PERSPECTIVE

The various ways that anadromous salmonids use lake habitats to complete their life history

Robert J. Lennox, Ulrich Pulg, Brendan Malley, Sven-Erik Gabrielsen, Erlend M. Hanssen, Steven J. Cooke, Kim Birnie-Gauvin, Bjørn T. Barlaup, and Knut Wiik Vollset

Abstract: Despite the preponderance of exorheic lakes in rivers home to anadromous salmonids, little research has focused on how salmon, trout, and char use lakes as part of their anadromous life histories. The literature on this subject has so far revealed that some parr move into lakes to feed and grow before smoltification but that smolts moving through lakes tend to have high mortality in disproportion to what is observed in other habitats they migrate in or through. Adults have been observed using lakes for behavioural thermoregulation prior to spawning, and kelts of iteroparous species often exploit lakes to overwinter before returning to sea to recondition. We summarized knowledge on lakes as salmonid habitat and identified knowledge gaps about the use of lakes by anadromous salmonids related to whether lakes are barriers that structure genetics of populations, whether mortality in lakes is compensatory or additive, and whether systems with lakes have higher rates of repeat spawning among iteroparous salmonids. Human activities that alter lakes require further study to understand how changes in temperature, oxygen, ice, or circulation affect navigation and fate.

Résumé : Malgré une prépondérance de lacs exoréiques le long de rivières où salmonidés anadromes sont résident, peu de recherche se sont penchés sur l'utilisation faite des lacs par les saumons, truites et ombles durant leurs cycles biologiques anadromes. La documentation à ce sujet a, à ce jour, révélé que certains tacons entrent dans des lacs pour se nourrir et croître avant la smoltification, mais les saumoneaux traversant des lacs tendent à présenter une forte mortalité comparativement à ce qui est observé dans d'autres habitats par ou dans lesquels ils migrent. L'utilisation de lacs par les adultes à des fins de thermorégulation avant le frai a été observée, et les saumons vides d'espèces itéropares exploitent souvent les lacs pour hiverner avant de retourner en mer pour se reconditionner. Nous présentons un résumé des connaissances sur les lacs comme habitats de salmonidés et cernons des lacunes dans les connaissances sur l'utilisation des lacs par les salmonidés anadromes, concernant un rôle éventuel des lacs comme barrières qui structurent la génétique de populations, le caractère compensatoire ou additif de la mortalité dans les lacs et une éventuelle fréquence accrue de frais répétés de salmonidés itéropares dans les réseaux comptant des lacs. Les activités humaines qui modifient les lacs doivent faire l'objet de plus d'études afin de comprendre l'influence des modifications de la température, des concentrations d'oxygène, de la glace ou de la circulation sur la navigation et le destin des poissons. [Traduit par la Rédaction]

Introduction

Salmonids (Subfamily Salmoninae) are distributed throughout the Holarctic in rivers, creeks, streams, ponds, and lakes. Species in this family are exceptional colonizers and have great capacity to move into saltwater to exploit the feeding opportunities provided by estuaries and coastal seas as well as the open ocean (Klemetsen et al. 2003; Drenner et al. 2012). The anadromous salmonids include species from the genera *Salvelinus*, *Oncorhynchus*, *Salmo*, and *Parahucho*. These species are riverine but many populations encounter lakes as part of their life cycle, including during migration to sea for feeding and eventually returning to spawn in the rocky gravel substrate where they hatched or to overwinter (Klemetsen et al. 2003; Hendry et al. 2004). Habitat is a primary focus of much research on anadromous salmonids (Jonsson and Jonsson 2011), including experiments to determine how water chemistry (Peterson and Gale 1991), substrate (Pulg et al. 2019; Finstad et al. 2009), and temperature (Richter

and Kolmes 2005; Frechette et al. 2018) influence the ability of salmonids to colonize and thrive in fresh water.

Anadromous salmon, trout, and char are native to freshwater systems that vary from large Arctic lakes (e.g., Baker Lake in Kivalliq, Nunavut, and Nettilling Lake in Qikiqtaaluk, Nunavut), to rivers thousands of kilometres long (e.g., Fraser River, British Columbia), to small creeks accessible only during the spring freshet (e.g., Ar Brook, Sweden; Limburg et al. 2001). The great diversity of the habitat types available to salmonids means that the freshwater ecology can differ greatly as an adaptation to life in their unique home system (Jonsson et al. 1991). For example, brown trout (*Salmo trutta*) living in small streams around the Baltic Sea may migrate into estuaries as parr to cope with low flows that preclude growth opportunities for young of the year in fresh water (Limburg et al. 2001). However, not all anadromous rivers are simply linear systems connecting with the sea; many postglacial watersheds are characterized

R.J. Lennox, U. Pulg, S.-E. Gabrielsen, E.M. Hanssen, B.T. Barlaup, and K.W. Vollset. Laboratory for Freshwater Ecology and Inland Fisheries (LFI) at NORCE Norwegian Research Centre, Nygårdsporten 112, 5008 Bergen, Norway.
B. Malley. Fisheries and Oceans Canada, Winnipeg, Man., Canada.
S.J. Cooke. Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ont., Canada.
K. Birnie-Gauvin. Section for Freshwater Fisheries and Ecology, National Institute of Aquatic Resources, Technical University of Denmark, Vejlsøvej 39, 8600 Silkeborg, Denmark.

Corresponding author: Robert J. Lennox (email: role@norceresearch.no).

by the presence of exorheic lakes, which are large, widened areas of very slow-flowing water (<0.01 m·s^{-1}), often with an inlet to the upper reaches of the river and always an outlet to the lower reaches of the river. The reliance on lake habitats varies among salmonids; for salmonids such as sockeye salmon (*Oncorhynchus nerka*), lake stratification may provide an opportunity for behavioural thermoregulation during an extensive migration (Newell and Quinn 2005). For anadromous Arctic char (*Salvelinus alpinus*), lacustrine environments are essential to most populations at various life-history stages, including reproduction, juvenile rearing, and overwintering (Johnson 1980; Power 2002; Moore et al. 2017). Lakes provide different habitat to anadromous salmonids in their riverine home, which makes systems that incorporate lakes of particular peculiarity in the life cycle of salmonids.

