whales based on temperature spikes and diving profiles, which may represent sperm whale (<i>Physeter macrocephalus</i>), beluga (<i>Delphinapterus leucas</i>), or a pilot whale (<i>Globicephala</i> spp.). Orca were recently directly observed consuming Atlantic salmon, and other delphinids may be predators, but direct data are lacking	Vester and Hammerschmidt 2013; Strøm et al. 2019

whether and how predation at different life stages has major population dynamic effects for salmon. We here sought to review evidence related to the impacts of predation on the Atlantic salmon, potential problems arising from predation and predator control, and the evidence available for addressing predation in the Atlantic salmon life cycle. To determine the impact of predation on a salmon population, important questions include how much do the predators eat, which life stages of salmon are targeted, what is the relationship between predation and other mortality causes, and what is the relationship between how many salmon are eaten and the salmon population status. We review and discuss all these questions in the following. The conclusions are drawn from considering knowledge on Atlantic salmon and their predators in a general theoretical framework from population ecology, and the narrative is intended to more broadly address the challenges of managing fish populations confronting predation.

Salmon predators

Salmon is vulnerable to predators at every stage of its life; predators that share the same water, predators that live on land and enter the water to catch them, and even predators in the air that swoop down or dive under the water. Predators range from large apex predators like Atlantic bluefin tuna (*Thunnus thynnus*) and toothed whales (Odontoceti) that eat salmon at sea, to conspecifics like salmon parr eating eggs in spawning redds (Table 1). Native species that salmon have shared rivers and coasts with for thousands of years represent important predators, including the congeneric brown trout (*Salmo trutta*) and closely related Arctic charr (*Salvelinus alpinus*) and brook charr (*Salvelinus fontinalis*; Table 1). Nearly all fish that salmon share a watercourse with, if big enough, will eat salmon eggs, fry, or parr. These piscivores include the northern pike (*Esox lucius*), pikeperch (*Sander lucioperca*), burbot (*Lota lota*), and sculpins (Cottidae). Many rivers and lakes have been affected by the intentional (for recreational fishing) or unintentional establishment of other fish species that are important predators of the salmon, especially pike (where not native), smallmouth bass (*Micropterus dolomieu*), and chain pickerel (*Esox niger*; Table 1). Other species may be shifting their range in response to climate change, including striped bass (*Morone saxatilis*) that are responsible for consuming a large share of salmon smolts migrating from rivers (e.g., Gibson et al. 2015; Table 1). Many marine fish predators may opportunistically take salmon, including cod (*Gadus morhua*) and other gadoid fish, Atlantic halibut (*Hippoglossus hippoglossus*) and Greenland halibut (*Reinhardtius hippoglossoides*) (Rikardsen et al. 2008), Atlantic bluefin tuna (Strøm et al. 2019), and various sharks, including the porbeagle (*Lamna nasus*) (Strøm et al. 2019).

Predation by fish is less visible to humans than predation by birds, which hunt fish from the shore, the air, or directly underwater. Herons (*Ardea cinerea*) hunt juvenile salmon in nearshore margins of rivers and lakes, mergansers (*Mergus merganser* and *Mergus serrator*) dive in slow flowing sections of rivers and lakes, and ospreys (*Pandion haliaetus*), cormorants (*Phalacrocorax* spp.), corvids (Corvidae), and dippers (e.g., *Cin-*

clus cinclus) will take migrating smolts directly out of the water. Predation by birds also occur in the marine phase, e.g., gulls (*Larus* spp.) and gannets (*Morus bassanus*) are shown to prey on post-smolts (Montevecchi et al. 2002; Thorstad et al. 2013).

Marine and semi-aquatic mammals target salmon at all life stages and in all habitats. Seals and toothed whales can eat fully grown fish as they travel through marine waters. Some harbour seals (*Phoca vitulina*) are observed to specialize as salmon predators during the migration period, although the species is mostly a generalist that will take whatever species is most available (Table 1). Pop-up satellite archival tag data have revealed several salmon in the open sea to be consumed by toothed whales based on temperature peaks and dive profiles (Strøm et al. 2019). Otters (e.g., *Lutra lutra*) in small rivers can also take adult salmon (Sortland et al. 2023).

Vulnerability to predation at different life stages

Salmon eggs are an energy-rich and popular food source for both birds and fish during the spawning period, and predatory trout and sculpin, along with cannibalistic salmon juveniles or juveniles of other salmonid species, can loiter around spawning grounds to snatch eggs from spawning females before they can be buried in the gravel (Cunjak and Therrien 1998; Näslund et al. 2015). Eggs drifting away from the redd with the water current are those mainly eaten. Such eggs will not survive in any case. Due to the large mortality from the egg stage to the end of the first summer in the river, egg predation is most likely not impacting the total smolt production from rivers.

Salmon fry are vulnerable to predation but the impacts are relatively small because there is strong density-dependent regulation of salmon populations in the juvenile phases, often related to shelter availability (see section on Vulnerability to different life stages below). As the salmon grows, it becomes less vulnerable, and predation more directly affects smolt production.

Atlantic salmon smolts undergo morphological, physiological, and behavioural changes to prepare for seaward migration. In some rivers, smolt mortality can be very high (Flávio et al. 2020) due to predation by trout (Hanssen et al. 2022), pike (Kekäläinen et al. 2008), and birds (Marquiss et al. 1991; Feltham 1995). Predators, such as pike, may aggregate at migration bottlenecks to target smolts (Kennedy et al. 2018). Vulnerability to predation seems to differ among size classes such that larger smolts have better survival (Gregory et al. 2019). Predation may also be higher for fish injured by turbines or affected by disease (Zydlowski et al. 2010) such that predation is partly compensatory. Predation risk also differs markedly among rivers depending on the habitat type, with lake habitats especially challenging for salmon to navigate through (Lennox et al. 2021).

