Chapter 7

Ocean Ecology of Steelhead

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Introduction

This chapter reviews information on the marine life history and ecology of steelhead—the ocean-migrating (anadromous) form of Rainbow Trout *Oncorhynchus mykiss*. While there are numerous scientific and common names for this species in North America and Asia (Table 1), the nomenclature in this chapter conforms to that accepted by western taxonomists. Both anadromous and freshwater resident forms of *O. mykiss* are best known as one of the world's premier species for aquaculture (predominantly resident form) and recreational fisheries (both anadromous and resident forms), and as such are very economically important. Nevertheless, most of the research on the ecology of *O. mykiss* has been conducted in freshwater habitats. In accordance with the theme of this book, however, information about the freshwater life history and ecology of Rainbow Trout is included only where needed to clarify this review.

An earlier review of the ocean ecology of steelhead by Burgner et al. (1992) includes references to most of the early scientific literature on this topic. My review, therefore, emphasizes new information published during the period 1992–2017. The chapter is divided into five major sections: (1) General Biology, (2) Migration, Distribution, and Abundance, (3) Feeding and Growth, (4) Survival, and (5) Concluding Remarks, which includes suggestions for future research on the ocean life history and ecology of steelhead.

In the ocean, the overall physical appearance of steelhead is similar to that of all other species of *Oncorhynchus*. For example, the ventral surface of the body (below the lateral line) is silvery due to guanine crystals in the skin under the scales. Nevertheless, steelhead have a more slender (compressed and elongated) body shape and a smaller head and anal fin (8–12 rays) than other Pacific salmon species (>12 anal fin rays). The posterior edge of the anal fin is vertical in steelhead, while it is slanted in other Pacific salmon species. The coloration of the dorsal surface of the steelhead body (above the lateral line) and head is typically a metallic gray-black or olive green and is covered with small black spots, in contrast to the blue or blue-green coloration in Coho Salmon *O. kisutch*, which also have small black spots on the dorsal surface of the body. The most unique physical characters that quickly distinguish steelhead from other Pacific salmon species in the ocean include the white mouth, tongue, and gums at the base of the teeth, the square shape of the caudal fin (very shallow forking), and the coloration of the caudal fin, which has radiating rows of small black spots covering the entire fin and silvery bars confined to the central portion of the fin. During the ocean life history phase, steelhead can be distinguished from anadromous Cutthroat Trout *O. clarki* by the

Table 1. Major taxonomic, phylogenetic, maturity, and migratory groups of *Oncorhynchus mykiss*.

Group	Description	Group locations	Source
Oncorhynchus mykiss, *Salmo gairdneri*, *Salmo mykiss; Parasalmo mykiss, Parasalmo penshinensis*, steelhead, steelhead trout, Kamchatka steelhead, Kamchatka mykiss. Rainbow Trout, Redband Trout, mikizha.	Taxonomic/Binomial names: *O. mykiss*: accepted by western taxonomists; *S. gairdneri* formerly used by western taxonomists, now unaccepted; *S. mykiss*, *P. mykiss*, and *P. penshinensis*, used by eastern taxonomists, are unaccepted by western taxonomists. Common names: steelhead, steelhead trout, Kamchatka steelhead used for anadromous form, Rainbow Trout and Kamchatka mykiss for resident form; Redband Trout for N. American inland form; mykiss or mikizha used in Russia for both anadromous and resident forms.	Resident and anadromous forms of *O. mykiss* are conspecifics and native to both Asia (Russia) and North America. In North America, *O. mykiss* is distributed from northern Mexico to western Alaska; redband trout are native only to the Fraser and Columbia River drainages east of the Cascade Crest. In Russia, mikizha are distributed primarily in Kamchatka. Resident forms occur in both eastern and western Kamchatka; coastal and typically anadromous forms are documented to occur only in western Kamchatka.	Savvaitova and Lebedev 1966; Savvaitova and Maksimov 1967; Savvaitova et al. 1973; Savvaitova 1975; Allendorf et al. 1980; Okazaki 1984b; Smith and Stearly 1989; Behnke 1992, 2002; Sheiko and Fedorov 2000; Pavlov et al. 2001; Chereshnev et al. 2002; Kuzishchin et al. 2002.
O. mykiss irideus, coastal; *O. mykiss gairdneri*, inland.	Phylogenetic groups: Two subspecies of *O. mykiss* proposed by Behnke (1992): coastal (*O. mykiss irideus)* and inland (*O. mykiss gairdneri)* based on differences in evolutionary development, history, and genetics; currently unaccepted.	California, Alaska, and Kamchatka have only the coastal group; Idaho has only the inland group; British Columbia, Washington, and Oregon have both inland and coastal groups; inland groups occur in tributaries of the Fraser R. (upstream from junction with Thompson R.) and Columbia R. (in and upstream from Klickitat and Deschutes rivers), east of the Cascade mountains.	Allendorf et al. 1980; Okazaki 1984b;Behnke 1992; Pavlov and Kuzishchin 1999; McCusker et al. 2000; McPhee et al. 2007.

Table 1. Continued.

Group	Description	Group locations	Source
Stream-maturing, summer, summer-run, fall, fall-run, hiemal race	Maturity group: fish not sexually mature at freshwater entry (May–October); commonly called summer steelhead; in Alaska called fall steelhead; in Kamchatka called heimel race.	Tend to spawn in upper reaches of North American streams; all Columbia R. inland steelhead are stream-maturing; in Kamchatka heimal race enters fresh water in fall with gonads at a low maturation stage and spawns in spring.	Busby et al. 1996; Pavlov et al. 2008.
Ocean-maturing, winter, winter-run, spring, spring-run, vernal race	Maturity group: fish are sexually mature at freshwater entry (November−April); commonly called winter or winter-run steelhead, except in Alaska called spring steelhead; in Russia called vernal race.	Dominant type in coastal streams of US Pacific Northwest; in Kamchatka the vernal race enters fresh water in spring right before spawning with gonads at high maturation stage.	Busby et al. 1996; Pavlov et al. 2008.
Kelt	Maturity group: a steelhead that has recently spawned or spawned more than once (repeat-spawner).	Kelts occur throughout the known geographic range of steelhead.	
Fluvial-anadromous	Migratory: Juveniles rear 1–2 (or sometimes more) summers in fresh water; smolts migrate to ocean, using the estuary only for acclimation to saltwater and as a migration corridor (also occasionally for spring-time feeding).	Southern California.	Shapavalov and Taft 1954; Smith 1990; Bond 2006; Boughton et al. 2005, 2007.
Lagoon-anadromous	Migratory: Juveniles spend 1st or 2nd summer in a seasonal lagoon at the mouth of the stream formed by a sandbar barrier between the ocean and river mouth.	Southern California.	Shapavalov and Taft 1954; Smith 1990; Bond 2006; Boughton et al. 2005, 2007.

Table 1. Continued.

Group	Description	Group locations	Source
A-run, B-run	Migratory: Designates bimodal peaks in inland steelhead runs in the Columbia River Basin, particularly the Snake River subbasin; A-run is young (ocean age 1), small size, and early (June–mid-August); B-run is older (ocean age 2), larger, and later (late August−October).	A-run spawn throughout Snake River subbasin (Idaho); B-run spawn only in Clearwater, Middle Fork Salmon, and South Fork Salmon (Idaho).	Busby et al. 1996.
Estuarine, riverine estuarine, riverine	Migratory: different in-river migratory patterns of resident forms of *O. mykiss*.	Asian and North America.	Pavlov et al. 1999; Savvaitova et al. 2005.
Half-pounders; migratory-B form	Migratory: After smoltification, half-pounders spend only 2−4 months in the ocean before returning to fresh water to overwinter; most are sexually immature and re-enter ocean in spring.	Rogue, Klamath, Mad, and Eel Rivers of southern Oregon and northern California, the California Current, and western Kamchatka (migratory-B form).	Snyder 1925; Busby et al. 1996; Pavlov et al. 1999, 2000, 2001; Behnke 2002; Savvaitova et al. 2005; Hayes et al. 2016.

lack of basibranchial teeth, which are located behind the tongue between the first and second gill clefts in Cutthroat Trout.

Oncorhynchus mykiss is an ancient species of Pacific salmon, ~6 million years old (McPhail 1996). All salmonids (members of the family Salmonidae) evolved as part of a diverse group of fishes in which diadromy (migration between fresh and marine water) is a key ancestral behavioral trait (McDowall 1993, 2002). The divergence of *Oncorhynchus* species from other salmonid fishes occurred during the late Miocene, ~8 million years ago, when formation of the cold Subarctic water mass provided cool and productive ocean conditions favorable to species diversification and range expansion of *Oncorhynchus* species (Neave 1958; Pearcy 1992). Thus, knowledge of the marine life history and ecology of *O. mykiss* is fundamental to understanding the evolution, adaptation, and survival of this species.

General Biology

Geographical Distribution and Abundance

Geographical distribution.—Steelhead and freshwater-resident forms of Rainbow Trout, henceforth collectively referred to as *O. mykiss*, are endemic to rivers tributary to the North Pacific Ocean and its adjacent seas in both Asia, specifically the Kamchatka Peninsula in the Russian Far East and western North America. On both continents, the coastal range of steelhead is less extensive than that of freshwater-resident Rainbow Trout (Figure 1).

In North America, the geographic distribution and population structure of *O. mykiss* appears to be closely related to the persistence over geological time scales of large westward-flowing rivers and inland lake systems, and the presence of ice-free refuges in western North America during periods of glacial maxima (Smith 1975; McPhail and Lindsey 1986; Minckley et al. 1986; Nielsen et al. 1994, 1998; McCusker et al. 2000; Gustafson et al. 2007; McPhee et al. 2007; Waples et al. 2001, 2008). The high genetic diversity of southern California steelhead compared to northern populations suggests that the current population structure of North American steelhead may have resulted from two Pleistocene refugia, the Gulf of California (proposed by Behnke 1992) and Beringia, and an ecotone (region of transition between populations) in southern California (Nielsen 1999). Ecotones occur in regions of divergent environmental conditions that drive genetic diversity. Thus, the hypothesis for a southern California ecotone is supported by oceanographic conditions in the California Transition Zone, located near 34°N (Point Conception, California), which is a region of steep thermal gradients (Nielsen 1999). The present geographic range of *O. mykiss* largely reflects distribution during the last glacial maximum in ice-free refuges in Alaska (Bering), British Columbia (Queen Charlotte), the Columbia River Basin (Cascadia), and California and Oregon, and postglacial recolonization over the past 10–25 thousand years.

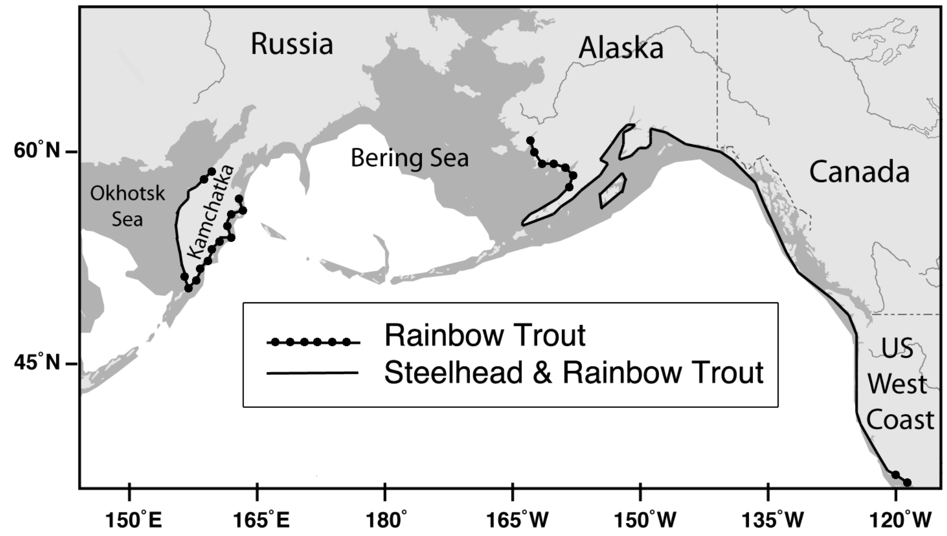

Figure 1. The endemic coastal range of steelhead and Rainbow Trout *Oncorhynchus mykiss*. Black line indicates region of overlap in coastal range of steelhead and Rainbow Trout. Dotted line indicates additional range of Rainbow Trout, which extends into northwestern Kamchatka and western Alaska (Bristol Bay northward to Kuskokwim River), and the extreme southern U.S. West Coast and northern Mexico. Not shown is the resident Rainbow Trout population on Great Shantar Island (56°54'N, 137°43'E) in the southwest Sea of Okhotsk (Augerot 2005).

In Asia, steelhead are documented to occur only in western Kamchatka Peninsula (Russia) streams tributary to the Sea of Okhotsk (Augerot 2005; Figure 1). Molecular genetic analysis suggests that Kamchatka may be the most recent region of postglacial recolonization by *O. mykiss*, via the Bering Strait after the Bering land bridge (Beringia) was submerged about 13,000–10,000 years ago (McCusker et al. 2000).

In Asia freshwater-resident forms of *O. mykiss* are much more abundant than steelhead, and their documented endemic range includes both eastern and western Kamchatka and the Great Shantar Island in the southwest Sea of Okhotsk (Augerot 2005). The current northern limit of resident *O. mykiss* forms in Asia appears to be the Ozernaya River on Kamchatka's east coast (57.5°N) and the Palana River (59.2°N) on Kamchatka's west coast (P.W. Soverel, Kamchatka Steelhead Project, personal communication, May 2013). Large spawning populations of steelhead are limited to tundra rivers and tributaries with special thermal conditions in western Kamchatka (Kuzishchin et al. 2008). Eastern Kamchatka rivers up to the Ozernaya River, however, are reported to produce small numbers of steelhead, i.e., individual fish rather than "runs" (Berg 1948; Savvaitova et al. 1973; P.W. Soverel, Kamchatka Steelhead Project, personal communication, May 2013). The documented geographic range of steelhead includes most rivers in western Kamchatka from the Opala River (52.3°N, 157.3°E) in southwestern Kamchatka to the Voyampolka River (58.1°N, 159.9°E) in northwestern Kamchatka (Savvaitova et al. 1973; Augerot 2005; McPhee et al. 2014). Previously reported regions of low steelhead abundance in Asia (Savvaitova et al. 1973; Burgner et al. 1992), i.e., the Okhotsk Sea continental coast (the Lonkovaya River near the Ola), the Amur River estuary south of the Amur River mouth (Kaganovski 1949), and possibly in the Commander Islands (Suvorov 1912) have not been verified.

In North America, *O. mykiss* are native to the Pacific and Bering slopes (regions west of the continental divide) from northwestern Mexico to the Kuskokwim River in western Alaska, and on the east slope of the continental divide of the Rocky Mountains in the headwaters of the Peace and Athabasca Rivers (Mackenzie River Basin) in Alberta, Canada (McPhail and Lindsey 1970; Behnke 2002). The documented native range of spawning steelhead currently extends from southern California (San Mateo Creek, 33.4°N, 117.6°W; NOAA 2005), northward to the upper Copper River drainage (Gulkana River, 62.2°N, 145.4°W) in southcentral Alaska (Burger et al. 1983; Wuttig et al. 2004), and westward to Russell Creek (55.2°N, 162.7°W) near Cold Bay on the southwest (Pacific Ocean side) of the Alaska Peninsula and the Sandy River (56.2°N, 160.4°W) on the north-central (Bering Sea side) of the Alaska Peninsula (Eaton and Adams 1995). The current extent of the southern range of spawning populations of steelhead is contracted from the endemic range, primarily due to human-built barriers to fish migration such as dams, culverts, and heavily engineered channels of concrete and riprap that have extirpated steelhead from at least a third of the basins in southern California where they occurred historically (Boughton et al. 2005).

In northern Mexico, the documented native range of spawning Rainbow Trout extends southward to (at least) the Rio Santa Domingo (25.5°N, 112.1°W) in Baja California and headwaters of the Sierra Madre Occidental from the Río Yaqui (27.6°N, 110.6°W) southward to (at least) the Río Culiacán (24.8°N, 107.4°W) (Needham and Gard 1959; Abadia-Cardoso et al. 2015). The disputed native range of Rainbow Trout in northern Mexico extends even further south to the Rio Presidio River in Mexico (23.1°N, 106.3°W) and perhaps Baluarte (23.3°N, 105.6°W) and Acaponeta (22.5°N, 105.4°W) river drainages (Hendrickson et al. 2002). The northern limit of the native range of Rainbow Trout in western Alaska is the Aniak River, (61.6°N, 159.5°W) in the Kuskokwim River Drainage (Alt 1986).

Abundance.—Data on abundance of steelhead are insufficient throughout most of the species range. There are no estimates of the total abundance of annual returns of adult steelhead in Kamchatka (Pavlov et al. 2007). In one tundra river system, the Utkholok River, the estimated 2007 run of adult steelhead, using a Dual-Frequency Identification sonar (DIDSON), was ~10,800 fish (Pavlov et al. 2009), an estimate considered to be far higher than what would be expected in most similar-sized (134 km) river systems in North America (P.S. Rand, Wild Salmon Center, Portland, Oregon, personal communication). Given that there are about 15–20 rivers with significant steelhead runs in western Kamchatka (Augerot 2005; P.W. Soverel, Kamchatka Steelhead Project, personal communication), a very rough estimate of recent total annual returns of adult Kamchatka steelhead is approximately 50,000–75,000 fish (P.W. Soverel, Kamchatka Steelhead Project, personal communication). The total annual abundance of adult steelhead returns in North America was roughly estimated at about 1.5–1.6 million fish (Sheppard 1972; Light 1987; see review by Burgner et al. 1992). Light (1987) estimated that about 50% of total annual adult steelhead returns to North America during 1970–1987 were wild (naturally produced) fish (Table 2). All Kamchatka steelhead are naturally produced.