Hundreds of river systems that support anadromous populations of salmon, trout, and char have lakes. Yet, most data about the life cycle and migration of salmonids is limited to fluvial river stretches without lakes. Seminal reviews about the biology of salmonids (e.g., Klemetsen et al. 2003; Birnie-Gauvin et al. 2019) and even the biology of salmon in fresh water (e.g., Bardonnet and Baglinière 2000; Arostegui and Quinn 2019) note the use of lakes by anadromous salmon, trout, and char and invite a more comprehensive discussion of their biology in lakes. Investigation of the biology of anadromous salmonids in lakes begins to reveal the unique patterns in the life cycles and migrations of salmonids through lakes, including the spawning habitats for some species, the growth opportunities offered to parr, the challenges confronted by smolts moving through lakes, the thermoregulatory opportunities conferred by lakes to adults, and the refuge for reconditioning exploited by postspawning kelts (e.g., Hutchings 1986; Newell and Quinn 2005; Kennedy and Allen 2016; Mulder et al. 2018). This literature is still diffuse and represents a minority of research on anadromous salmonids, but demonstrates that there is a uniqueness to biology in lakes that necessitates more focused research. There are ultimately two main questions that must be addressed with respect to the use of lakes by anadromous salmonids: (*i*) how do lakes affect production of anadromous salmonids, and (*ii*) how do lakes influence the pattern of migration expressed by anadromous salmonids? In this review, we seek answers to these questions in the literature and identify where gaps exist in our knowledge that limit the resolution of how lakes affect the production and migration of salmon, trout, and char. Our aims are to illustrate how lakes fit within the paradigm of salmonid migrations and identify priorities for better understanding how these species of high cultural and economic importance exploits this understudied habitat type throughout their distribution (Fig. 1).

What is a lake and what type of lakes are there in the context of salmonids?

Five major types of lakes are distinguished in the Holarctic, referring to their geomorphological origin (Hutchinson 1957): (*i*) tectonic lakes such as rift lakes (e.g., Thingvallavatn, Iceland; 64.1954°N, 21.1374°W); (*ii*) volcanic lakes such as crater lakes (e.g., Pulvermaar, Germany; 50.1310°N, 6.9250°E); (*iii*) glacial lakes such as lochs (e.g., Vangsvatnet, Norway; 60.6187°N, 6.3250°E); (*iv*) fluvial lakes, such as oxbows (e.g., Carter Lake, USA; 41.301889°N, 95.914917°W); and (*v*) artificial lakes such as reservoirs (e.g., Kinbasket Lake, Columbia River, Canada; 52.1306°N, 118.4362°W). Several more types are described, but they are extremely rare in the home range of salmon species, such as meteorite lakes and solution lakes. Exorheic lakes are those that are open and have an ultimate connection to the ocean by way of a connected river or stream, distinguished from endorheic counterparts that are closed and have no direct connection to the ocean. Although salmonids may inhabit both endorheic and exorheic lakes, exorheic

lakes provide unique habitat to anadromous fish that can reach the ocean and use lakes in diverse ways.

Most contemporary salmonid habitat has been shaped by glaciation during the ice ages of the Pleistocene. The distribution of anadromous salmonids in Europe, Asia, and North America overlaps very closely with the last glacial maximum 20 000 years ago. Only parts of Alaska, the western United States, and pockets of central Europe were ice-free. Where the glacier has receded, numerous lakes were formed, and glacial lakes are the most numerous in the world (Cohen 2003). On sedimentary terranes, most valleys where lakes could form have been filled with sediments in the Holocene. Lakes are therefore rare in these landscapes (Hauer and Pulg 2020). On plutonic and metamorphic terranes, postglacial rivers often develop a characteristic semi- and nonfluvial morphology, including the formation of lakes. Drainages are usually supply-limited, meaning that rivers incise in valley bottoms that are only marginally covered with sediments (Hauer and Pulg 2018). In these regions, most lakes formed by the ice during the Pleistocene have endured. Such regions are dominating the Scandinavian shield, the east Canadian Shield, Greenland, and Scotland, as well as minor parts of Alaska and British Columbia. In these regions, salmonids find many more lakes than on the sedimentary terranes and fluvial rivers south of the glaciated area, such as parts of Germany, France, Maine, California, or Oregon. Salmonids must therefore have survived the Pleistocene glaciation periods in fluvial river systems not covered by glaciers that are characterized by having fewer lakes, re-entering the lake-rich, postglacial habitats re-emerging from the glaciers in the Holocene a relatively short time ago (~10 000 years; McCusker et al. 2000; Olafsson et al. 2014).

Compared with rivers, lakes have slow current (<0.01 m·s^{-1}). Natural lakes in the home range of salmonids are usually stratified when deeper than 5–10 m. Fresh water has its highest density at 4 °C, and lakes thus develop a characteristic bottom layer of 4 °C (hypolimnion) with warmer layers in summer or colder layers in winter on top (epilimnion). When the temperature in the epilimnion reaches close to 4 °C, stratification collapses and water can be mixed by currents driven by mainly wind and river inlets (Wetzel 2001). In dimictic lakes, lake turnover happens in spring and autumn; in monomictic lakes, this happens once a year (summertime in the Arctic). Salmonids use both the hypo- and epilimnion. Spawning of sockeye occurs mainly in the epilimnion (0–5 m; Leonetti 1997). If oxygenated, the hypolimnion provides a permanent thermal refuge with cool water (4 °C) that is essential for salmonids, especially in southern parts of their distribution (Elliott and Elliott 2010).

River-fed lakes with a short retention time (i.e., small ratio of volume relative to river discharge) do not develop stratification. From a limnological perspective, such low-ratio lakes can be considered pools in a river rather than a lake, and they have complex currents and eddies dissimilar to lakes. Artificial lakes in salmonid rivers are usually created by damming (reservoirs and impoundments). Deep and large reservoirs develop stratification, but water levels may vary largely and affect food webs and life histories of fish (Murphy et al. 2019). Dams can alter downstream thermal regimes (Dripps and Granger 2013); for example, water discharged from bottom intakes in such lakes can therefore be colder than upstream reaches of rivers, with consequences for phenology, growth, and community dynamics within rivers. Spawning may therefore be later and growth slower in downstream reaches. Shallow impoundments that are common in run-of-the-river hydropower stations usually do not stratify but slow the water current considerably and may thus influence migration speed, navigation, and vulnerability to predators (Jepsen et al. 1998).