Post-smolts enter the ocean in spring as the water is warming. Although there is little evidence that predators migrate to river mouths to capitalize on the seasonal pulse, marine fish and birds can eat a substantial share of post-smolts during the early marine migration (Hvidsten and Lund 1988;

Jepsen et al. 2006; Thorstad et al. 2011, 2013). Outside River Surna (middle Norway), cod were implicated in 25% of smolt mortality (Hvidsten and Møkkelgjerd 1987). Alternative prey can buffer predation on smolts, for example, in the Tana River estuary (northern Norway), putative predators were mostly eating herring (Svenning et al. 2005a). Birds are also known to target smolts during their marine migration, for example, gannets in Canada (Montevocchi et al. 2002). Once arriving to the open ocean from the coast, salmon become vulnerable to large pelagic species. Pop-up satellite archival tags have revealed predation of Atlantic salmon kelts by toothed whales, cod and halibut, porbeagle shark, and bluefin tuna, and with higher mortality for southern than northern populations (Strøm et al. 2019).

As salmon return to coastal areas, they begin to overlap with harbour and grey seal (*Halichoerus grypus*) foraging grounds (Middlemas et al. 2006). Harbour and grey seals are generalist predators and salmon do not seem to comprise a major share of the diet even though they certainly catch and eat salmon in many regions (Carter et al. 2001; Matejusová et al. 2008; Sharples et al. 2009). There are indications from the Baltic Sea that declining post-smolt survival can be attributed to increased grey seal abundance (Mäntyniemi et al. 2012). Toothed whales, such as orca (*Orcinus orca*), which is a substantial predator of Pacific salmon returning to coastal areas, have also been observed to consume Atlantic salmon returning to northern Norway (Vester and Hammerschmidt 2013). Porpoise (*Phocoena phocoena* and *Tursiops truncatus*) may also attack salmon, and 5%–25% of returning salmon in Scotland had injuries consistent with attacks by some sort of marine mammal, suggesting predation pressure can be an important source of natural mortality for the population in the final phase of the marine migration.

Adult salmon have few predators in freshwater aside from humans. However, seals are known to occasionally swim up from estuaries into rivers to eat salmon. Moreover, Eurasian otters are zealous predators of salmon in freshwater and have been observed to kill salmon before, during, and after spawning (Carss et al. 1990; Sortland et al. 2023). Predation after spawning may reduce the number of repeat spawners in a population but in general, will be less impactful than predation before spawning. Such predation may also represent compensatory mortality if salmon are killed when near to death because of exhaustion, disease, or other factors that naturally limit post-spawning survival of Atlantic salmon. Sortland et al. (2023) noticed that predation was much more prevalent in a small river than a medium-sized river in western Norway and otter predation may be even less important in large rivers where salmon can more easily hide or escape.

Effects of predation on individual salmon

Predation can impact individual salmon both directly and indirectly. Direct effects are the capture and consumption of the individual, and indirect effects are mostly fear effects that impact behaviour and the distribution of individuals in their habitat (Laundré et al. 2014). Direct effects on individuals are most frequently lethal but can also maim animals, reducing

fitness by altering performance or sexual competitiveness because their features have been disfigured. Indirect effects of predators on performance can alter growth by excluding individuals from promising feeding opportunities, a concept termed landscape of fear (Laundré et al. 2014). Exposure to a decoy duck, for example, reduced the foraging of salmon in an experiment by Dionne and Dodson (2002). Such fear effects may have cascading effects on growth, maturation, and reproduction and can generate selective effects that determine the trajectory of evolution within a population.

Not all individuals from a population are equally vulnerable to predators. Size selection is one of the determinants of the magnitude of effects of predation on salmon populations (Gregory et al. 2019). If a predator selects small rather than large individuals, the individuals being eaten may have been more vulnerable to other sources of mortality, such as starvation. This may affect the population size less than when a predator selects the larger individuals, because in that case, it may be those with the greatest chance of later survival that are eaten by the predator (see section on additive versus compensatory mortality below). Several sources identified predators preferring smaller size classes of salmon (mink: Cuthbert 1979; merganser: Feltham 1990; Kålås et al. 1993; Marquiss et al. 1998; trout: Solås et al. 2019). An example of selection by sex was shown by Carss et al. (1990), who found male-biased predation of adult fish by otters in a UK river.

When an individual salmon is eaten by a predator, predation may have been either the proximate or the ultimate cause of death. When predation is the ultimate cause of death, it implies that a healthy individual was eaten and that predation was the reason for the animal dying, and there was no other underlying cause that could explain the increased likelihood of the death of the individual. Otherwise, predation may be the proximate cause of death; the most visible reason that the animal died, but not the primary, underlying factor. For sick, weak, disfigured, or otherwise less-fit animals that would fail to reproduce or simply die of other causes, predators may remove them from the population before they meet an alternative end (Milinski and Löwenstein 1980; Genovart et al. 2010; Krumm et al. 2010). This is one of the reasons why e.g., simple diet studies showing the extent to which salmon are eaten by different predators are not sufficient to evaluate the impact of predation on salmon populations, because they only identify the proximate cause of death. In practice, such simplified studies end up overestimating the significance of predation and provide a false image of the impact of predators.

Determining whether predation is a proximate or an ultimate cause of death is challenging. Thorstad et al. (2013) exposed Atlantic salmon smolts to aluminium and acidification and recorded the post-smolt mortality during the first phase of the marine migration in a combined laboratory and field experiment. Exposed groups had elevated mortality compared to the control group, showing that water quality was a factor implicated in the likelihood of mortality, but identification of predation events upon the tagged fish indicated that the proximate cause for mortality for many of the exposed fish was predation.

Effects of predation on populations

In most cases, the main parameter of interest for management when considering population effects of a predator is the effect it has on the population abundance at a given life stage, which in turn depends on the realized population growth rate at a given population abundance. Population growth is a function of births, deaths, and migration into and out of the population. Yet, understanding predation effects on population growth presents a challenge for two reasons. First, while predation can increase the rate at which individuals in a population are dying during a certain life stage, this does not necessarily translate into an equivalent effect on population growth. Second, predation rates are not constant, but rather can often be expected to respond to prey density, which in turn means that effects of predation on population growth can interact with other environmental stressors. Below, we outline the theory behind these two aspects of predation effects and how they may apply to Atlantic salmon.

How does predation rate translate to population growth?

