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# Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited

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## Abstract

Anadromy is a defining trait in salmonid fishes but it is expressed to different extents among the species in the family, as reviewed in a classic paper by Rounsefell (1958). The present paper re-examines the subject, assessing the degree of anadromy within the genus *Oncorhynchus*, using Rounsefell's six criteria: extent of migrations at sea, duration of stay at sea, state of maturity attained at sea, spawning habits and habitats, post-spawning mortality, and occurrence of freshwater forms of the species. The genus ranges from pink salmon (*O. gorbuscha*), the most fully anadromous species in the family, to entirely non-anadromous species closely related to rainbow trout (*O. mykiss*), including Mexican golden trout (*O. chrysogaster*), Gila and Apache trout (*O. gilae*), and sub-species of cutthroat trout (*O. clarki*). This paper provides updated information on anadromy and marine migration patterns, emphasizing the iteroparous species, cutthroat (*O. clarki*) and rainbow (*O. mykiss*) trout. These two species display widely ranging patterns of anadromy, including truly "landlocked" populations and residents with easy access to the sea. Anadromous rainbow trout (known as steelhead) populations also vary greatly in their distribution at sea, incidence of repeat spawning, and associated traits. We conclude, as did Rounsefell, that anadromy is not a single trait with two conditions (anadromous or non-anadromous). Rather, it reflects a suite of life history traits that are expressed as points along continua for each species and population. Further research is needed in the marine ecology of all species but especially trout, as they are less well known but apparently more variable in patterns of anadromy and life history than salmon species.

## Introduction

The family Salmonidae is characterized by three key life history patterns: anadromy (reproduction in freshwater, followed by migration to sea for feeding, and return to freshwater for reproduction), homing (the strong tendency to reproduce at the natal site), and semelparity (senescence and

mortality after the first season of reproduction). There is some debate as to whether salmonids evolved in freshwater or marine environments (McDowall, 2002) and the extent to which anadromy and homing co-evolved (McDowall, 2001). Regardless of the ancestral conditions and evolutionary trajectories, it is impossible to understand or conserve these fishes without careful consideration of these traits. Homing seems to be essentially universal within the family, but the other traits, anadromy and semelparity, vary greatly among and within species, often in association with each other. In his classic paper on anadromy in salmonids, Rounsefell (1958) argued that there are six criteria by which salmonids might be classified, and a combination of these indicates the extent of anadromy in the species. His criteria were as follows: (1) extent of migrations at sea, (2) duration of stay at sea, (3) state of maturity attained at sea, (4) spawning habits and habitats, (5) post-spawning mortality, and (6) occurrence of freshwater forms of the species. Since Rounsefell's paper was written, there has been a tremendous increase in our knowledge of salmon life history, behavior, and ecology. The purpose of this paper is to revisit his criteria, providing a brief update on marine migrations of Pacific salmon and trout. We emphasize new information (and remaining knowledge gaps) on anadromous trout (steelhead: *Oncorhynchus mykiss*, and cutthroat trout: *O. clarki*) and masu salmon (*O. masou*) because they have received less attention than the better-known salmon species (pink: *O. gorbuscha*, sockeye: *O. nerka*, chum: *O. keta*, coho: *O. kisutch*, and chinook: *O. tshawytscha*).

*Extent of migration at sea*

A great deal of information on the distribution of salmonids in the Pacific Ocean was collected by the United States, Canada, and Japan under the International North Pacific Fisheries Commission, and reviews of the species were published as bulletins (coho: Godfrey et al., 1975; sockeye: French et al., 1976; chum: Neave et al., 1976; chinook: Major et al., 1978; pink: Takagi et al., 1981; masu: Machidori and Kato, 1984; steelhead: Burgner et al., 1992). In addition, Hartt and Dell (1986) summarized information on the migrations of juvenile salmonids. These studies, and many that followed (e.g., Davis et al., 1990; Myers et al., 1996), have indicated a range of oceanic migration patterns. The most numerous species (pink, chum and sockeye) migrate to sea and use the epipelagic waters of the open ocean as their primary feeding area. Chum salmon spend a few days or weeks in estuaries but the other species seem to move directly to coastal waters (e.g. sockeye in Bristol Bay: Straty and Jaenicke, 1980, and the Fraser River: Groot et al., 1989; pink salmon in southeast Alaska: Jaenicke et al., 1984). North American populations migrate northward along the continental shelf, or westward along the Alaska Peninsula and across the eastern Bering Sea shelf, until sometime in late summer or early fall (Hartt and Dell, 1986). As they grow, they tend to move offshore, though the specific timing may vary among populations and years. Spatial and temporal variation in the early marine distribution, movements, growth, and survival of juvenile pink, chum, and sockeye salmon is closely linked to variation in physical (e.g., sea temperature, water currents) and biological factors, especially the distribution and abundance of their preferred zooplankton and micronekton food (see reviews by Myers et al., 2000; Beamish et al., 2003; Brodeur et al., 2003; Karpenko, 2003; Mayama and Ishida, 2003). Pink, chum, and sockeye salmon are not commonly found in coastal waters until they return at maturity. Some pink salmon apparently reside in Puget Sound, however, as recreational anglers caught them as early as March of the year in which they matured and as late as October of that year (Pressey, 1953).

The second migration pattern is shown by coho and chinook salmon. These species seem to migrate more slowly along the coast than the previous three, and they are commonly found in coastal and inland waters during their period at sea, though they are also found far offshore (Healey, 1991; Weitkamp and Neely, 2002). The more coastal distribution may result, at least in part, from the more southerly distributions of these species compared to the others. Chum salmon range only about as far south as the Oregon–California border, sockeye do not spawn south of the Columbia River, and pink salmon are scarce south of Puget Sound. Salmon entering the ocean off British Columbia and Alaska can find suitable water temperatures and prey offshore whereas populations off California and Oregon are largely limited to the coastal zone where upwelling brings cool, nutrient rich water to the

surface. Farther offshore, the waters are warm, less productive, and dominated by other fishes (Pearcy, 1992).

As shown by recoveries of coded-wire tags, coho salmon in coastal waters tend to be caught (generally in their second summer at sea) near their area of origin (Table 1; Weitkamp and Neely, 2002). More detailed analysis indicated differences among populations, and a tendency for coho salmon from southern Oregon to migrate south, whereas those entering the ocean north of Cape Blanco tend to migrate to the north. There are few opportunities to recover coded-wire tagged coho salmon in far offshore waters. A few high seas recoveries, however, demonstrate that some Washington and Oregon coho salmon migrate to waters far offshore in the North Pacific Ocean (Myers and Bernard, 1993).

The known ocean range of Asian coho salmon, as shown by high seas tagging experiments, extends from about 59° N in the Bering Sea, south to 46° N in the western North Pacific and 41° N in the central North Pacific, and east to 173° W in the central North Pacific and 179° W in the central Bering Sea (Myers et al., 1996). There are few high seas tag recoveries from western Alaska coho salmon, perhaps because runs are too late for fisheries and processors. There is no information from tagging experiments on the distribution of North American coho salmon in the Bering Sea. In the North Pacific, the known ocean range of North American coho salmon extends from about 42° N (just off the coast of the Oregon–California boarder), northward along the coast to the central Aleutian Islands, and further offshore throughout the eastern and central North Pacific (south to 44° N and west to 177° E). The known ranges of Asian and North American coho salmon overlap in the area just south of the central Aleutians and further south (to about 44° N) between 177° E and 173° W.

There are interesting differences in the offshore migrations of northern (Asian and western Alaska) and southern coho salmon stocks. Northern stocks are found farther offshore (averaging four times as far from tag recovery sites), compared to a more coastal distribution of southern stocks (Walker et al., 1992). From south central Alaska to California, there are progressively fewer recoveries from offshore tag releases and more recoveries from releases in coastal waters. Travel rates also reflect this difference. Although days at liberty after tagging are about the same for both northern and southern stocks (around 50 days), Asian and western Alaska coho travel about four times faster, over 40 km/day compared to about 10 km/day for coho salmon from southeastern Alaska and southward (Walker et al., 1992). South central Alaskan stocks seem to be intermediate between the two extremes.

Chinook salmon are also found in both coastal and offshore waters, however, their ocean life history is more complex than that of coho. Coho typically spend one (southern populations) or two (northern populations) full years in fresh water and one full year at sea (Sandercock, 1991) whereas chinook are classified as "ocean-type" (migrating to sea in their first year of life) and "stream-type" (migrating to sea after a full year in fresh water: reviewed by Healey, 1991). Ocean-type chinook tend to migrate downstream over a more protracted period, and then reside in estuaries for a much longer period than stream-type chinook (Healey, 1982; Simenstad et al., 1982; Dawley et al., 1986). Healey (1983) presented evidence that ocean-type chinook are predominately distributed in coastal waters whereas stream type are found primarily in offshore waters. Ocean-type chinook

*Table 1.* State or province where coho salmon originated, and the area where they were caught in North American coastal fisheries

| Area of origin | Catch area | | | | |
|---|---|---|---|---|---|
| | Alaska | British Columbia | Washington | Oregon | California |
| Alaska (2) | 98.8 | 1.3 | 0.0 | 0.0 | 0.0 |
| British Columbia (10) | 5.6 | 90.1 | 4.1 | 0.2 | 0.0 |
| Washington (33) | 0.1 | 37.9 | 42.3 | 17.8 | 1.8 |
| Oregon (16) | 0.0 | 4.0 | 14.8 | 58.5 | 22.7 |
| California (4) | 0.0 | 0.0 | 0.3 | 17.3 | 82.3 |

Numbers of hatcheries in each area that contributed to the averages are indicated in parentheses (from Weitkamp and Neely, 2002).

are most prevalent towards the southern end of the range of the species (Taylor, 1990; Healey, 1991), and so may feed over the continental shelf for the same reason as coho off Oregon and California. Interestingly, the chinook populations show a "break" between northward-migrating and southward-migrating populations at the same point along the Oregon coast as the coho (chinook: Nicholas and Hankin, 1989; coho: Weitkamp and Neely, 2002). Along much of the Oregon coast the chinook salmon tend to migrate north, and most of the adults from those populations are caught off British Columbia (56%) and Alaska (25%). Populations entering the ocean south of Cape Blanco migrate in a more southerly direction, with an average of 49% each caught off Oregon and California (Nicholas and Hankin, 1989).

In addition to the patterns of coastal and offshore migrations, there are also chinook and coho salmon that spend some or perhaps their entire marine lives in Puget Sound. Pressey (1953) reported catches of both species in every month from the fall of their first year at sea through to maturity the next fall in the case of coho salmon, and for three years in the case of chinook. The presence of salmon in all months of the year may indicate permanent residence by some individuals, but Brannon and Setter (1989) presented coded wire tag data supporting the hypothesis that some chinook salmon make short "loop" migrations north from Puget Sound in spring and back in fall each year until they mature.

As with coho, the tendency of chinook to migrate to the open ocean is incompletely known, in part because they are much less numerous than the other three species. The known range of North American chinook salmon, as shown by high seas tagging experiments, extends across almost the entire Bering Sea, north to about 64° N and west to 172° E (Myers et al., 1996). In the North Pacific, the known ocean range of North American chinook salmon extends north from about 40° N (in the coastal waters just off California) and west to the waters just south of Adak Island in the central Aleutians (176° W, 52° N). The known ranges of Asian and North American chinook salmon overlap in the area just south of the central Aleutians between 177° W and 172° W (Myers et al., 1996).

High seas recoveries of coded-wire tagged chinook salmon show that North American stocks originating south of the Alaska Peninsula (from central Alaska to the Sacramento River, California) range northward into the eastern Bering Sea (Myers et al., 1996). Coded-wire tag recoveries also provided the first information on winter distribution of western Alaska (Yukon Territory) chinook salmon in the Bering Sea, showing their distribution along the continental shelf break (200-m contour) from Unimak Pass and northwestward into the central Bering Sea. A recovery off the south central Oregon coast of a coded-wire tagged immature chinook salmon from the Kenai River, Alaska marks the southernmost recovery of an Alaska origin chinook salmon on the US Pacific Coast.