Lakes function as sediment traps. Fluvially transported material from inlet rivers and colluvial material from mountain slopes accumulates in lakes. Owing to slow velocity and shear stress, lacustrine sediments are often dominated by fine grains (<1 mm) and provide

Fig. 1. Illustration of an anadromous lake with generic salmonids. We find that some species use the lake for rearing, especially sockeye (limnetic) and Atlantic salmon and brown trout (littoral) before smoltifying. Smolts moving down to sea through lakes may be challenged to navigate based on current dynamics or thermal stratification that form during migration. However, adults can benefit from thermal stratification to behaviourally thermoregulate, especially sockeye. Only sockeye are known to spawn inside lakes along shore, but other species use inlets and outlets. Iteroparous Atlantic salmon and brown trout overwinter in lakes before returning to sea to recondition. There is still much more to learn about salmonids in anadromous lakes that can expand on this relatively rudimentary understanding of their role in the life cycle. [Colour online.]
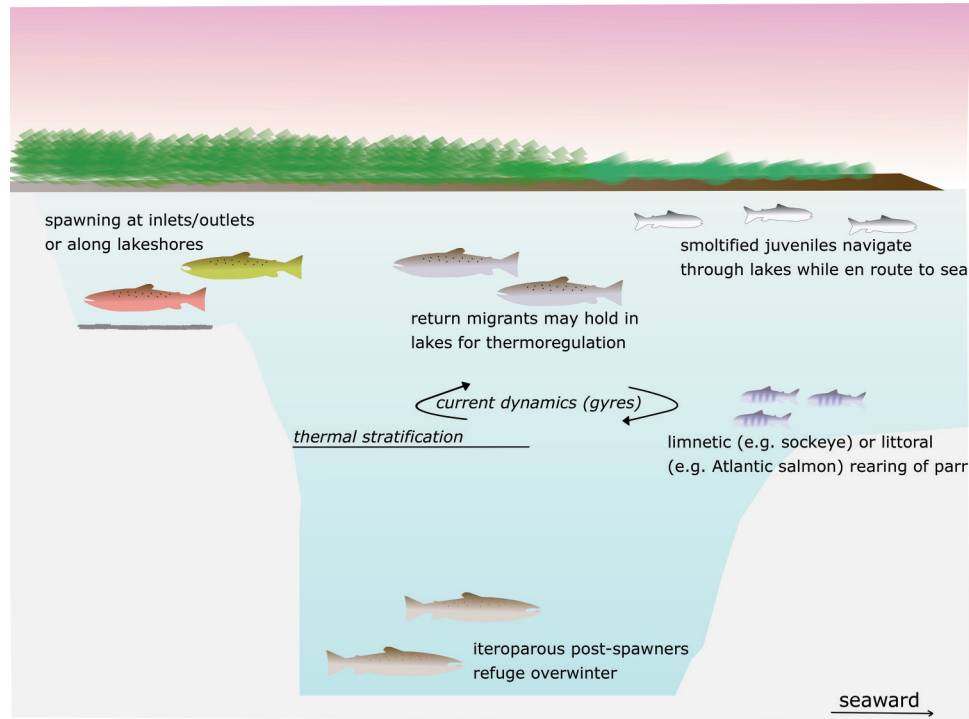
characteristic stratifications that may reflect past discharge events and bed load transport of tributaries (Hauer et al. 2019). This may create opportunities for studying anadromous populations in sediment cores (e.g., Gregory-Eaves et al. 2009). However, coarser material such as gravel and boulders may occur, especially at river inlets, at colluvial fans, and at the shore where waves and changing water levels create larger shear stress. These particular areas may be especially important for salmonids given they provide spawning habitat for anadromous salmonids in some watersheds (Arostegui and Quinn 2019).

The ways that anadromous salmonids exploit lakes

Growth habitat for parr

Anadromous lakes provide substantial potential habitat for the production of salmonids, although not all species exploit these habitats (Arostegui and Quinn 2019). For species such as brown trout, sockeye, and Atlantic salmon (*Salmo salar*), rearing in lakes may support a large proportion of a population's output in some systems (e.g., Atlantic salmon; Chadwick and Green 1985). Most colonization of lakes by juvenile salmonids seems to be immigration of parr spawned in the lake inlet, outlet, or tributaries (Halvorsen and Jørgensen 1996) or even farther away. Bodznick (1978) showed olfactory preference for lake water among sockeye fry, suggesting an early life migration from the river to these lake habitats for rearing. Tests on sockeye salmon fry from Alaska revealed genetic differences among lake-spawned, tributary-spawned, and outlet-spawned salmon, suggesting inherent differences driving behaviour and early life habitat selection (Raleigh 1967). Salmonid species seem to use lakes differently for rearing; sockeye salmon are described as limnetic zooplanktivores or insectivores with diel vertical migration

(Eggers 1978; Richardson et al. 2017). Pepper et al. (1985) explained that Atlantic salmonids thrive better in shallow lakes and preferentially colonize the littoral zone near shore. In addition, Godiksen et al. (2012) described a difference in temperature use at age for Arctic char, with young-of-the-year Arctic char also found in warmer, littoral habitats but shifting to colder habitats between 1 and 3 years of age (Godiksen et al. 2012). There is likely a broad variation in habitat quality among lakes, but they appear to provide good habitat for salmonids; comparison of proximate body composition between Atlantic salmon of fluvial and lacustrine provenance revealed higher protein and fat content among the lacustrine samples (Dempson et al. 2004). Contrastingly, Arctic char parr from rivers grew faster than lake-dwelling individuals (Gulseth and Nilssen 1999). Although lake production of anadromous salmonids can be high, there may be other limiting factors that temper the potential production and growth of salmon, trout, and char in lakes.

Competition and predation are important factors determining the suitability of lakes for salmonid parr to colonize and exploit for growth. It has been suggested that lake colonization by Atlantic salmon parr is a response to competitive exclusion by conspecifics in the river. Interspecific competition may be a driving force behind lake use by sockeye salmon, which share rivers with congeneric Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and rainbow (*Oncorhynchus mykiss*). The extent of trophic segregation when these species co-occur may be ascertained through experimental designs or comparisons between allopatric and sympatric systems. Trout were dominant to Atlantic salmon and Arctic char in most lakes in northern Norway, but mechanisms of competition differ across environments (Halvorsen and Jørgensen 1996). Char were excluded from the shallow littoral zone in many systems but were dominant in

lakes with deep Secchi depth (Halvorsen and Jørgensen 1996). In western Norway, competition between char and trout was mediated both by individual size and water temperature; trout displaced char either deeper in the littoral zone or into the pelagic zone (Gabrielsen 1999). Niche segregation may also be attributable to trophic differences among species (Jansen et al. 2002). Contrary to suggestions that lake-dwelling parr are pushed there by competitive exclusion from riverine habitat, several studies reveal fast growth among parr rearing in lakes, suggesting life in anadromous lakes may be beneficial (Hutchings 1986; Erkinaro et al. 1995; Halvorsen and Svenning 2000; Dempson et al. 2004). Whether this affects the rate of smoltification or maturation is unknown, but there may be more temperature choice available in lakes than in rivers to optimize growth.