Effects of predation on salmon population growth depend on to what degree the mortality is additive or compensatory. If predation mortality is additive, it comes in addition to other sources of mortality, and there are no benefits incurred by the population during later life stages that can counteract the negative effects of predation on population growth rate. In this case, predation mortality provides a proportional contribution to population growth rate. In contrast, if predation mortality is compensatory, the reduced population density results in a decrease in other causes of mortality (e.g., starvation, parasitism, and disease) such that total mortality from egg to adult changes less than what might be expected by considering predation mortality in isolation (Fig. 1). Alternatively (or additionally), the higher predation mortality at one life stage due to predation may be compensated for by a higher per *capita* reproductive success among breeding individuals, either because breeders that have experienced a lower density throughout their lives due to predation have achieved better growth conditions and thus a larger body size, or because of lower breeder density and less competition for suitable breeding grounds (however, the latter mechanism may be of less relevance for salmon managers attempting to maintain large spawner runs). Finally, compensation may occur if predators select prey individuals with a low expected fitness (e.g., individuals in poor health or of small size).

For Atlantic salmon, extensive experimental and observational studies have yielded considerable insights into the question of density dependence, which can be applied to understand potential population effects of predation. There is strong evidence for salmonid populations in general (review in Grossmann and Simon 2020) and for Atlantic salmon populations (review in Einum and Nislow 2011) to be regulated by density dependence during their juvenile freshwater life. Thus, density-dependent growth and survival are likely important compensatory mechanisms for the effects of predation in this species. The effects of density regulation

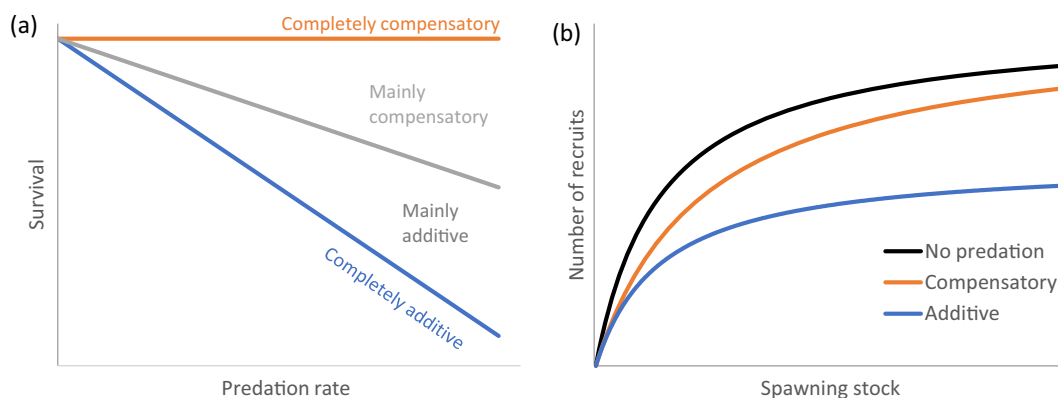
are evident at the population level, as shown by asymptotic or dome-shaped stock–recruitment relationships (Chadwick 1982; Jonsson et al. 1998; Prevost and Chaput 2001; Prevost et al. 2003). This implies that in Atlantic salmon populations, an increasing number of spawners will result in an increasing number of offspring (parr or smolts; Fig. 1) but will reach a maximum asymptote (or peak) at a level representing the production potential of the salmon population and the largest number of offspring that can be produced in a given river based on spawning ground area and accessible resources for the juveniles (Fig. 1b). In contrast, there appear to be no density regulation in the marine phase of Atlantic salmon (Jonsson et al. 1998). Thus, if we consider effects of predation on adult returns to rivers, a generalization might be that predation on juveniles in fresh water may be partly compensated, whereas predation at sea will be additive. Yet, more detailed knowledge about salmon juvenile biology may suggest that the potential for compensation in freshwater can often be limited. Upon emergence from nests, juveniles establish feeding territories (Keeley and Grant 1995), are strongly limited in the type of habitat that they can utilize with respect to water current velocity (Nislow et al. 2000; Armstrong and Nislow 2006), and show little willingness or ability to successfully disperse away from their nest areas to evade patches of high density (Einum and Nislow 2005; Einum et al. 2008; Foldvik et al. 2010). This results in strong local competition and density-dependent mortality during the first few weeks of their lives (Einum and Nislow 2005; Teichert et al. 2013). In contrast, later juvenile stages are more mobile and respond to high local density by dispersing to less-populated stream reaches (Einum et al. 2006; Teichert et al. 2017). This suggests that density-dependent mortality on the population level will be most intense during the first summer of their lives, and that predation that occurs at older stages to a lesser extent will be compensated. In some cases, such as in streams dominated by substrate suitable for spawning and where larger juveniles have poor access to shelters, density-dependent mortality can be significant for parr as well (Finstad et al. 2009; Teichert et al. 2013). However, it seems reasonable to assume that in most cases, predation on Atlantic salmon older than young-of-the-year is unlikely to be completely compensated prior to the return of adults to the stream, and thus is likely to cause some reduction in adult returns.

How does predation rate interact with other environmental stressors?

Currently, Atlantic salmon populations are experiencing a range of environmental stressors, and it seems likely that the management concerns about the role of predators will be particularly pronounced for populations that have experienced declines in abundance for other reasons (Forseth et al. 2017; Lennox et al. 2021). This makes it particularly important to evaluate to what extent predator impacts on salmon populations may depend on salmon population density.