The vast majority of anadromous salmonids in the Pacific Ocean are from one of the five semelparous *Oncorhynchus* species but interesting patterns are found in the other species. Masu salmon are exclusively Asian, and their marine distribution is largely limited to the Sea of Japan and Sea of Okhotsk rather than the open North Pacific (Machidori and Kato, 1984; Kato, 1991). There is, however, a fascinating but unverified report of masu spawning in recent years on Umnak Island, in the western Aleutians (Rowland and Sidorov, 2004).

Steelhead (anadromous rainbow trout) display a range of migration patterns. In most North American populations, the smolts are relatively large, having spent 1–3 or more years in fresh water (Busby et al., 1996). They seem to migrate rapidly through estuaries, as indicated by the short period of time when they are collected (e.g., Dawley et al., 1986) and leave coastal waters early in the summer, unlike sympatric coho and chinook salmon (Table 2). North American steelhead often migrate to distant ocean areas. The known ocean range of North American steelhead extends in a broad swath across almost the entire North Pacific, south to 40°58′ N (three coded-wire tagged fish from Snake River tributaries, Columbia River basin), and west to 163°32′ E (one coded-wire tagged fish

*Table 2.* Purse seine catches per set of juvenile salmonids off Washington and Oregon in 1980, indicating patterns of relative abundance (Miller et al., 1983)

| Species | 27 May–7 June | 4–15 July | 28 Aug.–8 Sept. |
|---|---|---|---|
| Chinook | 6.67 | 2.36 | 6.38 |
| Coho | 12.26 | 0.73 | 2.80 |
| Steelhead | 5.20 | 0.10 | 0.00 |

from the Quinault River, Washington, a distance approximately 5370 km from the river mouth). The combined results from all high seas tag recoveries suggest that steelhead from most streams along the North American Pacific coast have similar distributions offshore. Seasonal (summer and winter, also known as stream-maturing and ocean-maturing, respectively: Busby et al., 1996) runs of steelhead have broadly overlapping distributions, but have different seasonal patterns of marine distribution to accommodate the wide difference in time of return to fresh water exhibited by the two groups. In the Gulf of Alaska, coastal summer steelhead appear to have a more northerly distribution than inland summer run steelhead from the Columbia River basin. Steelhead from coastal Oregon and California may have more restricted westward migrations than more northern stocks. Spawning populations of steelhead in Asia are found in Russia along the mainland coast of the Sea of Okhotsk and on the Kamchatka Peninsula. The abundance of Russian steelhead is not well known but they are thought to be considerably less abundant than North American steelhead. At present, there are no reported recoveries of Asian steelhead that were tagged on the high seas. There is no information from tagging experiments on the distribution of Asian and North American populations in the Bering Sea, although some steelhead are caught in this area.

Information on steelhead migrations at sea is sketchy compared to the semelparous salmon, but information on other Pacific salmonids is even more limited. Cutthroat trout and several species of char (in North America, bull trout, *Salvelinus confluentus*; Dolly Varden, *S. malma*, and Arctic char, *S. alpinus*) have anadromous populations, though many non-anadromous populations also exist (Armstrong and Morrow, 1980; Johnson, 1980). The ratio of cutthroat to steelhead in coastal catches becomes more skewed towards cutthroat over the summer (e.g., Pearcy and Fisher, 1990; Table 3), indicating that the steelhead leave for the open ocean whereas the cutthroat remain in coastal waters. The relative abundance of the two trout species as a function of distance offshore also indicates differences in behavior. Pearcy et al. (1990) reported that steelhead were 25.0% of the trout caught <5 nautical miles (1 nm = 1.852 km) off the coast of Washington and Oregon, but their percentage of the catch increased steadily with distance offshore (26.5% from 5 to 10 nm, 48.5% from 10 to 15 nm, 60.5% from 15 to 20 nm, 61.2% from 20 to 25 nm, and 86.4% >25 nm offshore). Dolly Varden are generally thought to remain near their natal river but exceptionally long movements by some individuals indicate that this is not always the case (DeCicco, 1992).

*Table 3.* Catches per set of cutthroat and steelhead during the summer (numbers of purse seine sets made each month indicated in parentheses) off the Washington and Oregon coasts in 1981–1985, indicating patterns of relative abundance (Pearcy and Fisher, 1990)

| | May (180) | June (327) | July (130) | August (66) | September (152) |
|---|---|---|---|---|---|
| Cutthroat | 0.18 | 0.18 | 0.34 | 0.21 | 0 |
| Steelhead | 0.38 | 0.14 | 0.08 | 0.02 | 0 |
| % cutthroat | 32.7 | 55.7 | 81.5 | 93.3 | – |

As a rough measure of the relative extent of migration at sea by Pacific salmon and steelhead, distances between high seas tag release locations and coastal or freshwater recovery locations for Pacific salmon and steelhead were summarized by ocean age group (Table 4). Although Rounsefell (1958) considered pink salmon to be the most anadromous species, the mean and maximum distances of their migrations are far less than those of sockeye and chum salmon. In addition, because immature sockeye and chum salmon spend several years at sea, they are frequently more abundant than pink salmon in catches far offshore. Rounsefell categorized the migrations of steelhead as chiefly coastwise, and somewhat less extensive than those of Pacific salmon (chum, sockeye, pink, chinook, and coho) and Atlantic salmon. Since then, high seas tagging experiments have shown that steelhead make more extensive offshore migrations in their first year in the ocean than any other salmonid species. In addition, although steelhead are less abundant than chinook salmon in annual returns to coastal areas, they are frequently more abundant than chinook salmon in research vessel catches in waters far offshore, suggesting greater reliance on the high seas for feeding.

*Duration of stay in the sea and in fresh water*

The length of time individuals spend at sea, relative to time in fresh water, was Rounsefell's second

*Table 4*. Mean great circle distances (km) between high seas tag release and coastal or freshwater recovery locations for Pacific salmon and steelhead by ocean age group (i.e., number of winters at sea; pooled over all populations)

| Ocean Age | Distance (km) | Sockeye | Chum | Pink | Coho | Chinook | Steelhead | Grand total |
|---|---|---|---|---|---|---|---|---|
| 0 | *N* | 39 | 7 | 47 | 239 | 12 | 1 | 345 |
| | Mean | 842 | 635 | 265 | 538 | 672 | 2317 | 547 |
| | s.d. | 473 | 712 | 294 | 593 | 860 | | 585 |
| | Maximum | 2351 | 1648 | 1436 | 2303 | 2262 | 2317 | 2351 |
| 1 | *N* | 300 | 33 | 4203 | 841 | 73 | 46 | 5496 |
| | Mean | 1448 | 1918 | 506 | 544 | 290 | 2257 | 583 |
| | s.d. | 530 | 966 | 443 | 597 | 626 | 1477 | 574 |
| | Maximum | 4224 | 3186 | 2821 | 2706 | 4557 | 5106 | 5106 |
| 2 | *N* | 3300 | 493 | – | – | 25 | 24 | 3842 |
| | Mean | 952 | 2097 | – | – | 819 | 1960 | 1104 |
| | s.d. | 518 | 1075 | – | – | 761 | 1399 | 738 |
| | Maximum | 5597 | 5510 | – | – | 2574 | 4869 | 5597 |
| 3 or older | *N* | 1949 | 1683 | – | – | 13 | 15 | 3660 |
| | Mean | 829 | 1807 | – | – | 559 | 1332 | 1280 |
| | s.d. | 406 | 1113 | – | – | 332 | 836 | 948 |
| | Maximum | 3092 | 5595 | – | – | 1320 | 4075 | 5595 |
| All age groups | *N* | 5588 | 2216 | 4250 | 1080 | 123 | 88 | 13343 |
| | Mean | 935 | 1870 | 503 | 543 | 463 | 2013 | 923 |
| | s.d. | 501 | 1110 | 443 | 596 | 687 | 1384 | 802 |
| | Maximum | 5597 | 5595 | 2821 | 2706 | 4557 | 5106 | 5597 |

Data source: High Seas Salmon Research Program, University of Washington, Seattle, WA.

criterion for anadromy. In this respect the information he presented is in little need of revision. At one extreme are pink salmon that migrate seaward immediately after emerging from redds. Some populations actually spawn within the intertidal zone, especially in southeast Alaska, but others spawn 100–200 km or more upriver (reviewed by Heard, 1991). These latter populations experience some growth during downriver migration. Lacustrine rearing is much less common but in Lake Aleknagik, Alaska, pink salmon emerge from tributaries of the lake and grow from about 32 mm at emergence to 78 mm in a month before leaving the lake (Robins et al., in press). After pink salmon, chum salmon show the least reliance on fresh water for rearing. They commonly spend a few weeks in streams, then rear in estuaries, before migrating through coastal waters and out to the open ocean (Salo, 1991). The use of estuaries as a transition seems sensible enough for the relatively small migrants (ca. 40 mm) because both size-selective predation (Hargreaves and LeBrasseur, 1986) and osmoregulatory stress favor large size in salt water (Clarke et al., 1989). It is unclear why the even smaller pink salmon make less use of estuaries than chums. Virtually without exception, pink salmon in their natural range return to spawn after one winter at sea, for a total age of two years (including the winter spent as embryos during incubation). During this time they grow very fast; they may increase their weight 10000-fold, from about 0.2 to about 2 kg. Chums tend to spend 2–4 full years at sea (longer at northern latitudes; Salo, 1991).

Pink and chum salmon always migrate to sea in their first year of life, but seaward migration in the first year of life is also known (sometimes very common) in three other species: chinook, coho, and sockeye salmon. Many populations of chinook salmon, especially those at the southern end of the range and at lower elevations within this range, migrate to sea as either newly emerged fry or after a few months growth in rivers. This "ocean-type" life history extends to about 56° N latitude (i.e., the Skeena and Nass rivers; Taylor, 1990), beyond which chinook salmon are almost exclusively stream type (i.e., yearling migrants). The Situk River in south-central Alaska (59°30′ N) is an exception to this rule, producing almost exclusively ocean-type juveniles (Johnson et al., 1992). These juvenile life history types are

associated with growing conditions (fast growth with ocean-type and slow with stream type). However, they co-vary with the state of maturity of adults returning from the ocean, for reasons not fully understood but probably related to the challenges of migration to the spawning areas (see Section 3). Chinook salmon vary in duration of marine residence, with 2–4 years being typical (Roni and Quinn, 1995).

In sockeye salmon, the "classic" juvenile life history pattern involves one or two years of lake residence immediately after emergence from the gravel (Burgner, 1991) but some juveniles reside for a year in rivers if no lake is available (river-type) or migrate to sea in their first year of life ("sea-type", reviewed by Wood, 1995, see also Gustafson and Winans, 1999). Birtwell et al. (1987) reported that underyearling sockeye were very abundant in the Fraser River estuary, growing rapidly to 65–75 mm before leaving in early fall. Wood et al. (1987) reported that about 5% of the sockeye salmon smolts from the Stikine River, B.C. were sea-type, weighing about 1.0 g, 39–48% were river-type (about 3.0 g), and the rest were lake-type (about 3.6 g). Sockeye salmon show exceptional variation in the combinations of fresh water and marine ages (14 different combinations in females and 22 in males), though most spend 1 or 2 years in fresh water and 2 or 3 years at sea (Healey, 1987).

In coho salmon, the great majority of smolts are 1 or 2 years old, with a cline towards older fish in the north (Weitkamp et al., 1995). However, fry are often caught in downstream traps and in many coastal systems they enter the ocean shortly after emergence. Such migrants may be individuals unable to obtain territories, or displaced by floods (e.g., Hartman et al., 1982). It may be that these fish are really "downstream" rather than "seaward" migrants and it is only their misfortune to end up in salt water where they die instead of finding suitable riverine habitat downstream of their emergence site. The fate of these fry is not well known but recent work indicates that some spend the summer in estuaries and move back up into rivers in fall, and some remain at sea and contribute to the diversity of returning adults (Charles Simenstad, University of Washington, pers. comm.). Regardless of freshwater age, most coho salmon spend one winter at sea but some males (jacks) spend only the summer at sea before returning (Sandercock, 1991).

