

## Review Article

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# Differential migration in Pacific salmon and trout: Patterns and hypotheses

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**Abstract:** Migrations affect the population dynamics, life history, evolution, and connections of animals to natural ecosystems and humans. Many species and populations display partial migration (some individuals migrate and some do not), and differential migration (migration distance varies). Partial migration is widely distributed in fishes but the term differential migration is much less commonly applied, despite the occurrence of this phenomenon. This paper briefly reviews the extent of differential migration in Pacific salmon and trout (genus *Oncorhynchus*), a very extensively studied group. Three hypotheses are presented to explain the patterns among species: 1) phylogenetic relationships, 2) the prevalence of partial migration (i.e., variation in anadromy), and 3) life history patterns (iteroparous or semelparous, and duration spent feeding at sea prior to maturation). Each hypothesis has some support but none is consistent with all patterns. The prevalence of differential migration, ranging from essentially non-existent to common within a species, reflects phylogeny and life history, interacting with the geographic features of the region where juvenile salmon enter the ocean. Notwithstanding the uncertain evolution of this behavior, it has very clear implications for salmon conservation, as it strongly affects exposure to predators, patterns of fishery exploitation and also uptake of toxic contaminants.

**Keywords:** Partial migration; Anadromy; Life history; Phylogeny; Conservation; *Oncorhynchus*

## 1 Introduction

Migration is a widespread behavioral pattern in animals (1, 2), with profound consequences for the fitness of individuals and the conservation status of the population or species. Migration affects exposure to predators, pathogens, and contaminants, access to optimal feeding and breeding areas, spatio-temporal changes in abiotic conditions, and exploitation by humans (3-5). In many cases, migratory species, or the migratory forms of species, are in greater jeopardy than non-migratory species and forms (6-8). Migratory animals can also have profound effects on their ecosystems (9, 10).

Over the past decades it has been increasingly clear that there are many alternatives to migration displayed by individuals and populations, and the scientific literature on alternative migration patterns has been heavily influenced by work on birds (11, 12). With respect to birds, partial migration was defined as describing “... populations [that] include some individuals that do and some that do not migrate from the same breeding area” (13). This definition is consistent with general usage (14), and partial migration is known in many taxa (15-18) including fishes. For example, anguillid eels are famous for their catadromous migrations from marine areas where they are spawned to freshwater habitats where they feed and grow for years before migrating back to sea, but some juveniles do not ascend rivers (19). Many other diadromous fishes also show partial migration, including black bream, *Acanthopagrus butcheri*, in Australia (20), European perch, *Perca fluviatilis*, in the Baltic Sea (21), and white perch, *Morone americana*, on the Atlantic coast of North America (22). There are also many examples of marine fishes with migratory and non-migratory populations, and often the management and conservation hinge on understanding these patterns (e.g., Patagonian toothfish, *Dissostichus eleginoides* (23) and winter flounder, *Pseudopleuronectes americanus* (24)).

Perhaps the best studied example of partial migration in fishes is anadromy in salmonids (primarily the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*). In these fishes, the patterns and prevalence of anadromy can vary widely

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among and within populations (25-27), influenced by genotype and phenotypic plasticity (28). There is an extensive literature spanning all species, on the prevalence of anadromous and nonanadromous populations, and individuals within populations, including aspects related gene flow between forms (29), genomic association (30), relationship to growth among populations (31, 32), growth and energy storage of individuals (33-35), and sex (36).

The term differential migration is commonly used, especially in the avian literature, when referring to cases where individuals vary in the distance or timing of migration (37) or, more specifically, "... the situation in which migration in some distinguishable classes of individuals (ages, sexes, races) differs with respect to timing, distance, or both" (13). Typically, for example, female birds migrate farther than males, and males arrive earlier, or there is a difference between adults and young (38). Unlike partial migration, a term commonly applied to fishes in the scientific literature, differential migration is seldom applied to fishes in general and salmonids in particular, though the phenomenon certainly occurs. That is, many anadromous forms differ markedly in the spatial extent of their migrations. Striped bass, *Morone saxatilis*, vary in their movements in estuarine and marine waters (39), and Secor (40) revived this "contingent hypothesis" and revealed divergent patterns of movement among anadromous fish, in addition to a resident (nonanadromous) form (41, 42).

In a recent review of individual variation in animal movement, Shaw (43) concluded that "... the consequences of movement are less well understood than the causes." This may be the case for some taxa but I would argue that it is not so for salmon and their relatives. In these fishes, the consequences for growth, natural and anthropogenic mortality, and the productivity of populations, may be better understood than the causes, which are a complex blend of ancestral tendencies of the population, recent growth and condition of the individual, and environmental stimuli. Despite the voluminous scientific literature on the behavior, ecology, and evolution of salmonids (44, 45), and the existence of differential migration, the proximate and ultimate causes of this form of variation are very poorly understood.

The first purpose of this paper is to briefly review the prevalence and patterns of differential migration in anadromous Pacific salmon (genus *Oncorhynchus*) species. Definitions of differential migration often include variation in migration timing as well as spatial patterns (13), but this review follows Cristol, Baker (38) and limits the scope to differences in spatial extent of feeding migrations from the breeding areas. There is also widely recognized variation in migration timing, often referred to as

seasonal races or runs, in several families of migratory fishes, notably salmonids, sturgeons, and lamprey (46). Differential timing of migration is most dramatic among distinct breeding populations but within-population variation also occurs, with males and older salmon typically migrating earlier than females and younger salmon. These patterns and hypotheses were recently reviewed (47), and will not be detailed here.

Two important distinctions between the migrations of salmon and birds should be noted when reviewing concepts so well-established in the avian literature. First, differential migration in birds (in terms of distance) is often related to sex, with females typically migrating farther than males (38, 48, 49). Sex-biased distribution patterns are known in some fishes, for example sharks and rays (50, 51), but this is often related to parturition. Male salmon often migrate before females (though nest site selection and preparation are solely accomplished by females) but there seems to be no evidence of systematic differences in migration distance with sex. As noted at the conclusion of this paper, there may be data to test this hypothesis but it is not a prominent feature of research to date.

Even more fundamentally, salmon migrations differ from those of birds and some other animals in that, while the breeding site is a fixed location, the feeding grounds to which they migrate and from which they return are extremely broad. Salmon migrations are not seasonal changes in latitude between discrete breeding and feeding sites. Rather, juvenile salmon (naïve to the ocean, without adults to guide them) enter marine waters and disperse. Depending on the species and point of entry, individuals from one population may migrate north along the coast, both north and south, or mainly south. In many cases they feed out in the open North Pacific Ocean, more or less continuously moving, until they approach sexual maturity. They then migrate in a more directed manner homeward to the mouth of their natal river, ascend it, and spawn. Individual salmon can be caught at sea and in some cases tagged and later recovered, or assigned to a population of origin by genetic methods, but for the most part their feeding distribution and movements at sea are inferred indirectly. In comparison, the arrival of birds in feeding areas can be observed directly. The broad distributions of salmon during their feeding migrations at sea complicate determination of whether there are differential patterns or not; variation in distance travelled is so common as to be unimportant, especially in species that vary in the number of years spent feeding at sea prior to homeward migration. Consequently, this review focuses on distribution patterns that are bimodal or otherwise result in more discrete differences rather than a continuum.

Considering differential migration with respect to distance travelled rather than timing, patterns of variation might be explained, hypothetically, by three factors. First, the extent of differential migration might follow phylogeny (i.e., species more closely related would show more similar patterns). Second, the prevalence of differential migration might parallel that of partial migration (e.g., non-anadromy) among species. Third, the prevalence of differential migration might be associated with life history variation – specifically, the number of years spent at sea prior to maturation, and the prevalence of iteroparity. The review of species is arranged taxonomically, and a phylogeny is provided for reference (Fig. 1), though different studies, using different samples, markers, and analytical methods, vary somewhat in the relationships among species. Then, having reviewed the patterns and evaluated the support for these hypothesized factors as influencing differential migration, I discuss the evidence for the influences of genetic, internal (sex, size, physiological condition), and external (environmental) factors in differential migration, and end with an explanation for why these patterns are so important in these fishes, as with so many other migratory animals.

## 2 Species-Specific Patterns

### 2.1 Sockeye, Chum, and Pink Salmon

Salmon and trout enter the Pacific Ocean over a broad arc around the Pacific Rim, from California to Alaska in North America and from Korea to Russia in Asia (Fig. 2) so some generalization is needed in characterizing their migration patterns. The most numerous species are the pink (*O. gorbuscha*), chum (*O. keta*) and sockeye (*O. nerka*) salmon. These species, more closely related to each other than to others in the genus (52), typically migrate rapidly northward along the coast of North America and Asia during their first summer at sea, and then move into the open North Pacific Ocean and Gulf of Alaska and remain there before returning to spawn (53-55). Sockeye salmon commonly occur as self-sustaining non-anadromous populations (known as kokanee), that evolved independently from anadromous ancestors in many river systems (56). Nevertheless, the expression of differential migration is limited among anadromous populations of that species, and the others. For example, juvenile sockeye salmon migrate rapidly (57) and tend to vacate the inland waters of Puget Sound and the Strait of Georgia (Fig. 3), now often referred to as the Salish Sea, by mid-late summer

(58-60), and similarly rapid migrations are observed elsewhere (61). However, genetic analysis of juveniles caught in marine waters indicated that some populations left the Fraser River and migrated rapidly through the Strait of Georgia whereas others stayed longer there to feed, and some coastal B.C. populations remained in local areas into their first fall and winter at sea (62).

Juvenile chum salmon feed in estuaries longer than do sockeye and pink salmon but they also show a single migration pattern with few exceptions. Their distribution is in the open ocean, north of their river of origin. There are reports of some sub-adult chum salmon that remain in the Salish Sea and feed for a year or more (63), and I have sampled some while studying other salmon species in Puget Sound, but they seem to be quite unusual.