Individual predators change how much they eat relative to the prey density, which is termed a functional response de-

Fig. 1. (a) The effect of increasing predation rates on the survival of individuals in a salmon population determines the extent to which predation produces additive or compensatory mortality. If the predation is completely additive, each increase in predation will give an equal decrease in survival (blue line). If the predation is completely compensatory, an increase in predation will not affect overall survival (orange line). (b) Conceptual stock recruitment curves showing the relationship between spawning stock size and number of offspring with and without predation. Orange and gray lines show the relative effect of predation with mainly (or partially) compensatory and additive mortality. In both cases, 40% mortality from predation has been used, either on the spawning stock to simulate mainly (or partially) compensatory mortality, or on the offspring to simulate additive mortality.



describing the relationship between the average number of a prey that can be eaten by a predator per time unit relative to the density or abundance of prey (Holling 1959a, 1959b, 1965). The shape of this response is determined by different factors, such as the degree to which predators shift between different prey types in response to their relative abundance, and to what extent per capita food consumption becomes limited by time used for prey handling or satiation as the prey abundance increases. However, the crucial insights provided by this theory is that, depending on the functional response of the predator, mortality rates in the prey may either increase or decrease with increasing prey abundance. For example, a certain predator species may at any given time specialize on the single most common prey type available and ignore a given prey when it becomes rare. This will lead to low predation rates when the prey is at a low abundance and increasing predation rates with increasing prey abundance (it may decline again at even higher prey abundances, e.g., due to predator satiation). In contrast, other predators may catch their prey more indiscriminately, independent of their relative abundance, which can lead to high predation rates even when the prey abundance is low. Thus, it is predators imposing this latter type of response that may be particularly worrying for populations that experience additional environmental stressors.

In addition to the functional response, predator movements may also influence the potential for predator impact to depend on prey abundance. Predators may move among locations depending on the abundance of their prey. Such aggregative responses vary considerably among predators based on their mobility and ecology, and especially because of their relationship to the prey species (Peterman and Gatto 1978). Aggregative responses also manifest as co-migration, where predators migrate in synchrony with seasonal availability of their prey. Efforts to determine whether predators

have aggregative responses to salmon have not been conducted comprehensively. Hvidsten and Møkkelgjerd (1987) found indications for cod to aggregate in the estuary of River Surna to prey on outmigrating smolts during spring. Lennox et al. (2019) investigated co-migration of sea trout with the smolt run of salmon in a Norwegian river and found that the trout were not synchronizing their movements to exploit the smolt migrations in their marine environment. However, Kennedy et al. (2018) suggested that northern pike aggregated at river outlets into lakes where they could target migrating smolts in the spring. If they do this irrespective of the smolt cohort abundance, this will likely lead to higher mortality rates in years with low smolt abundance, but this remains unknown. Other marine predators and birds may flock towards rivers in the spring but too little is known about their movements to understand whether there is a strong aggregative response that is mechanistically linked to the salmon, and whether the extent to which they do this depends on the smolt cohort abundance.

Finally, the link between the population dynamics of predator and prey should be considered. The abundance of predators may be coupled to the abundance of prey species. Specialist predators that are tightly coupled to their prey will have population cycles because of the boom–bust dynamics of the prey and the demographic response of the predators (Krebs 1996). During the downcycle phase of the predator, the prey population can recover. In contrast, generalist predators can more effectively switch prey and persist through low densities of specific prey species, potentially maintaining high rates of predation when their preferred prey re-emerge (Smout et al. 2010). These generalist predators are therefore more likely to result in high mortality rates in the prey when the prey are at a low abundance.

For situations where a predator imposes a high mortality rate in their prey even as the prey abundance becomes low,

and where the prey population is pushed down to low densities due to some temporary environmental disturbance, three scenarios may occur. First, the prey population growth rate may become negative for both the current and all lower population densities, in which case the population will go extinct. Second, following the environmental disturbance, population growth rates increase again, and the population returns to its former state. Finally, the prey population may become stuck in a predation pit (Box 1), representing a new alternative stable state and being unable to reproduce sufficiently to achieve prior productivity even after the environmental disturbance has ended (Smout et al. 2010; Ward and Hvidsten 2011). Theoretical studies have shown that predation pits may occur in situations with different functional response types, with alternative prey type, through different feedback mechanisms between organisms in an ecosystem, with age-structured predation, and if a certain degree of the predation is stochastic (May 1977; Smout et al. 2010; Pavlová and Berec 2012; Clark et al. 2021; Box 1). It will, however, be difficult to predict the probability for the establishment of a predation pit, as detailed quantitative knowledge about these factors is rarely present. Simulations show that the predation pit probability increases with decreasing densities of alternative prey (Smout et al. 2010) and increasing stochasticity (Clark et al. 2021).

When salmon populations are demographically stuck in a predation pit, the normal compensatory processes that would otherwise allow them to re-populate with great efficiency, instead yield to increased predation rates and reduced population growth. In such scenarios, predation often operates as a synergistic factor with other mechanisms of mortality. In the Kootenays in Canada, the collapse of sockeye salmon (*Oncorhynchus nerka*) resulted in an increase in the predation rate by rainbow trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) from about 29% to over 70% predation mortality (Warnock et al. 2022). Although the collapse was not initiated by the predators, the demographic precarity of the population following overfishing seems to have rendered the juveniles easy to find and take for the predators. Because rainbow trout and bull trout populations do not decline in response to sockeye population reductions, they can maintain a high predation rate at low prey densities by opportunistically capturing vulnerable sockeye, a potential predation pit that could be challenging for the sockeye to climb out of.

When is predation problematic?

Salmon has always evolved in sympatry with predators. The salmon life cycle has clearly developed in response to pressure from predators, burying eggs in substrate to conceal them from predators and migrating to a vast and risky ocean despite abundant predators, in search of rich feeding areas in the ocean. Although predators have played a critical role in shaping the life cycle of salmon, there is little doubt that predation can challenge contemporary salmon populations that are destabilized by myriad stressors throughout the lifecycle. There are particularly four situa-

tions when predation may influence the population size of salmon.

The salmon population is reduced to low levels

In several cases, it has been shown that it is difficult to rebuild fish populations, even when the factor that caused the decline is removed (Hutchings 2000; Keith and Hutchings 2012). Marine fish stocks suffering overfishing may be an example of this, such as the cod populations of Newfoundland and the Baltic Sea (Swain and Benoit 2015; Neuenhoff et al. 2019). The ability of a population to recover and increase in abundance depends on how large the population decline was. In salmon populations, impacts from e.g., aquaculture, hydropower regulation, other habitat degradation, or overfishing may reduce the stock to below conservation limits (i.e., the spawning stock level below which recruitment would begin to decline significantly). If salmon populations do not recover in such situations even after the cause of this reduction has been removed, this indicates that the population growth rate is at an equilibrium where population growth is hindered by predation, i.e., being in a predation pit, as described above and in Box 1.