In Japan, masu salmon typically migrate to sea in spring and also return as adults in spring. Thus, these populations do not have jacks and all fish spend a winter at sea. There are, however, some populations in Miyagi and Fukushima prefectures that migrate to sea in the fall and return the following spring (Masahide Kaeriyama, Hokkaido Tokai University, pers. comm.). In Russia, there are four life history types of masu (Tsiger et al., 1994; Anton Ulatov, KamchatNIRO, pers. comm.). First, the typical anadromous form spends one winter at sea but a few individuals that spent two winters at sea are known from Primorye (in the Russian Far East). Second, the "neotenic" form matures as parr in their first or second fall of life. The great majority of these fish are males. Third, in rare cases males that matured once or twice as parr then undergo smolt transformation, migrate to sea for 2–3 months, and then return to spawn again. Fourth, there are resident populations.

Pacific salmon spawn in fall (though this may be as early as July or as late as February, depending on species and region) whereas the Pacific trout species (formerly in the genus *Salmo*) spawn in spring. In addition, the trout have somewhat smaller eggs (and higher fecundity, for a given length) than sympatric salmon with which they compete (notably coho; Quinn, 2004). Perhaps because of these traits the trout tend to spend more time in fresh water before migrating to sea than the salmon. A review of North American steelhead by Busby et al. (1996) indicated that most smolts are age 2 or 3, and older smolts predominate in the northern end of the range and younger smolts in the south (Table 5). Scale samples of from 3475 steelhead caught at sea from 1955 to 1985 indicated the following freshwater age composition: 17.0% were age 1, 27.2% were age 2, 42.3% were age 3, 12.5% were age 4, 0.9% were age 5, and a single fish was age 6 (Burgner et al., 1992).

Trotter (1989) reviewed data on cutthroat trout and found evidence of smolts aged 1–6 but 2, 3 and 4 were most common. There may be a cline in age composition with latitude, parallel to that seen in other salmonids (e.g., sea-run brown trout: L'Abée-Lund et al., 1989; Jonsson and L'Abée-Lund, 1993), but we have not seen data to demonstrate this in cutthroat. However, Johnston (1982) noted that cutthroat smolts in protected waters such as

*Table 5*. Percent of steelhead migrating to sea after different numbers of years in freshwater (i.e., smolt age), based on averages of populations from different regions of North America (sample size in parentheses; reported by Busby et al. (1996)

| Smolt age | Alaska (6) | B.C. (15) | Washington (9) | Columbia River (18) | Oregon (4) | California (8) |
|---|---|---|---|---|---|---|
| 1 | 0.0 | 0.7 | 6.3 | 3.8 | 3.8 | 23.3 |
| 2 | 15.2 | 34.9 | 85.7 | 79.0 | 79.3 | 69.0 |
| 3 | 73.8 | 60.5 | 8.0 | 16.6 | 16.3 | 7.5 |
| 4 | 11.0 | 3.9 | 0.0 | 0.6 | 0.6 | 0.3 |

Puget Sound and the Columbia River are smaller and younger than those on the open coast. He hypothesized that the extensive shoreline and productive nearshore habitat allow them to forage in the littoral zone (where they are caught by anglers). In contrast, the heavy surf of the ocean beaches may be less inhospitable and they forage farther from shore and so larger size is needed for survival. This hypothesis is supported by the lower smolt ages from Big Beef Creek, in Puget Sound, and tributaries of the Columbia River versus streams of the Washington and Oregon coasts (Table 6). Overall, the anadromous trout go to sea older and larger than the salmon, trading comparatively slow growth in fresh water for reduced mortality once they go to sea (Quinn, 2004). Care must be taken in considering smolt age, however, because the pattern may depend on whether smolt or adult samples are examined. For example, Shapovalov and Taft (1954) showed that the majority of smolts left Waddell Creek, California at age 1, but their survival at sea was much lower than that of older (and larger) smolts, so the adult run was most heavily represented by age 2 smolts (Table 7).

*Table 6*. Age composition of cutthroat trout smolts from the coast of Oregon (Sand Creek: Sumner 1962; 0.5% age 6 smolts omitted), the coast of Washington and larger rivers tributary to the Columbia River (data summarized by Johnston, 1982), and Big Beef Creek, tributary to Hood Canal, Puget Sound (Wenburg, 1998)

| | Age composition of smolts (%) | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Coastal Oregon (Sand Creek) | 0.3 | 6.4 | 46.3 | 38.8 | 7.7 |
| Coastal Washington | 0 | 0 | 23 | 59 | 18 |
| Columbia River | 0 | 65 | 33 | 2 | 0 |
| Puget Sound (Big Beef Creek) | 2.5 | 81.0 | 16.5 | 0 | 0 |

Most North American steelhead spend 1–3 full years at sea, though the timing of return migration can complicate assessment of marine age. Busby et al. (1996) obtained data on the ocean age at first spawning for 59 populations over the North American range and they averaged 0.1% age 0, 19.5% age 1, 60.5% age 2, 19.3% age 3 and 0.5% age 4. Scale samples from 9154 steelhead caught at sea indicated that 2.7% were in their first year, 66.2% in their second year, 29.6% in their third year, and 1.5% in their fourth year or more (Burgner et al., 1992). Most steelhead that spend only a single year at sea are males and are much smaller at return than older fish (e.g., Table 8). Moreover, in some populations from northern California and southern Oregon (notably the Klamath, Eel and Rogue rivers) there are fish that return after only a summer at sea. Owing to their small size, these fish are locally known as "half-pounders" (Kesner and Barnhart, 1972). These fish migrated to sea in spring and return that fall (August–October), at a size of about 250–350 mm, though some that had spent 3 years in the river prior to seaward migration were almost 500 mm when they returned. The half-pounders were mostly immature fish, tended to return earlier in the season than the larger steelhead, and also fed more heavily. Food was found in 67% of the

*Table 7*. The proportion of steelhead smolts aged 1–4, their modal lengths, percent surviving to adulthood, and representation in the adult run in Waddell Creek, California (data from Shapovalov and Taft, 1954)

| Smolt age | % of smolts | Modal length (mm) | % marine survival | % of adults |
|---|---|---|---|---|
| 1 | 59.8 | 100 | 2.4 | 34.8 |
| 2 | 37.3 | 160 | 5.8 | 52.4 |
| 3 | 2.9 | 220 | 18.1 | 12.7 |
| 4 | 0.03 | 270 | 16.7 | 0.1 |

*Table 8*. Number of years spent at sea and fork length (in mm) of 89 female and 93 male wild winter (ocean-maturing) steelhead from Forks Creek, Washington (T.P. Quinn, unpublished data)

| Sex | Trait | Years spent at sea | | | |
|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 |
| Female | Length | – | 670 | 739 | 820 |
| | Percent | 0.0 | 78.7 | 19.1 | 2.2 |
| Male | Length | 492 | 670 | 790 | 840 |
| | Percent | 8.6 | 76.3 | 14.0 | 1.1 |

stomachs of Klamath River steelhead < 350 mm, 44% for fish 350–449 mm, and 27% of the fish > 450 mm (Kesner and Barnhart, 1972).

Asian populations of steelhead occur primarily in the small tundra rivers of western Kamchatka (Maksimov, 1972, 1976; Savvaitova, 1975). Western Kamchatka steelhead smolts typically migrate to sea in June–July after 2 or 3 years in freshwater (range 1–6 yrs) and return to spawn for the first time after 2 or 3 years in the ocean (range 1–6 yrs; Savvaitova et al., 2003). In northern populations, spawning migrations occur from September through November (peaking in late October to early November: Maksimov, 1972). Adult steelhead overwinter in deep pools in the rivers, and migrate to spawning grounds in the spring. In southern populations such as the Bolshaya River, there is also a spring migration from the sea in April–May. Spawning occurs in late May to mid June, and kelts migrate downstream in June. Adult Kamchatka steelhead apparently do not feed during spawning runs but they feed actively in freshwater soon after spawning. Savvaitova et al. (2003) reported considerable annual variation in the percentages of first-time and repeat (typically 2–3 times, range 2–6 times) spawners. Juvenile steelhead from southern populations (e.g., the Bolshaya River) typically spend one year longer in freshwater than juveniles in northern rivers (the opposite pattern to that reported in North America by Busby et al., 1996). Adults in northern populations tend to be longer at maturity than in southern populations, probably because northern populations spend more time at sea (Maksimov, 1976).

Savvaitova and her colleagues identified four different life-history patterns in populations of western Kamchatka steelhead: (1) typical anadromous fish that migrate far offshore to the North Pacific Ocean to feed; (2) a coastal group that does not migrate far from the coast and probably feeds in the Sea of Okhotsk (including half pounders); (3) a river-estuarine group, which enters saltwater lagoons; and (4) a river group that does not migrate to the ocean, consisting mainly of males (Savvaitova, 1975). The typical, anadromous pattern dominates northern populations in western Kamchatka, whereas the coastal and river patterns are more common in southern populations. All life-history types occur in the Bolshaya River, which is the southern boundary of the range of Kamchatka steelhead (30% typical anadromous, 20% coastal, 50% river–estuarine and river; Maksimov, 1976). In addition to latitudinal clines in life history patterns, life-history type also appears to be related to the size of western Kamchatka rivers, i.e., typical-anadromous types dominate small, rivers ( < 100 km long, e.g., up to 96% in the Kvachina and Snatolvayam rivers); coastal and river types are more prevalent in larger rivers (up to 200 km long, e.g., 12% coastal and 3% river types in the Utkholok River), and coastal and river types dominate in large rivers (250–300 km long, e.g., 20% coastal and 50% river types in the Bolshaya River; Maksimov, 1976). In the Bolshaya River, spawning grounds and spawning periods of four life-history types overlap. The paucity of river-type females in small western Kamchatka rivers seems to be related to poor freshwater feeding conditions and the absence of diadromous forms in eastern Kamchatka is likely due to lack of suitable spawning habitat (Savvaitova, 1975).

Unlike salmon or steelhead, cutthroat trout characteristically spend only a summer at sea. During this time, their growth is modest and they reach a much smaller final size than steelhead (Table 9). As discussed in the next section on the state of maturity attained at sea, the number of months spent at sea in the "summer" and in fresh water depends on latitude. Some southern populations are largely marine after the smolt transformation, with a brief period in the river each year, whereas northern populations are largely freshwater residents with a brief jaunt to sea each year. In addition, the ability or tendency of cutthroat to overwinter at sea has been the subject of some debate. Wenburg (1998) marked individuals leaving and returning to Big Beef Creek (and other small nearby streams) in Hood Canal, Washington.

*Table 9*. Average fork length (mm) at age for anadromous cutthroat trout, compiled by Trotter (1989) based on data reported for populations from Oregon and Washington

| Stage/age | Age 2 smolts | Age 3 smolts | Age 4 smolts |
|---|---|---|---|
| Smolt | 165 | 203 | 216 |
| 1st return | 305 | 324 | 343 |
| 2nd return | 362 | 387 | 410 |
| 3rd return | 413 | 432 | 438 |
| 4th return | 438 | 457 | 470 |
| 5th return | – | 478 | – |

Most were only detected a few times but one individual was detected six times. It migrated to sea as a smolt on 15 April 1994, returned on 29 January 1995, left again on 19 April 1995, returned on 12 November 1995, was missed going downstream but entered again on 20 February 1996, and left on 7 April 1996 (Wenburg, 1998, Appendix Table G, Fish #BA4). Forty-eight fish that were marked while leaving one spring were detected upon their return in the fall/winter. Of these, 35 were detected after only one summer at sea but seven (all females) were next observed two winters later. Examination of scales indicated that they had not spawned but it was not possible to ascertain whether or not they had entered freshwater to feed. Wenburg (1998) noted that they could have escaped detection at the weirs but he concluded that "... some migrants remain at sea during the entire overwintering period."