The presence of other lake-dwelling species may exclude salmon from exploiting lakes; O'connell and Ash (1989) suggested that the absence of pike (Esox lucius) and cyprinids was the reason for high abundances of salmon parr in anadromous lakes of Newfoundland compared with mainland rivers. Lake trout (Salvelinus namaycush), Dolly Varden (Salvelinus malma), bull trout (Salvelinus confluentus), and European grayling (Thymallus thymallus) are also among the salmonid species that may co-occur in Arctic, Pacific, and Atlantic lakes. However, sticklebacks are also commonly co-occurring, and Richardson et al. (2017) revealed significant dietary differences between sockeye salmon and threespine stickleback (Gasterosteus aculeatus) in a shallow Alaskan lake. In winter, Swales et al. (1988) observed significant catches of coho parr in anadromous lakes but attributed higher catches of parr in one lake to the relatively low abundance of threespine stickleback, suggesting competition-mediated colonization of the lakes by coho. In addition to competition, predation has great potential to operate as a mechanism affecting lake exploitation by anadromous salmonids. At high latitudes where freshwater environments are less productive, resource pulse-adapted species such as Dolly Varden depend on cohabiting salmonids within lakes. Armstrong and Bond (2013) described how Dolly Varden gorge on Pacific salmon eggs, nearly accumulating their annual energy surplus needs in only ~5 weeks. Predators may also drive the behaviour of young salmon in lakes. Eggers (1978) observed diel vertical migration among zooplanktivorous sockeye salmon smolts in Lake Washington and inferred high rates of crepuscular feeding based on stomach fullness. Rapid growth of juvenile sockeye in the summer yielded to null or negative growth in the winter as feeding was greatly reduced, possibly to offset risk of predation by northern pikeminnow (Ptychocheilus oregonensis). Parr may school in the deep limnetic zone of lakes during the day before ascending to the shallows to feed on copepods and cladocerans (Narver 1970). Invasive predators may exclude salmonids from lakes entirely, including smallmouth bass (Micropterus dolomieu) and chain pickerel (Esox niger) in Nova Scotia.

Fry and parr of many anadromous salmonids may spend short or prolonged periods rearing in lakes before smoltification. Sampling these early life stages is needed to better survey how important these habitats are to various species, particularly those not well-resolved with respect to lake use. Arostegui and Quinn (2019) report on some seemingly exceptional examples of lake use by pink, chum, coho, and Chinook that suggests more research might reveal new knowledge about lake usage by these species. How community dynamics facilitate or interfere with lake colonization and whether juvenile anadromous salmonids benefit from different temperature or food availability in lakes may be relevant to understand how lakes provide heterogeneity to river systems yielding seagoing salmon, trout, and char.

Lakes as transitional habitats for migrating smolts

When salmonids undergo smoltification, morphological, physiological, and behavioral changes prepare them for life at sea, initiating the downstream migration towards the ocean (Folmar

and Dickhoff 1980; McCormick and Björnsson 1994; see review by Thorstad et al. 2012). In many catchments, smolts have to migrate through lakes to reach the river outlet. During the riverine migration, salmonids are in a shallow environment of rapid downstream currents. The transition into a lacustrine environment challenges smolts, with less-directed currents and formation of eddies potentially confounding navigation. Little is known of the navigational mechanisms guiding salmonid smolts through lakes, although flow is likely important in shallow or narrow lakes. Sockeye salmon smolts, a species whose juveniles frequently rear in lakes, have a directional preference towards the lake outlet, apparently using celestial visual orientation (Johnson and Groot 1963); navigational mechanisms are not resolved for other species. Smolts seem to have diel vertical migration within lakes, and Scheuerell and Schindler (2003) observed depths from 75 to 15 m for sockeye smolts. Telemetry studies of Atlantic salmon smolts reveal that they spend considerable time in lakes, an inefficiency suggesting poor navigation that costs valuable time and energy (Thorpe et al. 1981; Hansen et al. 1984; Honkanen et al. 2018; Babin et al. 2020; Hanssen 2020). However, this ignores the possibility that lakes have a role in the process of smolt maturation, which has not been studied before. Consequently, lakes have been identified as areas of high loss among smolts. In Lough Erne, Northern Ireland, Kennedy et al. (2018) observed a 31.2%·km^{-1} mortality in the first kilometres of the lake, suggested to be caused by predation by pike. In an artificial lake, Jepsen et al. (1998) observed a total 90% mortality for smolts migrating through Lake Tange and attributed this to predation by pike and avian predators. High mortality rates (35%) have also been observed for S. trutta smolts negotiating artificial impoundments in Denmark (Schwinn et al. 2018). At a lake outlet, Furey et al. (2015) discovered aggregations of bull trout predating on out-migrating sockeye salmon smolts, estimating the total consumption to account for a large portion (up to 12.6%) of sockeye biomass. Poe et al. (1991) described pikeminnow, channel catfish (Ictalurus punctatus), walleye (Sander vitreus), and smallmouth bass predation on Pacific salmon smolts in fluvial and reservoir reaches of the Columbia River. Encountering the navigational challenges that delay migration, along with entering a habitat potentially rich with piscivorous predators, makes lake areas hotspots for smolt losses, depending on the biology of the predator. Predation may be concentrated at lake inlets (northern pike; Kennedy et al. 2018), outlets (bull trout; Furey et al. 2015 — note, they describe bull trout aggregations at the "edge" of the lake–river interface, presumed to be the outlet), or within the lake (brown trout; Hanssen 2020). This corresponds to observations of antipredator behaviour in lakes including nocturnal migration, schooling, and diel vertical migration (Hartman et al. 1967; Eggers 1978; Thorpe et al. 1981; Scheuerell and Schindler 2003).