In Alaska, the documented distribution of wild steelhead includes 4,202 km of rivers and streams within 353 drainages; however, many streams have not been surveyed for steelhead (Marston 2012). Most of these rivers and streams support only small populations of steelhead spawners (≤1000 adults). Annual stock assessments (adult counts) of steelhead are limited to 15 index streams (snorkel surveys in 9 streams, weir counts in 6 streams). The most productive steelhead river, the Situk River near Yakutat in northern Southeast Alaska, has annual runs that vary from 3,000–15,000 adults (Harding and Coyle 2011) and average 7,000–9,000 adults (Marston 2012). Significant steelhead runs also occur in Southcentral Alaska on Kodiak Island and the Kenai Peninsula (Cook Inlet).

Table 2. Estimated historical (1970–1987) average annual abundance of North American steelhead (hatchery and wild stocks). Source: Light 1987.

	Number of Adults (nearest 1,000)[1]		
Region	Hatchery (%)	Wild (%)	Total
Alaska	2,000 (3)	73,000 (97)	75,000
British Columbia	34,000 (15)	190,000 (85)	224,000
Coastal Washington and Puget Sound	151,000 (70)	64,000 (30)	215,000
Columbia River Basin (Wash., Oregon, Idaho)	330,000 (73)	122,000 (27)	452,000
Coastal Oregon	222,000 (67)	108,000 (33)	330,000
California[2]	60,000 (22)	215,000 (78)	275,000
Total	799,000 (51)	772,000 (49)	1,571,000

[1] Rounding to the nearest 1,000 was for convenience only, and was not intended to reflect the precision of the estimates. The figures shown could fluctuate by more than one-third from year to year. See discussion in Light 1987.

[2] Does not include age .0 fish (half-pounders).

In British Columbia spawning populations of wild steelhead are distributed in an estimated 391 watersheds that contain 423 steelhead populations (Parkinson et al. 2005). British Columbia steelhead are classified into three ecotypes based on timing of freshwater entry and migratory distance of adults: coastal winter-run (300+ stocks; generally low abundance due to small, <200 km^2, watershed size and low productivity), coastal summer-run (the rarest ecotype, probably less that 40 stocks, and some possible local extinctions), and interior summer-run stocks (~70–80 stocks; distributed in mid- and upper tributaries of large watersheds, including the Fraser, Skeena, and Nass; productivity varies with latitude) (Pollard and Beere 2012). Adult steelhead catch data are not routinely monitored and accurate escapement estimates are available only for a few stocks.

The U.S. West Coast (Washington, Oregon, Idaho, and California) steelhead are delineated as 15 distinct population segments (DPSs), established by the federal National Oceanic and Atmospheric Administration (NOAA) for consideration as “species” under the U.S. Endangered Species Act (ESA) (Table 3). There are no estimates of total annual abundance of wild populations of U.S. West Coast steelhead in the 15 DPSs, although most are in long-term decline and listed under the ESA as species of concern, threatened, or endangered. If present trends continue, the southernmost native populations of U.S. Pacific Coast (California) steelhead will likely be extinct within 50–100 years due to climate change and human effects on the aquatic environment (Katz et al. 2012).

Harvests.—Steelhead have never been commercially fished in western Kamchatka, although illegal freshwater fishing (poaching) is reported to have reduced steelhead abundance during the 1970s–1990s (Augerot 2005). A small conservation research and ecotourism (catch and release) fishery operated in western Kamchatka between 1994 and 2005 and resumed in 2010 (Berejikian and Myers 1996; http://www.wildsalmoncenter.org/pubs/kamchatka_steelhead_bib.php; http://www.wildsalmonrivers.org/). No statistical data on catch-and-release recreational or subsistence fishery catches of steelhead in Kamchatka are available.

Burgner et al. (1992) reviewed historical harvests of steelhead in North American fisheries. During the 1980s, estimated annual recreational harvests in North America ranged from approximately 235,000–449,000 steelhead, and commercial and tribal catches ranged from 91,000–275,000 steelhead (estimated total annual harvests of 331,000–449,000 steelhead).

In the 1990s and 2000s, steelhead continued to support freshwater recreational and subsistence fisheries throughout most of their geographic range, although coastwide harvest data are incomplete (Tables 4 and 5; Figure 2). In British Columbia, annual harvests by recreational fisheries were low (average 5,700 fish; Table 4), and fishing effort decreased substantially (from >100,000 to ~50,000 angler-days per year) during 1990–2010 (Pollard and Beere 2012). In general, B.C. recreational fishing effort in the 2000s focused on northern B.C. steelhead, particularly Skeena River wild summer-run stocks (catch and release, as harvest of wild steelhead in B.C. recreation fisheries is prohibited), and the ten streams in B.C. stocked with hatchery fish (Bison 2008). For example, in 2006, approximately 35% of B.C. steelhead recreational fishing effort was in the Chilliwack River, which is stocked with hatchery fish that can be harvested. Reported subsistence harvests in B.C. averaged approximately 2,000 steelhead per year (Table 5). Recreational fishing for steelhead in Alaska in the 2000s was primarily catch and release (20,000–45,000 fish per year; 1/3 of the catch from the Situk River) and recreational harvests were very low, approximately 100–700 fish per year (Table 4; Marston 2010; Harding and Coyle 2011). Although statewide subsistence harvest estimates are

Table 3. Abundance status of US West Coast populations in Washington (WA), Oregon (OR), California (CA), and Idaho (ID) is delineated as distinct population segments (DPSs) by the federal National Oceanic and Atmospheric Administration (NOAA) for consideration as “species” under the U.S. Endangered Species Act (ESA). The "endangered" category indicates a DPS that is in danger of extinction within the foreseeable future throughout all or a significant portion of its range. The "threatened" category indicates a DPS that is less legally protected than the "endangered" category, but likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range. The "species of concern" category offers no legal protection but indicates that the DPS needs to be the focus of concentrated conservation actions. Source: http://www.nwr.noaa.gov/ESA-Salmon-Listings/Salmon-Populations/Steelhead. Maps showing the locations of DPS are available at http://www.nwr.noaa.gov/ESA-Salmon-Listings/Salmon-Populations/Maps/Steelhead-ESU-Maps.cfm.

Distinct Population Segment (DPS)	River basins included in DPS	Status under ESA
Puget Sound (Washington)	Strait of Juan de Fuca, Puget Sound, and Hood Canal, WA	Threatened
Olympic Peninsula	Olympic Peninsula, WA, west of the Elwha River and south to, but not including, Grays Harbor, WA	Not Warranted
Southwest Washington	Grays Harbor, WA, Willapa Bay, WA, and Columbia River below the Cowlitz River, WA, and below Willamette River, OR	Not Warranted
Lower Columbia River	Columbia River between Cowlitz and Wind Rivers, WA, and Willamette and Hood Rivers, OR Threatened	Threatened
Upper Willamette River	Willamette River and its tributaries upstream from Willamette Falls	Threatened
Middle Columbia River	Wind River, WA and Hood River, OR upstream to include the Yakima River, WA	Threatened
Upper Columbia River	Columbia River Basin upstream from the Yakima River, WA	Threatened
Snake River Basin	Snake River Basin of southeast WA, northeast OR, and ID	Threatened
Oregon Coast	Oregon coast north of Cape Blanco, OR	Species of Concern
Klamath Mountains Province	Elk River, OR to Klamath and Trinity Rivers, CA	Not Warranted
Northern California	Redwood Creek in Humboldt County, CA south to the Gualala River	Threatened

Table 3. Continued.

Distinct Population Segment (DPS)	River basins included in DPS	Status under ESA
California Central Valley	Sacramento and San Joaquin Rivers, CA, and their tributaries	Threatened
Central California Coast	Russian River to Soquel Creek, Santa Cruz County (inclusive) and the drainages of San Francisco and San Pablo Bays, CA	Threatened
South Central California Coast	Pajaro River, Santa Cruz County to (but not including) the Santa Maria River, CA; southern boundary near Pt Conception, CA	Threatened
Southern California	Santa Maria River, CA, to the southern extent of the species range	Endangered

not routinely reported, steelhead are an important subsistence food in some areas, e.g., Prince of Wales Island, Alaska, where a household survey in the mid 1990s estimated harvests of 700 steelhead during a 3-year period (Turek 2005). In the 1990s and 2000s, due to conservation concerns commercial fisheries for steelhead in North America were phased out in most areas except Oregon and Washington, where steelhead are commercially harvested by tribal fisheries (Table 6; Figure 2). The commercial fishery for steelhead in Alaska was terminated in 1994, when state regulation prohibited the commercial sale of steelhead, although small numbers are harvested incidentally by fisheries targeting other species (Table 6).

Hatchery Production

O. mykiss has been artificially produced in North America since the late 1800s (see historical review by Wahle and Smith 1979). The primary objectives of hatchery production of steelhead are to increase harvests and catches of adult steelhead, to mitigate for losses of natural populations due to human activities such as dam and road construction, logging, and overfishing, and more recently to conserve or recover natural populations. Coastwide releases of juvenile hatchery steelhead did not exceed 5 million fish during most of the first half of the 20th century and declined during World Wars I and II years (Mahnken et al. 1998). From 1960 to 1985, estimated annual releases increased by an order of magnitude (from about 3 million to over 30 million fish), producing estimated average annual returns of 738,000 adult steelhead from 1978 to 1987 (Light 1989). From 1989–1992, steelhead production decreased by about 20%, with more than 90% of total production in the Pacific Northwest (Mahnken et al. 1998). Subsequent coastwide releases of hatchery steelhead peaked in 1993–1999 at about 30 million fish, and decreased to about 20 million fish in the 2000s (2000–2009) (Table 7; Figure 2). Steelhead hatchery programs were reduced in British Columbia largely because of their poor performance in enhancing numbers of adult steelhead available to sport fisheries,

Table 4. Recreational harvest of adult steelhead (thousands of fish), 1993–2010. Source: NPAFC (2014a). NA = data are incomplete or not available.

Year	Alaska[1]	Washington[2]	Oregon[3]	California[4]	Idaho[5]	British Columbia[6]	Total
1993	3.8	124.3	95.0	40.5	34.8	7.1	305.5
1994	2.4	124.3	71.0	52.8	21.2	7.7	279.4
1995	1.0	105.7	74.6	31.4	22.4	6.7	241.8
1996	0.4	100.4	79.4	37.7	26.2	6.2	250.3
1997	0.3	67.8	83.4	31.0	32.9	5.8	221.2
1998	0.4	60.1	64.2	20.0	28.4	6.8	179.9
1999	0.7	75.3	64.8	25.0	31.8	4.9	202.5
2000	0.4	104.9	63.4	14.0	28.9	6.5	218.1
2001	0.4	194.0	103.4	19.0	69.5	5.8	392.1
2002	0.5	136.0	119.1	27.0	90.3	3.9	376.8
2003	0.4	124.2	80.0	3.3	77.9	5.1	290.9
2004	0.4	130.6	94.8	5.9	68.6	5.2	305.5
2005	0.6	134.4	66.3	2.9	53.3	3.6	261.1
2006	0.4	93.7	94.0	3.9	51.4	3.2	246.6
2007	0.2	104.1	81.7	7.2	57.7	4.1	255.0
2008	0.3	97.4	72.9	2.8	56.9	5.0	235.3
2009	0.4	176.3	85.6	3.0	87.6	7.1	360.0
2010	0.1	127.2	99.3	3.0	97.6	7.7	334.9
Mean	0.7	115.6	82.9		52.1	5.7	275.4

[1] Alaska harvest in 1996 updated with corrected data from Alaska Department of Fish and Game.

[2] Washington harvests in 2000 and 2001 from Manning and Smith (2004).

[3] Oregon harvests (1993–2010) updated with data from the Oregon Department of Fish and Wildlife: http://www.dfw.state.or.us/resources/fishing/sportcatch.asp

[4] California 1997–2002 harvests updated with statewide estimates from Jackson (2007). The 2003–2010 harvests were updated with catch report card data (expanded statewide estimates unavailable) provided by Farhat Bajjaliya, California Department of Fish and Wildlife, Sacramento, CA (January 28, 2015). Mean value is not given because of the lack of statewide estimates for the 2003–2010 period.

[5] Idaho harvests (1993–2010) updated with data provided by Alan Byrne, Idaho Fish and Game, Boise, ID (December 2, 2014).

[6] British Columbia harvests (1993–2010) updated with data provided by Mark Beere, Fish and Wildlife Branch, BC Ministry of Forests, Lands and Natural Resource Operations, Smithers, BC (December 3, 2014). Harvests were estimated by adult run year, e.g., data for 1993 are estimates for adult run year 1993–1994.

Table 5. Subsistence harvest of steelhead (thousands of fish), 1993–2010. Source: NPAFC (2014a). NA = data are not available. Data for Washington, Oregon, and Idaho are incomplete because some harvest statistics for the Columbia River and its tributaries in these states are not available.

Year	Alaska	Washington	Oregon	California	Idaho	British Columbia	Total
1993	NA	1.89	5.94	NA	NA	1.30	9.13
1994	NA	1.68	6.80	NA	NA	3.50	11.98
1995	NA	1.68	12.50	NA	NA	1.17	15.35
1996	NA	1.79	13.48	NA	NA	1.42	16.69
1997	NA	1.24	18.76	NA	NA	0.66	20.66
1998	NA	1.46	11.89	NA	NA	2.75	16.10
1999	NA	0.66	7.92	NA	NA	4.39	12.97
2000	NA	0.84	2.66	NA	NA	3.78	7.28
2001	NA	1.68	NA	NA	NA	2.36	4.04
2002	NA	0.01	NA	NA	NA	3.59	3.60
2003	NA	0.01	NA	NA	NA	1.19	1.20
2004	NA	0.01	NA	NA	NA	2.88	2.89
2005	NA	NA	NA	NA	NA	0.01	0.01
2006	NA	NA	NA	NA	NA	NA	
2007	NA	0.69	NA	NA	2.20	0.79	3.68
2008	NA	0.51	NA	NA	2.20	2.30	5.01
2009	NA	0.02	NA	NA	NA	1.68	1.70
2010	NA	0.12	NA	NA	NA	0.01	0.13
Mean		0.89	9.99		2.2	1.99	

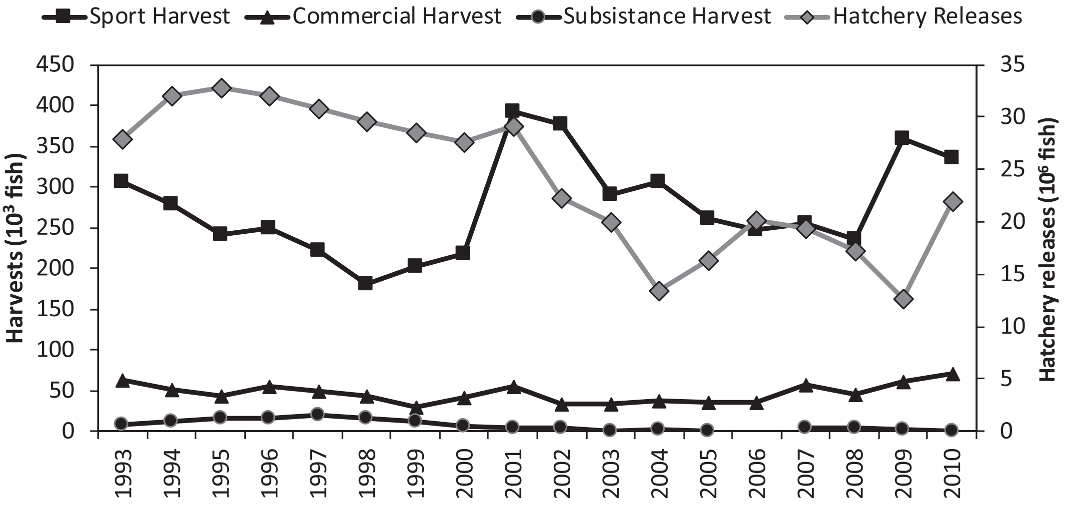

Figure 2. Trends in harvests and hatchery releases of North American steelhead, 1993–2010.

Table 6. Commercial harvest of adult steelhead (thousands of fish), 1993–2010. Source: NPAFC (2014a). NA = data are incomplete or not available.

Year	Alaska	Washington	Oregon[1]	California	Idaho	British Columbia	Total
1993	1.5	43.5	15.8	NA	NA	2.0	62.8
1994	0.8	39.0	8.9	NA	NA	2.0	50.7
1995	0.4	33.9	8.6	NA	NA	1.0	43.9
1996	0.7	52.0	1.4	NA	NA	1.0	55.1
1997	0.2	48.0	1.3	NA	NA	<0.5	49.5
1998	0.2	42.1	0.9	NA	NA	1.0	44.2
1999	0.3	28.5	0.4	NA	NA	<0.5	29.2
2000	0.2	33.7	7.8	NA	NA	<0.5	41.7
2001	0.1	54.8	0.1	NA	NA	<0.5	55.0
2002	0.1	34.5	0.1	NA	NA	<0.5	34.7
2003	0.1	33.3	0.1	NA	NA	<0.5	33.5
2004	0.3	38.0	0.4	NA	NA	<0.5	38.7
2005	0.2	35.7	0.8	NA	NA	0.0	36.7
2006	0.1	30.9	4.1	NA	NA	<0.5	35.1
2007	0.2	43.0	14.4	NA	NA	0.0	57.6
2008	0.1	37.0	8.5	NA	NA	0.0	45.6
2009	0.1	44.0	17.1	NA	NA	0.0	61.2
2010	0.1	48.6	21.4	NA	NA	0.0	70.1
Mean	0.3	40.0	6.2				45.9

[1] Oregon catches in 2001, 2005, 2006, and 2008, reported as "not available" (NPAFC 2014a), are from the NOAA Fisheries, Fisheries Statistics Division (http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index). Data were converted from metric tons to thousands of fish using an average body weight of 4.0 kg (1993–2000 NPAFC Statistical Yearbooks).

and particularly in recent years because of the lower marine survival of steelhead returning to hatchery-augmented streams compared to adjacent nonaugmented streams (Pollard and Beere 2012). The decrease in releases of U.S. hatchery steelhead in the 2000s is largely the result of hatchery reform practices to reduce potential risks of decreased fitness and survival of hatchery fish and increased predation on or competition with U.S. Endangered Species Act (ESA)-listed steelhead. In the 2000s the largest production of hatchery steelhead was in Washington State, where annual releases decreased from nearly 12 million fish in 2001 to 6.0 million fish in 2009 (Table 8). In the early 2010s, there was no hatchery steelhead production in Alaska (Marston 2012).