Dolly Varden char (*Salvelinus malma*) share many life history traits with cutthroat, and anadromous individuals had been believed to only spend the summer at sea. However, Bernard et al. (1995) estimated that 14–58% spent the winter at sea. Like cutthroat trout, most Dolly Varden were caught along shorelines but in some cases had crossed at least 10 km of open water (Bernard et al., 1995). More spectacular movements were reported by DeCicco (1992); two Dolly Varden tagged in the Wulik River of northwestern Alaska moved at least 1020 km down the Bering Strait and across the Bering Sea to the mouth of the Anadyr River in Russia, and then swam 540 and 670 km upriver. Other Dolly Varden moved 750 and 530 km away within Alaskan waters. Japanese research vessels routinely catch Dolly Varden in offshore waters of the central Bering Sea basin. It is certainly premature to conclude that cutthroat trout move this far at sea. However, so few are tagged that our opportunities to learn about their migrations are limited.

### *State of maturity attained at sea*

The maturity state attained by salmonids at sea varies enormously, and this fascinating subject remains in need of a thorough investigation. The great majority of pink and chum salmon enter freshwater in a nearly or completely mature state, and spawn only a short distance inland within a few days or weeks. There are populations of chum that migrate over 1000 km up the Amur River and 2400 km up the Yukon River, and these enter in a much less advanced state of maturity (Brett, 1995). As a rule pink salmon do not migrate as far inland but a few populations go more than 100 km upriver (Heard, 1991). Coho salmon often enter freshwater in a less advanced state of maturity and spawn a month or more later, though they do not necessarily migrate very far inland. However, all of these species generally spawn in the same season in which they left the ocean. Other salmonids show more complex patterns.

Some chinook salmon enter fresh water in fall and spawn within about a month. These "fall" chinook are most often ocean-type juveniles in the southern part of their range, though in the north then may be stream-type. However, in large rivers draining the interior plateau such as the Sacramento, Klamath, Columbia and Fraser rivers, much greater diversity in timing is seen (Healey, 1991; Myers et al., 1998). These rivers have "spring" chinook that enter in March–June (Figure 1) in a relatively immature state, migrate much of the way to their natal spawning grounds, and then hold during the summer and spawn in fall (e.g., September). In the Columbia River system, for example, these spring runs primarily originate in rivers of the interior, inland of the Cascade Mountains, but some coastal rivers also produce spring chinook in their upper reaches (Myers et al., 1998). We hypothesize that this life history pattern evolved because some areas suitable for spawning by adults and rearing by juveniles are inaccessible for reasons of flow or temperature in the months shortly before spawning. Therefore, the only option for adults is to leave the ocean early, get past the hazardous area, and then minimize energy losses until they spawn (Berman and

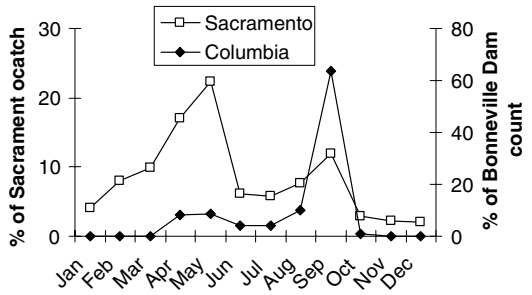


*Figure 1.* Timing of arrival of chinook salmon in the Sacramento River in 1872, inferred from catches at Rio Vista (Stone,1896), and the Columbia River (average of counts at Bonneville Dam from 1939 to 1948; US Army Corps of Engineers annual reports, Portland District).

Quinn, 1991). Genetic analyses indicate that most rivers were colonized by a single group of chinook salmon which then diverged into spring and fall runs. The two runs in a given river are now more closely related to each other than either is to runs with similar timing in other rivers (Waples et al., 2004). However, the interior of the Columbia River seems to have been colonized by a separate lineage from the coastal populations (Waples et al., 2004). Although genetic techniques can reveal differences between seasonal runs, the distinction between spring, summer and fall chinook salmon for counting purposes can be somewhat arbitrary, as adults migrate throughout much of the year (Figure 1). In the Sacramento River, there are also "winter" chinook that migrate in late winter and spawn in late spring, an apparently unique pattern in Pacific salmon (Fisher, 1994), so adults migrate in all months of the year (Figure 1).

"Premature" migration into fresh water is not restricted to chinook salmon. Some sockeye salmon populations enter in spring (as early as March or April) and then spawn in the fall (September to November). These are not populations with long migrations; rather, they are coastal populations in the southern end of the range that avoid warm temperatures in late summer by entering earlier in the year and remaining below the thermocline in lakes until they enter tributaries to spawn in the fall (Hodgson and Quinn, 2002). Even more extreme variation is seen in steelhead (Burgner et al., 1992; Busby et al., 1996). They are usually termed "winter" and "summer", referring to the seasons in which they enter freshwater; both types spawn in spring. Busby et al. (1996) suggested that these terms be replaced by "ocean-maturing" and "stream-maturing", respectively, to indicate the habitat in which maturation takes place. Ocean-maturing steelhead tend to occur in coastal rivers in the central and southern part of their range, entering fresh water in a relatively mature state in March or April, spawning in April or May, and leaving thereafter (Figure 2). Stream-maturing steelhead tend to spawn in the upper reaches of large rivers such as the Columbia, Fraser and Skeena (often in regions occupied by spring chinook salmon) and they enter the river in late summer or early fall (Robards and Quinn, 2002) in a less mature state, migrate part of the way home but then hold in suitable winter habitat and ascend to the spawning sites in late spring. In some cases a river will have both forms of steelhead, and their migration timing is still strikingly different. In the Kalama River, for example, the winter steelhead migration into the river increased gradually from late fall to a peak in April, then dropped off quickly (Figure 3), and the mean spawning date was 15 April (Leider et al., 1984). In contrast, the summer run's migration increased abruptly to a peak in July and then continued into the winter; the mean spawning date was 1 February. Thus the spring chinook enter in spring, hold all summer and spawn in the fall whereas the summer steelhead enter in summer or fall, hold all winter, and spawn in spring.

Premature migration into fresh water is a fascinating trait, documented in many Atlantic salmon populations (Went, 1964; Shearer, 1992) as well as Pacific salmon. In some cases the factor necessitating premature migration is obvious (e.g., high or low temperature or low water) but in other cases it is

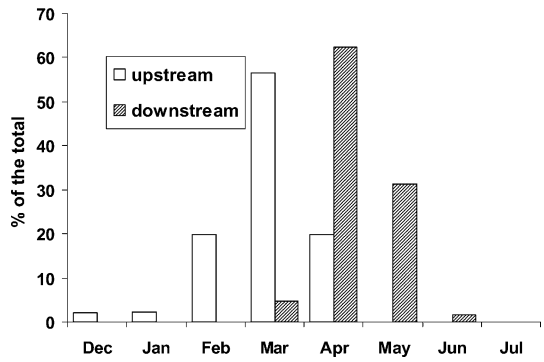


*Figure 2.* Timing of upstream migration by mature winter steelhead and downstream migration by kelts from Snow Creek, Washington (data from 1998 to 2003, Thom Johnson, Washington Department of Fish and Wildlife).

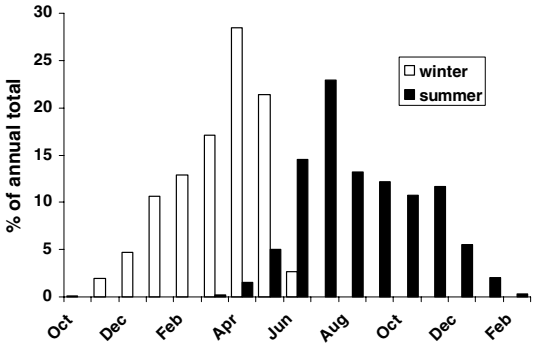


*Figure 3*. Timing of migration by wild adult "winter" or "ocean-maturing" and "summer" or "stream-maturing" steelhead at the Kalama Falls Hatchery trap on the Kalama River, Washington (Hulett et al.,1993, and additional Washington Department of Fish and Wildlife unpublished data).

not. This subject calls for further investigation, as it gets at the very essence of the anadromous life history: the relative benefits and costs of spawning in one environment and growing to maturity in another. As a very broad rule, the *Oncorhynchus* species do not return to fresh water unless they are prepared or preparing to spawn. Half-pounders in steelhead are an exception for that species, but in anadromous cutthroat trout (another spring-spawning species) many individuals return after their first summer at sea in an immature state. According to Johnston (1982), "In most Oregon and Washington coastal rivers (other than the Columbia), stocks are sexually mature at first return to freshwater, whereas a large percentage of Columbia River, Puget Sound, British Columbia and Alaska cutthroat females do not spawn during the winter of first return to fresh water."

In addition to the fact that not all sea-run cutthroat trout are mature when returning from the sea, the timing of cutthroat trout migration, hence the state of maturity, varies among areas. For example, in Eva Lake, Alaska the seaward migration was primarily in May and June and the return in September (Armstrong, 1971; Figure 4, top panel). Sand Creek, on the coast of Oregon, showed a longer period of marine residence, from April–May through October–December (Sumner, 1962; Figure 4, middle panel). In Washington, there seem to be two patterns. In large rivers the cutthroat enter relatively early, in September and October (Johnston, 1982), whereas in smaller streams they enter later (January–March), shortly before spawning, and leave primarily in April (e.g., Wenburg, 1998; Figure 4 bottom panel). Thus, the periods spent at sea and in freshwater in these three populations range from about 3.5 vs. 8.5 months in Eva Lake, to 6.5 vs. 5.5 months in Sand Creek, and 10 vs. 2 months in Big Beef Creek.

*Spawning habits and habitat*

Rounsefell (1958) distinguished four categories of spawning habits and habitats, and there has been much detail but few changes in this regard among Pacific species since his review. He distinguished species that can spawn successfully in the intertidal zone (pink and chum salmon), those spawning in streams (all species of *Oncorhynchus* and *Salvelinus* except lake trout, *S. namaycush*), lake spawners that build nests (sockeye salmon, and Arctic char,

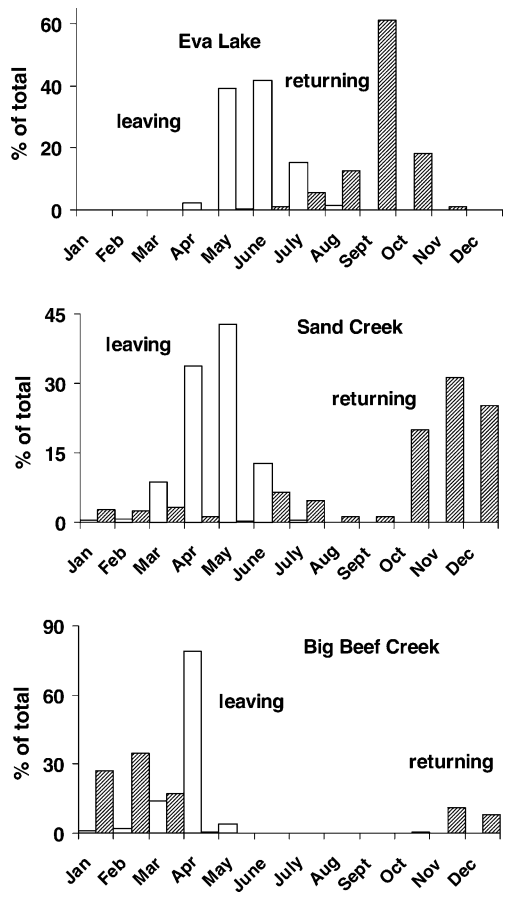


*Figure 4*. Timing of cutthroat trout migration leaving and returning to Eva Lake, in southeast Alaska (data from Armstrong,1971), Sand Creek, on the coast of Oregon (data from Sumner, 1962) and Big Beef Creek, in Hood Canal, Puget Sound, Washington (data from Wenburg, 1998).

*S. alpinus*), and lake spawners that broadcast their eggs rather than building nests (lake trout). In terms of anadromy, intertidal spawning may represent the greatest shift from the archetypal stream-spawning salmonid. This behavior is chiefly displayed by pink and chum salmon in small streams of southeast Alaska (e.g., Helle, 1970; Thorsteinson et al., 1971). The shortness of the streams in this area (often only a few km are accessible) and the high densities at which these species typically spawn may have contributed to the evolution of intertidal spawning.