An important message to managers is that a large reduction in salmon population size relative to a conservation limit should be a warning signal, because it will be increasingly difficult to rebuild the population from lower levels, due to predator-driven Allee effects. This is particularly the case when predation is an important source of mortality. Rivers with few hiding places from predators, few periods without predation, or with the most important predators being generalists that can be expected to target salmon as the salmon abundance declines may fit this description. Such processes are often not visible before the salmon population for other reasons is at a low level.

Predation rates are exacerbated due to human activity

Predation can be a synergistic stressor with other main effects, especially with human impacts on the river that modify the temperature, flow, habitat availability, water quality, or exposure to other stressors, such as disease or parasitism. Humans have dramatically altered rivers throughout the distribution of salmon; effects such as barricading and channelizing rivers can reduce shelter or create stopping points that aggregate salmon and make them vulnerable to predators. Hydropower regulation can lead to warmer water in winter, reducing ice cover and exposing eggs and fry to predators, such as diving ducks (Corser and Wilcox 2019). As juvenile salmon grow and smoltify to migrate to sea, they may encounter infrastructure, such as dams or reservoirs. Reservoirs have created novel habitats for pike and zander, greatly altering the relationships between predators and prey in favour of the predators. Such species may be of particular concern if the reservoirs contain alternative prey (i.e., other fish species), allowing them to act as generalist predators with a potential to create predation pits (Box 1).

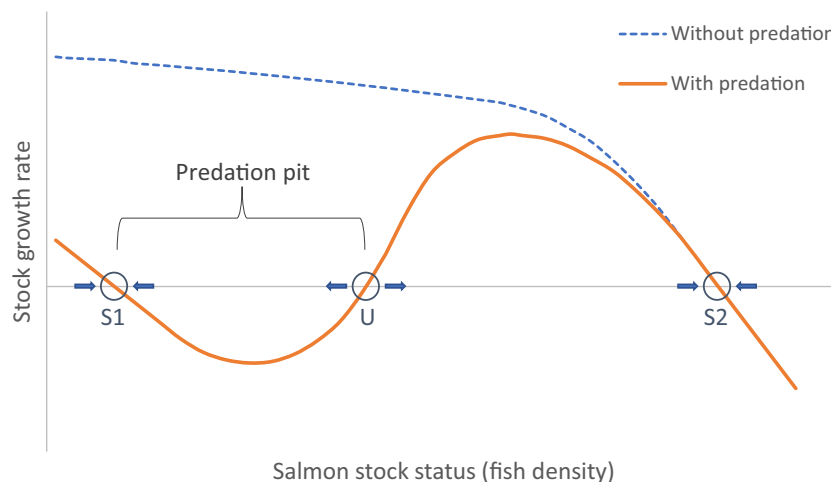
In two Danish studies (Jepsen et al. 1998; Aarestrup et al. 1999), it was estimated that 90% of the smolt died in the reser-

Box 1. Predation pits

Generalist predators, when numerous, can keep salmon populations at a low level, in a so-called predation pit (Smout et al. 2010). Predation pits occur when population recruitment becomes limited due to the force exerted by predators on the prey population, even as the latter declines to a low abundance. For instance, this will be the case if predators are able to maintain their population size through access to alternative prey while still opportunistically taking salmon, thereby maintaining the predation pressure on salmon with decreasing salmon population density.

An illustration of this is shown in the figure below, where the orange line shows the trajectory of a prey population that is forced into a predation pit. In the simple conceptual model without predation (dashed blue line, Fig. B1), only the density-dependent dynamics alters the growth rate of the population. If the mortality from predation is added, the relationship between population density and growth rate changes, and how this change will look like depends on the characteristics of the predator, for instance, which functional response the predator has, and the illustration below is one example.

Fig. B1. A description of the regulation of a prey population with density dependence, shown by the relationship between the density of salmon in a population (for instance the size of the spawning population from year to year) and how population increase and decrease impact the density of salmon. The dashed blue line shows the growth rate of the population without predation, while the orange line shows the growth rate with predation. The horizontal gray line shows a growth rate of 0, and the cross-points on this line show possible equilibrium points. Two of the points (S1 and S2) show stable equilibrium points (shown by arrows pointing towards the point), while the third cross point, U, is an unstable equilibrium point (shown by arrows pointing away from the point).



In the absence of other impact factors on the population, recruitment at population densities that intersect the horizontal axis at the stable equilibrium points (S1 and S2) results in a stable population size. Sometimes, poor conditions may lead to extra mortality and reduced population density, and the population will end up to the left of an equilibrium point, before a positive growth rate will cause the population to increase again (illustrated by the small arrow to the left of the equilibrium points S1 and S2, Fig. B1). On the opposite side, good conditions may result in reduced mortality and cause increased population density such that the population ends up on the right side of the equilibrium points. A subsequent negative population growth will then result in a reduced population density. In practice, the equilibrium points will be positioned at the long-term average of stochastic factors, because in nature, in addition to density-dependent dynamics, there will be factors that cause stochastic mortality from year to year and result in variation in the recruitment around an equilibrium point.

In this illustration, the increase in the population growth to the far left in the figure results from a predator that does not cause increased mortality at very low salmon densities. When the density of salmon becomes sufficiently large, the relative efficiency of the predator will increase fast and lead to a higher mortality and reduced population growth of the salmon. At even higher densities of salmon, factors, such as the handling time of individual prey, or when the predator becomes satisfied, will result in predation not increasing any longer. This again allows for a higher growth rate of the salmon population, as shown in the right half of Fig. B1. The theoretical framework for such a pattern with density-dependent predation at low population density and reverse density-dependent predation at high population density is further described by Sinclair and Pech (1996).