Life History Patterns in Freshwater and Ocean

O. mykiss exhibits a wide range of variation in freshwater and ocean life history patterns, e.g., degree of anadromy, seasonal races, adfluvial migration, freshwater residency, age structure, fecundity, run timing, and iteroparity (repeat spawning), that reflects both genetic

Table 7. Steelhead smolt production (millions of fish) by hatcheries in the 1980s (1978–1987; updated from Light 1989 and Busby et al. 1996), 1990s (1993–1999, updated from NPAFC 2014b), and 2000s (2000–2009, updated from NPAFC 2014b), listed from north to south. Sources: Alaska Department of Fish and Game, Freshwater Fisheries Society of British Columbia, Fisheries and Oceans Canada, California Department of Fish and Game, Idaho Department of Fish and Game, Oregon Department of Fish and Wildlife.

	No. of hatcheries		Average annual smolt production (millions of fish)			% of total		
Location	1980s	2000s	1980s	1990s	2000s	1980s	1990s	2000s
Alaska	4	1	0.1	0.1	<.01	0.3	0.2	0.0
British Columbia	22	10	0.5	0.6	0.5	2.6	2.9	3.1
Washington	44	60	6.8	10.9	9.1	34.7	35.6	45.7
Idaho	4	7	5.4	8.2	6.5	27.5	26.7	32.4
Oregon	26	26	4.5	5.9	1.9	23.2	19.1	9.5
California	9	8	2.3	4.8	1.9	11.8	15.5	9.2
Total	109	112	19.6	30.4	19.9	100.0	100.0	100.0

adaptation and plastic response to environmental conditions. Although variation in freshwater and ocean life history traits of *O. mykiss* might best be viewed as a continuum (e.g., Quinn and Myers 2004), scientists and fishery managers frequently classify fish with similar life history patterns into discrete groups (Table 1). These multiple life history strategies enable *O. mykiss* to adjust rapidly to new environmental conditions, providing a survival advantage over other less adaptable species.

The general life cycle and life history patterns of steelhead (Figure 3) are well known. Spawn timing (late winter and spring on rising temperature cycles) and capability for repetitive spawning are key reproductive features that distinguish steelhead from other species of Pacific salmon. Fecundity of steelhead ranges from about 2,500–10,000 eggs (average 3,500 eggs). Fry typically <30 mm fork length (FL) emerge from the gravel from late spring to midsummer. Fry and fingerlings may disperse to downstream freshwater overwintering habitats in late summer and fall. Juveniles can rear in freshwater for 1–7 years (Table 9; typically 2–3 years) before reaching a body size sufficient to smolt, which is the transitional stage between freshwater and ocean stages that occurs when fish are approximately 14–20 cm FL. Smolts enter the ocean from spring to early summer, and by midsummer juveniles (ocean age 0) are distributed in epipelagic open-ocean habitats. After their first summer at sea some juvenile steelhead called half-pounders (Table 1) may return to freshwater, where they overwinter and re-enter the ocean during the following spring. Steelhead typically spend from 1 to 3 years in the ocean before returning to freshwater to spawn for the first time. Seasonal races (spring, summer, fall, winter; Table 1) and maturation stage (immature, mature) at freshwater entry are highly variable. Typically, stream-maturing fish (often called summer or fall steelhead; Table 1) return to freshwater in May–October and overwinter in freshwater prior to spawning the following spring, whereas ocean-maturing fish (often called winter steelhead; Table 1) return in November–April and spawn shortly thereafter. Steelhead returning to the same river can include both stream-maturing and ocean-maturing races or ecotypes. Of the two distinct genetic groups of North American steelhead (coastal and inland; Table 1), the coastal

Table 8. Hatchery releases of juvenile steelhead (millions of fish), 1993–2010. Source: NPAFC 2014b. NA = data are incomplete or not available.

Year	Alaska	Washington	Oregon	California	Idaho	British Columbia	Total
1993	0.1	11.0	2.4	5.6	7.8	1.1	28.0
1994	–	9.8	6.6	6.4	8.1	1.1	32.0
1995	<0.05	10.6	6.8	5.8	8.7	0.9	32.8
1996	<0.05	10.6	6.5	5.3	8.9	0.7	32.0
1997	0.01	11.3	6.4	3.7	8.5	0.9	30.8
1998	<0.05	12.2	6.1	3.5	7.8	NA	29.6
1999	NA	11.0	6.3	3.0	7.6	0.7	28.6
2000	NA	10.9	5.8	2.4	7.9	0.6	27.6
2001	NA	11.6	5.4	3.3	8.2	0.6	29.1
2002	NA	10.0	1.4	2.2	8.0	0.7	22.3
2003	<0.01	8.4	1.3	2.1	7.5	0.7	20.0
2004	NA	8.8	0.3	0.6	3.1	0.7	13.5
2005	<0.01	8.0	1.3	1.9	4.4	0.7	16.3
2006	<0.01	9.4	1.3	1.1	7.7	0.6	20.1
2007	<0.01	9.3	1.2	2.4	6.0	0.5	19.4
2008	<0.01	8.9	0.4	1.7	5.7	0.6	17.3
2009	<0.01	6.0	0.2	0.1	5.8	0.6	12.7
2010	0.00	7.7	5.3	2.7	5.8	0.5	22.0
Mean		9.8	3.6	3.0	7.1	0.7	24.1

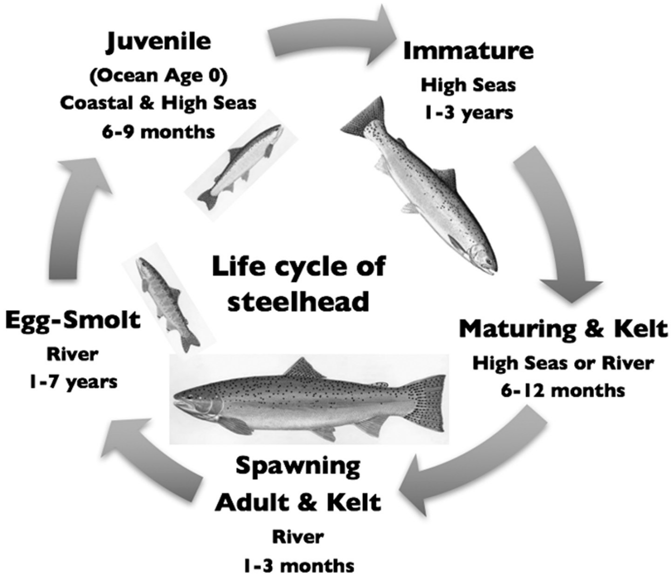

Figure 3. The life cycle of steelhead (*Oncorhynchus mykiss*).

Table 9. Smolt age frequency for selected wild steelhead populations (modal values are presented in bold). Data are from adult steelhead, except where noted otherwise. Populations are generally arranged from north to south (CA = California, Crk. = creek, I. = Island, ID = Idaho, N.F. = North Fork, M.F. = Middle Fork, OR = Oregon, R. = river, WA = Washington). Run type: S = stream-maturing, O = ocean maturing. *N* = sample size, n/a = not available, sample size not indicated in reference. U.S. West Coast populations are grouped by distinct population segment (see Table 3). Source: Updated from Busby et al. (1996) by addition of data for western Kamchatka steelhead.

Population	Run	Freshwater age							*N*	Reference
		1	2	3	4	5	6	7		
Western Kamchatka										
Snatolveyem R.	S	0.19	**0.74**	0.08	--	--	--	--	53	Savvaitova et al. 1973
Kvachina R.	S	0.01	**0.56**	0.42	0.01	--	--	--	217	Savvaitova et al. 1973
Utkholok R.	S	0.01	**0.86**	0.11	0.02	--	--	--	112	Maksimov 1972
Utka R.	S	0.22	**0.68**	0.10	--	--	--	--	68	Savvaitova et al. 1973
Bol'shaya R.	S	0.03	0.45	**0.49**	0.03	--	--	--	29	Maksimov 1976
Southcentral Alaska										
Karluk R. (Kodiak I.)	S	--	0.36	**0.63**	0.01	--	--	--	101	Sanders 1985
Anchor R. (Cook Inlet)	S	--	0.12	**0.85**	0.03	--	--	--	90	Sanders 1985
Copper R.	S	--	0.08	**0.89**	0.03	--	--	--	35	Sanders 1985
Southeast Alaska										
Situk R. (Yakutat)	S/O	--	0.13	**0.71**	0.16	--	--	--	284	Sanders 1985
Sitkoh Crk. (Chichagof I.)	O	--	0.04	**0.66**	0.30	--	--	--	656	Sanders 1985
Karta R.	O	--	0.18	**0.69**	0.13	--	--	--	808	Sanders 1985
British Columbia (mainland)										
Babine R.	S	--	0.02	**0.82**	0.15	0.01	--	--	100	Narver 1969
Cheakamus R.	O	--	0.45	**0.53**	0.02	--	--	--	64	Withler 1966
Capilano R.	O	--	0.46	**0.53**	0.01	--	--	--	70	Withler 1966
Capilano R.	S	0.01	0.16	**0.83**	--	--	--	--	86	Withler 1966
Seymour R.	O	--	0.33	**0.66**	0.02	--	--	--	58	Withler 1966
Seymour R.	S	--	0.40	**0.60**	--	--	--	--	25	Withler 1966

Table 9. Continued.

Population	Run	Freshwater age 1	2	3	4	5	6	7	*N*	Reference
British Columbia (Fraser R. Basin)										
Coquitlam R.	O	--	0.34	**0.66**	<0.01	--	--	--	146	Withler 1966
Alouette R.	O	0.08	**0.66**	<0.25	<0.01	--	--	--	131	Withler 1966
Chilliwack R.	O	0.02	**0.62**	0.36	<0.01	--	--	--	770	Maher and Larkin 1955
Chehalis R.	O	--	0.19	**0.68**	0.13	--	--	--	111	Withler 1966
Coquihalla R.	O	--	<0.28	**0.67**	0.05	--	--	--	39	Withler 1966
Coquihalla R.	S	<0.01	0.18	**0.75**	0.06	--	--	--	150	Withler 1966
British Columbia (Vancouver I.)										
Keogh R.	O	--	0.30	**0.60**	0.10	--	--	--	1,391	Ward and Slaney 1988
Nanaimo R.	?	--	**0.64**	0.35	0.01	--	--	--	228	Narver and Withler 1974
Nahmint R.	S	--	<0.21	**0.78**	0.02	--	--	--	58	Narver 1974
Puget Sound, WA										
Skagit R.	O	<0.01	**0.82**	0.18	<0.01	--	--	--	n/a	WDFW 1994
Deer Creek	S	--	**0.95**	0.05	--	--	--	--	n/a	WDF et al. 1993
Snohomish R.	O	0.01	**0.84**	0.15	<0.01	--	--	--	n/a	WDFW 1994
Green R.	O	0.16	**0.75**	0.09	--	--	--	--	100	Pautzke and Meigs 1941
Puyallup R.	O	0.05	**0.89**	0.06	--	--	--	--	n/a	WDFW 1994
Nisqually R.	O	0.19	**0.80**	0.01	--	--	--	--	n/a	WDFW 1994
Olympic Peninsula, WA										
Quillayute R.	O	0.03	**0.87**	0.10	<0.01	--	--	--	n/a	WDFW 1994
Hoh R.	O	0.03	**0.91**	0.06	--	--	--	--	n/a	Larson and Ward 1954
Chehalis R.	O	0.10	**0.88**	0.02	--	--	--	--	n/a	Larson and Ward 1954
Lower Columbia River										
Toutle R. (WA)	O	--	**0.86**	0.14	--	--	--	--	37	Howell et al. 1985
Cowlitz R. (WA)	O	--	**0.91**	0.09	--	--	--	--	56	Howell et al. 1985
Kalama R. (WA)	O	--	**0.87**	0.13	<0.01	--	--	--	1,363	Howell et al. 1985
Kalama R. (WA)	S	--	**0.89**	0.11	--	--	--	--	909	Howell et al. 1985
Washougal R. (WA)	S	--	**1.00**	--	--	--	--	--	7	Howell et al. 1985
Willamette R. (OR)	O	--	**0.92**	0.08	--	--	--	--	141	Howell et al. 1985
Wind River (WA)	S	0.05	**0.90**	0.05	--	--	--	--	19	Howell et al. 1985

Table 9. Continued.

Population	Run	Freshwater age							*N*	Reference
		1	2	3	4	5	6	7		
Middle Columbia River										
Klickitat R. (WA)	S	--	**0.94**	0.06	--	--	--	--	148	Howell et al. 1985
Deschutes R. (OR)	S	<0.29	**0.55**	0.14	0.02	--	--	--	100	Howell et al. 1985
John Day R. (OR)	S	--	**0.62**	0.38	--	--	--	--	112	Howell et al. 1985
Yakima R. (WA)	S	0.04	**0.91**	0.04	0.01	--	--	--	64	BPA 1992
Rock Island Dam (WA; RM 453.4)		0.70	43.20	**46.40**	8.60	0.80	0.10	0.10	722	Pevan et al. 1994
Rocky Reach Dam (WA; RM 473)		2.00	**45.40**	41.40	10.40	0.80	--	--	249	Pevan et al. 1994
Upper Columbia River										
Wenatchee R. (WA)	S	--	**0.76**	<0.24	--	--	--	--	17	Howell et al. 1985
Entiat R. (WA)	S	--	**1.00**	--	--	--	--	--	8	Howell et al. 1985
above Wells Dam (RM 515.8)	S	--	**0.57**	0.33	0.08	<0.01	--	<0.01	349	Mullan et al. 1992
Snake River Basin										
Lower Granite Dam (WA; Snake RM 107.5)	S	0.04	**0.62**	0.34	--	--	--	--	100	Hassemer 1992
Clearwater R. (ID)	S	<0.27	**0.59**	0.14	--	--	--	--	510	Whitt 1954
S. F. Salmon R. (ID)	S	--	0.31	**0.69**	--	--	--	--	65	BPA 1992
Lemhi River (ID)	S	--	**1.00**	--	--	--	--	--	353	BPA 1992
Oregon Coast						--				
Nehalem R.	O	0.05	**0.88**	0.07	--	--	--	--	310	Weber and Knispel 1977
Alsea R.	O	0.01	**0.80**	0.18	<0.01	--	--	--	978	Chapman 1958
Siuslaw R.	O	--	**0.83**	0.17	--	--	--	--	125	Lindsay et al. 1991
Rogue R.	O	0.09	**0.66**	<0.23	0.02	--	--	--	547	ODFW 1990
Klamath Mountains Province, CA										
Klamath R.	S	<0.27	**0.65**	0.08	--	--	--	--	391	Kesner and Barnhart 1972
N. F. Trinity R.	S	0.02	**0.95**	0.02	--	--	--	--	41	Freese 1982

Table 9. Continued.

Population	Run	Freshwater age							*N*	Reference
		1	2	3	4	5	6	7		
Northern California										
Mad R.	O	--	**0.97**	0.03	--	--	--	--	35	Forsgren 1979
Jacoby Creek	O	0.11	**0.78**	0.11	--	--	--	--	109	Harper 1980
Van Duzen R.	S	**1.00**	--	--	--	--	--	--	58	Puckett 1975
M. F. Eel R.	S	0.04	**0.79**	0.17	--	--	--	--	82	Puckett 1975
Central California Coast										
Waddell Creek	O	0.10	**0.69**	0.19	0.02	--	--	--	3,888	Shapovalov & Taft 1954
California Central Valley										
Sacramento R.	O	0.32	**0.69**	--	--	--	--	--	83	Hallock 1989

group includes both stream- and ocean-maturing fish and all inland steelhead are stream maturing. In contrast to salmon, spawning female steelhead do not guard the completed redd (nest). Female and male kelts (steelhead that have recently spawned; Table 1) may die after spawning, spend several months feeding in freshwater before returning to the ocean, or migrate to ocean feeding grounds immediately after spawning. Steelhead may spawn 1–5 times (typically 1 or 2 times) during their lifetime, typically either repeat spawning in consecutive years or skipping a year (skip spawning). Male steelhead are capable of early (precocious) maturation in freshwater as parr (life stage between fry and smolt). Breeding experiments indicate that smolting and precocious male maturation of steelhead are negatively genetically correlated (Thrower et al. 2004). Environmental factors such as water temperature that influence condition (higher growth and lipid storage) of individual fish also appear to play a key role in precocious maturation of male steelhead (McMillan et al. 2012). Precocious male parr can successfully mate with mature female steelhead, as indicated by genetic parentage analysis (e.g., Seamons et al. 2004).