On the other hand, many lakes support sockeye salmon populations that spawn on beaches. The juveniles of this species typically (but not invariably) rear in lakes, so this seems like a natural expansion of the breeding habitat for them. The spawning beaches are commonly at the outwash of a river, or the margins of the lake where groundwater flows down a hillside and wells up to irrigate the embryos (Wood, 1995). However, in Iliamna Lake, very many sockeye salmon spawn on low-lying islands with no groundwater. At these beaches the water is circulated through the gravel by wind-driven currents, and the substrate is very coarse (Kerns and Donaldson, 1968; Leonetti, 1997). Sockeye salmon commonly form non-anadromous populations (see below) but there is no apparent linkage between beach spawning and non-anadromy. Interestingly, coho salmon commonly rear in lakes and ponds, especially in winter, but we do not know of any beach spawning coho salmon populations.

### *Mortality after spawning*

Mortality after spawning is, strictly speaking, not a component of anadromy but the two traits are linked to some extent, presumably by the combined stresses of migration and reproduction. Rounsefell (1958) stated that all members of the genus *Oncorhynchus* (including anadromous and non-anadromous forms) die after spawning, and this is true with three exceptions. First, the Pacific trout species (classified in the genus *Salmo* at the time) are all iteroparous, and they are now in the genus *Oncorhynchus* (Smith and Stearley, 1989). Second, male masu salmon (*O. masou*) that mature in fresh water as parr are capable of surviving, migrating to sea, and spawning in a subsequent season (Ivankov et al., 1977; Tsiger et al., 1994), though anadromous males and females are semelparous. Third, under experimental conditions male chinook salmon can mature as parr, survive spawning, grow, and spawn again the following year, and even a third year (Unwin et al., 1999). This phenomenon, in a species that is normally exclusively semelparous, indicates that the separation between semelparous and iteroparous salmonids may not be as great as was once thought. The mature parr had very large gonads and depleted energy reserves, compared to parr that did not mature, and so the likelihood of their surviving the winter in rivers would be low.

The frequency of repeat spawning is higher in non-anadromous populations of both steelhead/rainbow trout and cutthroat trout (Fleming, 1998). Steelhead are iteroparous but sampling indicates that most (sometimes nearly all) spawn only once. For example, data from Petersburg Creek, Alaska indicated that 57% of the fish were returning to breeding for the first time (Jones, 1972, 1973; Table 10). At this site, females were more common than males among repeat spawners, consistent with general pattern for iteroparous salmonids (Fleming, 1998). Busby et al. (1996) reviewed data on 26 North American populations, and first time (maiden) spawners comprised 92% of the adults in British Columbia and Washington, 94% in the Columbia River, 85% in Oregon and 81.5% in California. This supports Withler's (1966) conclusion that repeat spawning is more common in southern compared to northern populations. In addition, sampling on the high seas produced primarily steelhead that had never spawned. Not only were the kelts less numerous but they were also distributed closer to shore, whereas the maiden fish migrated very extensively (Burgner et al., 1992). The apparently lower post-spawning survival of males compared to females is interesting

*Table 10*. Percent of male and female steelhead ascending Petersburg Creek, Alaska, that were spawning for the first through fifth times (Jones, 1972, 1973)

| Count | Spawning season | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | Total |
| Males | 60.9 | 31.3 | 6.8 | 1.0 | 0.0 | 294 |
| Females | 53.3 | 28.3 | 12.5 | 5.1 | 0.8 | 375 |
| % of total | 56.7 | 29.6 | 10.0 | 3.3 | 0.4 | 669 |
| % females | 52.8 | 53.5 | 70.1 | 86.4 | 100.0 | – |

because females devote much more energy to gonads than males. However, unlike semelparous females that guard their nest until they die, iteroparous females tend to leave shortly after spawning whereas males remain on the spawning grounds much longer. We might hypothesize that ocean-maturing steelhead would have a higher proportion of successful repeat spawners because they spend so much less time in freshwater than the stream maturing ones. The data provided by Busby et al. (1996) did not show a clear difference but other sources of variation in iteroparity confound the comparison. Data on wild steelhead from the Kalama River (Leider et al., 1986; Table 11) were consistent with the prediction that iteroparity would be more prevalent among winter (ocean maturing) steelhead.

There does not seem to be a comprehensive review of iteroparity in anadromous cutthroat trout, and the subject is complicated by the fact that some fish return to freshwater but do not spawn, especially on their first time back. However, data from four populations (Sand Creek, Oregon: Sumner, 1962; Snow and Salmon creeks, and the Stillaguamish River, Washington: Michael, 1989; Big Beef Creek, Washington: Wenburg, 1998) may serve to illustrate the general pattern: most fish are returning for the first time, and some of these may not spawn but only overwinter and leave again, so the proportion of successful repeat spawners is not great (Table 12). Wenburg (1998) pointed out that females were 58.5% of the first time returnees but 85.1% of those returning more often, consistent with the general pattern of higher post-breeding survival for iteroparous, anadromous salmonids.

*Occurrence of freshwater forms*

Pacific salmonids vary widely in the occurrence of freshwater forms within their native range. Pink and chum salmon apparently have no natural non-anadromous populations, and this is consistent with other aspects of their life histories indicating that they are the mostly strongly anadromous salmonids. To our knowledge there are no naturally occurring non-anadromous populations of chinook salmon in their native range. However, chinook salmon introduced to Lake Chelan, Washington in 1974 formed a self-sustaining, naturally reproducing population (spawning mainly in the Stehekin River system, and reaching about 7 kg; Charles Peven, Chelan County Public Utility District, pers. comm.). Another self-sustaining non-anadromous population spawns in tributaries of Lake Cushman, Washington. It is not clear if they are the descendents of anadromous fish that were trapped when the Skokomish River was dammed early in the 20th century, or if they were introduced later (James Myers, National Marine Fisheries Service, pers. comm.). It is interesting that both these non-anadromous populations are associated with lakes, though lakes are not a typical rearing habitat for this species.

Transplants outside the native range of Pacific salmon have produced a puzzling combination of failures and successes. Most transplants failed to established self-sustaining anadromous populations (Fedorenko and Shepherd, 1986; Harache, 1992) but the success of chinook salmon in New Zealand and their rapid evolution is a notable exception (Quinn et al., 2001). Landlocked, lacustrine chinook salmon occur in New Zealand as well (McDowall, 1990; Graynoth, 1999). Even more famous are the transplanted populations of salmonids in the Great Lakes. Crawford (2001) reviewed the long and complex history of these introductions, including the exceptional success of

*Table 11.* Percentage of adult winter (ocean-maturing) and summer (stream-maturing) steelhead returning to spawn in the Kalama River, Washington for the first, second, third and fourth time (Leider et al., 1986)

| | Spawning season | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Total |
| Winter | 88.76 | 9.18 | 1.70 | 0.45 | 3114 |
| Summer | 93.95 | 5.53 | 0.49 | 0.04 | 2841 |

*Table 12.* Percent of upstream migrating cutthroat trout returning for the first through fourth times in Snow and Salmon creeks and the Stillaguamish River, Washington (Michael, 1989), Sand Creek, Oregon (Sumner, 1962) and Big Beef Creek, Washington (Wenburg,1998)

| | Season of return | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Total |
| Snow and Salmon creeks | 69.4 | 27.4 | 3.2 | 0.0 | 62 |
| Stillaguamish River | 85.4 | 11.7 | 1.9 | 1.0 | 103 |
| Sand Creek | 68.4 | 26.6 | 4.5 | 0.5 | 376 |
| Big Beef Creek | 78.4 | 18.8 | 2.3 | 0.5 | 218 |

a very small, accidental transplant of pink salmon, and the more gradual transition from hatchery-produced to a mix of hatchery and natural production of coho and chinook salmon, and both stream-dwelling and migratory (steelhead) forms of rainbow trout. The salmon and steelhead seem to accept these huge lakes as a substitute for the ocean; they undergo the color changes normally seen in anadromous populations, and they move in open water (e.g., Haynes and Gerber, 1989). Semelparity still prevails, so at least at a proximate level it is not a function of the transition from salt to fresh water.

In addition to these introduced lacustrine populations, some stream-type chinook salmon populations include sexually mature male parr (Taylor, 1989; Myers et al., 1998). Coho salmon are essentially always anadromous, though there have been a few reports of "residual" populations (Foerster and Ricker, 1953; reviewed by Sandercock, 1991). It is not clear that these populations are truly self-sustaining (the bodies of water were all connected to the ocean so the fish were not landlocked), and they have received little attention from researchers. Interestingly, the residual coho salmon populations have been associated with lakes. Streams are the "classic" coho salmon habitat but many populations spend the winter in lakes and lakes are the primary rearing habitat for some populations. Given the abundance of non-anadromous sockeye salmon, it is unclear why non-anadromous coho salmon are so rare.

Sockeye salmon commonly form non-anadromous populations, known as kokanee. Ricker (1938) also noted the existence of "residuals" in some populations of anadromous sockeye. He hypothesized that these residuals are the non-anadromous offspring of anadromous parents, and they are the first step towards the evolution of a kokanee population. Recent studies have supported Ricker's hypothesis. Sockeye colonized lake systems during the post-glacial period, and in some instances their residual offspring eventually gave rise to kokanee populations. Thus kokanee are polyphyletic, having evolved from sockeye salmon on numerous, independent occasions (Taylor et al., 1996). The two forms can remain genetically distinct even in sympatry despite some interbreeding (Wood and Foote, 1996). Wood (1995) reviewed the ecological and evolutionary aspects of these life history patterns, and hypothesized that difficulty of migration for adults and productivity of the rearing lake for juveniles combine to determine the life history pattern of the sockeye. "Anadromy should be advantageous in situations in which food is much less abundant in freshwater than in the ocean and migration is neither hazardous nor energetically costly" (pp. 201–203). Thus unproductive lakes with easy migrations (i.e., near the ocean at low elevation) have only sockeye, whereas lakes in the interior that present more challenges to migration and are also more productive may have both forms. Transplants of sockeye salmon can result in non-anadromous populations, even when there is access to the ocean (e.g., in New Zealand: Graynoth, 1995; Quinn et al., 1998), further indicating the evolutionary flexibility of anadromy.

Rainbow and cutthroat trout commonly occur as non-anadromous forms, and indeed in large parts of their range only non-anadromous forms exist (Behnke, 1992, 2002). Steelhead are rare or absent from Alaska north of the Alaska Peninsula (e.g., in Bristol Bay) despite numerous robust rainbow trout populations with easy access to the ocean. Indeed, many of these adfluvial trout take advantage of the eggs and juveniles from the very abundant sockeye salmon populations (e.g., Eastman, 1996) to grow very large (Seidelman et al., 1973). Thus, unlike the case with kokanee, non-anadromy in these trout seems to be determined more by growing opportunities than difficulty of migration. At the southern end of their range, rainbow trout exist as landlocked populations in northern Mexico (Nielsen and Sage, 2001; Behnke, 2002). At these sites, the migration to sea may be impossible or the conditions at sea unsuitable for trout, but they persist in fresh water. In between, there are examples of sympatric rainbow and steelhead trout populations, existing with some degree of genetic isolation. Zimmerman and Reeves (2000) studied such cases and found that the resident trout spawned earlier in the season, and used slightly different habitat for redd sites, consistent with their smaller size relative to sympatric steelhead. However, the extent of genetic divergence seems to vary among sites. Docker and Heath (2003) found genetic differences between sympatric pairs of rainbow and steelhead populations in one of the five river systems they studied, and Narum et al. (2004) found differences in one of the two they studied.