A predation pit occurs if the salmon prey population has two equilibrium points; one at low and one at high density (S1 and S2, Fig. B1), and when there is a negative population growth between these two points. Such a pattern in population growth has significant management consequences. When the population is at a level shown to the right half of the figure, in the area with positive population growth, the tolerance to fishing mortality or other negative impacts of human activities is relatively high. But if the population ends up in the left half, the problems will escalate if the impact continues. This is because the intercept in the middle (U) is an unstable equilibrium, and the population density to the left of this point is an area with negative growth that will quickly move the population to the left, to the lower equilibrium point S1. An area with a negative population growth (between S1 and U, Fig. B1) is termed a predation pit because the mortality from normal predation at low density of salmon is high enough to keep the salmon population at a low equilibrium level, perhaps even if the mortality from the human impact is significantly reduced or even removed. This situation has severe consequences for salmon populations.

voirs, where pike accounted for more than half of the mortality and birds for a third. Damage caused by collisions with rotating turbine blades and other structures, as well as sudden pressure changes, can lead to both direct and indirect mortality as injuries and disorientation can lead to predation (Ruggles 1980). Below a power station, damaged smolt will be an easy prey for predators, for example, around 70% of the radio tagged smolt was taken by predators below a power plant in Gudenå in Denmark (Koed et al. 2002). Fishways trying to move salmon beyond barriers have provided hiding spots for invasive Wels catfish (*Silurus glanis*) where they target the adult fish (Boulêtreau et al. 2018). Water quality has also been shown to affect behaviour and predation risk of juvenile salmon, for example, salmon tethered in an acidic stream in Canada suffered higher predation rates than counterparts in neutral control sites (Elvidge and Brown 2014). Tests with toxin exposure have also revealed important consequences for juvenile salmonid behaviour (Moore et al. 2007) and predation (Hatfield and Anderson 1972). These chemicals include anxiolytic pharmaceuticals that enter watercourses and can alter the boldness of salmon, resulting in increased predation (Klaminder et al. 2019). Post-release predation may also be enhanced in rivers where seals or otters can capture tired fish that are released by recreational fishers (Raby et al. 2014). It is important to point out that when other human impacts result in increased predation rate of salmon, it is not the predator that is the ultimate cause for the population decline. Even though predation is the endpoint for individual fish, it is important for the management to identify and mitigate the ultimate cause for the increased predation risk and eventual population decline.

Alien species

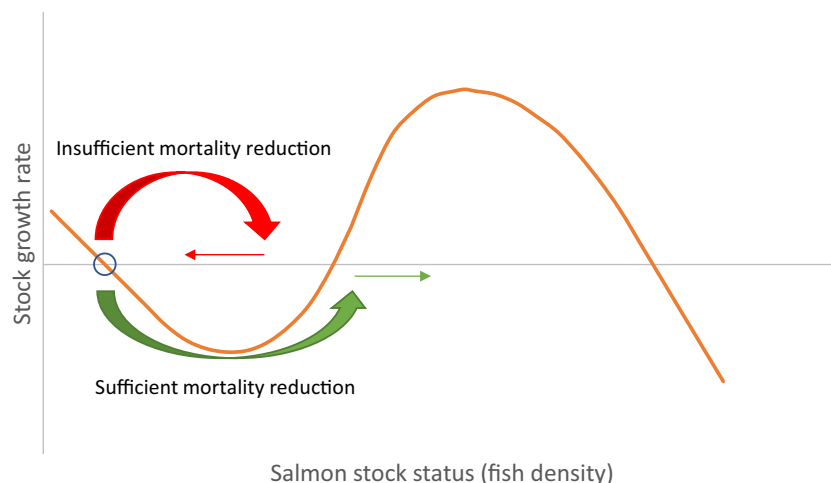
Alien species have been transported beyond the species' native range; alien predators are a major driver of global biodiversity loss as they have escaped regulation by predators and pathogens that help regulate them in their native distribution (Doherty et al. 2016). Invasive species have become salmon predators throughout the entire distribution of salmon. Several invasive fish species have emerged as important predators of juvenile salmon, most notably, several esocid species. The northern pike is a major predator where it has invaded Atlantic salmon rivers, as is the chain pickerel. Suitable refuge from pike predation seems to be a factor de-

termining the extent of pike predation as a mechanism for mortality of juvenile salmonids based on research from the Pacific (Sepulveda et al. 2013). In Canada, smallmouth bass has invaded rivers in Nova Scotia and New Brunswick and is considered a significant threat to the survival of juvenile Atlantic salmon (Ramberg-Pihl et al. 2023). The striped bass in Canada is not invasive but now represents a major predator of Atlantic salmon smolts in rivers and estuaries (Gibson et al. 2015), including below power stations (Andrews et al. 2018). Biological invasions are challenging problems to overcome for fisheries managers, particularly where they are intentionally stocked; stopping the spread of invasive predators is easier than eliminating them once they establish. Furthermore, many of the invasive species are generalist predators, enabling them to become invasive in the first place, and may therefore be particularly relevant to consider in a predation pit context (Box 1).

Climate interactions

Warming has the potential to destabilize salmon populations where their predators outperform them in warming lakes, rivers, estuaries, and in the open sea. Atlantic salmon is a cold-water species that is vulnerable to temperature warming beyond about 20 °C (Elliott and Elliott 2010). Climate change is accelerating the rate of global warming, particularly in freshwater, which threatens the physiological performance of Atlantic salmon, including swimming (Thorstad et al. 2021). Salmon are expected to have some local adaptations to thermal regimes (Anttila et al. 2014) and their predators will also adapt. However, warming of rivers may tip the balance towards predators if they maintain performance better than Atlantic salmon do. This may be particularly true for invasive predators that are often characterized as being physiologically flexible and tolerant (Zerebecki and Sorte 2011). Experimental evidence of the interplay between predator and prey performance suggests that northern pike are ineffective trout predators below 11 °C but very effective above 11 °C (Öhlund et al. 2015), but field evidence is lacking. When adult salmon return to freshwater from the ocean to spawn, warming estuaries and rivers may delay their migration and promote inactivity (Baisez et al. 2011), which can render them vulnerable to predation when they fail to elicit appropriate escape responses or diligence due to the physiological overloading. Although there are many unknowns about the tra-

Fig. 2. Example of a possible reconstruction of a salmon stock that has ended up in a predation pit and has a density at a low equilibrium level (crossing point marked with a circle). If the mortality reduction is too low (shown with a red arrow), the population effect will be too low to get past the area with a negative growth rate. With a sufficiently high reduction in mortality, the population will emerge from the density range with a negative growth rate and the population will rebuild.



jectory of salmon populations in response to predation in a warming world, it can be predicted that endothermic species and warm water-adapted ectotherms will become increasingly problematic predators of salmon in warming rivers.