Despite many large lakes in the range of Pacific salmon, research has not focused very much on the migration of the native species through lakes. There are still substantial knowledge gaps related to the migration of smolts through lakes, with most data coming from Atlantic salmon, which suggests further research is needed on lakes where other smolts species transit. Additionally, with lakes functioning as survival bottlenecks for migrating smolts, research should focus on whether these areas can act as genetic barriers in river systems. Several studies have highlighted the genetic diversity among locations within a river (Burger et al. 1997; Elo et al. 1994; Primmer et al. 2006; Vähä et al. 2008; Larson et al. 2014). A compelling research question is whether adult spawners above and below an anadromous lake differ genetically. Brannon (1972) described differences in behaviour of parr born below or above lakes, suggesting innate differences, but whether similar behavioural adaptations exist among smolts to survive downstream through lakes is not known. This is important to consider, because many populations contemporaneously rely on hatchery programs to enhance the smolt

production, and the genetic source may be relevant to consider to ensure adaptations for efficient lake navigation and survival. Another relevant research question that arises from the high mortalities observed in lakes is what type of functional response is present in the predator–prey system. Predator-driven Allee–Bowen effects can threaten small populations when the predator numerical response does not respond to the small prey population (Gascoigne and Lipcius 2004). For species that depend on predator swamping to survive the type II functional response of aggregative predators, populations at low abundance, such as small salmon populations, can struggle to recover to pre-impact abundance because of predation.

Adult salmon refuge in lakes during the upriver spawning migration

Adult salmon must survive and thrive in lakes to spawn successfully. The navigational mechanisms for moving through lakes remain poorly described. Sockeye salmon were described to move up to five times the minimum distance necessary to travel upstream from outlet to inlet based on radio tracking by Young and Woody (2007). Salmon may remain in lakes for months during the migration (premature migration; Quinn et al. 1997; Newell and Quinn 2005; Quinn et al. 2016). Rivers with lakes in particular tend to have more premature migration timing by the salmon, presumably because the population has evolved to exploit the availability of refuge (Reed et al. 2017). In Lough Neagh, Atlantic salmon seemed to ascend lakes slowly until later in the season when time was more limited to make it to spawning grounds (Kennedy and Allen 2016). Diverse and complex lake spawning strategies are emphasized by a 2-year cycle of migration and maturation (Johnson 1980) in which char overwinter in Nauyuk Lake, access upstream spawning grounds in Willow Lake during the spring freshet, and spawn more than a year after migration was initiated. Ablation experiments on lake-spawning sockeye in Lake Toya, Japan, suggest that visual cues are important for finding the general spawning area followed by olfactory sensing for precise fine-scale homing (Ueda et al. 1998). However, displacement experiments by Blair and Quinn (1991) showed that site characteristics serve a role in sockeye spawning site selection because individuals did not consistently return to their capture site. Clearly, salmon, trout, and char can navigate lakes but require time and perhaps other resources (genetic information, experience from previous spawning or downstream migration as smolt) to enhance passage. Delays in lakes may have both costs and benefits to the individuals that seek out holding territory in preparation for spawning.

One of the most substantive implications of lake usage by adult salmonids is the change in temperature encountered relative to the river. The impact that lakes have on the thermal landscape of rivers is considerable, and rivers with lakes tend to have earlier migration timing than rivers without (Reed et al. 2017). Lentic water bodies, which are typically stratified, create opportunities for behavioural thermoregulation given the manifold effects of water temperature on the biology and ecology of fish. In the Lake Washington basin, it is typical for sockeye salmon to return to the lake during the warmest period of the year and exploit cooler temperatures at depth (Newell and Quinn 2005). Fish typically spent ~6 days approaching in river water ~18 °C before entering the lake, which was generally <13 °C. The majority of temperature records obtained from fish in the lake were between 9 and 11 °C, corresponding to depths of 18–30 m. Fish remained in the lake for an average of 83 days before ascending to spawning grounds. Using a combination of telemetry and thermal biologgers, Mathes et al. (2010) inferred that fish were retarding pathogen development by selecting cool temperatures. However, the role of anadromous lakes in behavioural thermoregulation may not apply to all species. Keefer et al. (2019) used radiotelemetry and temperature biologgers to characterize Chinook salmon

thermal biology during use of impounded reaches of the Columbia and Snake rivers. Fish in that study exhibited little diel temperature variation but did engage in frequent and extensive vertical movements. During the depth-seeking behaviour, fish did experience slightly cooler body temperatures (~0.01 to 0.02 °C·m⁻¹). However, the authors did not find evidence of long-term (beyond minutes) cool-water thermal refuges in reservoirs. Similarly, Goetz and Quinn (2019) found that adult Chinook salmon in Lake Washington spent time both above and below the thermocline and failed to fully exploit the available thermal refuge in deep water.

The disparity in findings (especially relative to Newell and Quinn 2005; conducted in the same system) regarding lake use by anadromous salmonids is worthy of more research, as we seek to understand intra- and interspecific variation. There is evidence of intraspecific variation with respect to the usage of lakes among upriver migrating sockeye. For example, females with lowest levels of somatic energy preferred the coolest temperatures in natal lakes (Roscoe et al. 2010), and Minke-Martin et al. (2018) combined telemetry, temperature biologgers, and nonlethal blood sampling and found that ~33% of fish occupied temperatures within an optimal temperature window (13.4–19.5 °C; range generated using respirometry in a swim tunnel) where ≥90% of maximum aerobic scope was maintained. There was a positive relationship between time spent in the T_{opt} for aerobic scope during lake residency with reproductive longevity and an inverse probability of egg retention, suggesting successful spawning. This study reveals that behavioural thermoregulation may be particularly important for regulating physiological processes, yet relatively little is known about how use of lake habitats relates to maturation processes. Newell and Quinn (2005) reported that the apparent thermal preference of lake-refuging sockeye salmon decreased over the summer, which may be a function of sexual maturation, agreeing with findings by Kennedy and Allen (2016) that later arriving Atlantic salmon navigated lakes more rapidly than early arrivals.

Studies on anadromous lake usage by adult salmonids have been largely observational in nature, but one study has implemented an experimental approach. Naughton et al. (2018) assessed behaviour and survival of adult Chinook salmon as part of a reintroduction program where fish were released either in a reservoir or immediately downstream of spawning grounds in Oregon. Seventy percent of salmon released into the reservoir entered an upriver tributary after spending a median (across 5 years) of 3–95 days in the reservoir. Biologgers recovered from salmon revealed that fish selected temperatures that were 3 to 6 °C cooler per day in the reservoir than in the river. When cumulative exposure was calculated, researchers revealed that reservoir-released fish had 64 degree days less, on average relative to river-released fish. The cumulative aspects of thermal experience seem to be quite important and should become a focus of future research.