In the case of pink salmon, there are two forms of differential migration to note. First, though the great majority feed on the open ocean, the populations from Asia (e.g., the east coast of the Kamchatka Peninsula) travel farther at sea than do North American populations, based on tagging studies, and the Asian populations also migrate homeward much faster than do the North American ones at the onset of sexual maturity (64). In addition to this variation in distribution and migration rate at sea, Jensen (65) reported that some pink salmon entering Puget Sound remained there rather than migrating to the ocean as most do. Haw, Wendler (66) measured a sample of these fish and they were markedly smaller than conspecifics caught along the coast at the same time of year. This differential migration pattern was never explained and now seems to be increasingly rare, as indicated by my examination of catch records reported by the Washington Department of Fish and Wildlife. Pink salmon, as a species, are currently more numerous in the Salish Sea than they were in the past (67), so differential migration would likely be detected if it was still common.

Thus within this evolutionary group, differential migration is limited, being mostly a matter of degree (i.e., oceanic distributions and migration rates) or uncommon alternative patterns such as the Puget Sound residents. Given the shared evolutionary lineage of this group, the results are thus consistent with a hypothesis related to phylogeny. In sockeye salmon, non-migratory populations evolved repeatedly, but the anadromous form showed only limited differential migration, so the connection between partial and differential migration is not supported. In terms of life history, the three species vary in terms of how long they stay at sea, from one year in pink salmon to typically two or three in sockeye and two to four or more in chum salmon (44), so there is no clear link between this aspect of life history and migration. All

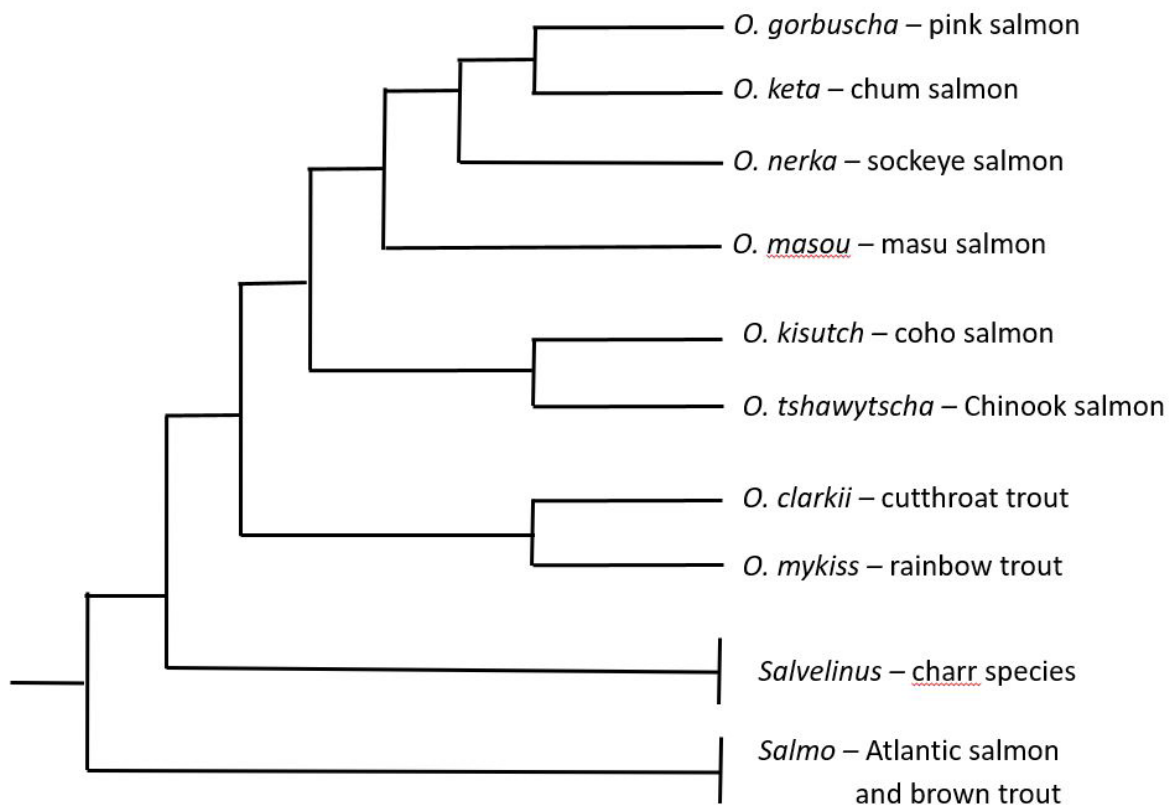
three species are invariably semelparous but, as the next section indicates, so are other species in which differential migration is common.

## 2.2 Chinook and coho salmon

The second major grouping of migration patterns involves Chinook and coho salmon, another evolutionary lineage (Fig. 1), and was recently reviewed (68, 69). In their native range these species are almost exclusively anadromous, though in some cases individuals mature without having gone to sea. This so-called precocious maturation is almost exclusively seen in males and in Chinook salmon rather than coho salmon. It is associated with rapid growth (70) but the tendency to do so varies among populations (71). These species are invariably semelparous under normal circumstances, though under experimental conditions males that mature can survive and spawn in subsequent years (72). Thus the life history patterns differ from those of pink, chum, and sockeye salmon.

Chinook and coho salmon breed in rivers farther south than do pink, chum and sockeye salmon, and the

southern populations of coho and Chinook salmon feed primarily in the cool, productive coastal upwelling zone from California to southern British Columbia. Populations farther north feed along the coast and also in offshore waters. These patterns suggest that the area where salmon enter the ocean determines their feeding areas but this is not the case. Decades ago it was reported that Chinook salmon from different populations breeding within the Columbia River system had very different marine distribution patterns despite entering at the same point along the coast (73). Healey (74) pointed out that populations with juveniles entering the ocean in their first year of life, termed ocean-type, were distributed along the coast (rather than offshore) to a much greater extent than the “stream-type” that spend a full year in streams prior to seaward migration. The ocean-type juveniles tend to be smaller when they enter the ocean, enter over a longer period, and make greater use of estuaries, suggesting a relationship to differential migration. However, the real divide in migratory patterns seems to be between lineages that evolved in the continental interior or coastal areas (75), rather than a divide between juvenile life history patterns (76). Thus the evolutionary lineage within the





species seems, in this case, to have more influence on differential migration (i.e., coastal vs. offshore distributions) than does the region of the coast where the fish enter the ocean, or their juvenile life history. Even among those distributed along the coast, some populations differ in how far they go. In particular, juveniles from the Columbia River migrate rapidly northward in their first summer at sea, dispersing over almost 3000 km along the continental shelf, whereas many others remain within about 100 – 200 km of their natal rivers (77). It should also be noted that Chinook salmon vary in the number of years spent at sea, and in general the older fish are found farther from their natal river than are younger fish (78).

As with Chinook salmon, the marine distribution patterns of coho salmon populations vary considerably, even among those entering the ocean near each other (79). In contrast to Chinook salmon, coho salmon do not seem to show the “offshore vs. coastal” differential migration pattern within a given region, but only the general latitudinal gradient from distribution within the coastal upwelling zone of the California Current region, to a mix of nearshore and offshore distribution farther north, where the offshore waters are more suitable in temperature, productivity, and biotic community. However, it has also been known for more than a century that both

Chinook and coho salmon display another form of differential migration; some members of these species feed throughout the year in the inland marine waters of the Salish Sea rather than along the ocean coast (Figs. 4, 5). Indeed, these salmon were so numerous that the leading ichthyologists of the day wrote [p. 475] that “King Salmon and Silver Salmon of all sizes are taken with the seine at almost any season in Puget Sound. This would indicate that these species do not go far from the shore” (80). The latter statement, that they do not migrate to the open ocean, was clearly incorrect, but their presence within the Salish Sea is undeniable, and has been common knowledge in the fishing and fisheries management communities of the region for decades (66, 81) but has not been discussed in the broader context of differential migration.

The existence of salmon making such limited marine migrations poses several inter-related questions: 1) what proportion of the salmon displays this form of differential migration, 2) has the proportion changed over the past decades, 3) do the migratory variants reflect discrete modes of behavior or points along a continuum, 4) what costs and benefits might accrue to the two migratory forms, and 5) to what extent are the patterns under environmental and genetic control?