Relevant New Information on Freshwater Trout Ecology

Anadromy and freshwater residency in *O. mykiss* reflects interactions among genetics, individual fish condition, and the environment (see review by Kendall et al. 2015). The co-occurrence of spawning populations of resident Rainbow Trout and steelhead in freshwater is well known. In some streams, resident and anadromous forms of *O. mykiss* interbreed, and progeny can include both forms (e.g., Pavlov and Savvaitova 2008; Christie et al. 2011; Courter et al. 2013; Sloat and Reeves 2014). The lack of reproductive isolation between anadromous and resident forms indicates the important role of the freshwater environment in the expression of life history diversity in *O. mykiss* (Table 10; McPhee et al. 2007). Environmental variation and homing to specific spawning grounds combine to produce a broad range of local phenotypic adaptations. Conserved haplotypes (a set of alleles inherited by an individual from a single parent) can control parallel adaptation of geographically distant *O. mykiss* populations, e.g., development rate of embryos in response to temperature (Miller et al. 2012). Expression of anadromy in *O. mykiss* in the John Day River watershed, Oregon, appears to be driven by environmental variation, e.g., ecological and physical processes related to stream size, at a range of spatial and temporal scales (Mills et al. 2012). In Kamchatka, proportions of resident versus anadromous life strategies may be regulated by the ratio of suitable spawning area to feeding area and stream productivity (Pavlov et al. 2008). Thermal conditions for successful steelhead reproduction in Kamchatka are found only in tundra rivers and tributaries, and include rapid warming of water in May (water temperature 4.5–4.8°C) and a sufficient sum of degree-days (over 500) from mid May to mid July (Kuzishchin et al. 2008). The short-term extinction risk (i.e., risk of extinction in 10 or fewer years) of steelhead might be mitigated by reproductive contributions from resident trout (Good et al. 2005), leading to the view that interbreeding trout and steelhead should be managed as a single population rather than as separate populations (e.g., McPhee et al. 2007). Interbreeding between steelhead and resident trout can buffer the genetic impact of fluctuating anadromous run size on effective population size per generation (Araki et al. 2007). Courter et al. (2013) were the first to successfully quantify steelhead production rates from female resident Rainbow Trout in a large watershed using otolith microchemistry (20% in 2010 and 7%

Table 10. Summary of studies comparing reproductive isolation between sympatric anadromous and resident *O. mykiss*. Source: Updated from McPhee et al. 2007.

Location	Description	Data type	Reproductive isolation	Reference
Kamchatka Peninsula Russia	No within-drainage divergence detected. Isolation by distance evident among populations sampled over 1200 km range.	Microsatellite (10 loci)	No	McPhee et al. 2007
Krasnaya River, Nilkinka River (Kol River tributaries) Kamchatka Russia	Joint spawning of anadromous and resident forms	Observation	No	Kuzishchin et al. 2007, 2008
Copper River Alaska	Indistinguishable within 2 locations, differ significantly between 2 locations	Microsatellite (13 loci)	No	Olsen et al. 2006
British Columbia Canada	MtDNA showed significant difference in only one (Meziadin) of five rivers; all nuclear comparisons non-significant	mtDNA (ND3, D-loop), Nuclear GH2D (3,4GATT)	Yes? (mtDNA), No (nuclear)	Docker and Heath 2003
Snow Creek Washington	Genetic parentage analysis provided indirect evidence that resident mature male steelhead parr successfully mated with anadromous female steelhead	Microsatellite (12 loci)	No	Seamons et al. 2004
Quileute River Washington	Visual evidence of mating behavior during late spawning season between wild resident males and steelhead females in all reaches studied	Observation	No	McMillan et al. 2007
Klikitat River Washington	Heterozygosity of resident and anadromous life history types limited at high elevation sites; high stream gradients and barriers limited anadromous distribution to lower elevation sites	Microsatellite (13 loci)	Yes & No	Narum et al. 2008b

Table 10. Continued.

Location	Description	Data type	Reproductive isolation	Reference
Yakima River Washington	Visual evidence of anadromous and resident interbreeding consistent with allele frequencies of progeny collected in same reaches	Observation, Allozyme (22 loci)	No	Pearsons et al. 2007
Walla Walla River Washington	Genetic divergence of resident and anadromous populations in mainstem, but not in one tributary (Touchet R.). Mainstem differences may reflect out-of-basin stocking.	Microsatellite (6 loci)	Yes & No	Narum et al. 2004
Hood River Oregon	High levels of reproductive contribution of nonanadromous parents to anadromous offspring when anadromous run size is small, suggesting a genetic compensation between life-history forms	Microsatellite (8 loci)	No	Araki et al. 2007
Hood River Oregon	A 3-generation genetic pedigree analysis provided indirect evidence that anadromous steelhead mate with residualized hatchery steelhead and resident Rainbow Trout	Microsatellite (8 loci)	No	Christie et al. 2011
Deschutes River Oregon	Resident female parentage (low ratios) dominated in mainstem progeny steelhead (high ratios dominated below falls and in tributaries)	Otolith SR:Ca ratios	Yes? (female parent) & No	Zimmerman and Reeves 2000, 2002

in 2011), and concluded that production of cross-life history forms may be critical to persistence of anadromy in areas where abundance of steelhead is low. Steelhead conservation and management programs need to incorporate information on the genetic contributions of wild resident Rainbow Trout to endangered steelhead populations (Christie et al. 2011). Furthermore, the role of oceanic environmental drivers of anadromy and extinction risk, e.g., ocean temperature, needs to be recognized and evaluated.

Migration, Distribution, and Abundance

Timing of Entry into Seawater

Entry of juvenile steelhead into seawater is preceded by parr-to-smolt transformation (smoltification) that is characterized by major physiological, morphological, and behavioral changes (e.g., Zaugg and Wagner 1973; McCormick 2013). Smoltification is influenced by environmental rearing conditions, particularly water temperature and growth. For example, juvenile steelhead from different populations reared in common environments grew faster and smolted earlier in warmer water temperatures than in cooler temperatures (Doctor et al.

2014). High freshwater temperatures (>12°C) can inhibit or reverse smoltification in steelhead (Zaugg and Wagner 1973; Adams et al. 1975; Hoar 1988; see review by Richter and Kolmes 2005). Steelhead growth rates or body size (average smolt fork length of ~16 cm, range 12.5–22.5 cm) are more important determinants of timing of seaward migration than age (e.g., see review by Burgner et al. 1992). Body size may be a proxy for physiological readiness of smolts to migrate seaward. For example, in central California, early steelhead migrants are larger smolts that move directly to the ocean in February–April, while later migrants are smaller fish that move to the estuary in May–June, where they may rear for several months before entering the ocean or moving back upstream to overwinter in freshwater, entering the ocean as larger smolts the following spring (Hayes et al. 2011; Hayes and Kocik 2014). There appears to be a strong genetic influence on smolt transformation in steelhead, but resident and anadromous life history strategies are not fixed phenotypes (Hayes et al. 2012b). For hatchery steelhead, freshwater residualism and low survival rates may result from early (non-volitional) release of steelhead presmolts or parr (e.g., see review by California HSRG 2012; Sandstrom et al. 2013a; Tatara et al. 2017).

Timing of entry of steelhead smolts into seawater is an important adaptive trait related to juvenile-to-adult survival (Scheuerell et al. 2009; Moore et al. 2010b). Timing is diverse (mid-March to mid-July; peak mid-April to mid-May), and is associated with key environmental factors, for example, peak spring river flows (Burgner et al. 1992). For example, in Alaska steelhead smolts enter saltwater during March through June, usually corresponding with high spring flows caused by melting snow (Lohr and Bryant 1999). In the Columbia River, steelhead smolts move rapidly through the estuary during periods of peak river flows in spring, using the main river channel as a migratory pathway (Ledgerwood et al. 1991; Weitkamp et al. 2012; see review by Weitkamp et al. 2014). Juvenile-to-adult survival of Columbia River Basin (Snake River) steelhead migrating in early to mid May was 4–50 times greater than that of mid-June migrants (Scheuerell et al. 2009). In a small coastal stream (Alsea River) in northwest Oregon, acoustic tracking of hatchery- and naturally-reared steelhead smolts showed highly variable migratory timing and low survival (<50%) to the lower estuary for all release groups, and the degree of hatchery domestication and rearing environment (concrete raceway versus natural stream) did not significantly influence rate of downstream movement or residence time within the estuary (Johnson et al. 2010). A subsequent acoustic tracking study in two small northwest Oregon coastal streams (Alsea River and Nehalem River) also showed low survival (40–50%) of wild steelhead smolts, and for most release groups survival was negatively correlated with stream flow and not correlated with fork length of smolts (Romer et al. 2012). In addition, most smolt mortality occurred in the lower estuary near the ocean despite a very short estuarine residence time, typically less than 1 d (Romer et al. 2012). In a central California coastal stream, archival tag data indicate that steelhead (Scott Creek population) time their smolt out-migration to a narrow temperature window between February and April (Hayes et al. 2011), when ocean entry conditions are suitable for survival. In central and southern California streams, before ocean entry steelhead smolts may rear for extended periods at the mouths of streams in lagoons, formed by a sandbar barrier between the ocean and river mouth (see lagoon-anadromous, Table 1). The Scott Creek, California, population adopts a mixed-habitat use strategy, whereby some smolts enter coastal marine waters when winter storms reconnect the estuary to the ocean, and others rear in the estuary for the summer and then move upstream in the fall to spend an additional winter in freshwater (Hayes et al. 2011).

In an intermittently-closed estuary in Northern California (Russian River), the movements of juvenile steelhead tagged with temperature sensor-encoded acoustic tags indicated that when the inlet to the ocean is temporarily closed by barrier beach formation juvenile steelhead relocate and aggregate near coldwater refugia in the lagoon (Matsubu et al. 2017). Relatively little is known about the physiological and behaviorial adaptations of steelhead smolts to dynamic habitat changes in nearshore and open ocean habitats, and this an important topic for future research.

Age-specific movements of juvenile steelhead between freshwater and ocean habitats have been correctly predicted by theoretical and computational state-dependent life history models at the population level (Mangel and Satterthwaite 2008; Satterthwaite et al. 2009, 2010) and individual-fish level (Satterthwaite et al. 2012). These models indicate that much of the variation in steelhead age and timing at ocean entry can be explained by a mortality-growth tradeoff. Mixed habitat use (freshwater versus ocean) by juveniles of the same state (body length) may result from density-dependent reduction in growth rates (Satterthwaite et al. 2012).

Ocean Distribution and Abundance of Juvenile, Immature, and Mature Fish

Information on the ocean distribution and abundance of steelhead is based primarily on commercial and research vessel catch and effort data (e.g., Sutherland 1973; Okazaki 1983, 1985; Hartt and Dell 1986; Pearcy et al. 1990; Burgner et al. 1992; Welch et al. 1998; Kovalenko and Shubin 2000; Brodeur et al. 2003, 2004; Kovalenko et al. 2003, 2005). Composite analyses of these data show that distribution of steelhead extends across the entire subarctic North Pacific (north of 38°N) from the North American coastline to at least 150°E, including portions of the Sea of Okhotsk and Bering Sea (Figure 4). Throughout this extensive oceanic range, steelhead are sparsely distributed, and abundance in research catches is usually low compared to other species of Pacific salmon, excepting Chinook Salmon (e.g., Myers et al. 1993). Within this broad range, steelhead distribution varies substantially by ocean age and maturity group (Figures 5 and 6). In general, steelhead abundance is highest in the Gulf of Alaska and eastern North Pacific, lower in the central North Pacific Ocean, and lowest in the western North Pacific Ocean, western Aleutian Islands, and western and central Bering Sea (Sutherland 1973; Burgner et al. 1992; Welch et al. 1998).

High seas research vessel data for juvenile (ocean age-0) steelhead are insufficient to describe distribution, particularly in late autumn and winter. Autumn-winter movements must be extensive, however, because by the following spring the distribution of ocean age-1 steelhead (by convention all fish become one year older on January 1) extends across the North Pacific (125°W–155°E), and has shifted southward—generally south of 52°N in the Gulf of Alaska and south of 48°N in the central North Pacific (Burgner et al. 1992). Despite relatively extensive research vessel sampling with fine-mesh nets, there are no reported catches of juvenile steelhead in the Bering Sea and Aleutian Islands region (Figure 5). Nevertheless, North Alaska Peninsula streams tributary to the southeastern Bering Sea host small populations of steelhead, and the early-ocean distribution and life history of these populations in the Bering Sea has yet to be investigated.

The high seas distribution of immature (ocean age-1 and older) steelhead is more extensive than that of juvenile (ocean age 0) steelhead (Figures 5 and 6). The overall seasonal patterns of distribution among all age groups are similar, however, ocean age-1 steelhead are typically the most abundant age-group in high seas time-area strata, and have the most

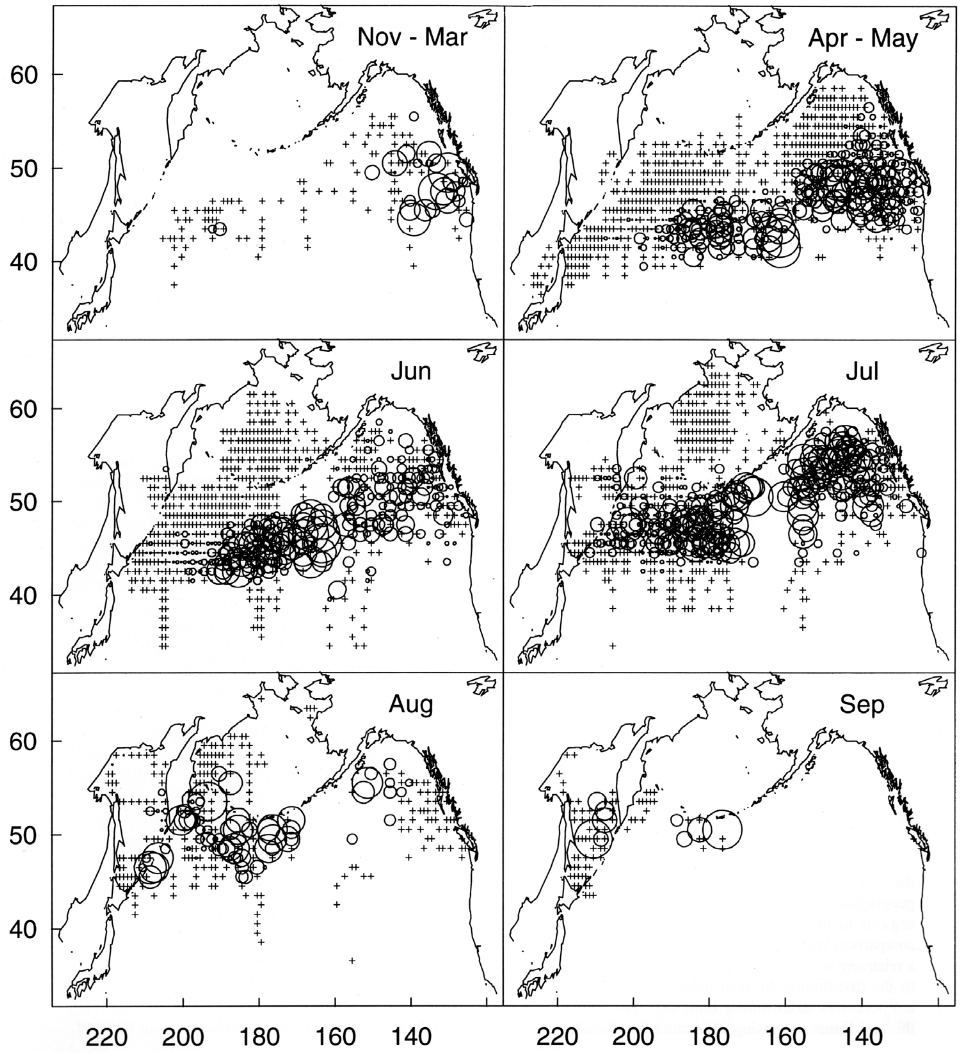

Figure 4. Relative abundance and distribution of steelhead (all age and maturity groups combined) in winter (November–March), spring (April–May), and summer months (June, July, August, and September), 1956–1996. Source: Welch et al. 1998. A "+" indicates no catch. An open circle is used to indicate relative abundance, i.e., catch-per-unit effort (CPUE), and circle radius is proportional to $\log_{10}$ (CPUE). Data were averaged over 1°-latitude by 1°-longitude statistical areas. Data comprise all available observations (*N* = 20,397) from Canadian longline (and some similar U.S. sampling) and gillnet surveys during the 1950s and 1960s, Canadian longline, gillnet, and surface rope trawl surveys during the 1980s and 1990s, and Japanese (1972–1996) research vessels surveys (gillnets and longlines). Individual observations were first normalized by dividing the average annual catch for each sampling gear in order to remove effects due to interannual variations in abundance and gear type.