Cutthroat trout have an even longer and more complex history of non-anadromy, as there are sub-species in drainages that do not connect with the Pacific Ocean (Behnke, 1992, 2002). For example, there are native cutthroat trout in Yellowstone Lake, in the upper reaches of the Missouri River system, which flows into the Mississippi River and into the Gulf of Mexico; in the Rio Grande River, which also flows into the Gulf of Mexico; in the Colorado River, which flows into the Gulf of California; and in the Lahontan basin of Nevada and California, without a present connection to the ocean. Even among the coastal cutthroat trout, there are anadromous, fluvial, adfluvial and resident trout, and several of these forms may occur in the same basin. In some cases there is a barrier to migration, and cutthroat may be the only salmonid in some small, isolated streams, but in other cases the non-anadromy is facultative (Northcote, 1997).

In addition to the non-anadromous populations of rainbow and cutthroat trout, a fraction of the males mature as parr in anadromous populations. This phenomenon has been closely studied in Atlantic salmon (Fleming, 1998; Hutchings and Jones, 1998) and brown trout (L'Abée-Lund et al., 1990), and in these Atlantic species rapid growth in fresh water is associated with a higher proportion of males maturing as parr. However, the reports for Pacific trout species (e.g., Shapovalov and Taft, 1954; reviewed by Busby et al., 1996) are rather anecdotal and there does not seem to be a systematic survey of the proportion of male parr in steelhead or anadromous cutthroat trout populations. This topic needs further investigation, because rapid growth in hatcheries may result in residual males that mature without going to sea.

## Linkages among life history traits

Rounsefell (1958) correctly pointed out that anadromy is really a matter of degree rather than being an absolute trait among salmonid species, and that anadromy is not even a single trait but rather a series of interrelated traits. He produced a figure and ranked salmonids according to their degree of anadromy. Among the Pacific species, he ranked pink salmon as the most strongly anadromous, followed by chum salmon, chinook salmon, coho salmon, sockeye salmon, rainbow/steelhead trout, cutthroat trout, Dolly Varden char (bull trout were not classified separately at that time), Arctic char, and lake trout. Recent work has not changed the essential continuum of salmonid species very much, though one might make a case that chinook salmon are less strongly anadromous than coho by virtue of the existence of mature male parr, and iteroparity under experimental conditions. However, our understanding of the traits related to anadromy has been enriched for all the species, and we have come to appreciate the extensive variation within species. Information has also been collected and hypotheses have been developed concerning the interactions among traits, and they are the focus of this final section.

First, anadromy is linked to semelparity. Fleming (1998) and Fleming and Reynolds (2004) summarized data showing that anadromous populations are less likely to breed iteratively than non-anadromous ones of the same species. This may result from the energetic demands of migration, the physiological stress of changing osmotic environments, or the higher rates of mortality among adults at sea than in freshwater. In addition, it is becoming clear that semelparity is not as fixed a trait as was once thought. As was mentioned earlier, male masu salmon that matured as parr can survive, migrate to sea, and return to spawn as jacks or older fish (e.g., Ivankov et al., 1977; Tsiger et al., 1994). Sexually mature chinook salmon parr can survive after spawning, recover, grow, and spawn in a second and even a third year under artificial conditions (Unwin et al., 1999). Interestingly, male chinook salmon that are mature in their first year of life routinely return to the University of Washington's hatchery. These fish, released in their first spring of life as smolts, return that same fall. Thus they are the same age as the mature parr studied by Unwin et al. (1999), but have undergone smolt transformation. Efforts to get these "mini-jacks" to feed and survive the spawning season were unsuccessful (Quinn, unpublished results). Thus it would seem that once the Pacific salmon undergo smolt transformation and go to sea, they are destined for semelparity, but maturation as parr leaves open the possibility of iteroparity. There are no reports of iteroparous kokanee, so the smolt-like transformation that

they undergo (Foote et al., 1992) may be sufficient to preclude repeat spawning.

Another interesting connection is between sexual maturity and homing. Decades of research have demonstrated that the homing of adults to the natal stream is guided by the memory of odors imprinted during residence in fresh water and migration to sea (Hasler and Scholz, 1983; Dittman and Quinn, 1996). This learning process is presumably the same for all smolts within a population without regard to their subsequent life history. However, individuals that return to freshwater at an immature state are less likely to home than are maturing fish. Satterthwaite (1988) reported that the straying rates of half-pounders were 87% higher than those of maturing steelhead. Homing patterns by anadromous Dolly Varden depend on whether the fish is going to spawn, and whether the natal river is associated with a lake (providing suitable overwinter habitat) or not (Armstrong, 1984; Bernard et al., 1995). Such variation in behavior greatly complicates management of the populations. Tagging of cutthroat trout by Wenburg (1998) revealed a low level of straying among nearby creeks, but significant population structure was evident from DNA microsatellite loci, indicating restricted gene flow (Wenburg and Bentzen, 2001). More research is certainly needed on the patterns of movement into and among streams by immature and maturing individuals in the iteroparous, anadromous species.

More broadly, anadromy and homing may be deeply rooted traits in salmonids. McDowall (2002) considered whether salmonids are ancestrally marine or freshwater fishes and concluded that this is "a question for which an answer seems likely to be elusive" (p. 171). Broadly distributed marine species might have colonized freshwater for breeding, in which case homing to natal streams might be an evolved trait, and the present complex population structure would have been the result. On the other hand, resident freshwater species might have gradually exploited marine feeding areas, in which case highly structured populations would have been the ancestral condition and anadromy would have facilitated gene flow. Both scenarios are consistent with the relative levels of genetic heterogeneity within species of marine, anadromous and fresh water fishes (Gyllensten, 1985; Ward et al., 1994). McDowall (2001) hypothesized that homing might actually have been a critical preadaptation for the evolution of anadromy (assuming a freshwater ancestry) because it would preserve the local adaptations so important for survival. However, he recognized that "alternatively, anadromy having evolved, the development of homing could have been a mechanism that increased the adaptive value of anadromy and/or made the evolution of longer-distance anadromous migrations possible" (p. 82). In the end, McDowall (2001) found the evidence insufficient to support a firm conclusion regarding the evolution of homing and anadromy, other than to characterize them as synergistic traits.

Fascinating and intriguing though it is, a determination of the ancestral condition of salmonids is probably not critical for their current management. However, anadromy (with all the traits this term includes), and its interactions with homing, and iteroparity are essential features of salmonids. Further research, especially on the Pacific trout and char species and masu salmon, and comparisons with Atlantic species, would prove very useful in conservation efforts as well as advancing our understanding of the ecology of the family as a whole. In particular, the extent of genetic control over the suite of anadromy-related traits needs more study, and the patterns probably vary among species. This issue is not a new one; Huntsman (1947) decried "the utter lack of published data from experiments to distinguish the effects of heredity and environment" and called for experiments to "discover possible hereditary differences in migratory behavior of supposed 'races' or 'strains' in salmonid species." The relatively sharp distinction between sockeye and kokanee may not be characteristic of salmonids. Various lines of evidence indicate plasticity of anadromy within polymorphic populations of brown trout (e.g., Jonsson, 1985) and Arctic char (Nordeng, 1983; Svenning et al., 1992; Rikardsen et al., 1997). On the other hand, sympatric, genetically distinct anadromous and resident populations have been reported in Atlantic salmon (Verspoor and Cole, 1989) and brown trout (Skaala and Nævdal, 1989). It is likely that salmonid species vary in the plasticity of anadromy, and this is an especially fruitful area for future research.

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## References

Armstrong, R.H. (1971) Age, food, and migration of sea-run cutthroat trout, *Salmo clarki*, at Eva Lake, Southeastern Alaska. *Trans. Am. Fish. Soc.* **100**, 302–306.

Armstrong, R.H. (1984) Migration of anadromous Dolly Varden charr in southeastern Alaska - a manager's nightmare. *In*: Johnson, L. and Burns, B. (eds.), *Biology of the Arctic Charr. Proceedings of the International Symposium on Arctic Charr*. University of Manitoba Press, Winnipeg, MB, pp. 559–570.

Armstrong, R.H. and Morrow, J.E. (1980) The Dolly Varden charr, *Salvelinus malma*. *In*: Balon, E.K. (ed.), *Charrs: Salmonid Fishes of the Genus* Salvelinus. Dr. W. Junk, Publishers, The Hague, pp. 99–140.

Beamish, R.J., Pearsall, I.A. and Healey, M.C. (2003) A history of the research on the early marine life of Pacific salmon off Canada's Pacific coast. *N. Pac. Anad. Fish Comm. Bull.* **3**, 1–40.

Behnke, R.J. (1992) *Native Trout of Western North America*. American Fisheries Society Monograph 6. Bethesda, MD.

Behnke, R.J. (2002) *Trout and Salmon of North America*. The Free Press, New York.

Berman, C.H. and Quinn, T.P. (1991) Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *J. Fish Biol.* **39**, 301–312.

Bernard, D.R., Helper, K.R., Jones, J.D., Whalen, M.E. and McBride, D.N. (1995) Some tests of the "migration hypothesis" for anadromous Dolly Varden (southern form). *Trans. Am. Fish. Soc.* **124**, 297–307.

Birtwell, I.K., Nassichuk, M.D. and Beune, H. (1987) Underyearling sockeye salmon (*Oncorhynchus nerka*) in the estuary of the Fraser River. *Can. Sp. Publ. Fish. Aquat. Sci.* **96**, 25–35.

Brannon, E. and Setter, A. (1989) Marine distribution of a hatchery fall chinook salmon population. *In*: Brannon, E. and Jonsson, B. (eds.), *Proceedings of the Salmonid Migration and Distribution Symposium*. School of Fisheries, University of Washington, Seattle, WA, pp. 63–69.

Brett, J.R. (1995) Energetics. *In*: Groot, C., Margolis, L. and Clarke, W.C. (eds.), *Physiological Ecology of Pacific Salmon*. University of British Columbia Press, Vancouver, BC, pp. 1–68.

Brodeur, R.D., Myers, K.W. and Helle, J.H. (2003) Research conducted by the United States on the early ocean life history of Pacific salmon. *N. Pac. Anad. Fish Comm. Bull.* **3**, 89–131.

Burgner, R.L. (1991). Life history of sockeye salmon (*Oncorhynchus nerka*). *In*: Groot, C. and Margolis, L. (eds.), *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, BC, pp. 1–117.

Burgner, R.L., Light, J.T., Margolis, L., Okazaki, T., Tautz, A. and Ito, S. (1992) Distribution and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* **51**, 92 pp.

Busby, P.J., Wainwright, T.C., Bryant, G.J., Lierheimer, L.J., Waples, R.S., Waknitz, F.W. and Lagomarsino, I.V. (1996) Status review of west coast steelhead from Washington, Idaho, Oregon and California. National Marine Fisheries Service Technical Memorandum NMFS-NWFSC-27. Seattle, WA.

Clarke, W.C., Shelbourn, J.E., Ogasawara, T. and Hirano, T. (1989) Effects of initial daylength on growth, seawater adaptability and plasma growth hormone levels in underyearling coho, chinook, and chum salmon. *Aquaculture* **82**, 51–62.

Crawford, S.S. (2001) Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects. *Can. Sp. Publ. Fish. Aquat. Sci.* **132**, 205 pp.

Davis, N.D., Myers, K.W., Walker, R.V. and Harris, C.K. (1990) The Fisheries Research Institute's high seas salmonid tagging program and methodology for scale pattern analysis. *Amer. Fish. Soc. Symp.* **7**, 863–879.

Dawley, E.M., Ledgerwood, R.D., Blahm, T.H., Sims, C.W., Durkin, J.T., Kirn, R.A., Rankis, A.E., Monan, G.E. and Ossiander, F.J. (1986) Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966–1983. Final Report to the Bonneville Power Administration, Project 81–102. Portland, OR, 256 pp.

DeCicco, A.L. (1992) Long-distance movements of anadromous Dolly Varden between Alaska and the U.S.S.R. *Arctic* **45**, 120–123.

Dittman, A.H. and Quinn, T.P. (1996) Homing in Pacific salmon: mechanisms and ecological basis. *J. Exp. Biol.* **199**, 83–91.

Docker, M.F. and Heath, D.D. (2003) Genetic comparison between sympatric anadromous steelhead and freshwater resident rainbow trout in British Columbia, Canada. *Cons. Genetics.* **4**, 227–231.