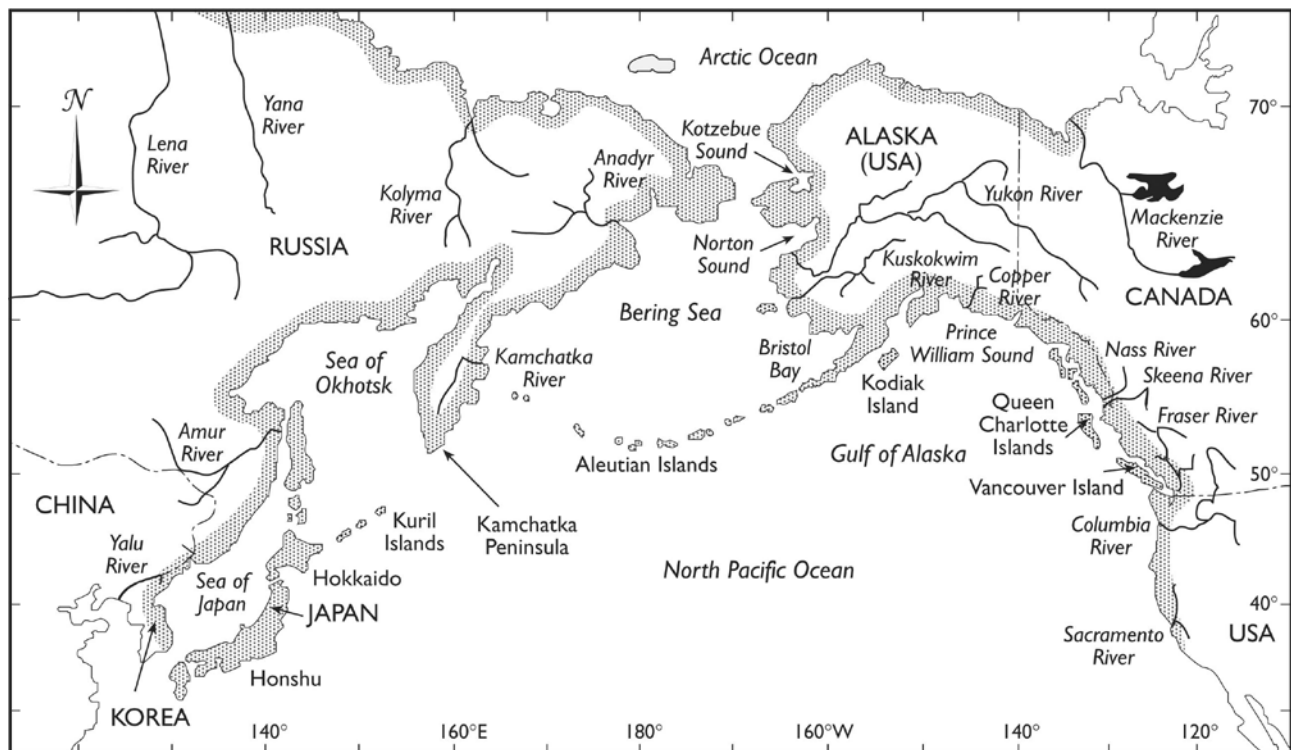
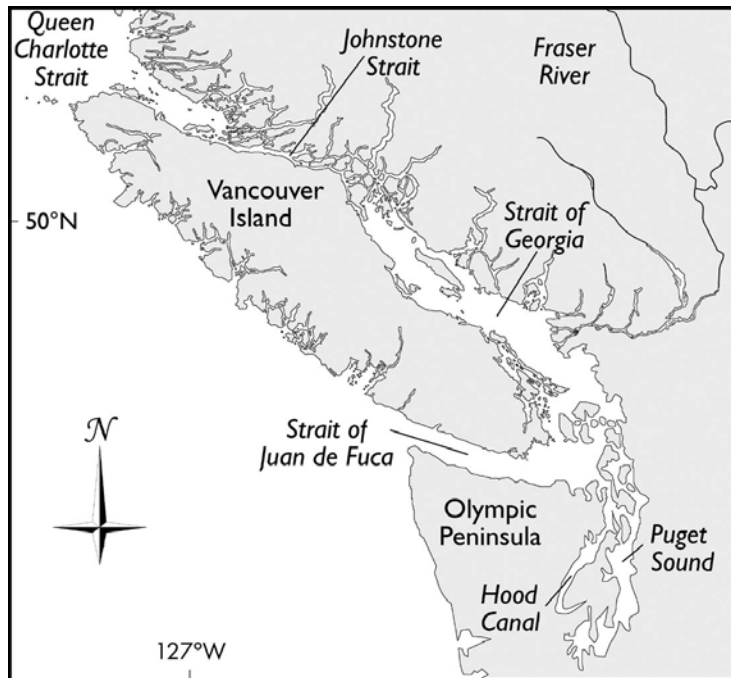


Figure 2: Map of the North Pacific Rim, showing the area, stippled, where Pacific salmon and trout enter marine waters [46].



**Figure 3:** Map showing the Strait of Georgia, Puget Sound and associated inland marine waters where differential migration is displayed by some salmon, as an alternative to migration to west coast of Washington along the Olympic Peninsula, west coast of Vancouver Island, or central coast of British Columbia north of Queen Charlotte Strait [46].



**Figure 4:** Chinook salmon, caught in Puget Sound in August, when such fish normally return from the Pacific Ocean coast to inland marine waters prior to migrating upriver to spawning areas. Photo credit: Thomas Quinn, used with permission of the angler, Leonard O'Neill.



**Figure 5:** Immature Chinook salmon caught in Puget Sound in November, as part of the anadromous but “resident” contingent that represents an alternative to the pattern of migration to the coastal ocean. Photo credit: Thomas Quinn, used with permission of the angler, Justin Wong.

Tagging data indicated that the great majority of coho (79) and Chinook salmon (78) feeding in Puget Sound originated from rivers flowing into the Salish Sea. However, many salmon originating from the same rivers migrate farther, out to the ocean coast, and feed there rather than remaining in the Salish Sea. Analysis of the recoveries of tagged coho salmon entering the Strait of Georgia indicated that the residents decreased as a proportion of the total from the mid-1970s (ca. 60%) to almost nil by the late 1990s (82). The authors concluded (p. 514), “Despite our inability to understand all of the details of the mechanisms that affected the movement of coho, there is little doubt that the recent behaviour change in coho is related to a change in climate.” Further analyses of tagging data (83) indicated that only small a proportion of coho salmon produced in Puget Sound remained as residents – the considerable majority migrated to the coast. A mix of long and short distance migrants was seen in all years and population groups, but the proportions varied with the region of Puget Sound that they entered. In addition, salmon that entered marine waters later in the year were more likely to remain in Puget Sound than those entering earlier. There was also considerable year to year variation in the proportions of long and short distance migrants. These findings suggest that the environmental conditions encountered when entering marine waters influenced migration but the mechanism is not clear, and the evidence not complete.

O’Neill and West (84) also used data on the recovery patterns in space and time of Chinook salmon tagged as juveniles, and concluded that those remaining in Puget Sound were a large fraction of the total population. The tendency to remain within Puget Sound was greater for salmon that had spent a full year in fresh water prior to ocean entry as juveniles (hence were larger) compared to those migrating to sea in their first year of life. Subsequent analysis of similar data over a longer period of record by Chamberlin, Essington (85) also indicated that a substantial fraction of the juveniles entering Puget Sound fed there for most or all of their period at sea. As was the case with the coho salmon, the tendency to remain as residents was primarily affected by where they entered marine waters, with a secondary effect of size (larger being more likely to remain resident) and substantial variation among years. Interestingly, the annual indices of residency were positively correlated between coho and Chinook salmon (Pearson correlation coefficient: 0.58,  $P < 0.01$ ), and warmer water was associated with a greater tendency for migration to the coast in both species (Race Rocks, British Columbia July mean vs. Chinook salmon:  $R^2 = 0.37$ ,  $P < 0.01$ ; coho salmon:  $R^2 = 0.33$ ,  $P = 0.015$ ).

The influence of body size and entry date could be interpreted as consistent with some interaction between individual condition and the environment, and the effects of geographic region and environmental conditions on migration indicate external influences. The fact that in both species, both forms of migration are seen within breeding populations would seem to argue against a strong genetic control of short and long migration patterns in this case (e.g., some population adopt one pattern, and other populations adopt the alternative pattern). However, as discussed in more detail below (Section 4.1), recent studies have uncovered strong associations between genomic signatures and the timing of migration from the ocean into freshwater habitats, and the tendency for juveniles to migrate between breeding sites in streams and the ocean (86), or a large lake (87). Consequently, the extent of genetic influence on alternative migration distances may be greater than one might infer from the presence of both migratory forms in a given population. Indeed, it was recently reported that the tendency of coho salmon to feed as residents or migrate northward differed between populations, and even some family-level variation in distribution was detected (88).

Regardless of the controlling factors, body size differs dramatically between salmon feeding in the Salish Sea and those migrating to the coast (Fig. 6). Jensen (89) wrote that “... both the silver [coho] and chinook salmon remaining in Puget Sound are much smaller than their brothers feeding off our coast. This may be due to lack of feed in the Sound, or it is possible there is a definite relationship between the size of the fish and the distance they migrate



**Figure 6:** Immature coho salmon caught in Puget Sound in May, displaying the small size that is typical of such residents, in contrast to the larger conspecifics of the same age that feed along the Pacific Ocean coast. Photo credit: Thomas Quinn.



from their home stream.” Essentially, he was posing two hypotheses: fish of similar size enter two environments and then grow at different rates, or initial size predisposes individuals to migrate long or short distances. Milne (90) reported the same growth rate differential between coho salmon feeding in British Columbia inland marine water and the coast. He pointed out that the slower-growing, short distance migrants do not represent separate breeding populations but, rather, some fish from all populations seem to show this pattern. Pressey (81) reported that Chinook salmon sampled in June within Puget Sound were much smaller than those in outer Juan de Fuca Strait (averaging 54.0 vs. 84.2 cm in length or about 2 vs. 7 kg). Those fish might represent a range of ages but Haw, Wendler (66) reported similar size differences between coho salmon sampled within Puget Sound and near the coast (46.4 cm vs. 70 cm or about 1 vs 4 kg in mass), and 42.1 vs. 56.0 cm in pink salmon. Both coho and pink salmon spend a single year at sea so all would have been the same age when sampled. Thus, there seem to be fundamental differences between the water bodies that affect growth in all three species. Given the strong relationship between body size and the number and size of eggs females can produce, and the advantages of large size through sexual selection in males, these differences in body size would reflect very substantial fitness costs (44).

The slower growth of salmon remaining in the Salish Sea does not mean that this differential migration pattern is necessarily maladaptive. For example, if Salish Sea resident salmon experienced higher survival rates than those migrating to the coast, there might be a form of tradeoff of benefits and costs. The inter-annual trends in survival at sea differ between populations entering marine waters in the Salish Sea and the coastal ocean in coho (91) and Chinook salmon (92), and in coho salmon the survival rates have been higher for Salish Sea populations. This does not prove that the members of each population remaining in the Salish Sea enjoy a higher probability of surviving than members of their cohort migrating to the coast, but it is at least consistent with that hypothesis.

In summary, coho and Chinook salmon are phylogenetically close to each other and each species shows one or more forms of differential migration, but partial migration is rare in coho and uncommon in Chinook salmon, and largely restricted to males. That is, neither species forms nonanadromous populations in their native range, though some male Chinook salmon can mature and spawn without going to sea, and some coho salmon of both sexes can do so if a lake is available for rearing. Thus partial and differential migration are not linked in these species. As

with pink, chum, and sockeye salmon, coho and Chinook salmon are invariably semelparous under natural conditions.