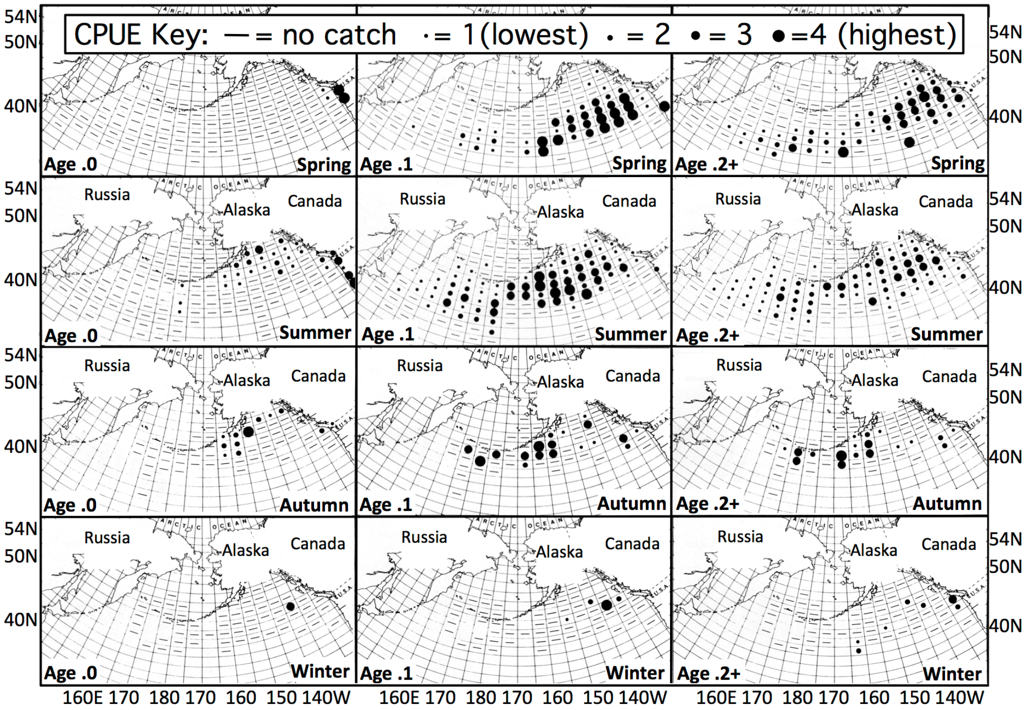

Figure 5. Abundance and distribution of juvenile (ocean age .0), ocean age .1, and ocean age .2 or older (ocean age .2+) steelhead in spring (March–May), summer (June–August), autumn (September–November), and winter (December–February) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955–1985) and Japanese (1981–1985) research vessels fishing with purse seines, gillnets, and longlines (Source: Burgner et al. 1992). Seasonal catch and effort data were stratified by International North Pacific Fisheries Commission 2°-latitude by 5°-longitude statistical areas. To account for differences in efficiency and selectivity of each gear type, four CPUE ranks from 1 (lowest CPUE) to 4 (highest CPUE) were calculated for each gear type and then averaged for all gear types fished in each season-area strata to produce a single weighted average for each time-area combination.

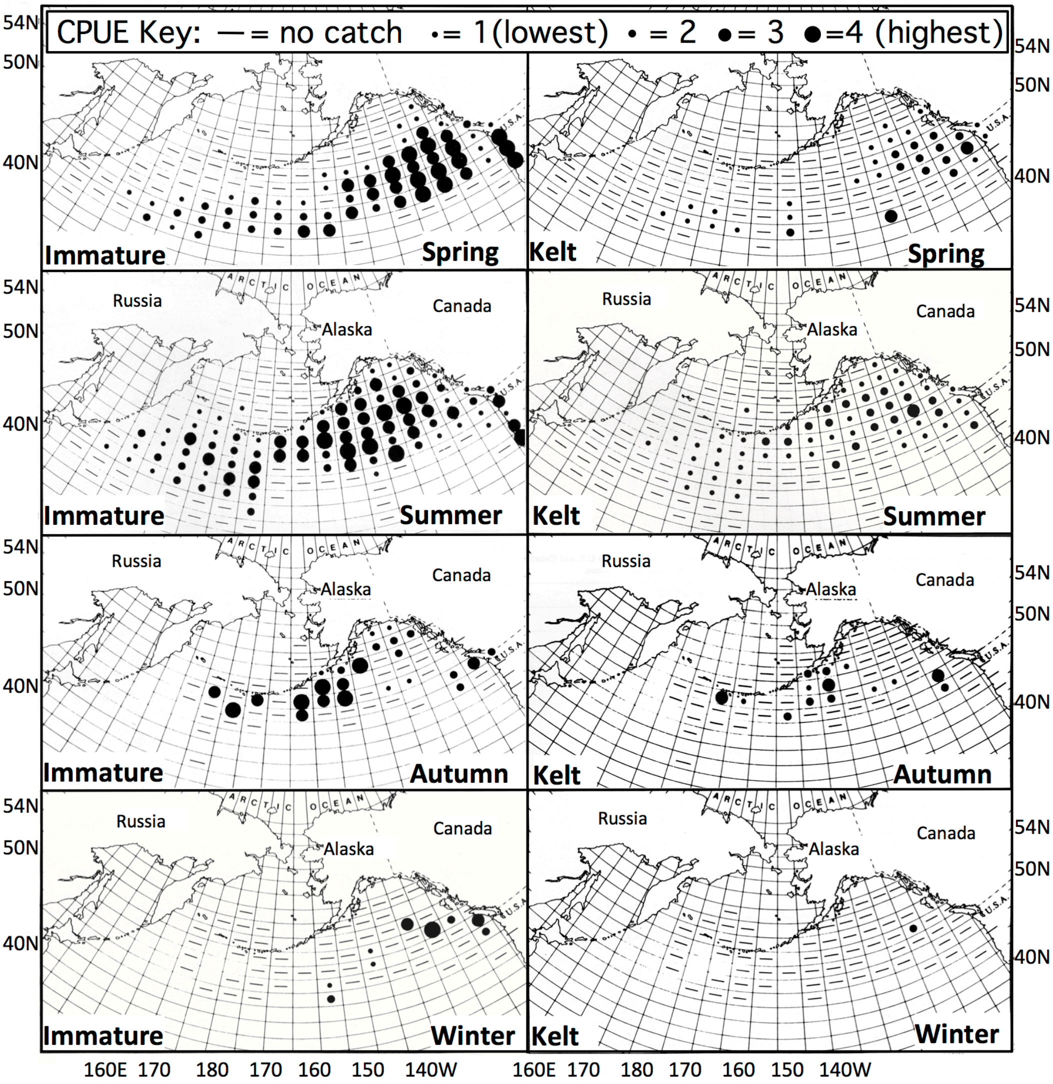

Figure 6. Abundance and distribution of immature and mature (kelt) steelhead in spring (March–May), summer (June–August), autumn (September–November), and winter (December–February) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955–1985), U.S.S.R. (1983–1985) and Japanese (1981–1985) research vessels fishing with purse seines, gillnets, and longlines (Source: Burgner et al. 1992). Seasonal catch and effort data were stratified by International North Pacific Fisheries Commission 2°-latitude by 5°-longitude statistical areas. To account for differences in efficiency and selectivity of each gear type, four CPUE ranks from 1 (lowest CPUE) to 4 (highest CPUE) were calculated for each gear type and then averaged for all gear types fished in each season-area strata to produce a single weighted average for each time-area combination.

extensive westward distribution. During early spring immature steelhead are concentrated near the southern limit of their range in the North Pacific Ocean, between 42°N and 52°N latitude (Figures 5 and 6) (Burgner et al. 1992). During summer, distribution extends northward and westward, while remaining largely south of the Aleutian Islands (Hartt and Dell 1986; Burgner et al. 1992; Welch et al. 1998), and by July and August, steelhead are distributed as far west as North Pacific waters off the southern Kuril Islands, Russia (Figure 7) (Kovalenko et al. 2003, 2005). In the vicinity of the Kuril Islands, approximately 75% of small-sized (<66 cm) and 50% of large-sized (>66 cm) male and female steelhead were immature (Kovalenko et al. 2003, 2005). Relatively little is known about late autumn and winter migrations of immature steelhead in the open ocean, due to the difficulty of conducting field surveys during those seasons when large storms cross the North Pacific (Welch et al. 1998). Mature (kelt or postspawning steelhead) are less abundant and have a less extensive ocean distribution than immature steelhead (Figure 6; Burgner et al. 1992).

Composite estimates of relative abundance of all age and maturity groups of steelhead from five decades of high-seas salmon research vessel sampling indicate that steelhead make extensive seasonal migrations across broad fronts in the North Pacific Ocean—moving to the north and west in spring through summer and to the south and east from autumn through winter (Sutherland 1973; Okazaki 1985; Burgner et al. 1992; Welch et al. 1998). The observed directional pattern of broad-scale seasonal movements appears to reflect an innate oriented swimming response to magnetic fields (see below—Migration behavior and mechanism, *Orientation*). The directions of seasonal migrations of steelhead are similar to those of other more abundant species of Pacific salmon such as Pink (*O. gorbuscha*), Chum (*O. keta*), and

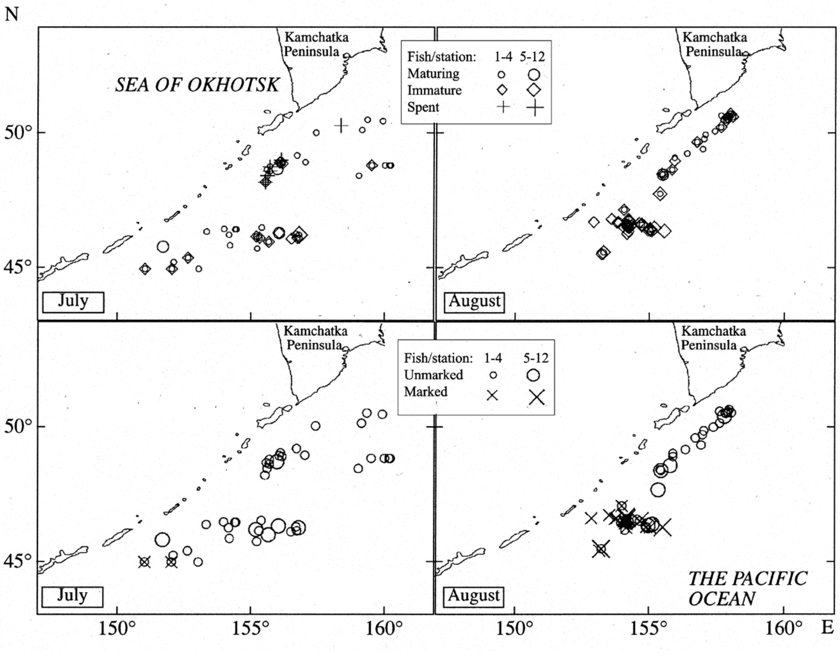

Figure 7. Distribution and relative abundance (catch in research gillnets, number of fish per station) of maturing, immature, and spent (kelt) steelhead (top panels) and unmarked and marked steelhead (bottom panels) in July and August 2001 in the Russian Exclusive Economic Zone (EEZ) in the western North Pacific and southern Okhotsk Sea (Kovalenko et al. 2005).

Sockeye (*O. nerka*) salmon (e.g., Myers et al. 2007). In winter and spring, steelhead distribution is most concentrated in areas well to the south of the Commander-Aleutian Islands chain and far to the east of the Kuril Islands chain (Figure 4). Although research vessel survey data are limited, abundance in winter and spring appears to be highest in eastern and central regions of the subarctic North Pacific near the southern limit of steelhead distribution. In summer and autumn steelhead distribution shifts to the north and west, and abundance is highest in the northwestern Gulf of Alaska, central North Pacific near the Aleutian Islands chain, western North Pacific near the Kuril Islands chain, southwestern Bering Sea off the eastern Kamchatka Peninsula and Commander Islands, and southeastern Sea of Okhotsk near the western Kamchatka Peninsula (Figure 4).

Seasonal Migration Model of Major Stocks

Kamchatka steelhead include anadromous forms that migrate to the North Pacific Ocean, as well as coastal and half-pounder (sometimes called migratory-B form) steelhead that may remain for their entire ocean life in the Okhotsk Sea (Table 1). There are no stock-specific data on the early ocean distribution and abundance of juvenile (ocean age-0) Kamchatka steelhead, and this is an important topic for future research. Kovalenko et al. (2003, 2005) suggested a seasonal migration model for Kamchatka steelhead related to sea surface temperature (SST). According to this model, in winter (November–March) Kamchatka steelhead distribution is limited by the 5–10°C area of the northeastern North Pacific Ocean. In April, Kamchatka steelhead start migrating westward towards the Asian continent. In May they reach 160°E, but only in the area south of 45°N. In late June, maturing Kamchatka steelhead start to move into the Russian Exclusive Economic Zone, i.e., the 200-mi zone near the North Pacific side of the Kuril Islands, where they migrate northward following the 6°C isotherm. Maturing Kamchatka steelhead feed in the western North Pacific Ocean and Okhotsk Sea for 2 months before entering western Kamchatka rivers in September. Immature Kamchatka steelhead enter the Russian Exclusive Economic Zone later than maturing fish, during second half July when SSTs are higher, and are the dominant maturity group of steelhead by the second half of August. During summer, immature steelhead (including North American stocks) occur in low abundance in the Russian Exclusive Economic Zone from the southern Kuril Islands to southern Kamchatka, and enter the Okhotsk Sea and southwestern Bering Sea (e.g., Myers et al. 1990, 1993; Welch et al. 1998) (Figure 4). All immature steelhead return to overwintering areas located far to the east of the Kuril Islands in the central and eastern North Pacific Ocean (Kovalenko et al. 2003, 2005).

In North America, most coastal field investigations of juvenile (ocean age-0) steelhead have emphasized spring and summer (April–September) research in waters off the U.S. West Coast, mainly within 200 km from the shoreline (Brodeur et al. 2003). The timing and extent of migration of juvenile steelhead in U.S. West Coast waters is diverse. Catches of juvenile steelhead in research vessel surveys off Oregon and Washington during springs and summers, 1981–1985, were generally low and decreased from May to August, and no juvenile steelhead were present in September, indicating they had already migrated out of coastal waters (Pearcy and Fisher 1990). The highest relative abundances of juvenile steelhead occurred offshore (27.8 or 37.1 km) of the mouth of the Columbia River (46°15’N), a major source of steelhead (Pearcy and Fisher 1990). Coded-wire tag and genetic data (incomplete baseline) indicate that steelhead populations originating from California rivers north of San Francisco Bay and southern coastal Oregon rivers south of Cape Blanco, Oregon (42°50’N, 124°33’W) reside in the coastal zone off northern California and southern Oregon during their entire ocean life (Pearcy et al. 1990; Brodeur et al. 2004). However, only a few juvenile steelhead (typically <30 cm) were captured during 10 years of central California coastal research surveys focusing on juvenile Chinook Salmon (MacFarlane, unpublished data, as cited by Hayes et al. 2012a). A reconstruction of the early ocean (3-months) migration route of a Central California juvenile steelhead, as determined by archival tag and remote sensing (satellite) temperature data, suggested rapid northwestward migration to an oceanic region between Vancouver Island and Southeast Alaska and far offshore into the Gulf of Alaska (Hayes et al. 2013). In addition, a few historical recoveries of high-seas tagged southcentral, central, and northern California steelhead (n = 9; tagged between 45 and 54°N latitude, west to approximately 160°W longitude) show that at least some California steelhead migrate far offshore into the Gulf of Alaska during juvenile and subsequent life history stages (Myers et al. 1996).

Research surveys off the Oregon and Washington coasts indicate that juvenile steelhead from rivers north of Cape Blanco, Oregon, migrate offshore (~30–50 km) and northward shortly after ocean entrance during May to August, and by September most fish have migrated far offshore (Pearcy et al. 1990; Brodeur et al. 2003, 2004; Daly et al. 2014). Juvenile Columbia River steelhead migrate northward and farther offshore than most juvenile Chinook and Coho Salmon from the Oregon-Washington region (Miller et al. 1983; Brodeur et al. 2004). A few coded-wire tagged juvenile steelhead released from lower Columbia River, Snake River Basin, Olympic Peninsula, and Vancouver Island hatcheries in spring were recovered in July in the eastern North Pacific and Gulf of Alaska during cooperative Japan–U.S. tagging programs (Pearcy and Masuda 1982, 1987; Myers et al. 2001). The CWT recovery data, however, are insufficient to estimate exact timing and migration routes of juvenile steelhead to the high seas (Brodeur et al. 2003).

Overall, the high seas migrations of North American juvenile (ocean age-0) steelhead are more extensive than those of any other juvenile salmonid species (Brodeur et al. 2003). Research vessel surveys indicate that juvenile steelhead begin leaving nearshore waters over the continental shelf of North America soon after entering saltwater in the spring (Hartt 1980; Hartt and Dell 1986). Some juvenile steelhead move to the high seas as early as June, and spend their first summer–fall in the northeastern North Pacific Ocean and Gulf of Alaska (Pearcy and Masuda 1982, 1987; Hartt and Dell 1986; Burgner et al. 1992; Myers et al. 2001). Most juvenile steelhead from North America probably remain in the Gulf of Alaska throughout their first summer and fall, although the known westward range of juvenile steelhead in summer extends to 180° longitude in the central North Pacific Ocean (Figure 5) (Burgner et al. 1992).