Eastman, D.E. (1996) Response of freshwater fish communities to spawning sockeye salmon (*Oncorhynchus nerka*). Master of Science thesis. University of Washington, Seattle, WA.

Fedorenko, A.Y. and Shepherd, B.G. (1986) Review of salmon transplant procedures and suggested transplant guidelines. *Can. Tech. Rept. Fish. Aquat. Sci.* **1479**, 144 pp.

Fisher, F.W. (1994) Past and present status of Central Valley chinook salmon. *Cons. Biol.* **8**, 870–873.

Fleming, I.A. (1998) Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Can. J. Fish. Aquat. Sci.* **55** (Suppl. 1), 59–76.

Fleming, I.A. and Reynolds, J.D. (2004) Salmonid breeding systems. *In*: Hendry, A.P. and Stearns, S.C. (eds.), *Evolution Illuminated: Salmon and their Relatives*. Oxford University Press, Oxford, pp. 264–294.

Foerster, R.E. and Ricker, W.E. (1953) The coho salmon of Cultus Lake and Sweltzer Creek. *J. Fish. Res. Board Can.* **10**, 293–319.

Foote, C.J., Wood, C.C., Clarke, W.C. and Blackburn, J. (1992) Circannual cycle of seawater adaptability in *Oncorhynchus nerka*: genetic differences between sympatric sockeye salmon and kokanee. *Can. J. Fish. Aquat. Sci.* **49**, 99–109.

French, R., Bilton, H., Osako, M. and Hartt, A. (1976) Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* **34**, 113 pp.

Godfrey, H., Henry, K.A. and Machidori, S. (1975) Distribution and abundance of coho salmon in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* **31**, 80 pp.

Graynoth, E. (1995) Spawning migrations and reproduction of landlocked sockeye salmon (*Oncorhynchus nerka*) in the Waitaki catchment, New Zealand. *N. Zeal. J. Mar. Freshw. Res.* **29**, 257–269.

Graynoth, E. (1999). Recruitment and distribution of juvenile salmonids in Lake Coleridge, New Zealand. *N. Zeal. J. Mar. Freshw. Res.* **33**, 205–219.

Groot, C., Bailey, R.E., Margolis, L. and Cooke, K. (1989). Migratory patterns of sockeye salmon *(Oncorhynchus nerka)* smolts in the Strait of Georgia, British Columbia, as determined by analysis of parasite assemblages. *Can. J. Zool.* **67**, 1670–1678.

Gustafson, R.G. and Winans, G.A. (1999) Distribution and population genetic structure of river- and sea-type sockeye salmon in western North America. *Ecol. Freshw. Fish.* **8**, 181–193.

Gyllensten, U. (1985). The genetic structure of fish: differences in the intraspecific distribution of biochemical genetic variation between marine, anadromous, and freshwater species. *J. Fish Biol.* **26**, 691–699.

Harache, Y. (1992) Pacific salmon in Atlantic waters. *ICES Mar. Sci. Symp.* **194**, 1955–1977.

Hargreaves, N.B. and LeBrasseur, R.J. (1986) Size selectivity of coho (*Oncorhynchus kisutch*) preying on juvenile chum salmon (*O. keta*). *Can. J. Fish. Aquat. Sci.* **43**, 581–586.

Hartman, G.F., Anderson, B.C. and Scrivener, J.C. (1982) Seaward migration of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia. *Can. J. Fish. Aquat. Sci.* **39**, 588–597.

Hartt, A.C. and Dell, M.B. (1986) Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. *Int. N. Pac. Fish. Comm. Bull.* **46**, 1–105.

Hasler, A.D. and Scholz, A.T. (1983) *Olfactory Imprinting and Homing in Salmon*. Springer-Verlag, Berlin.

Haynes, J.M. and G.P. Gerber. (1989) Movements and temperatures of radiotagged salmonines in Lake Ontario and comparisons with other large aquatic systems. *J. Freshw. Ecol.* **5**, 197–204.

Healey, M.C. (1982) Juvenile Pacific salmon in estuaries: the life support system. *In* Kennedy, V.S. (ed.), *Estuarine Comparisons*. Academic Press, New York, pp. 315–341.

Healey, M.C. (1983) Coastwide distribution and ocean migration patterns of stream- and ocean-type chinook salmon, *Oncorhynchus tshawytscha*. *Can. Field-Nat.* **97**, 427–433.

Healey, M.C. (1987) The adaptive significance of age and size at maturity in female sockeye salmon (*Oncorhynchus nerka*). *Can. Sp. Publ. Fish. Aquat. Sci.* **96**, 110–117.

Healey, M.C. (1991) Life history of chinook salmon (*Oncorhynchus tshawytscha*). *In*: Groot, C. and Margolis, L. (eds.), *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, pp. 311–393.

Heard, W.R. (1991) Life history of pink salmon (*Oncorhynchus gorbuscha*). *In*: Groot, C. and Margolis, L. (eds.), *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, BC, pp. 119–230.

Helle, J.H. (1970) Biological characteristics of intertidal and fresh-water spawning pink salmon at Olsen Creek, Prince William Sound, Alaska, 1962–63. United States Fish and Wildlife Service, Washington, D.C., Special Scientific Report, Fisheries 602: 19 pp.

Hodgson, S. and Quinn, T.P. (2002) The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. *Can. J. Zool.* **80**, 542–555.

Hulett, P.L., Bradford, R.H., Wagemann, C.W. and Leider, S.A. (1993) Studies of hatchery and wild steelhead in the lower Columbia region. Progress report for fiscal year 1992. Washing Department of Wildlife, Fisheries Management Division Report 93–12, 70 pp.

Huntsman, A.G. (1947) Are lake salmon hereditarily distinct? *Science* **105**, 289–290.

Hutchings, J.A. and Jones, M.E.B. (1998) Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* **55(**Suppl. 1**),** 22–47.

Ivankov, V.N., Padetskiy, S.N. and Chikina, V.S. (1977). On the postspawning neotenic males of the masu, *Oncorhynchus masu*. *J. Ichthyol.* **15**, 673–678.

Jaenicke, H.W., Celewycz, A.G., Baily, J.E. and Orsi, J.A. (1984). Paired open beach seines to study estuarine migrations of juvenile salmon. *Mar. Fish. Rev.* **46(**3**)**, 62–67.

Johnson, L. (1980). The arctic charr, *Salvelinus alpinus*. *In*: Balon, E.K. (ed.), *Charrs: Salmonid Fishes of the Genus Salvelinus*. Dr. W. Junk, Publishers, The Hague, pp. 15–98.

Johnson, S.W., Thedinga, J.F. and Koski, K.V. (1992). Life history of juvenile ocean-type chinook salmon (*Oncorhynchus tshawytscha*) in the Situk River, Alaska. *Can. J. Fish. Aquat. Sci.* **49**, 2621–2629.

Johnston, J.M. (1982) Life histories of anadromous cutthroat with emphasis on migratory behavior. *In*: Brannon, E.L. and Salo, E.O. (eds.), *Proceedings of the Salmon and Trout Migratory Behavior Symposium*. University of Washington, School of Fisheries, Seattle, WA, pp. 123–127.

Jones, D.E. (1972) A study of steelhead-cutthroat trout in Alaska. Alaska Department of Fish and Game, Division of Sport Fish, Rept. G-11–1. Juneau, AK.

Jones, D.E. (1973) Steelhead and sea-run cutthroat life history in southeast Alaska. Alaska Dept. Fish Game, Division of Sport Fish, Rept. AFS-42–1. Juneau, AK.

Jonsson, B. (1985) Life history patterns of freshwater resident and sea-run brown trout in Norway. *Trans. Am. Fish. Soc.* **114**, 182–194.

Jonsson, B. and L'Abée-Lund, J.H. (1993) Latitudinal clines in life-history variables of anadromous brown trout in Europe. *J. Fish Biol.* **43**(Supplement A), 1–16.

Karpenko, V.I. (2003) Review of Russian marine investigations of juvenile Pacific salmon. *N. Pac. Anad. Fish Comm. Bull* **3**, 69–88.

Kato, F. (1991) Life histories of masu and amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodurus*). *In*: Groot, C. and Margolis, L. (eds.), *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, BC, pp. 448–520.

Kerns, O.E., Jr. and Donaldson, J.R. (1968) Behavior and distribution of spawning sockeye salmon on island beaches in Iliamna Lake, Alaska. *J. Fish. Res. Board Can.* **24**, 485–494.

Kesner, W.D. and Barnhart, R.A. (1972) Characteristics of the fall-run steelhead trout (*Salmo gairdneri gairdneri*) of the Klamath River system with emphasis on the half-pounder. *Cal. Fish Game* **58**, 204–220.

L'Abée-Lund, J.H., Jonsson, B., Jensen, A.J., Sættem, L.M., Heggberget, T.G., Johnsen, B.O. and Næsje, T.F. (1989) Latitudinal variation in life-history characteristics of sea-run migrant brown trout, *Salmo trutta*. *J. Anim. Ecol.* **58**, 525–542.

L'Abée-Lund, J.H., Jensen, A.J. and Johnsen, B.O. (1990) Interpopulation variation in male parr maturation of anadromous brown trout (*Salmo trutta*) in Norway. *Can. J. Zool.* **68**, 1983–1987.

Leider, S.A., Chilcote, M.W. and Loch, J.J. (1984) Spawning characteristics of sympatric populations of steelhead trout (*Salmo gairdneri*): evidence for partial reproductive isolation. *Can. J. Fish. Aquat. Sci.* **41**, 1454–1462.

Leider, S.A., Chilcote, M.W. and Loch, J.J. (1986) Comparative life history characteristics of hatchery and wild steelhead trout (*Salmo gairdneri*) of summer and winter races in the Kalama River, Washington. *Can. J. Fish. Aquat. Sci.* **43**, 1398–1409.

Leonetti, F.E. (1997) Estimation of surface and intragravel water flow at sockeye salmon spawning beaches in Iliamna Lake, Alaska. *N. Amer. J. Fish. Mgmt.* **17**, 194–201.

Machidori, S. and Kato, F. (1984) Spawning populations and marine life of masu salmon (*Oncorhynchus masou*). *Int. N. Pac. Fish. Comm. Bull.* **43**, 138 pp.

Maksimov, V.A. (1972) Some data on the ecology of the Kamchatka trout (*Salmo mykiss* Walbaum) from the Utkholok River. *J. Ichthyol.* **12**, 759–766.

Maksimov, V.A. (1976) The ecology of the Kamchatka trout *Salmo mykiss* population for the Bol'shaya River (western Kamchatka). *J. Ichthyol.* **16**, 12–17.

Major, R.L., Ito, J., Ito, S. and Godfrey, H. (1978) Distribution and origin of chinook salmon (*Oncorhynchus tshawytscha*) in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* **38**, 54 pp.

Mayama, H. and Ishida, Y. (2003) Japanese studies on the early ocean life of juvenile salmon. *N. Pac. Anad. Fish Comm. Bull.* **3**, 41–67.

McDowall, R.M. (1990) *New Zealand Freshwater Fishes*. Heinemann Reed, Auckland.

McDowall, R.M. (2001) Anadromy and homing: two life-history traits with adaptive synergies in salmonid fishes? *Fish and Fish.* **2**, 78–85.

McDowall, R.M. (2002). The origin of the salmonid fishes: marine, freshwater … or neither? *Rev. Fish Biol. Fish.* **11**, 171–179.

Michael, J.H., Jr. (1989) Life history of anadromous coastal cutthroat trout in Snow and Salmon creeks, Jefferson County, Washington, with implications for management. *Cal. Fish Game* **75**, 188–203.

Miller, D.R., Williams, J.G. and Sims, C.W. (1983) Distribution, abundance and growth of juvenile salmonids off the coast of Oregon and Washington, summer 1980. *Fish. Res.* **2**, 1–17.

Myers, K.W. and Bernard, R.L. (1993) Biological information on Pacific salmon and steelhead trout in observer samples from the Japanese squid driftnet fishery in 1990. *Int. N. Pac. Fish. Comm. Bull.* **53**(II), 217–238.