In general, almost all of the research on lentic behavioural thermoregulation and physiological energetics has occurred in the Pacific Northwest of North America. Atlantic salmon have been observed to modify behaviour to maintain optimal body temperatures in rivers and may capitalize on lakes to do so as well (Frechette et al. 2018). Virtually nothing is known about how other salmon species use lentic parts of systems during upriver migration and the extent to which such areas benefit or impede migration and fitness. It is clear that not only does behavioural thermoregulation impact energy use and maturation (Minke-Martin et al. 2018), it may also play an important role in retarding pathogen development (Mathes et al. 2010). The complex ways in which fish use lentic habitats during upriver migration presents many fascinating opportunities for behavioural ecologists and physiologists to collaborate.

Spawning habitat

Salmonids predominantly spawn in fluvial reaches of rivers where gravel interstitial spaces are well-oxygenated and cleaned of sediment by the flow (Esteve 2005). However, it is increasingly clear that salmonids can make use of diverse habitats for spawning, including brackish estuaries (Landergren and Vallin 1998), as long as the eggs receive enough oxygen, are not smothered by sediment, are safe from predators, and there is spawning gravel available that attracts the female salmon to construct a redd. Lakes do provide habitat for salmonids to spawn (Arostegui and Quinn 2019) have a comprehensive review of this), but most of the research focus is on resident species. For example, populations of resident lake-spawning brown trout use wave action (Barlaup et al. 1998) or upwelling areas (Brabrand 2002) to keep gravel clean. Char will readily construct redds in lakes with suitable gravel; however, where redd construction is not feasible, broadcast spawning is documented among resident populations (Sigurjónsdóttir and Gunnarsson 1989). Spawning without making a redd is also practiced by lake trout and does not include the prespawning cleaning of gravel as found for nest-digging species (Gunn 1995; Esteve et al. 2008). For many species, exploitation of lakes is only at inlets and outlets with flow, which are indeed important spawning areas for many species (Arostegui and Quinn 2019).

There is limited evidence of anadromous salmonids spawning in lakes, but there are interesting exceptions. So far, sockeye salmon are the primary anadromous species documented to use the habitat within lakes as spawning grounds, which has been reported in lakes throughout the distribution (Burger et al. 1995). Postglaciation patterns of habitat emergence may have driven selection for novel spawning phenotypes in sockeye, and there is evidence of genetic differentiation between lake shoreline (also referred to beach spawning) and river-spawning individuals among sockeye (Burger et al. 1997; Larson et al. 2014), as well as in a rare ecotype of chum salmon that spawns in Lebedinoe Lake of the Kurilka River, Russia (Zhivotovsky et al. 2012). Lake-spawning sockeye have distinct run timing phenotypes, arriving later than the river reproducing counterparts (Burger et al. 1995). A multiple-origin introduction experiment suggested that individuals originating from a line of tributary-spawning sockeye can contribute to lakeshore spawning (Burger et al. 2000). Exceptional lake spawning by chum salmon has been observed in both North America and Asia (e.g., Zhivotovsky et al. 2012; see Arostegui and Quinn 2019). The closest description of another anadromous salmonid spawning within lakes may be Einarsson et al. (1990), who speculated that Atlantic salmon may have been spawning near tributary outlets within a lake in Iceland, but did not make direct observations. Although not directly within the lake, the inlets, outlets, and straits between two lakes where water is flowing are commonly used for spawning, meaning that lakes provide some suitable spawning habitat for anadromous salmonids (e.g., pink salmon; Fukushima and Smoker 1997). Spawning surveys in Norway have suggested lake outlets to be important for spawning, whereas spawning is sporadic at best at inlets.

Habitat conditions required and the rather common occurrence of lake spawning in resident populations render lake spawning likely to occur in anadromous populations that has not yet been found or reported. The description of lake-spawning sockeye salmon phenotypes was relatively recent in western science, and perhaps lakes are more important spawning zones than presently recognized for some other species. Lakes are clearly not the predominant source of spawning habitat for anadromous salmonids but perhaps provide some additional habitat in certain systems. Despite this, the spawning targets assigned at a national level in Norway are calculated in part based on the perimeter of the system and many do not exclude lakes from the calculation, artificially inflating the spawning targets of rivers with lakes (Hindar et al. 2007).

Refuge habitat for postspawners

Reproduction is one of the most energetically costly events for anadromous salmonids, involving migrations from sea to fresh water (sometimes exceeding hundreds of kilometres), the development of sexually dimorphic traits, gonadal development, as well as intrasexual competition (Stearns 1992; Hendry and Berg 1999; Stephens et al. 2009). This has promoted semelparity in several species of salmonids, but iteroparous species and phenotypes must still migrate back to sea after spawning and do so on a very limited energy budget (Jonsson et al. 1997; Jørgensen et al. 1997; Hutchings et al. 1999). After spawning, iteroparous Atlantic salmon, sea trout, anadromous Arctic char, anadromous brook trout, and steelhead are energy-depleted and must be physiologically prepared for marine re-entry before migrating back to seawater (i.e., osmoregulatory processes). In this case, anadromous lakes may act as important refuge habitats for postspawners to conserve energy before starting their return to sea. Indeed, anadromous lakes are a feature of rivers that can help support greater rates of repeat spawning among iteroparous species (Cunjak et al. 1998).

For some fall-spawning species, lakes may serve as overwintering habitats for postspawners, hypothesized to be due to a combination of low salinity tolerance and critically low winter marine temperatures (Svenning and Gullestad 2002; Elliott and Elliott 2010; Mulder et al. 2018). This is particularly well documented for Arctic char, but less so for other salmonids. Arctic char lack "anti-freeze" proteins, preventing them from surviving temperatures below −0.99 °C (Fletcher et al. 1988; Svenning and Gullestad 2002). Ice-covered lakes typically range between 0 and 4 °C and as such may provide thermal refuge for some anadromous salmonids. A study from two lakes in Labrador, Canada, revealed that char occupy a narrow range of temperatures (0.5–2 °C), thought to be a strategy that minimizes metabolic costs and energetic expenditure to preserve stored resources for overwinter survival and return migration to sea (Mulder et al. 2018). This energy-saving strategy may be necessary for survival, meaning that lakes represent a critical refuge habitat for resource-depleted postspawners. However, overwintering brown trout in Vassbygdi Lake (Aurland River) mostly selected the warmest water available (never less than 4.2 °C), suggesting some species-specific optimization of temperature selection to modulate energetic expenditure while overwintering (Lunde 2014). The differences likely reflect the life histories of the animals, and Monsen (2019) revealed that overwintering trout in the Botn River occupied surface layers and were less active (3–5 m) than Arctic char, which stayed at 12–15 m deep.