Information on the open-ocean distribution North American steelhead has been obtained primarily by tagging studies (e.g., Hartt 1980; Pearcy and Masuda 1982, 1987; Hartt and Dell 1986; Light et al. 1988; Davis et al. 1990; Myers et al. 1990, 1993, 1996, 2005; Pearcy et al. 1990; Burgner et al. 1992; McKinnell et al. 1997; Klovach et al. 2002; Beamish et al. 2005). A composite summary of tag recovery data shows the known open-ocean distribution of North American steelhead, primarily during spring and summer months (Figure 8). Kovalenko et al. (2003, 2005) found that many of the immature steelhead caught during Russian research vessel surveys in the western North Pacific near the Kuril Islands were marked by fin clips (Figure 7), indicating North American origin, similar to catches of marked and coded-wire tagged steelhead in the central and eastern North Pacific (e.g., Pearcy and Masuda 1982, 1987; Myers

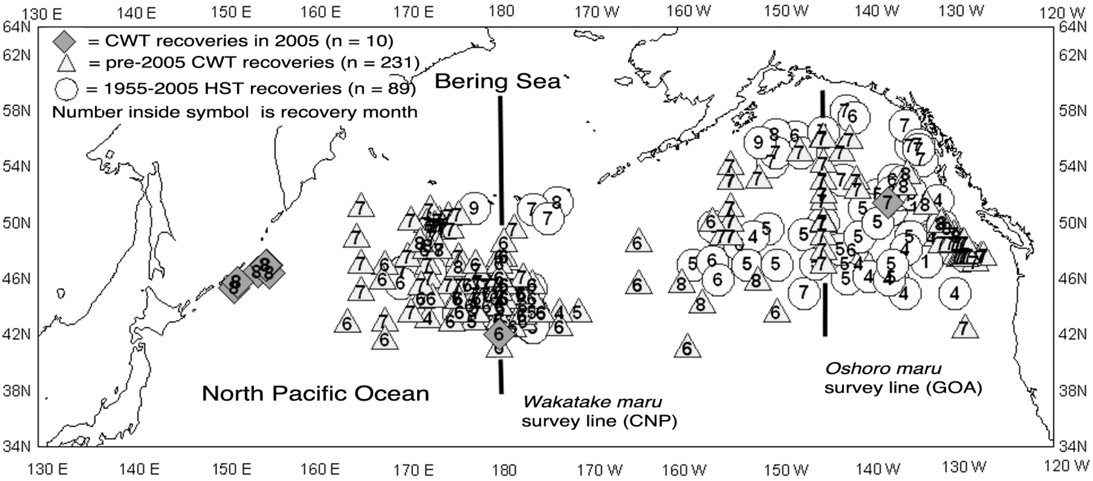

Figure 8. The known ocean distribution of North American steelhead as determined by high seas tagging experiments, 1955–2004. New coded-wire tag (CWT) recoveries are those reported for the first time in 2005. High seas tags (HST) are external tags attached to salmon at sea and later recovered in North America. Month is high seas recovery month for CWT fish or high seas release month for HST fish and *n* = total number of tagged fish that were recovered. The *Wakatake maru* survey line in the Central North Pacific (CNP) and the *Oshoro maru* survey line in the Gulf of Alaska (GOA) were the two primary open-ocean locations for HST releases and CWT tag recoveries of steelhead during the 1990s and 2000s. Source: Myers et al. 2005.

et al. 1990, 1996; Burgner et al. 1992; Fukuwaka et al. 2007). Coded-wire tag recoveries from some of these marked steelhead established the known western range limit of North American steelhead in the North Pacific Ocean (Myers et al. 2005). The tagged steelhead recovered farthest to the west, caught off the Kuril Islands (151°16’E, 45°21’N) on 28 August 2004, was an immature age 1.1 (655 mm FL, 3.04 kg) female B-run steelhead (see Table 1) released from the Dworshak National Fish Hatchery, Snake River Basin, Idaho. The fish was released as a smolt on 23 April 2003 into the mainstem Clearwater River, Idaho (46°30’N, 116°18’W), a point-to-point great-circle distance of 6,705 km from the recovery location. This is the long-distance freshwater-ocean migratory range record for all *Oncorhynchus* spp.

Although sample sizes are small, tag recovery data indicate that open-ocean seasonal migrations of North American steelhead are diverse, varying by phylogenetic group (inland versus coastal), life history type, age, and regional stock groups (Tables 11 and 12) (Light et al. 1988; Myers et al. 1990, 1996, 2005; Burgner et al. 1992; McKinnell et al. 1997). For example, in the Gulf of Alaska coastal stream-maturing steelhead, largely of B.C. origin, appear to have a more northerly distribution than inland (Columbia River Basin) steelhead (Burgner et al. 1992). Columbia River steelhead are more abundant in the central North Pacific (near 180°) at an earlier age (age 1.1) than Georgia Basin (Georgia Strait, Puget Sound, and adjacent waters) steelhead (McKinnell et al. 1997). In the central and western North Pacific, inland Snake River Basin steelhead are distributed farther to the west than coastal stream-maturing steelhead (Burgner et al. 1992; Myers et al. 2005). Among inland steelhead, the westward extent of Idaho A-run steelhead, which typically return to spawn after only 1 winter at sea (Table 1), is less extensive than Idaho B-run steelhead (Table 11). In the Gulf of Alaska in summer, winter-run steelhead are distributed farther offshore (none in the eastern Gulf of

Table 11. Summary of high seas and coded-wire tag steelhead recovery data (1956–2010) by month, ocean age-group, ocean location, migratory type (Snake A-run, Snake B-run), phylogenetic (interior, coastal), and maturity type of coastal steelhead (summer = stream maturing, winter = ocean maturing) (*N* = 317 fish). All recoveries are steelhead of North American origin. All recoveries of interior steelhead are stream-maturing fish from the Columbia R. and Snake R. basins. Phylogenetic, maturity, and migratory groups are described in Table 1. Latitude (Lat, °N) and longitude (Long) are in decimal degrees. *N* = sample size (number of fish), Max = maximum, Min = minimum, SD = standard deviation. Latitude and longitude for Gulf of Alaska = latitude ≥ 50.0 (50°00′N), longitude 125.0–165.0 (125°00′W–165°00′W), Northeastern North Pacific Ocean = latitude <50.0 (50°00′N), longitude 125.0–165.0 (125°00′W–165°00′W), Central North Pacific Ocean = longitude 165.0–190.0 (165°00′W–170°00′E), 180.0 = International dateline, Western North Pacific Ocean = longitude >190.0 (west of 170°00′E). Data Sources: High Seas Salmon Research Program, University of Washington, Seattle, and North Pacific Anadromous Fish Commission, Vancouver, B.C., Canada.

Month	Ocean age	Ocean location	Snake A-run	Snake B-run	Interior	Coastal	Coastal summer	Coastal winter
January	2	*N*			1	1		
		Lat-Mean			51.0	47.2		
		Lat-SD						
		Lat Max			51.0	47.2		
		Lat-Min			51.0	47.2		
		Long-Mean			135.0	133.8		
		Long-SD						
		Long-Max			135.0	133.8		
		Long-Min			135.0	133.8		
April	1	*N*			1	2		1
		Lat-Mean			48.9	48.9		51.6
		Lat-SD			3.9			
		Lat Max			48.9	51.6		51.6
		Lat-Min			48.9	46.1		51.6
		Long-Mean			133.3	136.3		132.5
		Long-SD				5.3		
		Long-Max			133.3	140.0		132.5
		Long-Min			133.3	132.5		132.5
	2	*N*				3		3
		Lat-Mean				44.9		44.9
		Lat-SD				2.8		2.8
		Lat Max				48.1		48.1
		Lat-Min				43.1		43.1
		Long-Mean				165.8		165.8
		Long-SD				26.7		26.7
		Long-Max				187.8		187.8
		Long-Min				136.0		136.0
May	1	*N*				9	1	7
		Lat-Mean				46.7	46.0	46.8
		Lat-SD				1.9		2.1
		Lat Max				49.2	46.0	49.2
		Lat-Min				43.5	46.0	43.5
		Long-Mean				152.1	142.4	155.6

Table 11. Continued.

Month	Ocean age	Ocean location	Snake A-run	Snake B-run	Interior	Coastal	Coastal summer	Coastal winter
		Long-SD				14.7		14.9
		Long-Max				177.5	142.4	177.5
		Long-Min				137.5	142.4	142.5
	2	*N*				8	3	5
		Lat-Mean				45.4	46.1	45.0
		Lat-SD				3.2	5.1	2.2
		Lat Max				52.0	52.0	47.7
		Lat-Min				42.9	42.9	42.9
		Long-Mean				165.5	164.5	166.1
		Long-SD				21.0	22.8	22.6
		Long-Max				182.9	182.9	182.9
		Long-Min				129.6	139.0	129.6
	3	*N*			2	5	2	
		Lat-Mean			50.5	49.7	50.3	
		Lat-SD			0.7	0.8	1.0	
		Lat Max			51.0	51.0	51.0	
		Lat-Min			50.0	49.0	49.6	
		Long-Mean			138.2	140.8	144.3	
		Long-SD			1.1	6.0	9.5	
		Long-Max			139.0	151.0	151.0	
		Long-Min			137.5	135.5	137.6	
June	1	*N*	9	20	38	20	2	18
		Lat-Mean	43.7	43.8	43.8	46.4	49.6	46.0
		Lat-SD	2.0	1.4	1.6	3.2	9.3	2.2
		Lat Max	47.0	47.0	47.5	56.2	56.2	50.0
		Lat-Min	41.0	41.0	41.0	41.0	43.0	41.0
		Long-Mean	175.9	182.3	179.4	171.2	164.0	172.0
		Long-SD	9.4	5.0	7.2	12.7	22.7	11.9
		Long-Max	184.5	192.5	192.5	184.3	180.1	184.3
		Long-Min	159.7	176.5	159.7	141.8	148.0	141.8
	2	*N*	2	6	12	33	7	20
		Lat-Mean	44.0	44.5	43.9	46.0	48.4	45.1
		Lat-SD	1.4	1.9	1.5	3.1	5.1	1.4
		Lat Max	45.0	47.5	47.5	57.6	57.6	47.5
		Lat-Min	43.0	42.0	42.0	42.5	42.5	42.7
		Long-Mean	180.0	180.0	177.6	176.6	170.5	181.8
		Long-SD	0.0	2.5	9.0	14.6	22.5	7.9
		Long-Max	180.0	184.3	185.3	196.5	192.7	196.5
		Long-Min	180.0	176.5	150.0	137.3	137.3	157.0
	3	*N*			1	4		4
		Lat-Mean			52.1	47.4		47.4
		Lat-SD				3.6		3.6
		Lat Max			52.1	52.1		52.1
		Lat-Min			52.1	43.9		43.9

Table 11. Continued.

Month	Ocean age	Ocean location	Snake A-run	Snake B-run	Interior	Coastal	Coastal summer	Coastal winter
		Long-Mean			137.6	169.9		169.9
		Long-SD				22.2		22.2
		Long-Max			137.6	188.1		188.1
		Long-Min			137.6	137.6		137.6
July	0	*N*	2	2	4	6	2	4
		Lat-Mean	51.8	51.2	51.5	53.0	54.0	52.5
		Lat-SD	0.4	1.6	1.0	2.2	1.4	2.5
		Lat Max	52.0	52.3	52.3	56.0	55.0	56.0
		Lat-Min	51.5	50.0	50.0	50.0	53.0	50.0
		Long-Mean	145.0	143.1	144.1	144.8	144.4	145.0
		Long-SD	0.0	2.7	1.9	2.0	4.3	0.0
		Long-Max	145.0	145.0	145.0	147.5	147.5	145.0
		Long-Min	145.0	141.3	141.3	141.4	141.4	145.0
	1	*N*	4	21	52	38	11	22
		Lat-Mean	46.9	45.6	46.8	51.5	52.7	50.9
		Lat-SD	0.7	1.8	2.1	3.1	3.1	3.1
		Lat Max	47.6	50.4	54.2	56.5	56.0	56.5
		Lat-Min	46.0	42.9	42.4	44.8	45.5	44.8
		Long-Mean	143.8	184.5	155.0	152.8	148.3	155.9
		Long-SD	18.5	4.3	26.6	13.8	14.2	14.0
		Long-Max	164.0	195.0	195.0	188.5	181.5	188.5
		Long-Min	127.6	177.5	127.6	132.1	134.3	142.9
	2	*N*	1	1	4	32	12	19
		Lat-Mean	51.4	45.5	47.0	50.3	51.3	49.6
		Lat-SD			3.4	2.7	3.7	1.5
		Lat Max	51.4	45.5	51.4	58.0	58.0	53.0
		Lat-Min	51.4	45.5	43.5	45.4	45.5	45.4
		Long-Mean	138.0	180.5	157.2	174.7	162.0	184.4
		Long-SD			28.4	19.0	20.4	10.3
		Long-Max	138.0	180.5	182.5	195.5	195.0	195.5
		Long-Min	138.0	180.5	127.8	142.1	142.1	145.0
	3	*N*			1	7	3	2
		Lat-Mean			49.0	50.9	53.8	49.8
		Lat-SD				3.5	3.5	0.3
		Lat Max			49.0	56.9	56.9	50.1
		Lat-Min			49.0	47.6	50.0	49.6
		Long-Mean			145.0	152.0	143.9	188.5
		Long-SD				26.3	7.3	1.6
		Long-Max			145.0	189.6	150.5	189.6
		Long-Min			145.0	127.6	136.1	187.4
August	1	*N*	2	14	21	2		2
		Lat-Mean	51.2	46.9	48.0	52.3		52.3
		Lat-SD	3.2	1.7	2.3	5.6		5.6
		Lat Max	53.4	51.2	53.4	56.3		56.3

Table 11. Continued.

Month	Ocean age	Ocean location	Snake A-run	Snake B-run	Interior	Coastal	Coastal summer	Coastal winter
		Lat-Min	49.0	45.4	45.4	48.3		48.3
		Long-Mean	133.2	185.8	173.6	169.0		169.0
		Long-SD	3.8	28.9	32.8	26.6		26.6
		Long-Max	135.9	208.7	208.7	187.8		187.8
		Long-Min	130.5	132.2	130.5	150.1		150.1
	2	*N*		3	3			
		Lat-Mean		46.3	46.3			
		Lat-SD		2.4	2.4			
		Lat Max		49.0	49.0			
		Lat-Min		44.1	44.1			
		Long-Mean		146.9	146.9			
		Long-SD		14.5	14.5			
		Long-Max		158.1	158.1			
		Long-Min		130.5	130.5			
September	0	*N*				1		1
		Lat-Mean				55.7		55.7
		Lat-SD						
		Lat Max				55.7		55.7
		Lat-Min				55.7		55.7
		Long-Mean				151.8		151.8
		Long-SD						
		Long-Max				151.8		151.8
		Long-Min				151.8		151.8
	1	*N*				1		1
		Lat-Mean				51.0		51.0
		Lat-SD						
		Lat Max				51.0		51.0
		Lat-Min				51.0		51.0
		Long-Mean				182.7		182.7
		Long-SD						
		Long-Max				182.7		182.7
		Long-Min				182.7		182.7

Table 12. Summary of high seas and coded-wire tag steelhead recovery data (1956–2010) by month, ocean age-group, ocean location, and stock conservation or management unit (*N* = 305 fish). Alaska steelhead are designated by geographic regional management units (Southcentral Alaska, Southeast Alaska). British Columbia steelhead are designated by watershed or basin-scale population conservation units (Stikine and Taku, Nass and Skeena, Lower Fraser River, Lower Mainland, Vancouver Island). U.S. West Coast stocks are designated by Distinct Population Segments (DPS) (Table 2). Latitude (Lat) and longitude (Long) locations are in decimal degrees. *N* = sample size (number of fish), Max = maximum, Min = minimum, SD = standard deviation. Latitude and longitude for Gulf of Alaska = latitude ≥50.0 (50°00′N), longitude 125.0–165.0 (125°00′W–165°00′W), Northeastern North Pacific Ocean = latitude <50.0 (50°00′N), longitude 125.0–165.0 (125°00′W–165°00′W), Central North Pacific Ocean = longitude 165.0–190.0 (165°00′W–170°00′E), 180.0 = International dateline, Western North Pacific Ocean = longitude >190.0 (west of 170°00′E). Data Sources: High Seas Salmon Research Program, University of Washington, Seattle, and Pacific States Marine Fisheries Commission, Portland, Oregon.

	Month	April		May			June			July				August	
Stock	Ocean age	1	2	1	2	3	1	2	3	0	1	2	3	1	2
Southcentral Alaska	*N*							1					1		
	Lat-Mean							42.5					50.0		
	Lat-SD														
	Lat Max							42.5					50.0		
	Lat-Min							42.5					50.0		
	Long-Mean							173.5					145.0		
	Long-SD														
	Long-Max							173.5					145.0		
	Long-Min							173.5					145.0		
Southeast Alaska	*N*							1			1	2			
	Lat-Mean							47.0			48.0	49.6			
	Lat-SD											0.2			
	Lat Max							47.0			48.0	49.8			
	Lat-Min							47.0			48.0	49.5			
	Long-Mean							180.0			186.6	185.8			
	Long-SD											0.7			
	Long-Max							180.0			186.6	186.3			
	Long-Min							180.0			186.6	185.3			
Stikine and Taku, BC	*N*							1							
	Lat-Mean							53.0							
	Lat-SD														
	Lat Max							53.0							

Table 12. Continued.

Stock	Month	April		May			June			July				August	
	Ocean age	1	2	1	2	3	1	2	3	0	1	2	3	1	2
	Lat-Min							53.0							
	Long-Mean							137.3							
	Long-SD														
	Long-Max							137.3							
	Long-Min							137.3							
Nass and Skeena, BC	*N*	1			1	3	1	1	1		3	1	2		
	Lat-Mean	48.9			52.0	50.2	56.2	57.6	52.1		55.2	58.0	55.6		
	Lat-SD					0.7					0.6		1.8		
	Lat Max	48.9			52.0	51.0	56.2	57.6	52.1		55.6	58.0	56.9		
	Lat-Min	48.9			52.0	49.6	56.2	57.6	52.1		54.5	58.0	54.4		
	Long-Mean	133.3			139.0	142.5	148.0	141.7	137.6		134.8	142.5	143.3		
	Long-SD					7.4					0.6		10.2		
	Long-Max	133.3				151.0	148.0	141.7	137.6		135.5	142.5	150.5		
	Long-Min	133.3			139.0	137.5	148.0	141.7	137.6		134.3	142.5	136.1		
Lower Fraser River, BC	*N*		1		1			4			2	3	3		
	Lat-Mean		43.5		43.5			44.2			52.5	48.4	48.3		
	Lat-SD							0.9			4.9	2.5	1.2		
	Lat Max		43.5		43.5			44.8			56.0	49.9	49.6		
	Lat-Min		43.5		43.5			42.9			49.0	45.4	47.6		
	Long-Mean		173.5		176.5			183.0			150.0	185.7	147.5		
	Long-SD							6.4			7.1	3.7	34.5		
	Long-Max		173.5		176.5			188.5			155.0	187.9	187.4		
	Long-Min		173.5		176.5			177.5			145.0	181.4	127.6		
Lower Mainland, BC	*N*							2							
	Lat-Mean							44.4							
	Lat-SD							1.6							
	Lat Max							45.5							
	Lat-Min							43.3							
	Long-Mean							180.5							
	Long-SD							4.2							
	Long-Max							183.5							
	Long-Min							177.5							
Vancouver Island, BC	*N*				2			6		1	10	15	1	1	
	Lat-Mean				43.2			45.6		55.0	52.7	50.5	50.1	48.3	

Table 12. Continued.