## 2.3 Masu salmon

The first five species discussed above are all distributed on both the Asian and North American sides of the Pacific Ocean, though each has its own latitudinal range. A sixth species, masu salmon, *O. masou*, restricted to Asia, has long been recognized. In some taxonomies it was divided into two species (93) but it is now more widely recognized as a single species with four subspecies, some of which evolved as isolated, nonanadromous forms (94). The taxonomic relationship between masu salmon and the rest of the Pacific salmon and trout is not entirely clear, and its ecology and life history has elements of many different species. The most widely distributed subspecies, *O. masou masou*, is commonly anadromous and in the northern part of its range both males and females typically migrate to sea. However, farther south, more males reach sexual maturity after feeding in freshwater habitats and thus the great majority of seaward migrants are females (31). Under conditions of especially rapid growth, females also mature without migrating to sea. The anadromous individuals die after spawning but those maturing in fresh water can spawn again (95). Thus this species displays sex-biased partial migration, and also some deviation from the semelparity that otherwise characterizes Pacific salmon. However, there seem to be no indications of differential migration, only variation related to where they enter marine waters. The timing of migration to sea and back by masu salmon varies but few if any spend more than a single winter at sea, and their feeding distribution is largely restricted to the Sea of Japan and Sea of Okhotsk (96).

## 2.4 Cutthroat trout and steelhead – anadromous rainbow trout

Cutthroat trout, *O. clarkii*, and rainbow trout, *O. mykiss*, were formerly classified in the genus *Salmo*, with Atlantic salmon and brown trout but were reassigned to the same genus as Pacific salmon (97). Both species include subspecies and very distinct genetic lineages in their natural ranges (98), and both exist in many areas as exclusively nonanadromous populations, either landlocked above barriers to migration, or volitionally so. Juveniles of the two species are often difficult to distinguish visually,



habitat use patterns in streams overlap (99), and naturally-produced hybrids are not uncommon (100-102). Both species breed in the spring, in contrast to the fall-spawning Pacific salmon. Moreover, both species are iteroparous, and the offspring migrate to sea at similar body sizes, ages, and times of the year. All these attributes would suggest similar and limited marine migrations in both species; this is the case with the coastal cutthroat trout subspecies, *O. clarkii clarkii*, but not rainbow trout.

In Puget Sound, the great majority of cutthroat trout do not move more than about 20 – 30 km from their natal streams, based on genetic assignment of fish to rivers of origin (103), and sonic tracking (104). They feed very close to shore and display spotting patterns that camouflage them when seen against a background of gravel, sand, and shells along beaches (Fig. 7). In other regions such as the Columbia River estuary (105) and coastal Alaska (106), complex patterns of movement are displayed between marine and freshwater habitats for feeding, breeding, and overwintering but there are no indications of long distance movement or differential migration. Populations along the open ocean coast may differ in distribution; some move offshore (107-109) whereas others remain within or near their natal estuaries (110). Nevertheless, there are presently no indications of long distance migrations in some members of the species that would exemplify differential patterns, relative to the characteristic pattern of limited movement.

Given the extensive range of non-anadromy and partial migration in rainbow trout, and the ecological similarity to cutthroat in many aspects, one might predict that

anadromous rainbow trout would show limited marine migration comparable to that in cutthroat trout. However, in stark contrast to cutthroat trout, seaward migration by the anadromous form of rainbow trout, known as steelhead, is typically quite rapid, directed, and primarily in open water, as revealed by studies in the Salish Sea (111-113), and rivers along the North American coast (114, 115). Sub-adult steelhead quickly move to the open ocean, travelling far out to sea (108, 116) and display the countershading needed for camouflage in the ocean – gray backs, silver sides, and white undersides (Fig. 8). There is some variation in marine distribution related to where the fish entered the ocean and how long they stay before returning (116), but these seem more a matter of degree and thus not clearly an example of differential migration.

One study serendipitously provided insights into the genetic basis of migration in these species. Wild steelhead and cutthroat trout smolts were trapped as they left a river flowing into Hood Canal, part of Puget Sound, and sonic transmitters were implanted to track their movements. Subsequent DNA analysis revealed that 89 steelhead, 52 cutthroat trout, and 42 naturally-produced hybrids (23%) had been tagged. As expected, the steelhead moved rapidly seaward and the cutthroat remained near their natal river, and the movement patterns of the hybrids were intermediate between the two pure forms (117).

Thus the life history and freshwater ecology of these two related species, cutthroat and rainbow/steelhead trout, are similar, yet they have completely different patterns of migration at sea, and neither displays clear differential migration at sea. In partially migratory populations



**Figure 7:** Coastal cutthroat trout caught in Puget Sound in December, displaying the spotting pattern typical of this subspecies in rivers and marine waters. Photo credit: James Losee, Washington Department of Fish and Wildlife.



**Figure 8:** Female steelhead, caught in a tributary of Puget Sound in January prior to spawning, displaying the countershading that is typical of the anadromous form of rainbow trout. Photo credit: Bill McMillan.

of rainbow trout, the sex ratio of seaward migrants is often female-biased (118-121) and this may also be the case with cutthroat trout but I have not seen data to test the idea. It should be noted that the above description of steelhead reflects the large literature on the form in North America, but there are indications of greater migration diversity in Russia. Interpretation of scales from the Kol and Kekhta rivers of Kamchatka indicated that in addition to the dominant forms (river resident and anadromous), some individuals used the estuary without going to the ocean (122). It is unclear whether these forms are now, or ever were, prevalent in North America, how distinct they are, and what factors cause them to occur in some rivers, and some individuals.

### 3 Discussion

As noted in the Introduction, the consequences of migration in salmonids in general, and especially partial and differential migration, are much better understood than the evolution and causes. The consequences of differential migration can include exposure to higher rates of fishing pressure in coastal waters than offshore for Chinook salmon (76), higher concentrations of chemical contaminants for those feeding in Puget Sound compared to the ocean coast (84), and different growth rates. This review considers three hypothetical frameworks for comparing patterns of differential migration: phylogenetic affinity, patterns of partial migration, and life history variation (duration of marine residence, and iteroparity).

There is some support for the hypothesized connection between differential migration and phylogeny, but not for a connection to partial migration (i.e., anadromy vs. non-anadromy). Pink, chum, and sockeye salmon are most closely related to each other and they show only a limited degree of differential migration; virtually all anadromous individuals of all three species migrate to the open ocean. The presence of a common nonanadromous form of sockeye salmon, kokanee, thus seems disconnected from differential migration. Coho and Chinook salmon are related to each other and both show differential migration but only slight partial migration (and almost exclusively males in their native range). Rainbow and cutthroat trout are related to each other, and each shows almost exclusively a single migration pattern, though they differ greatly from each other in the duration and spatial extent of migrations at sea. The phylogenetic position of masu salmon is unclear, and they show several forms of partial migration but apparently no differential migration.

The connection between phylogeny and the extent of differential migration but not with partial migration among species, seems somewhat counter-intuitive. Phylogeny would be expected to be linked to the more fundamental trait of anadromy or freshwater residency, owing to the profound physiological adaptations needed for this migration, compared to the primarily behavioral adaptations for differential migration. Importantly, the patterns of partial and differential migration are not closely connected.

There was also little or no support for the hypothesized connection between life history traits such as the number of years spent at sea or the prevalence of iteroparity, and differential migration. The duration of marine residence varies among species, ranging from less than a year in cutthroat trout, typically or invariably one full year at sea in pink, masu, and coho salmon, commonly two or three in steelhead and sockeye salmon, one to four in Chinook salmon, and two to four in chum salmon. Thus the species with best-developed differential migration, coho and Chinook salmon, are not distinguished in the duration of marine residence. Similarly, neither semelparous nor iteroparous species seem predisposed to differential migration, though partial migration (i.e., non-anadromy) is much more common in the iteroparous species.

### 4 Key questions to guide future research

Movement decisions by individuals result from complex combinations of internal and external factors, as the genotype interacts with the immediate biotic and abiotic conditions experienced by the individual, as summarized by efforts to synthesize the vast research on migration patterns of diverse taxa (43, 123). Similar conclusions have been drawn regarding the variation in anadromy in salmonids; movement decisions reflect genetic tendencies at the population and individual levels, growth and condition of the individual, and proximate environmental conditions presented to the population (28, 44). If progress is to be made on some of the complex issues related to differential migration in salmon (and, by extension, other less closely studied species), then hypotheses need to be framed to address these influences (124).

#### 4.1 What is the genetic contribution to differential migration?

There is evidence for some degree of genetic control over migration in many taxa (125), and especially birds (126). It is beyond the scope of this review to consider all aspects of genetic control and evolution of migration in salmonids (44), but selected examples related to anadromy may prove useful. Salmonid species show a wide range of patterns, from invariably anadromous to entirely non-anadromous (25, 26). In sockeye salmon, anadromous populations colonized suitable habitat after glacial retreat, and in many independent river systems the slower growth in fresh water was sufficiently offset by the survival advantage of not going to sea and back, leading to the evolution of and non-anadromous “kokanee,” often in sympatry with anadromous conspecifics (56, 127). Genetic separation is achieved through a combination of assortative mating and lower survival of the hybrids, which not uncommonly occur (128). In contrast to this relatively strong genetic separation between forms in this species, most salmonids show more conditional control, with sex-specific norms of reaction related to the growth rate of the juveniles (36, 129), an exemplified in *O. mykiss* (28). Consequently, some genetic influence on differential migration would not be surprising.