Most anadromous salmonids are known to reduce or cease feeding prior to spawning until they return to sea. Exorheic lakes are not documented to provide feeding habitats for anadromous postspawners. However, sea trout (*S. trutta*) overwintering in lakes are observed feeding on Atlantic salmon smolts in the springtime (Hanssen 2020). These lakes could provide refuge against predators for postspawners, including mammals such as otters (*Lutra lutra*) that seem to be successful at taking fish around or after spawning (Carss et al. 1990). The somewhat limited data available on the use of lakes by postspawning anadromous salmonids support the idea that lakes serve as refuge to conserve energy, where fish opt for utilizing areas of low variability to improve bioenergetics efficiency, reduce energy consumption, and preserve energetic resources for future metabolic demands (e.g., Mulder et al. 2018). Although it may be assumed that overwintering fish are relatively inactive in the slow-flowing, cold lakes while waiting for summer, Monsen (2019) calculated that Arctic char and brown trout were swimming up to 70–80 km per day within the lake and must have actively been feeding to maintain energy supplies.

Generally, studies that have explored the role of lakes for salmonids have centered on lakes as spawning habitat or rearing

habitat or have strictly considered lake-dwelling phenotypes (Arostegui and Quinn 2019). There is a substantial knowledge gap on the use of lakes by anadromous postspawners, and the existing studies on the topic have focused on Arctic char. This is perhaps because most systems with exorheic lakes are home to wild Arctic char or because char are known to use lakes extensively. Although some systems are also home to other anadromous salmonids, almost nothing is known about their potential use of lakes after spawning. If the assumption that other anadromous postspawning salmonids use exorheic lakes as refuge for energy conservation is correct, there is a great opportunity to explore this strategy, as climate change is likely to impact the condition and duration of lake ice cover (Prowse and Brown 2010), and hydropower regulation can alter the temperatures and ice cover on anadromous lakes. Changing ice cover conditions will impact the stability of the lake environment, reduce the availability and duration of stable water temperatures, and therefore impact the conditions that facilitate energy-conserving strategies after spawning, with subsequent negative impacts on survival.

Methods to study the ecology of anadromous salmonids in lakes

One of the biases towards studies of salmonids in rivers compared with lakes is most likely related to the difficulties of obtaining relevant data on fish ecology and habitat in lakes compared with rivers. Capture of anadromous salmonids can be easily done by backpack electrofishing equipment or seine nets in rivers, but such methods have limited suitability in most areas of lakes, though electrofishing boats can be a suitable method in some shallow lakes. On the other hand, other methods that can be used in standing waters such as gill- or trap nets or angling are possible to use and can be cost-effective particularly for catching large migratory individuals. A crucial consideration here is capture bias, which can occur if sampling gears are disproportionately targeting animals of a certain phenotype. Animal personality affects catchability and also influences traits such as activity and migration (Biro and Post 2008), so care must be taken to gather a representative sample when studying behaviour. It is particularly important to sample at all depths to avoid biasing towards deep or shallow phenotypes or species. Acoustic echo-sounding has been applied to observe smolt migrations in lakes but is nonspecific (Groot and Wiley 1965). Telemetry tagging (including simple passive integrated transponders (PIT tags), acoustic and radio transmitters) is widely used for studying salmonids and has been critical to revealing how these fishes use lakes (e.g., Mathes et al. 2010; Kennedy et al. 2018; Mulder et al. 2018). Depth renders the short reading distance of PIT tags ineffective and triangulation with radio tags in lakes is challenging, so acoustic tagging systems are commonly applied, with receiver arrays that can collect fine- or coarse-scale data on various aspects of behavior with high dimensionality, as well as sensors to reveal aspects of environmental relations (e.g., depth, temperature) or their physiology (e.g., acceleration). Innovations in this field of science include the development of tagging systems that allows accurate identification of predation events (e.g., Hanssen 2020) and open source triangulation systems allowing fine-scale 3D tracking (Baktoft et al. 2017). Other sensors are available in logging tags that must be retrieved from the animal to yield information (which can result in survivor bias because recovery of tags from dead individuals is challenging) and include heart rate loggers that reveal physiological responses to the environment (Prystay et al. 2020) and magnetometers that reveal orientation and aspects of navigation (Chakravarty et al. 2019); these tools may soon become important to revealing some of the finer-scale details of lake use by anadromous salmonids.

Other methods that are of particular interest in studying lake ecology of salmonids is the study of sediment cores. Lakes are particularly suitable for these methods because they are natural deposits of sediments, and sediment core samples are widely available from research programs studying paleo records of climate and ecological processes, particularly within botany (Epp et al. 2015). Traditionally, studies have used stable isotopes analysis and records of plankton remains (such as diatom scales; Rühland et al. 2008) and have allowed scientists to build historical records going back thousands of years on biomass of salmonids in lakes. The development of highly sensitive molecular methods, such as environmental DNA (in this context called sediment DNA), will allow even more detailed analysis on lake ecology; using methods such as metabarcoding will enable scientists to get insights into how whole communities vary with salmonid presence and abundance of salmonids in lakes (Nelson-Chorney et al. 2019).

Synthesis of lingering questions and research opportunities

Lakes are a part of the habitat available to anadromous salmonids that can drive the expression of different life-history traits. Rivers tend to have greater biodiversity than lakes because they offer a greater diversity of habitat (Irz et al. 2006); however, there may be important differences among lakes that drive the biotic interactions of the fauna. The influence of lake scale (size, depth) on use by parr, adults, and postspawners is an important avenue of research and one that has not been adequately addressed by the available research. Lakes can be relatively narrow, shallow, and straight, but we predict that wide, deep lakes with unpredictable bends and contours will be most relevant to contrast with biology in rivers. Deep lakes with thermoclines likely provide the best habitat for salmon to thermoregulate, providing choices of temperature not available in the river. Adding new studies on systems with lakes of varying sizes will assist in better understanding how lakes are exploited by anadromous salmonids.