	Month	April		May			June			July				August	
Stock	Ocean age	1	2	1	2	3	1	2	3	0	1	2	3	1	2
	Lat-SD				0.4			1.6			2.0	2.3			
	Lat Max				43.5			47.5		55.0	56.0	55.9	50.1	48.3	
	Lat-Min				42.9			43.5		55.0	49.0	47.5	50.1	48.3	
	Long-Mean				177.2			183.9		147.5	153.0	171.8	189.6	187.8	
	Long-SD				8.1			7.1			4.2	18.5			
	Long-Max				182.9			192.7		147.5	155.0	187.3	189.6	187.8	
	Long-Min				171.5			175.5		147.5	144.9	142.1	189.6	187.8	
Puget Sound, WA	*N*						2	2	1		5	1		1	
	Lat-Mean						46.2	46.8	45.3		51.2	53.0		56.3	
	Lat-SD						3.2	4.1			1.3				
	Lat Max						48.4	49.7	45.3		53.0	53.0		56.3	
	Lat-Min						43.9	43.9	45.3		49.9	53.0		56.3	
	Long-Mean						167.0	169.1	176.6		149.0	145.0		150.1	
	Long-SD						18.3	17.3			5.5				
	Long-Max						179.9	181.3	176.6		155.0	145.0		150.1	
	Long-Min						154.0	156.8	176.6		145.0	145.0		150.1	
Olympic Peninsula, WA	*N*			1	1		14	8	2	2	9	4			
	Lat-Mean			43.5	43.9		45.9	44.9	46.0	54.0	49.7	50.1			
	Lat-SD						2.3	1.7	2.9	2.8	3.0	2.0			
	Lat Max			43.5	43.9		50.0	47.5	48.0	56.0	53.0	53.0			
	Lat-Min			43.5	43.9		41.0	42.5	43.9	52.0	44.8	48.9			
	Long-Mean			176.4	182.7		174.2	183.0	182.7	145.0	159.0	175.7			
	Long-SD						8.7	6.4	7.6	0.0	14.6	23.0			
	Long-Max			176.4	182.7		184.3	196.5	188.1	145.0	188.5	195.5			
	Long-Min			176.4	182.7		157.0	176.5	177.4	145.0	145.0	142.9			
Southwest Washington	*N*		1	1	1			1				2			
	Lat-Mean		43.1	49.2	47.0			44.0				47.6			
	Lat-SD											3.0			
	Lat Max		43.1	49.2	47.0			44.0				49.8			
	Lat-Min		43.1	49.2	47.0			44.0				45.5			
	Long-Mean		187.8	147.0	159.0			189.0				186.3			
	Long-SD											1.1			
	Long-Max		187.8	147.0	159.0			189.0				187.0			
	Long-Min		187.8	147.0	159.0			189.0				185.5			

Table 12. Continued.

	Month	April		May			June			July				August	
Stock	Ocean age	1	2	1	2	3	1	2	3	0	1	2	3	1	2
Lower Columbia River	*N*	1		2	1		2	2		3	3	4			
	Lat-Mean	51.6		45.8	42.9		45.5	45.8		51.7	49.1	50.5			
	Lat-SD			1.7			3.5	0.4		1.5	3.3	2.5			
	Lat Max	51.6		47.0	42.9		48.0	46.0		53.0	52.0	53.0			
	Lat-Min	51.6		44.6	42.9		43.0	45.5		50.0	45.5	47.0			
	Long-Mean	132.5		160.0	182.9		161.0	178.3		143.8	152.9	180.6			
	Long-SD			24.7			27.0	2.5		2.1	25.6	24.0			
	Long-Max	132.5		177.5	182.9		180.1	180.0		145.0	181.5	195.0			
	Long-Min	132.5		142.5	182.9		141.8	176.5		141.4	132.1	145.0			
Middle Columbia River	*N*						1								
	Lat-Mean						43.5								
	Lat-SD														
	Lat Max						43.5								
	Lat-Min						43.5								
	Long-Mean						182.5								
	Long-SD														
	Long-Max						182.5								
	Long-Min						182.5								
Upper Columbia River	*N*						2				5			2	
	Lat-Mean						43.7				48.5			49.0	
	Lat-SD						1.6				0.0			0.7	
	Lat Max						44.8				48.5			49.5	
	Lat-Min						42.5				48.4			48.5	
	Long-Mean						175.6				130.2			160.1	
	Long-SD						2.9				0.5			40.4	
	Long-Max						177.7				130.8			188.7	
	Long-Min						173.5				129.7			131.5	
Snake River Basin	*N*						35	11		4	47	4	1	19	3
	Lat-Mean						43.8	44.0		51.5	46.6	47.0	49.0	47.9	46.3
	Lat-SD						1.7	1.6		1.0	2.2	3.4		2.4	2.4
	Lat Max						47.5	47.5		52.3	54.2	51.4	49.0	53.4	49.0
	Lat-Min						41.0	42.0		50.0	42.4	43.5	49.0	45.4	44.1
	Long-Mean						179.5	177.6		144.1	157.7	157.2	145.0	175.0	146.9
	Long-SD						7.4	9.5		1.9	26.6	28.4		32.9	14.5

Table 12. Continued.

	Month	April		May			June			July				August	
Stock	Ocean age	1	2	1	2	3	1	2	3	0	1	2	3	1	2
	Long-Max						192.5	185.3		145.0	195.0	182.5	145.0	208.7	158.1
	Long-Min						159.7	150.0		141.3	127.6	127.8	145.0	130.5	130.5
Oregon Coast	*N*	1		2	1	1		2			2				
	Lat-Mean	46.1		48.1	47.7	49.0		46.8			50.3				
	Lat-SD			1.5				1.7			6.7				
	Lat Max	46.1		49.2	47.7	49.0		48.0			55.0				
	Lat-Min	46.1		47.0	47.7	49.0		45.7			45.5				
	Long-Mean	140.0		150.1	129.6	135.5		167.9			164.3				
	Long-SD			4.3				32.3			20.0				
	Long-Max	140.0		153.1	129.6	135.5		190.7			178.4				
	Long-Min	140.0		147.0	129.6	135.5		145.1			150.1				
Klamath Mountains Province	*N*			1					1		1				
	Lat-Mean			46.0					52.1		56.5				
	Lat-SD														
	Lat Max			46.0					52.1		56.5				
	Lat-Min			46.0					52.1		56.5				
	Long-Mean			142.4					137.6		145.0				
	Long-SD														
	Long-Max			142.4					137.6		145.0				
	Long-Min			142.4					137.6		145.0				
Northern California	*N*		1	1		2		1			1				
	Lat-Mean		48.1	47.0		49.5		49.7			53.0				
	Lat-SD					0.7									
	Lat Max		48.1	47.0		50.0		49.7			53.0				
	Lat-Min		48.1	47.0		49.0		49.7			53.0				
	Long-Mean		136.0	137.5		140.0		156.8			142.9				
	Long-SD					1.5									
	Long-Max		136.0	137.5		141.1		156.8			142.9				
	Long-Min		136.0	137.5		139.0		156.8			142.9				
Central California Coast	*N*							1							
	Lat-Mean							47.3							
	Lat-SD														
	Lat Max							47.3							
	Lat-Min							47.3							

Table 12. Continued.

	Month	April			May				June				July					August	
Stock	Ocean age	1	2		1	2	3		1	2	3		0	1	2	3		1	2
	Long-Mean									157.0									
	Long-SD																		
	Long-Max									157.0									
	Long-Min									157.0									
Southcentral California Coast	*N*				1														
	Lat-Mean				47.1														
	Lat-SD																		
	Lat Max				47.1														
	Lat-Min				47.1														
	Long-Mean				145.8														
	Long-SD																		
	Long-Max				145.8														
	Long-Min				145.8														
Total *N*		3	3	0	9	8	6	0	57	44	5	0	10	89	36	8	0	23	3

Alaska) than summer-run fish, likely due to differences in timing of adult returns to freshwater (Burgner et al. 1992). The westward extent of offshore migrations of coastal Oregon and California steelhead may be less than other regional stock groups (Burgner et al. 1992). A statistical analysis of CWT recovery data indicated that at least some hatchery steelhead populations aggregate on the high seas, however, sampling was insufficient to determine the size, structure, or stability of these aggregations (McKinnell et al. 1997).

Acoustic tracking and archival tagging studies of North American steelhead kelts indicate diverse ocean migration patterns. Acoustic telemetry showed that California Central Valley hatchery steelhead kelts exhibit both anadromous and nonanadromous postspawning migration strategies, and some individuals alternate these strategies between years (Null et al. 2012; Teo et al. 2013). Anadromy, the most common strategy, was characterized by short-term residence near the release site, followed by sustained downstream emigration. For example, one California Central Valley (Sacramento River) kelt double-tagged with acoustic and geolocation archival tags remained in freshwater most of the time after release (285 d), while another tagged kelt migrated to California coastal marine waters (219 d at liberty) (Teo et al. 2013). Central California Coast (Scott Creek) kelts (2 fish) tagged with temperature-recording archival tags appeared to time their out-migration to a narrow temperature window between February and April, feeding in the California Current while moving northward, and migrating offshore to the same high-seas areas of the North Pacific as more northern North American steelhead populations (Hayes et al. 2012a). Although sample sizes were small, observed differences in migratory behavior between California Central Valley and Central California Coast steelhead might be related to the relative size of the river-estuary systems in the study populations (Teo et al. 2013). In British Columbia, one acoustic-tagged Keogh River kelt migrated slowly in Queen Charlotte Strait (15.6 km in 3 d) and spent a considerable amount of time milling (34 h) at one location (Welch et al. 2004). After spending up to 10 months in the Ninilchik River (Cook Inlet, southcentral Alaska), acoustic-tagged kelts migrated rapidly downstream with no apparent problems adapting to salt water, and held in marine water near the river mouth for 0–35.5 h (84 fish; Nielsen et al. 2011). The downstream migration to Cook Inlet was diurnal, and significantly related to tidal stage (high tide and ebbing flow). Minimum winter sea temperature data (6.2–6.9°C in December 2002) from two archival tagged Ninilchik River kelts indicated a potential maximum southern distribution of 44–45°N in the North Pacific Ocean (Nielsen et al. 2011). Future innovative and cost-effective use of remote sensing and acoustic and data storage tagging technology is likely to greatly expand our knowledge of stock-specific seasonal distribution of steelhead in the open ocean (e.g., Hayes et al. 2013).

To fill gaps in information on seasonal migrations of major stocks, Burgner et al. (1992) proposed an age-specific seasonal model of North American steelhead. The model of Burgner et al. (1992) was derived from a previously reported comprehensive model of seasonal migrations of both Asian and North American steelhead (Light et al. 1989). A maturity-specific model for typically anadromous Kamchatka and North American steelhead (Figure 9), updated with more recent information from tagging studies (Tables 11 and 12), is similar to earlier models (Light et al. 1989; Burgner et al. 1992; Kovalenko et al. 2005). Briefly, like other Okhotsk Sea stocks of Pacific salmon, juvenile (ocean age-0) Kamchatka steelhead may spend their first summer-autumn in the Sea of Okhotsk and western North Pacific off southeastern Kamchatka. In subsequent years, again like other Okhotsk Sea stocks of Pacific salmon, Kamchatka steelhead are probably distributed primarily west of the international

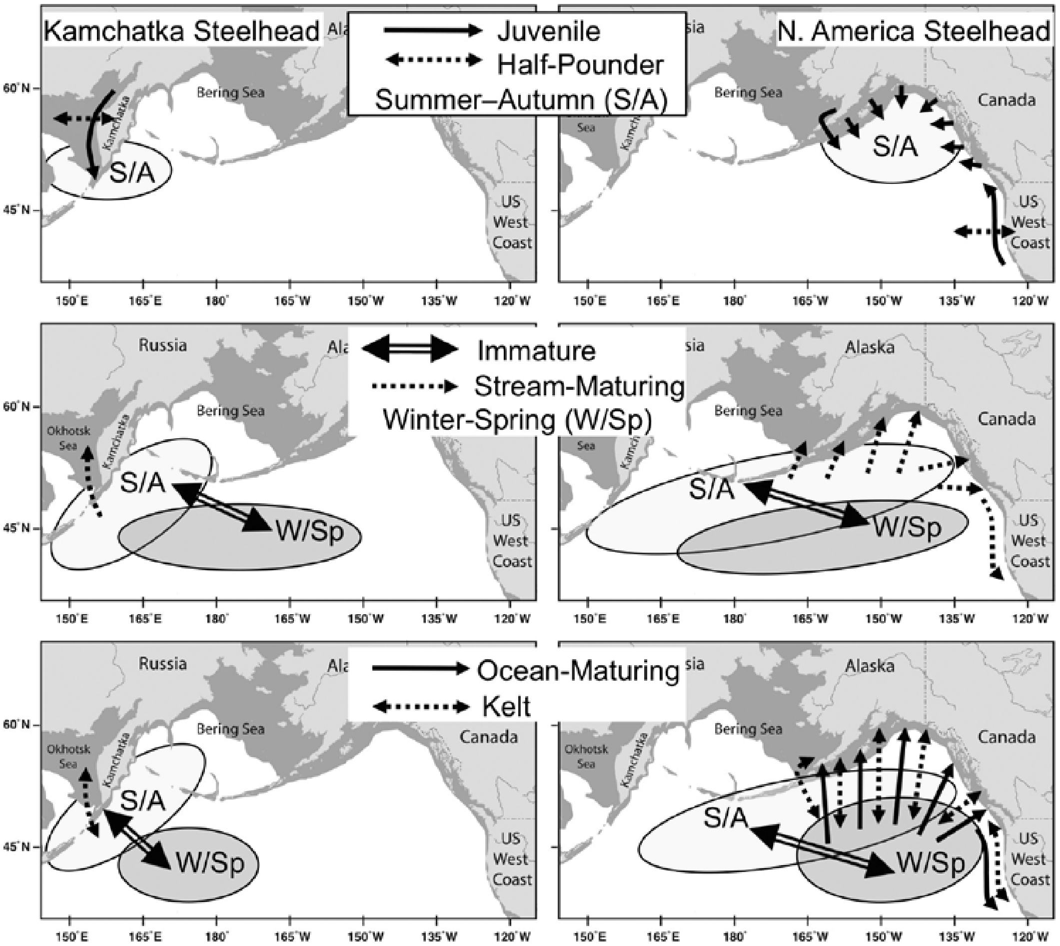

Figure 9. Conceptual model of seasonal ocean distribution of Kamchatka steelhead (left panels) and North America steelhead (right panels) by maturity stage and type: juvenile, including half-pounders (top panels); immature, including stream-maturing (middle panels); and kelts and ocean-maturing (bottom panels) and maturation type (stream-maturing, ocean maturing) based on research vessel catch, age, and maturity data, and tag recovery (only N. America) data. Elipses indicate approximate seasonal area of distribution. Open-shaft arrows indicate overall pattern of seasonal shift in high seas distribution of steelhead to the south and east in winter-spring (W/Sp) and to the north and west in summer-autumn (S/A). Solid-shaft and dotted-shaft arrows indicate movements to and from the seasonal ocean distribution areas to home streams by steelhead of various maturity stages and maturation types.

date line (180° longitude) and south of 46°N in the western and central North Pacific Ocean (e.g., Myers et al. 1993). Winter-spring distribution of immature Kamchatka steelhead may extend far to the east into the northeastern North Pacific Ocean, and summer-autumn distribution likely extends into the western Bering Sea (Kovalenko et al. 2003, 2005). Steelhead at advanced maturity stages and maturing steelhead distributed in the Okhotsk Sea are likely of local (Kamchatka) origin (Kovalenko et al. 2003, 2005). North American steelhead during their first summer-autumn at sea are distributed in coastal and offshore (Gulf of Alaska) habitats (Figure 9). In subsequent years immature steelhead make extensive seasonal migrations across broad fronts, moving to the north and west in spring through summer and to the south and east from autumn through winter. The open ocean distribution of maturing (winter run or ocean-maturing) and kelt (repeat-spawning) steelhead follows similar seasonal patterns but is less extensive than that of immature steelhead (Figure 9).

Only a few studies have attempted to develop quantitative estimates of stock proportions of steelhead in mixed-stock high seas samples. Dalton (1991) used a natural parasite tag (*Nanophyetus salmincola*), found in roughly 60% of U.S. Pacific Northwest (Washington to northern California) steelhead, to estimate proportions of this stock in summer (1986–1987) samples collected in the central North Pacific Ocean (170°W–165°E, 40°N–52°N). Estimates indicated that ~50% of steelhead distributed in this region were infected with *N. salmincola*, however, the origin of uninfected fish could not be determined. Margolis (1998) reviewed the use of *N. salmincola* for quantitative estimates of steelhead stock composition, and concluded that U.S. Pacific Northwest steelhead baselines may need to be re-established annually to account for annual variation in parasite prevalence (% of stock with the parasite) and intensity (numbers of parasites in each host).

A comprehensive genetic database for estimating stock proportions of steelhead and application of this database to high seas mixture samples of steelhead is needed to validate the assumptions of existing seasonal migration models and advance scientific knowledge of stock-specific migrations. This might be accomplished by application of new genetic stock-identification technologies to existing biological collections of steelhead scales collected during high seas research vessel surveys.