Predation and the restoration of reduced salmon populations

Predation rarely instigates the collapse of prey populations due to compensatory mechanisms, and we have found no examples describing such events for Atlantic salmon in the scientific literature. As discussed above, predation is problematic in some specific instances, most of which are attributable to human interventions, often through multiplicative stressors, that have created reduced population sizes. If high mortality due to human impact is not compensated by mitigation effort, this can contribute to a continued reduction in population size, where the relative negative impact of predators increases. The population can enter a predator pit that is hard to escape where the population stabilizes at a low level, or in worst case, can go extinct.

If a population is reduced to population sizes far below the conservation limit, there is a need to develop a restoration plan with mitigation measures that will contribute to decreased mortality or increase production. The most important mitigation measure will be to remove or reduce the human impact that has reduced the population. A high natural mortality rate when there are few salmon left may necessitate strong mitigation efforts to increase the population size above the low density where Allee effects are acting a potential predation pit (Fig. 2; Box 1). It is relatively easy to reduce a salmon population to a low density due to human impacts, such as aquaculture, hydropower development, other habitat destruction or overfishing, but when the population is reduced, increased mortality from predation may hinder the rebuilding of the population and an increased abundance.

The risk of such effects calls for a precautionary approach, including implementing relatively small measures to keep the salmon population safely above possible tipping points, rather than having to implement large and costly measures later.

Increasing productivity by removing stressors may be an important and actionable way to buffer the impacts of predation. Barriers in rivers can negatively affect sediments and the availability of hiding places for juvenile salmon, and shoreline development or channelization can eliminate suitable undercut banks or areas that salmon use as refuge from predators. Restoring habitat and connectivity can be an important factor in improving population productivity, which may help lift some populations out of predator pits. The best available evidence suggests that interventions aiming to restore salmon populations affected by predation should focus as much as possible on identifying and resolving the driving factors behind the population's demise while considering predation as a potential synergistic factor.

If natural mortality cannot easily be adjusted by management, a second lever is available, which is altering the number of individuals in a population. A common way in which this is conducted is to cultivate and release salmon, thereby increasing the number of eggs, fry, parr, or smolts in the population. Assuming that the attack rate of the predators is largely density-independent, this will serve to reduce the share of natural mortality experienced by the population, releasing more individuals and kickstarting recovery of the population by lifting the population out of the predation pit (Box 1). Hatchery cultivation does not, unfortunately, work so elegantly in practice. Hatchery-reared individuals have reduced fitness compared to wild counterparts (Milot et al. 2013) and may be more vulnerable to predation themselves (e.g., Hawkins et al. 2004; Jackson and Brown 2011; Thorstad et al. 2012). Solås et al. (2019) emphasized how challenging this is, showing that enrichment efforts to improve fit-

ness of hatchery fish were insufficient to buffer the predation salmon that were exposed when released to the wild. Hatcheries should only be used as a last resort to forestall extinction and where efforts are being made to identify and resolve stressors that are affecting the production of the population (Lennox et al. 2021; Thorstad et al. 2021). In addition, it is important to point out that if hatchery fish are added to a system, predator's aggregative and numerical responses to the hatchery fish may lead to increased predation on the few remaining wild fish (Alvarez and Ward 2019).

Does predation control work?

Humans have endeavoured to control predators for millennia, trying to limit the abundance and distribution of predators to protect property, increase yields available to hunting or fishing, and enhance human safety. There are many efforts to manage salmon predators, both sanctioned and unsanctioned, throughout the distribution. Ducks and seals are shot, otters and mink are trapped, and trout, pike, and other fish are captured or netted and discarded. Ideally, evidence that predators are the main factor regulating salmon abundance should be available before initiating management. However, efforts have largely failed to identify such a relationship. Harris et al. (2008) concluded a review of bird predation on salmon in Scotland finding a lack of clear evidence to support the prediction that birds were controlling salmonid abundance. A global meta-analysis of cormorant (Phalacrocoracidae) predation on fish identified no significant relationship (Ovegård et al. 2021). Carter et al. (2001) found that harbour seals in rivers Dee and Don were eating Atlantic salmon and sea trout but also a variety of marine species, such that the impact of the seals on salmon was not considered to be a major mortality factor.

In general, evidence that removing predators is helpful is weak at best. Yodzis (1998) and Morrisette et al. (2012) conducted modelling exercises to determine whether it would be advantageous to cull marine mammals and release the fish that they consumed to fisheries but found that these efforts would most likely be in vain, potentially even decreasing fisheries yields in the process. Killing some predatory animals will usually be compensated for by local immigration. In Canada, 954 ducks were shot along the Atlantic salmon River Restigouche (Anderson 1986) and in the Dee, 49 ducks were shot (Marquiss et al. 1998); neither case substantially reduced the number of ducks nor did the action contribute to an increased estimate of successfully migrating salmon. If the predator population is successfully reduced, it can create a gap in the ecosystem that is filled by invasive species; indeed, otters seem to exclude invasive mink from areas, an ecosystem service that limits the other damages initiated by mink (Guidos 2019). Alternatively, predator removal may yield mesopredator release, in which subordinate predators in the food chain rapidly reproduce to fill the gap left by a culled apex predator. This occurred in the River Lee, Scotland where ~72 000 pike were removed over 8 years, only to be replaced by increased production of the opportunistic brown trout that readily replaced the pike in eating smolts (Twomey 1976). Generally, the costs of removing predators have been

found to exceed the benefits accrued from the efforts (Lennox et al. 2018).

Removing predators to improve salmon populations may be justified in some cases, although there are no general rules that might help guide decision-making. Some individuals within a population may specialize on salmon, for example, a small proportion of seals were deemed to be responsible for salmon predation in the River Conon, Scotland (Graham et al. 2011). Accurate identification of these perpetrators and targeted removal would be more efficient than a general seal cull, which may promote the immigration of new salmon-eating seals to fill the territories left by the animals removed. Predators such as otters that can capture spawning salmon before or during spawning could have a disproportionately high impact on the population, and removing these individuals may be a step towards effective management. However, removing individuals may cause rapid immigration, often of smaller animals with smaller territories leading to an increase in overall predation. Instead of removal, temporary measures, such as exclusion by fencing or non-lethal control by translocation, may be effective for reducing predation during these critical windows. These solutions may be more challenging for birds and piscivorous fish that are more difficult to target at specific places and times.