It is very possible that the spatial extent of migration has a genetic basis. Indeed, there is strong evidence of population-specific patterns of salmon distribution at sea, as indicated by juveniles tagged in fresh water and recovered as adults at sea (130), and by the maintenance of migration patterns after transplantation to a new site and hybridization between populations (131). The Chinook salmon from the interior part of the Columbia River basin are genetically distinct as a lineage from those breeding farther downriver, and differ in marine distribution (75, 76). However, the alternative tendencies to feed in inland marine waters or migrate to the ocean coast are evident within populations of Chinook (85) and coho salmon (83), so the evidence for a genetic basis is mixed and ambiguous, and conclusions await controlled experiments. Alternatively, recent developments in genetic analyses allow what is known as parentage-based tagging of hatchery produced salmon. That is, all parents used for spawning are genotyped and then fisheries are sampled so that individual adult salmon can be linked to not only their population of origin (as prior tagging programs have done) but also to their parents. This remarkable capacity now permits detailed assessment of the spatial and temporal patterns of salmon at sea in areas where fishing occurs (88, 132). Application of this approach revealed that

some coho salmon populations produced more fish that remained in the Salish Sea rather than migrating farther north, and that siblings were closer to each other when recovered at sea than non-siblings among those migrating long distances (88). This kind of approach, associating behavior patterns with population or family of origin, likely will be complemented in the future with genomic approaches such as those used to investigate within-species variation in the timing of return from the ocean (133), and the distinction between non-anadromous and anadromous forms (30).

#### 4.2 How does individual condition affect differential migration?

In many taxa, patterns of differential migration are related to body size, sex, or both (especially in cases of sexual dimorphism). For example, male elephant seals, *Mirounga angustirostris*, are much larger than females, and travel farther to forage than do females, likely to meet their metabolic needs (134). Segregated foraging areas by age and sex are also known in many other animals, including beluga whales, *Delphinapterus leucas* (135), many species of sharks (50), songbirds (136), and more. Given the notable sex bias in anadromy (more common in females if the species varies), it is plausible that differential migration (e.g., use of inland marine waters vs. the coastal ocean) is sex-biased. To my knowledge such patterns have not been reported but data could be obtained from fishery samples to evaluate this hypothesis.

With respect to size, it is widely known that the fastest growing individuals (especially males) of many salmonid species transition directly to sexual maturity without migrating to sea, for example in masu salmon (32), Atlantic salmon, *Salmo salar* (137), and Chinook salmon (138). Thus a connection between body size and differential migration is plausible. There are at least two obvious hypotheses related to body size and differential migration alternatives in salmon of migration to the coast and occupancy of interior marine waters. First, juveniles of all sizes might enter inland marine waters and some factor other than size determines whether they remain or migrate to the coast. In this scenario, those remaining grow slower, for ecological reasons, than do those along the coast. Second, small (or large) size may predispose juveniles to follow one migration alternative or the other. Studies on the migration pathways of individuals of known size have not been conducted. However, cohorts of juvenile salmon (i.e., those migrating to sea in a given year from a given hatchery or river or origin) that were larger on average

tended to produce more fish that remained in Puget Sound rather than migrating to the coast in Chinook salmon (85). However, the effect was not consistent among regions, and was not detected in coho salmon using similar analyses (83), so evidence that large size influences differential migration in these salmon is at present mixed. It thus seems that poorer growing conditions in the inland marine waters reduce growth, rather than that small fish tend to remain there while larger members of the cohort migration to the coast.

### 4.3 How do environmental conditions affect differential migration?

In the case of juvenile Chinook and coho salmon cohorts entering Puget Sound in a given year, the proportions of the two species that remain there rather than migrating farther out to the coastal ocean were positively correlated between years (83, 85). Moreover, in years when sea surface temperatures in late spring (when the juveniles enter marine waters) were cooler, larger proportions remained as residents whereas warmer temperatures were associated with larger proportions of distant migrants, in both salmon species. These findings were all consistent with environmental influences on migration, though the mechanism is unclear. The changes in temperature among

decades have been slight, and in general these waters are characterized by very moderate seasonal changes. For example, from 1970 – 2010, the mean surface temperatures at Race Rocks, British Columbia in June ranged from 9.1 to 11.4 and the seasonal variation was from a mean monthly low of 7.6° in winter to a high of 11.3°. Conditions within Puget Sound may be more variable but it still seems unlikely that thermal conditions alone are responsible for the changes in migratory behavior. Rather, there are probably other ecological processes that are either causally connected with temperature or coinciding over the period of record, that affect the fish.

### 4.4 Are differential migration patterns alternatives, or points along a continuum?

In some cases, differential migration is a matter of discrete alternative feeding areas or distances (50, 134), but in other cases it is a matter of degree, for example the latitudinal clines in sex ratio reported in some migratory birds (48, 49). In some taxa, new research is challenging previous paradigms. For example, it was concluded that “Mysticete [whale] migration should be thought of as a continuum of different strategies” (139). In the case of Pacific salmon, there has been a tendency to view those remaining in inland marine waters as distinct from those migrating to

**Table 1:** Summary of variation among Pacific salmon (*Oncorhynchus*) species in the prevalence of anadromy and partial migration (within the native range, discounting transplants and populations artificially landlocked), life history (iteroparity or semelparity), general marine migration pattern, and extent differential migration.

Species	Anadromy	Life history	Marine migration	Differential migration
Pink salmon	Invariably so	Semelparous	Extensive, offshore	Negligible
Chum salmon	Invariably so	Semelparous	Extensive, offshore	Negligible
Sockeye salmon	Typical, but non-anadromous populations are common	Semelparous	Extensive, offshore	Negligible
Coho salmon	Almost invariably so; in a few lakes some fish mature without going to sea	Semelparous	Primarily nearshore; northern populations more often offshore	Two forms; moderately common; residents in inland marine waters and migration to the ocean coast
Chinook salmon	Almost invariably so; some males mature without going to sea	Semelparous	Primarily nearshore; northern populations more often offshore	Three moderately common forms; residents in inland marine waters, coastal, and offshore
Masu salmon	Populations may be anadromous, nonanadromous, or mixed	Semelparous, with exceptions when not anadromous	Primarily nearshore	Negligible
Rainbow trout	Populations may be anadromous, nonanadromous, or mixed	Iteroparous	Extensive, offshore	Negligible
Cutthroat trout	Populations may be anadromous, nonanadromous, or mixed	Iteroparous	Limited to the area near the natal stream	Negligible



the coast. This idea is based largely on recovery patterns of tagged salmon in fisheries, and such data only indicate their location at capture, not their movement history. More recently, telemetry has indicated that most salmon tagged in Puget Sound as residents remained there until they reached sexual maturity, but some later moved out to the coast, and a few of those came back into Puget Sound prior to the normal return migration for spawning (140, 141). However, most of the salmon tracked remained within Puget Sound, and limited their movements to a small area (140, 142). These observations are consistent with the idea that the differential migration alternatives in Pacific salmon are more like modes along a continuum rather than discrete, absolute alternatives, or the two tails of a single normal distribution of behavior.

Finally, we may ask, “Why does this matter?” There is wide recognition that migratory animals link ecosystems and provide important services of many kinds (9), though they may also play a role in disease transmission (143). Many migratory species are threatened, often at least in part because their migrations heighten vulnerability (6, 7). However, the diversity of migration patterns may confer some greater resilience to the effects of human activities, including a changing climate (144). Migratory fishes often provide food for humans in addition to other ecosystem services, and there is increasing recognition that variable migration patterns affect fisheries exploitation (24, 42, 145). Alternative migration patterns also affect uptake of chemical contaminants in species such as Pacific bluefin tuna, *Thunnus orientalis* (146, 147), striped bass (148), Pacific herring (149), Atlantic salmon (150, 151), and Chinook salmon (84). These contaminants can be a health concern for humans, and also a conservation concern for the natural predators that feed on the salmon (152). Thus differential migration patterns can be very consequential for the fishes themselves and their consumers, both human and otherwise. Understanding the causal mechanisms is vital in salmon, because their genotype and phenotype are altered by the hatchery production that has increasingly come to dominate many populations complexes (153). To the extent that migration patterns are influenced by body size, date of seawater entry, and genotype, we may be affecting migration patterns. Finally, climate-driven changes in temperature and flow regimes are altering both the selective forces on migration patterns and timing, and some of the cues that trigger migration.

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## References

- [1] Baker RR. The Evolutionary Ecology of Animal Migration. New York: Holmes and Meier; 1978.
- [2] Dingle H. Migration: The biology of life on the move. New York: Oxford University Press; 1996. 474 p.
- [3] Bairlein F. Migratory birds under threat. *Science*. 2016;354:547-8.
- [4] Hardesty-Moore M, Deinet S, Freeman R, Titcomb GC, Dillon EM, Stears K, et al. Migration in the Anthropocene: how collective navigation, environmental system and taxonomy shape the vulnerability of migratory species. *Philosophical Transactions of the Royal Society, B*. 2018;373:20170017.
- [5] Tamario C, Sunde J, Petersson E, Tibblin P, Forsman A. Ecological and Evolutionary consequences of environmental change and management actions for migrating fish. *Frontiers in Ecology and Evolution*. 2019;7:271.
- [6] Horns JJ, Şekercioğlu Ç. Conservation of migratory species. *Current Biology*. 2018;28:R980–R3.
- [7] Runge CA, Martin TG, Possingham HP, Willis SG, Fuller RA. Conserving mobile species. *Frontiers in Ecology and the Environment*. 2014;12:395–402.
- [8] Wilcove DS, Wikelski M. Going, going, gone: Is animal migration disappearing? *PLoS Biology*. 2008;6(7):e188.
- [9] Bauer S, Hoyer BJ. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*. 2014;344:1242552.
- [10] Polis GA, Anderson WB, Holt RD. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*. 1997;28:289–316.
- [11] Lack D. Bird migration and natural selection. *Oikos*. 1968;19:1-9.
- [12] Lack D. The problem of partial migration. *British Birds*. 1944;37:122-30, 43-50.
- [13] Terrill SB, Able KP. Bird migration terminology. *Auk*. 1988;105:205-6.
- [14] Chapman BB, Brönmark C, Nilsson J-A, Hansson L-A. The ecology and evolution of partial migration. *Oikos*. 2011;120:1764–75.