Salmonid behaviour differs in lakes compared with rivers, which has relevant implications for conservation and management of populations. Parr exploit these habitats for feeding, and lakes could buffer density-dependent effects of competition that regulate populations in rivers (Pulg et al. 2019). Adults and smolts appear to have difficulty navigating lakes, and this seems to contribute to high smolt mortality when passing through lakes; however, the mechanisms for this remain poorly understood. Observations from acoustic telemetry have suggested a role of predation on mortality of smolts. A lingering question here is whether predation in these systems is compensatory, acting on fish that were unlikely due to poor condition or simply a consequence of ineffective navigation. Inability to find the lake outlet in a timely manner would likely kill a smolt, and Honkanen et al. (2018) observed inefficient movement of smolts. Hanssen (2020) also estimated smolts moving tens of kilometres before finding the exit of the lake, only 6 km directly from the inlet. Ineffective and energetically inefficient behaviours in lakes may also kill smolts even in the absence of predators, thus separating whether predation pressure on smolts in lakes represents additive mortality. Salmon are known to overwinter in lakes when they are available (Hubley et al. 2008). Cunjak et al. (1998) specifically pointed to lakes as important for successful reconditioning of iteroparous Atlantic salmon. Comparisons of behaviour and survival between kelts overwintering in lakes, riverbeds, and estuaries are lacking, but presence of lakes may support higher survival of kelts and better contribution of repeat spawning fish (Cunjak et al. 1998).

Some systems have multiple lakes that salmon must pass before reaching the ocean, and it is unknown whether they learn successful navigation techniques. Experimental displacement studies could be used to test whether smolts that have already passed a lake pass a second lake faster or with higher survival. Perhaps there is a genetic component to surviving this challenge

as well, with stock-specific genes separated by lakes or inherited traits from parents that may help offspring navigate these challenges (Elo et al. 1994; Primmer et al. 2006; Vähä et al. 2008). This would be difficult to test directly, but would have immense implications for programs that stock hatchery fish to ensure that the information needed for juveniles to transit lakes is not disrupted by stocking. It also suggests questions about how the creation of artificial reservoirs affect selective pressures in rivers and introduce a barrier to successful smolt migration.

Understanding how exploitation of salmon habitat affects their behaviour and survival is an established field of applied ichthyology. However, exploitation of rivers affects lake habitat generally differently from rivers and coastal areas. Recreational fishing efforts targeting anadromous salmonids tends to be focused in rivers, meaning that salmonids may be less vulnerable to angling when they refuge in lakes, but this remains to be tested directly. Discharge of hypolimnetic water from reservoirs or mountain intakes leads to colder water temperature in summer and warmer in the winter. In lakes, the cold water sinks to the bottom in the summer, altering circulation patterns and potentially disrupting the cues used by salmon smolts when moving through lakes. The cold water in the summer could also provide a thermal refuge to adults as they move through the system, allowing them to save energy if they exploit these areas, but this is unknown.

Tag effects studies are needed to understand whether tagging fish with transmitters affects their survival probability. Acoustically transmitted depth data from smolts tagged by Haugen et al. (2016) revealed unexpected patterns in depth use and may suggest a buoyancy effect of the tag. Such effects would not be expected in rivers, which are relatively shallow. Fresh water provides less buoyancy than salt water, meaning that tag effects on buoyancy are likely to be more pronounced in deep lakes than in shallow rivers or the marine environment. The same may also apply to adults. Wright et al. (2019) recorded high mortality of tagged adult salmon in snorkel-style sea cages compared with untagged fish, although no fish died in unmodified cages in which fish had access to the surface, where they regulate the filling of the swim bladder.

Many rivers are managed based on the carrying capacity of fish in the river, and it is presently uncertain precisely how lakes influence management paradigms. Spawning counts in rivers are generated by snorkel surveys in many rivers (Mahlum et al. 2019); surveys of lakes are rare, but anadromous salmonids in lakes could be monitored by boat, drone, plane, or echo sounder. These surveys can be used to estimate total river production based on eggs per spawner, and underestimates caused by fish residing in lakes has consequences for fisheries and future management efforts (Forseth et al. 2013). So little is known about lake production of Pacific salmonids other than sockeye, and this clearly creates a potential barrier affecting the management of spawning rivers considering how frequently glacial rivers incorporate lakes where salmon can refuge and rear.

Lastly, research is needed to understand the constraints that may cause an individual to use a lake. Are certain individuals more likely to use lakes than others, and why? Genetic differences structuring stocks seem to be partly responsible for the use of lakes among sockeye and chum salmon (Burger et al. 1997; Zhivotovsky et al. 2012). Among iteroparous species, individuals that invest more in reproduction are likely more energy-depleted and may require a place to rest and recondition, such as a lake, if one is nearby. Alternatively, lakes may provide an intermediate location to recondition given that species such as sea trout are observed foraging in lakes before returning to sea (Hanssen 2020). On the other hand, due to the greater availability of food items at sea, it may be more advantageous to return to sea sooner to recondition. These types of questions would help to understand the drivers of these different life-history strategies and the role of physiology in that context.

Summary and conclusions

Exorheic lakes provide important habitat to Pacific and Atlantic salmon, steelhead, sea trout, Arctic char, and other anadromous salmonids (Fig. 1). Lakes may provide refuge from temperature, flow, predators, and anglers and provide a large volume of potential habitat for supporting fish production, if the species can use it effectively. Many salmonid-producing rivers incorporate lakes, but these areas have been scarcely studied compared with rivers without lakes or riverine reaches of rivers with lakes. Consequently, most models of salmonid migrations exclude the movement down and back up through lakes. Parr may also find good feeding habitat in lakes that can contribute to smolt production or encourage better growth or higher rates of residency. High-quality lake habitat may also encourage precocious maturation where feeding conditions are especially good (Myers et al. 1986). Smolts consistently have high mortality in these areas, and there may be unstudied genetic factors or learning involved in assisting migration through lakes, but perhaps the smolt production in lakes acts to offset some of the mortality among smolts. Atlantic salmon and sea trout kelts seem to overwinter in lakes, and systems with lakes may have better contributions of repeat spawning (Cunjak et al. 1998).

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