Myers, K.W., Aydin, K.Y., Walker, R.V., Fowler, S. and Dahlberg, M.L. (1996) Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1995. *N. Pac. Anad. Fish Comm. Doc.* **192**. School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA.

Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Lierheimer, L.J., Wainwright, T.C., Grant, W.S., Waknitz, F.W., Neely, K., Lindley, S.T. and Waples, R.S. (1998) Status review of chinook salmon from Washington, Idaho, Oregon and California. National Marine Fisheries Service, NOAA Technical Memorandum NMFS-NWFSC-35. Seattle, WA.

Myers, K.W., Walker, R.V., Carlson, H.R. and Helle, J.H. (2000) Synthesis and review of U.S. research on the physical and biological factors affecting ocean production of salmon. *N. Pac. Anad. Fish Comm. Bull* **2**, 1–9.

Narum, S.R., Contor, C., Talbot, A. and Powell, M.S. (2004) Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, U.S.A. *J. Fish Biol.* **65**, 471–488.

Neave, F., Yonemori, T. and Bakkala, R.G. (1976) Distribution and origin of chum salmon in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* **35**, 79 pp.

Nicholas, J.W. and Hankin, D.G. (1989) Chinook salmon populations in Oregon's coastal river basins. Oregon Department of Fish and Wildlife, Portland, OR, 359 pp.

Nielsen, J.L. and Sage, G.K. (2001) Microsatellite analyses of the trout of northwest Mexico. *Genetica* **111**, 269–278.

Nordeng, H. (1983) Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. *Can. J. Fish. Aquat. Sci.* **40**, 1372–1387.

Northcote, T.G. (1997) Why sea run? An exploration into the migration/residency spectrum of coastal cutthroat trout. *In: Sea-run Cutthroat Trout: Biology, Management, and Future Conservation*. Oregon Chapter, American Fisheries Society, pp. 20–26.

Pearcy, W.G. (1992) *Ocean Ecology of North Pacific Salmonids*. Washington Sea Grant Program, University of Washington, Seattle, WA.

Pearcy, W.G. and Fisher, J.P. (1990). Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981–1985. National Marine Fisheries Service, NOAA Technical Report 93, Corvallis, OR, 83 pp.

Pearcy, W.G., Brodeur, R.D. and Fisher, J.P. (1990) Distribution and biology of juvenile cutthroat trout *Oncorhynchus clarki clarki* and steelhead *O. mykiss* in coastal waters off Oregon and Washington. *Fish. Bull.* **88**, 697–711.

Pressey, R.T. (1953) The sport fishery for salmon on Puget Sound. *Fish. Res. Papers, Wash. Dept. Fish.* **1**(1), 33–45.

Quinn, T.P. (2004) *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press, Seattle, WA.

Quinn, T.P., Graynoth, E., Wood, C.C. and Foote, C.J. (1998) Genotypic and phenotypic divergence of sockeye salmon in New Zealand from their ancestral British Columbia populations. *Trans. Am. Fish. Soc.* **127**, 517–534.

Quinn, T.P., Kinnison, M.T. and Unwin, M.J. (2001) Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* **112/113**, 493–513.

Ricker, W.E. (1938) "Residual" and kokanee salmon in Cultus Lake. *J. Fish. Res. Board Can.* **4**, 192–218.

Rikardsen, A.H., Svenning, M.-A. and Klemetsen, A. (1997) The relationships between anadromy, sex ratio and parr growth of Arctic charr in a lake in North Norway. *J. Fish Biol.* **51**, 447–461.

Robards, M.D. and Quinn, T.P. (2002) The migratory timing of adult summer-run steelhead trout (*Oncorhynchus mykiss*) in the Columbia River: six decades of environmental change. *Trans. Am. Fish. Soc.* **131**, 523–536.

Robins, J.B., Abrey, C.A., Quinn, T.P. and Rogers, D.E. (2005). Lacustrine growth of juvenile pink salmon, *Oncorhynchus gorbuscha*, and a comparison with sympatric sockeye salmon, *O. nerka*. *J. Fish Biol.* (in press).

Roni, P. and Quinn, T.P. (1995) Geographic variation in size and age of North American chinook salmon (*Oncorhynchus tshawytscha*). *N. Am. J. Fish. Mgmt.* **15**, 325–345.

Rounsefell, G.A. (1958) Anadromy in North American Salmonidae. *Fish. Bull.* **131**, 171–185.

Rowland, R. and Sidorov, G. (2004) Lost salmon? *Redd Fish: Alaska's Sustainable Fisheries Newsletter* **1**(1), 10–11.

Salo, E.O. (1991) Life history of chum salmon (*Oncorhynchus keta*). *In*: Groot, C. and Margolis, L. (eds.), *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, BC, pp. 231–309.

Sandercock, F.K. (1991) Life history of coho salmon (*Oncorhynchus kisutch*). *In*: Groot, C. and Margolis, L. (eds.), *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, BC, pp. 395–445.

Satterthwaite, T.D. (1988) Influence of maturity on straying rates of summer steelhead into the Rogue River, Oregon. *Cal. Fish Game* **74**, 203–207.

Savvaitova, K.A. (1975) The population structure of *Salmo mykiss* in Kamchatka. *J. Ichthyol.* **15**, 876–888.

Savvaitova, K.A., Kuzishchin, K.V., Gruzdeva, M.A., Pavlov, D.S., Stanford, J.A. and Ellis, B.K. (2003). Long-term and short-term variation in the population structure of Kamchatka steelhead *Parasalmo mykiss* from rivers of western Kamchatka. *J. Ichthyol.* **43**, 757–768.

Seidelman, D.L., Cunningham, P.B. and Russell, R.B. (1973) Life history studies of rainbow trout in the Kvichak drainage of Bristol Bay. Alaska Dept. Fish and Game, Sport Fish Division, Vol. 14, Study G-11, Juneau, AK.

Shapovalov, L. and Taft, A.C. (1954) The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. *California Department of Fish and Game, Fish Bulletin* **98**, 375 pp.

Shearer, W.M. (1992) *The Atlantic Salmon. Natural History, Exploitation and Future Management*. Fishing News Books, Oxford.

Simenstad, C.A., Fresh, K.L. and Salo, E.O. (1982) The role of Puget Sound estuaries in the life history of Pacific salmon: an unappreciated function. *In*: Kennedy, V.S. (ed.), *Estuarine Comparisons*. Academic Press, New York, pp. 343–364.

Skaala, O. and Naevdal, G. (1989) Genetic differentiation between freshwater resident and anadromous brown trout, *Salmo trutta*, within watercourses. *J. Fish Biol.* **34**, 597–605.

Smith, G.R. and Stearley, R.F. (1989) The classification and scientific names of rainbow and cutthroat trouts. *Fisheries* **14**(1), 4–10.

Straty, R.R. and Jaenicke, H.W. (1980) Estuarine influence of salinity, temperature, and food on the behavior, growth, and dynamics of Bristol Bay sockeye salmon. *In:* McNeil, W.J. and Himsworth, D.C. (eds.), *Salmonid Ecosystems of the North Pacific*. Oregon State University Press, Corvallis, OR, pp. 247–265.

Stone, L. (1896) The artificial propagation of salmon on the Pacific coast of the United States, with notes on the natural history of the quinnat salmon. *Bull. U.S. Fish Comm.* **16**, 203–235.

Sumner, F.H. (1962) Migration and growth of the coastal cutthroat trout in Tillamook County, Oregon. *Trans. Am. Fish. Soc.* **91**, 77–83.

Svenning, M.-A., Astrid, S.-N. and Jobling, M. (1992) Sea water migration of Arctic charr (*Salvelinus alpinus* L.) correlation between freshwater growth and seawater migration, based on back-calculation from otoliths. *Nordic J. Freshw. Res.* **67**, 18–26.

Takagi, K., Aro, K.V., Hartt, A.C. and Dell, M.B. (1981) Distribution and origin of pink salmon (*Oncorhynchus gorbuscha*) in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* **40**, 195 pp.

Taylor, E.B. (1989) Precocial male maturation in laboratory-reared populations of chinook salmon, *Oncorhynchus tshawytscha*. *Can. J. Zool.* **67**, 1665–1669.

Taylor, E.B. (1990) Environmental correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *J. Fish Biol.* **37**, 1–17.

Taylor, E.B., Foote, C.J. and Wood, C.C. (1996) Molecular genetic evidence for parallel life-history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). *Evolution* **50**, 401–416.

Thorsteinson, F.V., Helle, J.H. and Birkholz, D.G. (1971) Salmon survival in intertidal zones of Prince William Sound streams in uplifted and subsided areas. *In*: The Great Alaska earthquake of 1964: biology. *National Academy of Science Publication* **1604**, 194–219.

Trotter, P.C. (1989) Coastal cutthroat trout: a life history compendium. *Trans. Am. Fish. Soc.* **118**, 463–473.

Tsiger, V.V., Skirin, V.I., Krupyanko, N.I., Kashlin, K.A. and Semenchenko, A.Y. (1994) Life history form of male masu salmon (*Oncorhynchus masou*) in South Primoré, Russia. *Can. J. Fish. Aquat. Sci.* **51**, 197–208.

Unwin, M.J., Kinnison, M.T. and Quinn, T.P. (1999) Exceptions to semelparity: Postmaturation survival, morphology, and energetics of male chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* **56**, 1172–1181.

Verspoor, E. and Cole, L.J. (1989) Genetically distinct sympatric populations of resident and anadromous Atlantic salmon, *Salmo salar*. *Can. J. Zool.* **67**, 1453–1461.

Walker, R.V., Davis, N.D. and Myers, K.W. (1992). High seas distribution of coho and chinook salmon. *In:* Proceedings of the 1992 chinook and coho workshop, Boise, Idaho, September 28–30, 1992. American Fisheries Society, Bethesda, MD, pp. 120–134.

Waples, R.S., Teel, D.J., Myers, J.M. and Marshall, A.R. (2004) Life-history divergence in chinook salmon: historic contingency and parallel evolution. *Evolution* **58**, 386–403.

Ward, R.D., Woodwark, M. and Skibinski, D.O.F. (1994) A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. *J. Fish Biol.* **44**, 213–232.

Weitkamp, L. and Neely, K. (2002) Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. *Can. J. Fish. Aquat. Sci.* **59**, 1100–1115.

Weitkamp, L.A., Wainwright, T.C., Bryant, G.J., Milner, G.B., Teel, D.J., Kope, R.G. and Waples, R.S. (1995) Status review of coho salmon from Washington, Oregon, and California. National Marine Fisheries Service, NOAA Technical Memorandum NMFS-NWFSC-24, Seattle, WA.

Wenburg, J.K. (1998) Coastal cutthroat trout (*Oncorhynchus clarki clarki*): genetic population structure, migration patterns, and life history traits. Ph.D. dissertation. University of Washington, Seattle, WA.

Wenburg, J.K. and Bentzen, P. (2001) Genetic and behavioral evidence for restricted gene flow among coastal cutthroat trout populations. *Trans. Am. Fish. Soc.* **130**, 1049–1069.

Went, A.E.J. (1964) Irish salmon – a review of investigations up to 1963. *Sci. Proc. Royal Dublin Soc., Ser. A* **1**(15), 365–412.

Withler, I.L. (1966) Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific coast of North America. *J. Fish. Res. Board Can.* **23**, 365–393.

Wood, C.C. (1995) Life history variation and population structure in sockeye salmon. *Amer. Fish. Soc. Symp.* **17**, 195–216.

Wood, C.C. and Foote, C.J. (1996) Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). *Evolution* **50**, 1265–1279.

Wood, C.C., Riddell, B.E. and Rutherford, D.T. (1987) Alternative juvenile life histories of sockeye salmon (*Oncorhynchus nerka*) and their contribution to production in the Stikine River, northern British Columbia. *Can. Sp. Publ. Fish. Aquat. Sci.* **96**, 12–24.

Zimmerman, C.E. and Reeves, G.H. (2000) Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. *Can. J. Fish. Aquat. Sci.* **57**, 2152–2162.