- [15] Berg JE, Hebblewhite M, St. Clair CC, Merrill EH. Prevalence and mechanisms of partial migration in ungulates. *Frontiers in Ecology and Evolution*. 2019;7:325.
- [16] Menz MHM, Reynolds DR, Gao B, Hu G, Chapman JW, Wotton KR. Mechanisms and consequences of partial migration in insects. *Frontiers in Ecology and Evolution*. 2019;7:403.
- [17] Chapman BB, Hulthén K, Brodersen J, Nilsson PA, Skov C, Hansson L-A, et al. Partial migration in fishes: causes and consequences. *Journal of Fish Biology*. 2012;81:456–78.
- [18] Chapman BB, Skov C, Hulthén K, Brodersen J, Nilsson PA, Hansson L-A, et al. Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*. 2012;81:479–99.
- [19] Tsukamoto K, Nakai I, Tesch W-V. Do all freshwater eels migrate? *Nature*. 1998;396:635–6.
- [20] Gillanders BM, Izzo C, Doubleday ZA, Ye Q. Partial migration: growth varies between resident and migratory fish. *Biology Letters*. 2015;11:20140850.
- [21] Tibblen P, Koch-Schmidt P, Larsson P, Stenroth P. Effects of salinity on growth and mortality of migratory and resident forms of Eurasian perch in the Baltic Sea. *Ecology of Freshwater Fish*. 2012;21:200–6.
- [22] Kerr LA, Secor DH, Piccoli PM. Partial migration of fishes as exemplified by the estuarine-dependent white perch. *Fisheries*. 2009;34:114–23.
- [23] Boucher EM. Disentangling reproductive biology of the Patagonian toothfish *Dissostichus eleginoides*: skipped vs obligatory annual spawning, foraging migration vs residential life style. *Environmental Biology of Fishes*. 2018;101:1343–56.
- [24] Ziegler CM, Zacharias JP, Frisk MG. Migration diversity, spawning behavior, and habitat utilization of winter flounder. *Canadian Journal of Fisheries and Aquatic Sciences*. 2019;76:1503–14.
- [25] Rounsefell GA. Anadromy in North American Salmonidae. *Fishery Bulletin*. 1958;58:171–85.
- [26] Quinn TP, Myers KW. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. *Reviews in Fish Biology and Fisheries*. 2004;14:421–42.
- [27] Spares AD, Dadswell MJ, Dickinson MP, Stokesbury MJW. A critical review of marine adaptability within the anadromous Salmoninae. *Reviews in Fish Biology and Fisheries*. 2015;25:503–19.
- [28] Kendall NW, McMillan JR, Sloat MR, Buehrens TW, Quinn TP, Pess GR, et al. Anadromy and residency in steelhead and rainbow trout *Oncorhynchus mykiss*: a review of the processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*. 2015;72:319–42.
- [29] Johnson JR, Baumsteiger J, Zydlewski J, Hudson JM, Ardren W. Evidence of panmixia between sympatric life history forms of coastal cutthroat trout in two lower Columbia River tributaries. *North American Journal of Fisheries Management*. 2010;30:691–701.
- [30] Narum SR, Zendt JS, Frederiksen C, Campbell N, Matala A, Sharp WR. Candidate genetic markers associated with anadromy in *Oncorhynchus mykiss* of the Klickitat River. *Transactions of the American Fisheries Society*. 2011;140:843–54.
- [31] Morita K, Nagasawa T. Latitudinal variation in the growth and maturation of masu salmon (*Oncorhynchus masou*) parr. *Canadian Journal of Fisheries and Aquatic Sciences*. 2010;67:955–65.
- [32] Morita K, Tamate T, Kuroki M, Nagasawa T. Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish. *Journal of Animal Ecology*. 2014;83:1268–78.
- [33] Silverstein JT, Shimma H, Ogata H. Early maturity in amago salmon (*Oncorhynchus masu ishikawai*): an association with energy storage. *Canadian Journal of Fisheries and Aquatic Sciences*. 1997;54:444–51.
- [34] Shearer KD, Swanson P. The effect of whole body lipid on early sexual maturation of 1+ age male chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture*. 2000;190:343–67.
- [35] Sloat MR, Reeves GH. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (*Oncorhynchus mykiss*) life histories. *Canadian Journal of Fisheries and Aquatic Sciences*. 2014;71:491–501.
- [36] Sloat MR, Fraser DJ, Dunham JB, Falke JA, Jordan CE, McMillan JR, et al. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. *Reviews in Fish Biology and Fisheries*. 2014;24:689–707.
- [37] Ketterson ED, Nolan V. The evolution of differential bird migration. *Current Ornithology*. 1983;1:357–402.
- [38] Cristol DA, Baker MB, Carbone C. Differential migration revisited: latitudinal segregation by age and sex class. *Current Ornithology*. 1999;15:33–88.
- [39] Clark J. Seasonal movements of striped bass contingents of Long Island Sound and the New York Bight. *Transactions of the American Fisheries Society*. 1968;97:320–43.
- [40] Secor DH. Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research*. 1999;43:13–34.
- [41] Secor DH, Rooker JR, Zlokovitz E, Zdanowicz VS. Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. *Marine Ecology Progress Series*. 2001;211:245–53.
- [42] Secor DH, O'Brien MHP, Gahagan BI, Watterson JC, Fox DA. Differential migration in Chesapeake Bay striped bass. *PLoS ONE*. 2020;15(5):e0233103.
- [43] Shaw AK. Causes and consequences of individual variation in animal movement. *Movement Ecology*. 2020;8(12):1–12.
- [44] Quinn TP. *The Behavior and Ecology of Pacific Salmon and Trout*, second edition. Seattle: University of Washington Press; 2018.
- [45] Jonsson B, Jonsson N. *Ecology of Atlantic Salmon and Brown Trout: Habitat as a Template for Life Histories*. New York: Springer; 2011. 708 p.
- [46] Berg LS. Vernal and hiemal races among anadromous fishes. *Journal of the Fisheries Research Board of Canada*. 1959;16:515–37.
- [47] Quinn TP, McGinnity P, Reed TE. The paradox of 'premature migration' by adult anadromous salmonid fishes: Patterns and hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences*. 2016;73:1015–30.
- [48] Catry P, Lecoq M, Araújo A, Conway G, Felgueiras M, King JMB, et al. Differential migration of chiffchaffs *Phylloscopus collybita* and *P. ibericus* in Europe and Africa. *Journal of Avian Biology*. 2005;36:184–90.

- [49] Jenkins K, Cristol DA. Evidence of differential migration by sex in white-throated sparrows (*Zonotrichia albicollis*). *The Auk*. 2002;119:539-43.
- [50] Chapman DD, Feldheim KA, Papastamatiou YP, Hueter RE. There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. *Annual Reviews of Marine Science*. 2015;7:547-70.
- [51] Omori KL, Fisher RA. Summer and fall movement of cownose ray, *Rhinoptera bonasus*, along the east coast of United States observed with pop-up satellite tags. *Environmental Biology of Fishes*. 2017;100:1436-49.
- [52] Crête-Lafrenière A, Weir LK, Bernatchez L. Framing the Salmonidae family phylogenetic portrait: A more complete picture from increased taxon sampling. *Public Library of Science*. 2012;7(10):e46662. doi:10.1371/journal.pone.0046662.
- [53] Radchenko VI, Beamish RJ, Heard WR, Temnykh OS. Ocean ecology of Pink Salmon In: Beamish RJ, editor. *The Ocean Ecology of Pacific Salmon and Trout*. Bethesda: American Fisheries Society; 2018. p. 15-160.
- [54] Urawa S, Beacham TD, Fukuwaka M, Kaeriyama M. Ocean ecology of Chum Salmon. In: Beamish RJ, editor. *The Ocean Ecology of Pacific Salmon and Trout*. Bethesda: American Fisheries Society; 2018. p. 161-318.
- [55] Farley Jr EV, Beacham TD, Bugaev AV. Ocean ecology of Sockeye Salmon. In: Beamish RJ, editor. *The Ocean Ecology of Pacific Salmon and Trout*. Bethesda: American Fisheries Society; 2018. p. 319-90.
- [56] Taylor EB, Foote CJ, Wood CC. Molecular genetic evidence for parallel life-history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). *Evolution*. 1996;50:401-16.
- [57] Welch DW, Melnychuk MC, Rechisky ER, Porter AD, Jacobs MC, Ladouceur A, et al. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array *Canadian Journal of Fisheries and Aquatic Sciences*. 2009;66:736-50.
- [58] Neville CM, Johnson SC, Beacham TD, Whitehouse T, Tadey J, Trudel M. Initial estimates from an integrated study examining the residence period and migration timing of juvenile sockeye salmon from the Fraser River through coastal waters of British Columbia. *North Pacific Anadromous Fish Commission Bulletin*. 2016;6:45-60.
- [59] Groot C, Bailey RE, Margolis L, Cooke K. Migratory patterns of sockeye salmon (*Oncorhynchus nerka*) smolts in the Strait of Georgia, British Columbia, as determined by analysis of parasite assemblages. *Canadian Journal of Zoology*. 1989;67:1670-8.
- [60] Groot C, Cooke K. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? *Canadian Special Publication of Fisheries and Aquatic Sciences*. 1987;96:53-60.
- [61] Farley EV, Jr., Murphy JM, Wing BW, Moss JH, Middleton A. Distribution, migration pathways, and size of western Alaska juvenile salmon along the eastern Bering Sea shelf. *Alaska Fishery Research Bulletin*. 2005;11:15-26.
- [62] Beacham TD, Beamish RJ, Candy JR, Wallace C, Tucker S, Moss JH, et al. Stock-specific migration pathways of juvenile Sockeye Salmon in British Columbia waters and in the Gulf of Alaska. *Transactions of the American Fisheries Society*. 2014;143:1386-403.
- [63] Jensen HM. Recoveries of immature chum salmon tagged in southern Puget Sound. *Fisheries Research Papers, Washington Department of Fisheries*. 1956;1(4):32.
- [64] Hiramatsu K, Ishida Y. Random movement and orientation in pink salmon (*Oncorhynchus gorbuscha*) migrations. *Canadian Journal of Fisheries and Aquatic Sciences*. 1989;46:1062-6.
- [65] Jensen HM. Migratory habits of pink salmon found in the Tacoma Narrows area of Puget Sound. *Fisheries Research Papers, Washington Department of Fisheries*. 1956;1(4):21-4.
- [66] Haw F, Wendler HO, Deschamps G. Development of Washington State salmon sport fishery through 1964. *Washington Department of Fisheries, Research Bulletin* 7, 1967.
- [67] Losee JP, Kendall NW, Dufault A. Changing salmon: an analysis of body mass, abundance, survival, and productivity trends across 45 years in Puget Sound. *Fish and Fisheries*. 2019;20:934-51.
- [68] Riddell BR, Brodeur RD, Bugaev AV, Moran P, Murphy JM, Orsi JA, et al. Ocean ecology of Chinook Salmon. In: Beamish RJ, editor. *The Ocean Ecology of Pacific Salmon and Trout*. Bethesda: American Fisheries Society; 2018. p. 555-696.
- [69] Beamish RJ, Weitkamp LA, Shaul LD, Radchenko VI. Ocean ecology of Coho Salmon. In: Beamish RJ, editor. *The Ocean Ecology of Pacific Salmon and Trout*. Bethesda: American Fisheries Society; 2018. p. 391-554.
- [70] Clarke WC, Blackburn J. Effect of growth on early sexual maturation in stream-type chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture*. 1994;121:95-103.
- [71] Taylor EB. Precocial male maturation in laboratory-reared populations of chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Journal of Zoology*. 1989;67:1665-9.
- [72] Unwin MJ, Kinnison MT, Quinn TP. Exceptions to semelparity: postmaturation survival, morphology and energetics of male chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*. 1999;56:1172-81.
- [73] Wahle RJ, Chaney E, Pearson RE. Areal distribution of marked Columbia River basin spring chinook salmon recovered in fisheries and at parent hatcheries. *Marine Fisheries Review*. 1981;43(12):1-9.
- [74] Healey MC. Coastwide distribution and ocean migration patterns of stream- and ocean-type chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Field-Naturalist*. 1983;97(4):427-33.
- [75] Waples RS, Teel DJ, Myers JM, Marshall AR. Life-history divergence in chinook salmon: historic contingency and parallel evolution. *Evolution*. 2004;58:386-403.
- [76] Sharma R, Quinn TP. Linkages between life history type and migration pathways in freshwater and marine environments for Chinook salmon, *Oncorhynchus tshawytscha*. *Acta Oecologica*. 2012;41:1-13.
- [77] Trudel M, Fisher J, Orsi JA, Morris JFT, Thiess ME, Sweeting RM, et al. Distribution and migration of juvenile Chinook salmon derived from coded wire tag recoveries along the continental shelf of western North America. *Transactions of the American Fisheries Society*. 2009;138:1369-91.