The benefits of alternative actions to address predation conflicts should be considered. Predation is a source of natural mortality and a strategy to reduce natural mortality, prolong survival, and increase abundance may be to take an ecosystem approach. Where predators have lost alternative prey species, they may be more damaging to salmon; therefore, efforts could be made to restore alternative populations of species that salmon predators could target. Many salmon predators are generalists and switch to salmon because their alternative prey are depleted. Leach et al. (2022) noticed a declining trend in seal injuries on salmon coincided with increasing populations of alternative prey for the seals, which seemed to switch prey from salmon when there were good alternatives for them to eat. Otters prefer to target slower moving species, and conservation efforts focused on an ecosystem approach may help relieve predation pressure on salmon via apparent competition between salmon and other prey species (Erlinge 1968). Focusing on restoration and having an ecosystem approach to address perceived challenges with predators may be the most durable, sustainable, and cost-effective measures. Odden et al. (2013) suggested such a relationship for lynx (*Lynx lynx*) whereby conflicts with farm de-predations could be mitigated by restoring the cat's natural prey base, the roe deer (*Capreolus capreolus*). This was demonstrated for Atlantic salmon in the Penobscot River, where seal injuries noted on salmon at a counting facility were less frequent as the river herring (*Alosa alosa*) recovered (Leach et al. 2022).

Predator control to improve populations of one species, such as Atlantic salmon, will often be problematic, because the predators may also be reduced, vulnerable, and red-listed species that need protection and mitigation measures on their own. There will often also be conflicts between different interest groups, where fishers tend to focus on protecting salmon, and for instance, birders tend to focus on the protec-

tion of birds, and other groups may be more willing to spend resources on protecting marine mammals.

Conclusions

There is no clear relationship between the number of eggs, fry, and parr that are eaten by predators and how much this reduces the number of smolts leaving the river, due to large, density-dependent mortality on these life stages. When salmon parr become older, it is more likely that predation may reduce the number of smolts leaving the river than when predation acts on the earlier life stages, and predation on later life stages may even more likely have population effects, but there is still often not a simple numeric relationship between the number of salmon eaten by predators and population effects. We therefore warn against drawing conclusions based on simple cause–effect relationships in predation studies. Simply counting the number of predators and the number of salmon individuals they eat will often not lead to insightful conclusions on population effects in the salmon population.

We conclude that in salmon populations reaching the conservation limits, it is unlikely that predation from a natural predator will drive the salmon population to very low levels or extinction. In a salmon population that is strongly reduced due to increased mortality because of human impacts related to aquaculture, hydropower development, other habitat alterations, and overfishing, predation may reduce the population further and make recovery very difficult, particularly if the predators in question are generalists that continue to target salmon as the salmon abundance declines (Box 1) and show little numerical response to a decline in salmon abundance. Managing or controlling the level of predation through human intervention is difficult, and there are few examples showing satisfactory results of such interventions can be achieved, at least over time. A salmon population can quickly be reduced to a low level through human impacts, but when it is reduced, increased natural mortality from predation may hamper rebuilding and recovery of the population, such that it is much easier to reduce than to rebuild the population. There is a great risk that strongly reduced populations remain at a low level, among other reasons also due to natural predation. Even when the initial cause of decline is reduced or removed, it has proven difficult to recover reduced population. We therefore recommend managers to not let salmon populations decline to such low levels where it might enter a predator pit and remove the causes of decline as early as possible. It is better with early management efforts aiming to keep salmon populations in a watercourse at a safe level above possible tipping points, rather than having to implement large and expensive efforts later.

Managers estimating the impacts of predation on their rivers may come to two conclusions, first, that the population has become too small to sustain pressure from predators and the salmon population is nearly incapable of recovery in its present state and second, that predation is limiting the effectiveness of management levers to reduce mortality and increase the abundance of salmon. The bur-

den of evidence for most conservation interventions is quite high, yet there are essentially no strong examples that clearly demonstrate the efficacy of managing predators to recover threatened salmon populations. Nevertheless, there are clearly knowledge gaps in the literature that require some generalizations about salmon–predator relationships across contexts.

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Data availability

The paper is based on published literature and not on primary research data.

Author information

Author ORCIDs

Morten Falkegård <https://orcid.org/0000-0003-2853-2749>

Robert J. Lennox <https://orcid.org/0000-0003-1010-0577>

Eva B. Thorstad <https://orcid.org/0000-0002-7373-6380>

Sigurd Einum <https://orcid.org/0000-0002-3788-7800>

Peder Fiske <https://orcid.org/0000-0003-2253-900X>

Øyvind A. Garmo <https://orcid.org/0000-0001-9169-3735>

Åse H. Garseth <https://orcid.org/0000-0002-8507-3246>

Helge Skoglund <https://orcid.org/0000-0003-4303-6292>

Monica F. Solberg <https://orcid.org/0000-0002-5844-9498>

Kjell R. Utne <https://orcid.org/0000-0002-6428-3690>

Knut W. Vollset <https://orcid.org/0000-0003-0210-4316>

Leif Asbjørn Vøllestad <https://orcid.org/0000-0002-9389-7982>

Vidar Wennevik <https://orcid.org/0000-0002-3329-8769>

Torbjørn Forseth <https://orcid.org/0000-0002-1066-2839>

Author contributions

Conceptualization: MF, RJL, EBT, SE, TF

Funding acquisition: TF

Investigation: MF, RJL, EBT

Methodology: MF, RJL, EBT, SE

Project administration: MF

Resources: TF

Visualization: MF

Writing – original draft: MF, RJL, EBT, SE

Writing – review & editing: MF, RJL, EBT, SE, PF, ØAG, ÅHG, HS, MFS, KRU, KWV, LAV, VW, TF

Competing interests

The authors declare that they have no competing interests.

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