- [78] Weitkamp LA. Marine distributions of Chinook salmon from the west coast of North America determined by coded wire tag recoveries. *Transactions of the American Fisheries Society*. 2009;139:147-70.
- [79] Weitkamp L, Neely K. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. *Canadian Journal of Fisheries and Aquatic Sciences*. 2002;59:1100-15.
- [80] Jordan DS, Evermann BW. The Fishes of North and Middle America. Washington, D. C.: Smithsonian Institution; 1896.
- [81] Pressey RT. The sport fishery for salmon on Puget Sound. Fisheries Research Papers, Washington Department of Fisheries. 1953;1(1):33-48.
- [82] Beamish RJ, McFarlane GA, Thomson RE. Recent declines in the recreational catch of coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia are related to climate. *Canadian Journal of Fisheries and Aquatic Sciences*. 1999;56:506–15.
- [83] Rohde J, Fresh KL, Quinn TP. Factors affecting partial migration in Puget Sound Coho Salmon (*Oncorhynchus kisutch*). *North American Journal of Fisheries Management*. 2014;34:559-70.
- [84] O'Neill SM, West JE. Marine distribution, life history traits, and the accumulation of polychlorinated biphenyls in Chinook salmon from Puget Sound, Washington. *Transactions of the American Fisheries Society*. 2009;138:616-32.
- [85] Chamberlin JW, Essington TE, Ferguson JW, Quinn TP. The influence of hatchery rearing practices on salmon migratory behavior: Is the tendency of Chinook salmon to remain within Puget Sound affected by size and date of release? . *Transactions of the American Fisheries Society*. 2011;140:1398-408.
- [86] Hecht BC, Campbell NR, Holecek DE, Narum SR. Genome-wide association reveals genetic basis for the propensity to migrate in wild populations of rainbow and steelhead trout. *Molecular Ecology*. 2012.
- [87] Arostegui MC, Quinn TP, Seeb LW, Seeb JE, McKinney GJ. Retention of a chromosomal inversion from an anadromous ancestor provides the genetic basis for alternative freshwater ecotypes in rainbow trout. *Molecular Ecology*. 2019;28:1412–27.
- [88] Beacham TD, Wallace C, Jonsen K, McIntosh B, Candy JR, Willis D, et al. Variation in migration pattern, broodstock origin, and family productivity of coho salmon hatchery populations in British Columbia, Canada, derived from parentage-based tagging. *Ecology and Evolution*. 2019.
- [89] Jensen HM. Puget Sound salmon investigation. Washington Department of Fisheries, 1948.
- [90] Milne DJ. The difference in the growth rate of coho salmon on the east and west coasts of Vancouver Island in 1950. Fisheries Research Board of Canada, Progress Report of the Pacific Coast Stations. 1950;85:80-2.
- [91] Zimmerman MS, Irvine JR, O'Neill M, Anderson JH, Greene CM, Weinheimer J, et al. Spatial and temporal patterns in smolt survival of wild and hatchery Coho Salmon in the Salish Sea. *Marine and Coastal Fisheries*. 2015;7:116-34.
- [92] Ruff CP, Anderson JH, Kemp IM, Kendall NW, McHugh PA, Velez-Espino A, et al. Salish Sea Chinook salmon exhibit weaker coherence in early marine survival trends than coastal populations. *Fisheries Oceanography*. 2017;26:625–37.
- [93] Kato F. Life histories of masu and amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodurus*). In: Groot C, Margolis L, editors. Pacific salmon life histories. Vancouver: University of British Columbia Press; 1991. p. 448-520.
- [94] Morita K. General biology of masu salmon. In: Beamish RJ, editor. The Ocean Ecology of Pacific Salmon and Trout. Bethesda, MD: American Fisheries Society; 2018. p. 703-30.
- [95] Tsiger VV, Skirin VI, Krupyanko NI, Kashlin KA, Semenchenko AY. Life history form of male masu salmon (*Oncorhynchus masou*) in South Primor'e, Russia. *Canadian Journal of Fisheries and Aquatic Sciences*. 1994;51:197-208.
- [96] Nagasawa T. Ocean life history of Masu Salmon from ocean entry to upstream migration. In: Beamish RJ, editor. The Ocean Ecology of Pacific Salmon and Trout. Bethesda, MD: American Fisheries Society; 2018. p. 731-66.
- [97] Smith GR, Stearley RF. The classification and scientific names of rainbow and cutthroat trouts. *Fisheries*. 1989;14(1):4-10.
- [98] Behnke RJ. Native trout of western North America. Bethesda: American Fisheries Society; 1992.
- [99] Bisson PA, Sullivan K, Nielsen JL. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. *Transactions of the American Fisheries Society*. 1988;117:262-73.
- [100] Baumsteiger J, Hankin D, Loudenslager EJ. Genetic analyses of juvenile steelhead, coastal cutthroat trout, and their hybrids differ substantially from field identifications. *Transactions of the American Fisheries Society*. 2005;134:829-40.
- [101] Kennedy BM, Baumsteiger J, Gale WL, Ardren WR, Ostrand KG. Morphological, physiological, and genetic techniques for improving field identification of steelhead, coastal cutthroat trout, and hybrid smolts. *Marine and Coastal Fisheries*. 2009;1:45-56.
- [102] Campton DE, Utter FM. Natural hybridization between steelhead trout (*Salmo gairdneri*) and coastal cutthroat trout (*Salmo clarki clarki*) in two Puget Sound streams. *Canadian Journal of Fisheries and Aquatic Sciences*. 1985;42:110–9.
- [103] Losee JP, Seamons TR, Jauquet J. Migration patterns of anadromous Cutthroat Trout in South Puget Sound: A fisheries management perspective. *Fisheries Research*. 2017;187:218-25.
- [104] Goetz FA, Baker B, Buehrens T, Quinn TP. Diversity of movements by individual anadromous coastal cutthroat trout in Hood Canal, Washington. *Journal of Fish Biology*. 2013;83:1161-82.
- [105] Zydlewski GB, Zydlewski J, Johnson J. Patterns of migration and residency in coastal cutthroat trout *Oncorhynchus clarkii clarkii* from two tributaries of the lower Columbia River. *Journal of Fish Biology*. 2009;75:203-22.
- [106] Saiget DA, Sloat MR, Reeves GH. Spawning and movement behavior of migratory coastal cutthroat trout on the western Copper River Delta, Alaska. *North American Journal of Fisheries Management*. 2007;27:1029-40.
- [107] Pearcy WG, Brodeur RD, McKinnell SM, Losee JP. Ocean ecology of anadromous coastal cutthroat trout. In: Beamish RJ, editor. The Ocean Ecology of Pacific Salmon and Trout. Bethesda, MD: American Fisheries Society; 2018. p. 905-30.
- [108] Pearcy WG, Brodeur RD, Fisher JP. Distribution and biology of juvenile cutthroat trout *Oncorhynchus clarki clarki* and



- steelhead *O. mykiss* in coastal waters off Oregon and Washington. *Fishery Bulletin*. 1990;88:697-711.
- [109] Pearcy WG, Fisher JP. Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981-1985. Corvallis, Oregon: National Marine Fisheries Service, 1990.
- [110] Krentz LK. Habitat use, movement, and life history variation of coastal cutthroat trout *Oncorhynchus clarki clarki* in the Salmon River estuary, Oregon. Corvallis: Oregon State University; 2007.
- [111] Moore ME, Berejikian BA, Goetz FA, Berger AG, Hodgson SS, Connor EJ, et al. Multi-population analysis of Puget Sound steelhead survival and migration behavior. *Marine Ecology Progress Series*. 2015;537:217-32.
- [112] Melnychuk MC, Welch DW, Walters CJ, Christensen V. Riverine and early ocean migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the Cheakamus River, British Columbia. *Hydrobiologia*. 2007;582:55-65.
- [113] Goetz FA, Jeanes E, Moore ME, Quinn TP. Comparative migratory behavior and survival of wild and hatchery steelhead (*Oncorhynchus mykiss*) smolts in riverine, estuarine, and marine habitats of Puget Sound, Washington. *Environmental Biology of Fishes*. 2015;98:357-75.
- [114] Chapman ED, Hearn AR, Singer GP, Brostoff WN, LaCivita PE, Klimley AP. Movements of steelhead (*Oncorhynchus mykiss*) smolts migrating through the San Francisco Bay Estuary. *Environmental Biology of Fishes*. 2015;98:1069-80.
- [115] Romer JD, Leblanc CA, Clements S, Ferguson JA, Kent ML, Noakes D, et al. Survival and behavior of juvenile steelhead trout (*Oncorhynchus mykiss*) in two estuaries in Oregon, USA. *Environmental Biology of Fishes*. 2013;96:849-63.
- [116] Myers KW. Ocean ecology of steelhead. In: Beamish RJ, editor. *The Ocean Ecology of Pacific Salmon and Trout*. Bethesda: American Fisheries Society; 2018. p. 779-904.
- [117] Moore ME, Goetz FA, Van Doornik DM, Tezak EP, Quinn TP, Reyes-Tomassini JJ, et al. Early marine migration patterns of wild coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. *PLoS one*. 2010;5(9):E12881.
- [118] Kelson SJ, Miller MR, Thompson TQ, O'Rourke SM, Carlson SM. Do genomics and sex predict migration in a partially migratory salmonid fish, *Oncorhynchus mykiss*? *Canadian Journal of Fisheries and Aquatic Sciences*. 2019;76:2080-8.
- [119] Rundio DE, Williams TH, Pearse DE, Lindley ST. Male-biased sex ratio of nonanadromous *Oncorhynchus mykiss* in a partially migratory population in California. *Ecology of Freshwater Fish*. 2012;21:293-9.
- [120] Ohms HA, Sloat MR, Reeves GH, Jordan CE, Dunham JB. Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*. 2014;71:70-80.
- [121] Pavlov DS, Savvaitova KA. On the problem of ratio of anadromy and residence in salmonids (Salmonidae). *Journal of Ichthyology*. 2008;48:778-91.
- [122] Pavlov DS, Savvaitova KA, Kuzishchin KV, Gruzdeva MA, Mal'tsev AY, Stanford JA. Diversity of life strategies and population structure of Kamchatka mykiss *Parasalmo mykiss* in the ecosystems of small salmon rivers of various types. *Journal of Ichthyology*. 2008;48:37-44.
- [123] Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltze D, et al. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*. 2008;105:19052-9.
- [124] Shaw AK. Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*. 2016;30:991-1007.
- [125] Liedvogel A, Åkesson S, Bensch S. The genetics of migration on the move. *Trends in Ecology and Evolution*. 2011;26:561-9.
- [126] Pulido F. Evolutionary genetics of partial migration – the threshold model of migration revis(it)ed. *Oikos*. 2011;120:1776-83.
- [127] Wood CC. Life history variation and population structure in sockeye salmon. *American Fisheries Society Symposium*. 1995;17:195-216.
- [128] Wood CC, Foote CJ. Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). *Evolution*. 1996;50:1265-79.
- [129] Dodson JJ, Aubin-Horth N, Thériault V, Páez DJ. The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biological Reviews*. 2013;88:602-25.
- [130] Weitkamp L. Marine distributions of coho and Chinook salmon inferred from coded wire tag recoveries. *American Fisheries Society Symposium*. 2012;76:191-214.
- [131] Quinn TP, Chamberlin J, Brannon EL. Experimental evidence of population-specific spatial distributions of Chinook salmon, *Oncorhynchus tshawytscha*. *Environmental Biology of Fishes*. 2011;92:313-22.
- [132] Beacham TD, Wallace C, Jonsen K, McIntosh B, Candy JR, Willis D, et al. Insights on the concept of indicator populations derived from parentage-based tagging in a large-scale coho salmon application in British Columbia, Canada. *Ecology and Evolution*. 2020.
- [133] Prince DJ, O'Rourke SM, Thompson TQ, Ali OA, Lyman HS, Saglam IK, et al. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. *Science Advances*. 2017;3:e1603198.
- [134] Stewart BS. Ontogeny of differential migration and sexual segregation in northern elephant seals. *Journal of Mammalogy*. 1997;78:1101-16.
- [135] Loseto LL, Richard P, Stern GA, Orr J, Ferguson SH. Segregation of Beaufort Sea beluga whales during the open-water season. *Canadian Journal of Zoology*. 2006;84:1743-51.
- [136] Woodworth BK, Newman AEM, Turbek SP, Dossman BC, Hobson KA, Wassenaar LI, et al. Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. *Oecologia*. 2016;181:413-22.
- [137] Myers RA, Hutchings JA, Gibson RJ. Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*. 1986;43:1242-8.
- [138] Larsen DA, Beckman BR, Strom CR, Parkins PJ, Cooper KA, Fast DE, et al. Growth modulation alters the incidence of early male maturation and physiological development of hatchery-reared spring Chinook salmon: a comparison with wild fish. *Transactions of the American Fisheries Society*. 2006;135:1017-32.

- [139] Geijer CKA, Notarbartolo de Sciara G, Panigada S. Mysticete migration revisited: are Mediterranean fin whales an anomaly. *Mammal Review*. 2016;46:284-96.
- [140] Kagley AN, Smith JM, Fresh KL, Frick KE, Quinn TP. Residency, partial migration, and late egress of sub-adult Chinook salmon (*Oncorhynchus tshawytscha*) and comparisons with coho salmon (*O. kisutch*) in Puget Sound, Washington. *Fishery Bulletin*. 2017;115:544-55.
- [141] Rohde J, Kagley AN, Fresh KL, Goetz FA, Quinn TP. Partial migration and diel movement patterns in Puget Sound Coho Salmon. *Transactions of the American Fisheries Society*. 2013;142:1615-28.
- [142] Arostegui MC, Smith JM, Kagley AN, Spilsbury-Pucci D, Fresh KL, Quinn TP. Spatially clustered movement patterns and segregation of sub-adult Chinook Salmon within the Salish Sea. *Marine and Coastal Fisheries*. 2017;9:1-12.
- [143] Altizer S, Bartel R, Han BA. Animal migration and infectious disease risk. *Science*. 2011;331:296-302.
- [144] Gilroy JJ, Gill JA, M. Butchart SHM, Jones VR, Franco AMA. Migratory diversity predicts population declines in birds. *Ecology Letters*. 2016;19:308-17.
- [145] Braccini M, Aires-da-Silva A, Taylor I. Incorporating movement in the modelling of shark and ray population dynamics: approaches and management implications. *Reviews in Fish Biology and Fisheries*. 2016;26:13-24.
- [146] Colman JA, Nogueira JI, Pancorbo OC, Batdorf CA, Block BA. Mercury in Pacific bluefin tuna (*Thunnus orientalis*): bioaccumulation and trans-Pacific Ocean migration. *Canadian Journal of Fisheries and Aquatic Sciences*. 2015;72:1015-23.
- [147] Madigan DJ, Baumann Z, Carlisle AB, Snodgrass O, Dewar H, Fisher NS. Isotopic insights into migration patterns of Pacific bluefin tuna in the eastern Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*. 2018;75:260-70.
- [148] Zlokovitz ER, Secor DH. Effect of habitat use on PCB body burden in Hudson River striped bass (*Morone saxatilis*). *Canadian Journal of Fisheries and Aquatic Sciences*. 1999;56((Suppl. 1)):86-93.
- [149] West JE, O'Neill SM, Ylitalo GM. Spatial extent, magnitude, and patterns of persistent organochlorine pollutants in Pacific herring (*Clupea pallasii*) populations in the Puget Sound (USA) and Strait of Georgia (Canada). *Science of the Total Environment*. 2008;394:369-78.
- [150] Svendsen TC, Vorkamp K, Rønsholdt B, Frier J-O. Retrospective determination of primary feeding areas of Atlantic salmon (*Salmo salar*) using fingerprinting of chlorinated organic contaminants. *ICES Journal of Marine Science*. 2008;65:921-9.
- [151] Svendsen TC, Vorkamp K, Svendsen JC, Aarestrup K, Frier J-O. Organochlorine fingerprinting to determine foraging areas of sea-ranched Atlantic salmon: a case study from Denmark. *North American Journal of Fisheries Management*. 2009;29:598-603.
- [152] Cullon DL, Yunker MB, Alleyne C, Dangerfield NJ, O'Neill S, Whitticar MJ, et al. Persistent organic pollutants in Chinook salmon (*Oncorhynchus tshawytscha*): implications for resident killer whales of British Columbia and adjacent waters. *Environmental Toxicology and Chemistry*. 2009;28:148-61.
- [153] Naish KA, Taylor JE, Levin PS, Quinn TP, Winton JR, Huppert D, et al. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*. 2007;53:61-194.