Migration Behavior and Mechanism (Speed, Diel Patterns, Vertical Movement, Orientation)

Migration speed.—A synthesis of the results of 207 tagging studies indicates that salmonids (Pacific salmon, Atlantic Salmon *Salmo salar*, Brown Trout *Salmo trutta*, steelhead, and Cutthroat Trout *O. clarkii*) at all life stages swim at an average speed of approximately one body length per second, likely the speed of minimal energy costs of transport (Drenner et al. 2012). Nevertheless, migration speeds and travel rates of steelhead in the ocean are highly variable depending on life stage and habitat (Table 13), even among individuals within a single population. For example, acoustic-tagged steelhead smolts quickly exited (95% in ≤3 d) the mouth of the Columbia River and plume (McMichael et al. 2011). Acoustic-tagged steelhead smolts rapidly transited San Francisco Bay Estuary (2–4 d), using flows in the main channel (Chapman et al. 2015). Minimum migration speeds, body lengths (BL) per second, of acoustic-tagged Cheakamus River steelhead smolts during their migration through Howe Sound to the Strait of Georgia or Johnstone Strait to Queen Charlotte Strait, British Columbia, varied from <1 BLs^{-1} to >4 BLs^{-1} (Melnychuk et al. 2007). Average movement rates of acoustic-tagged native steelhead smolts were higher in the estuary, San Pablo Bay and San Francisco Bay, California, than in the coastal ocean (Sandstrom et al. 2013b). Wide variation in travel times of individual fish is exemplified by two acoustic-tagged steelhead smolts tracked from the Golden Gate Bridge in San Francisco to Pt. Reyes, California (a straight line distance of 54 km); one fish traveled the distance in 16 d and the other in 145 d (Del Real et al. 2012). In general travel rates of steelhead smolts (Table 13) are similar to those reported for other species of Pacific salmon (e.g., see summary by Brodeur et al. 2003), although acoustic telemetry data for Salish Sea (Puget Sound, Strait of Georgia, Johnstone Strait, Queen Charlotte Strait)

Table 13. Summary of information on steelhead migration rates. Two measures of travel speed were commonly reported: length-specific rates in mean BL•$^{s–1}$ (body lengths per second) and mean or median (bold font, ± SD when reported) absolute rates in km•d–1. *N* = sample size (number of fish), n/a = sample size not reported; habitat: rkm = river kilometers; Life stage: smolt EM is an early-migrant smolt, smolt PM is a peak-migrant smolt. Habitat: FW is freshwater release site. Tag type: AT = acoustic tag, CWT = coded-wire tag, DST = data storage tag, HST = high seas tag, RT = radio tag. TDS = transmitter, depth sensing; rkm = river kilometer.

				BL• s^{-1}	Migration rate km•day^{-1}			
Life stage	N	Location	Habitat	Mean	Mean or **median**	Range	Tag type	Source
Smolt	12	San Pablo Bay	Estuary		36.6	18.4–53.2	AT	Sandstrom et al. 2013b
Smolt	9	San Francisco Bay	Estuary		28.9	5.1–77.8	AT	Sandstrom et al. 2013b
Smolt	6	San Francisco Bay to Pt. Reyes CA	Open coast		4.1	1.8–9.8	AT	Sandstrom et al. 2013b
Smolt	3	San Francisco Bay to Pt. Reyes CA	Open coast		1.6	0.4–4.0	AT	Del Real 2012
Smolt	1	San Francisco Bay to Pt. Reyes CA	Open coast		4.8		AT	Del Real 2012
Smolt EM	10	Alsea River, Oregon	FW to estuary (rkm 55 to 0.2)		**2.7**	1.3–3.7	AT	Romer et al. 2012
Smolt PM	28	Alsea River, Oregon	FW to estuary (rkm 55 to 0.2)		**4.2**	1.7–9.1	AT	Romer et al. 2012
Smolt EM	13	Nehalem River, Oregon	FW to estuary (rkm 33 to 1.2)		**3.2**	1.1–7.6	AT	Romer et al. 2012
Smolt PM	27	Nehalem River, Oregon	FW to estuary (rkm 33 to 1.2)		**4.2**	2.6–7.0	AT	Romer et al. 2012
Smolt	2408	Columbia River	Estuary (rkm 153 to 8.3)		**78.0**		AT	McMichael et al. 2011
Smolt	2408	Columbia River	Estuary (rkm 49.6 to 22)		**40.7**		AT	McMichael et al. 2011

Table 13. Continued.

				BL• s^{-1}	Migration rate km•day^{-1}			
Life stage	N	Location	Habitat	Mean	Mean or **median**	Range	Tag type	Source
Smolt	2408	Columbia River	Estuary (rkm 22 to 8.3)		**106.2**		AT	McMichael et al. 2011
Smolt	211	Hood Canal WA	Inland marine			8.0–10.0	AT	Moore et al. 2010a
Smolt	34	N. Puget Sound & Strait of Juan de Fuca WA	Inland marine			26.0–28.0	AT	Moore et al. 2010a
Smolt	1000	San Francisco Bay CA	Estuary	1.4			AT	Chapman et al. 2015
Smolt	25	Queen Charlotte St. BC	Inland marine			0.5–1.0	AT	Welch et al. 2004
Smolt	74	Howe Sound	Inland marine	2.5			AT	Melnychuk et al. 2007
Smolt	55	St. of Georgia BC	Inland marine	1.0			AT	Melnychuk et al. 2007
Smolt	28	N. St. of Georgia-Queen Charlotte St. BC	Inland marine	1.8			AT	Melnychuk et al. 2007
Smolt	28	Howe Sound-Queen Charlotte St. BC	Inland marine			~9.0–21.0	AT	Melnychuk et al. 2007
Smolt	n/a	Queen Charlotte & Juan de Fuca	Inland marine	0.9	13.9		AT	Melnychuk et al. 2010
Juvenile	1	Alsea R. OR to northern GOA	Open coast to open ocean		21.5/16.7	--/14.8–18.5	HST	[1]Royce et al. 1968/Hartt and Dell 1986
Juvenile	2	Gulf of Alaska	Open ocean		21.9	19.9, 23.9	CWT	McKinnell et al. 1997
Immature	3	Central North Pacific Ocean	High seas		28.8		AT	Ogura and Arai 1993
Maturing	12	North Pacific Ocean	High seas to coast		33.0	8.7–62.0	HST	Burgner et al. 1992

Table 13. Continued.

				BL• s^{-1}	Migration rate km•day^{-1}			
Life stage	N	Location	Habitat	Mean	Mean or **median**	Range	Tag type	Source
Maturing	1	Central Gulf of Alaska to Copper R. Delta AK	High seas to coast		25.9		DST	Walker et al. 2000b
Adult	19	Dean & Fisher channels to Dean R. mouth, BC	Inland marine		17.2	6.5–42.0	RT	Ruggerone et al. 1990
Adult	6	Dean & Fisher channels	Inland marine	0.73[2]	18.0	9.6–24.0	AT	Ruggerone et al. 1990
Kelt	1	San Francisco Bay to Pt. Reyes CA	Open coast		31.9		AT	Del Real 2012
Kelt	10	Queen Charlotte Strait	Inland marine	0.1			AT	Welch et al. 2004
Kelt	38	Ninilchik River to Cook Inlet AK	FW to near-shore inland marine		5.10 ± 4.40		AT	Nielsen et al. 2011
Kelt	46	Ninilchik River to Cook Inlet AK	FW to near-shore inland marine		8.55 ± 9.9		AT	Nielsen et al. 2011

[1] The two studies used different assumptions (open coast vs. open ocean) about migration routes of the same fish.

[2] Average ground speed; net movement back to river of origin was lower ($0.24BL \cdot s^{-1}$) indicating milling behavior.

populations indicate that after ocean entry Coho and Chinook Salmon have much slower and more variable rates of migration than steelhead and sockeye salmon (Welch et al. 2011). Variation in migration speed of steelhead smolts likely reflects a complex balance between foraging and predator avoidance requirements (Melnychuk et al. 2010). In the only acoustic/radio-tag tracking study of steelhead on the high seas, the average ground speed of three fish for 4, 19, and 144 h, respectively, was 1.2 km/h (Ogura and Arai 1993). During similar tracking studies on other species (Ogura 1990, 1991; Ogura and Ishida 1995), the speeds of Sockeye, Chum, and Pink Salmon were about twice those of steelhead, and speeds of Coho and Chinook Salmon were similar to steelhead. Direction of migration during high-seas steelhead tracking was not consistent, and fish often seemed to be drifting (Ogura and Arai 1993).

Diel migration patterns.—Acoustic telemetry research indicates that steelhead smolts prefer diurnal (daytime) travel during their emigration to the ocean, e.g., downstream in California's Sacramento River, through the San Francisco Bay estuary, and into the Pacific Ocean (Chapman et al. 2013). Acoustic-tagged steelhead smolts were first detected at arrays in the lower Columbia River estuary during daylight hours, although timing and arrival appeared to be most influenced by tide with most fish emigrating on ebb tides (McMichael et al. 2011). An earlier study, based on beach seine and purse seine catches in the Columbia River estuary, also indicated the greatest downstream movement of steelhead smolts during daylight hours (noon to early evening); however, there was no apparent relationship between tidal cycle and catch (Ledgerwood et al. 1991). In contrast, in-river migrations of acoustic-tagged Cheakamus River, British Columbia, smolts occurred only at night, and early marine migrations of B.C. steelhead through Howe Sound and the Strait of Georgia or Johnstone Strait to Queen Charlotte Strait, B.C., did not show any consistent diel patterns (Melnychuk et al. 2007). Diel movements of acoustic-tagged Green River (Puget Sound) steelhead smolts were predominantly nocturnal (nighttime) in the river, transitioned from nocturnal to diurnal (daytime) in the upper estuary (perhaps in response to tidal currents), and were predominantly diurnal in the lower estuary and inland marine waters (Goetz et al. 2015). Variation in diel patterns of steelhead smolts may reflect differences in behavioral responses to predators, prey, and other environmental conditions.

Data on diel patterns of distribution of steelhead in the open ocean are rare. A unique open-ocean biotelemetry study of three immature steelhead, tracked for 4, 19, and 144 h, respectively, in the central North Pacific in July 1992 showed no significant diurnal patterns in swimming depths or direction of movement (Table 14) (Ogura and Arai 1993). Due to the relatively short tracking period, however, the fish might not have fully recovered from the effects of tagging. The only long-term (36-d) electronic data storage tag record of ambient sea temperature from a maturing steelhead, tagged in the open ocean (central Gulf of Alaska) on 9 July 1998 and recovered in a Copper River Delta (southcentral Alaska) salmon fishery on 14 August 1998, showed diel patterns of behavior (Walker et al. 2000b). Temperatures experienced by the fish were significantly higher at night (mean 12.2°C, SD 1.2°C) than during the day, and significantly more variable during the daytime (mean 11.9°C, SD 2.0°C), with fish exhibiting rapid movements between warmer and cooler waters (Figure 10). A comparison of the data storage tag record with concurrent field-based oceanographic temperature-depth profiles indicated that the coolest daytime temperature (6.4°C) recorded on the data storage tag was at about 50-m depth. Although the temperature data indicated that the steelhead was located primarily at the surface at night, it may have been actively swimming, as

Table 14. Diurnal depth distribution of steelhead (mean depth from the water surface in meters) as shown by tagging experiments. Stock: *N* = number of fish tagged; BC = British Columbia, CA = California, R. = River; Location: NPO = North Pacific Ocean; Habitat: FW = fresh water; Tag type: AT = acoustic transmitters with depth sensing, LAT = light-, temperature-, depth-recording data storage tags, LTD = temperature- and depth-recording data storage tags; Depth: NS = no significant difference in day-night depths.

			Depth (mean ± SD)		Travel Rate (km/hr)			
Stock (*N*)	Location	Stage/Habitat	Day (m)	Night (m)	Day	Night	Tag type	Study
Dean R., BC (6)	Dean and Fisher Channel	Adult/Inland marine	1.5	2.8	2.3	1.1	AT	Ruggerone et al. 1990
Unknown (3)	Central North Pacific Ocean	Immature/ epipelagic ocean	≤10.0	NS			AT	Ogura and Arai 1993
Ninilchik R., AK (1)	Cook Inlet/ NPO (16 months at sea)	Epipelagic ocean	3.8± 1.8	NS			LTD	Nielsen et al. 2010
Ninilchik R., AK (1)	Cook Inlet/ NPO (16 months at sea)	Epipelagic ocean	3.5± 2.7	NS			LTD	Nielsen et al. 2010
Central Valley, CA (1)	Sacramento R	Kelt #1/ initial FW	3.08± 1.50	1.65± 1.15			LAT	Teo et al. 2013
Central Valley, CA (1)	Sacramento R	Kelt #1/ estuary, Ocean	1.32± 1.161	5.63± 6.11			LAT	Teo et al. 2013
Central Valley, CA (1)	Sacramento R	Kelt #1/ return FW	1.56± 0.8	1.4± 0.97			LAT	Teo et al. 2013

Table 14. Continued.

			Depth (mean ± SD)		Travel Rate (km/hr)			
Stock (*N*)	Location	Stage/Habitat	Day (m)	Night (m)	Day	Night	Tag type	Study
Central Valley, CA (1)	Sacramento R	Kelt #2/ initial FW	1.23± 0.33	0.72± 0.35			LAT	Teo et al. 2013
Central Valley, CA (1)	Sacramento R	Kelt #2/ estuary	3.59± 1.27	2.57± 1.70			LAT	Teo et al. 2013
Central Valley, CA (1)	Sacramento R	Kelt #2/FW resident	1.17± 0.36	0.79± 0.38			LAT	Teo et al. 2013
Central Valley, CA (1)	Sacramento R	Kelt #2/ FW resident	1.56± 0.8	1.4± 0.97			LAT	Teo et al. 2013

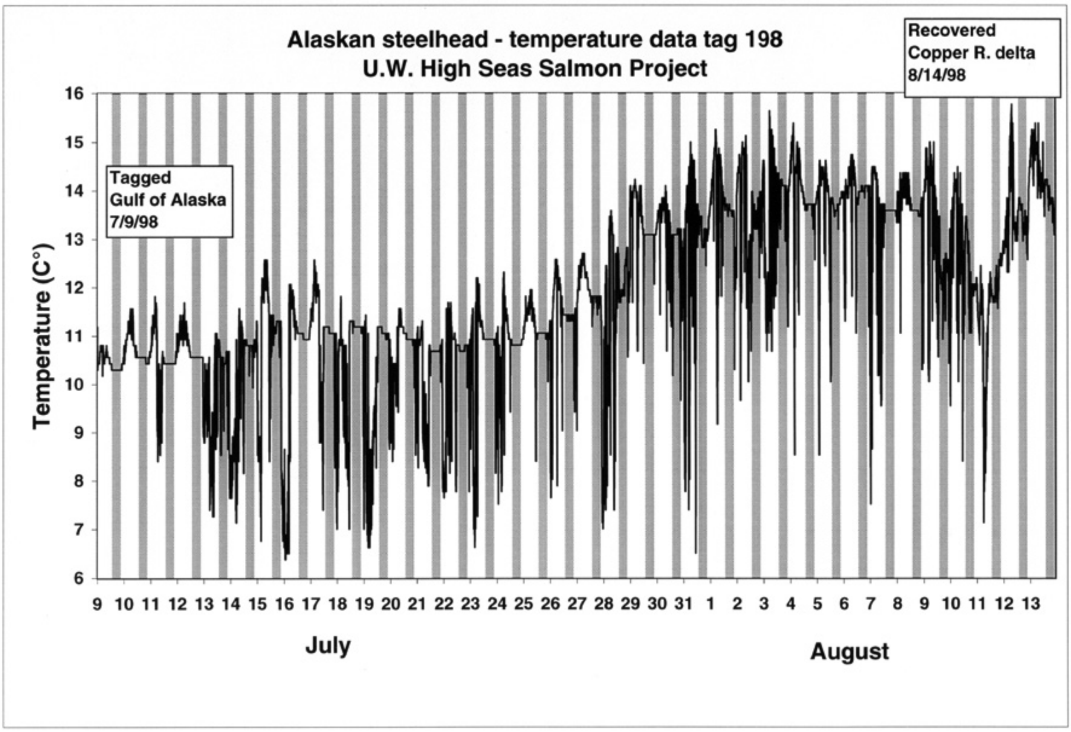

Figure 10. Ambient temperatures recorded every 7.5 minutes (6909 data points) on a data storage tag externally attached to a male steelhead (age 2.3, 690 mm FL) tagged on 7/9/98 in the central Gulf of Alaska (49°58'N, 144°58'W) and recovered on 8/14/98 in Alaska (Copper R. delta, 60°13'N, 144°40'W). An initial 4-day recuperation period of fish after release is indicated by limited variation in temperature. Shaded bars indicate approximate hours of darkness. Initially, the fish is located in the central Gulf of Alaska gyre (maximum temperatures of 11–12°C), then the fish crosses the warmer surface waters of the Alaska Current (12–13°C maxima), then moves into cooler coastal waters (Walker et al. 2000b). Original data source: High Seas University of Washington, High Seas Salmon Research Project, University of Washington, Seattle.

indicated by similar data for other salmon species (Walker et al. 2000b) (Figure 10). In contrast, an acoustic tracking study of adult steelhead in inland marine waters showed steelhead were distributed at shallower mean depths and had faster travel rates during the day than at night (Table 14), and displacement at night resulted from drift (Ruggerone et al. 1990). This might reflect diurnal variation in navigation behavior or predator avoidance as adult fish approach their home stream. Records from two data storage tagged Sacramento steelhead kelts that exhibited different migratory strategies showed diurnal variation in swimming depths by habitat (Table 14; Teo et al. 2013). However, diurnal variation in swimming depths of two data storage tagged Ninilchik River, Alaska, steelhead kelts, recovered after 16 months at sea, was not significant (Table 14; Nielsen et al. 2011).

Vertical movements.—Data on the vertical movements of steelhead are sparse, but indicate that steelhead are surface oriented, and have a shallower vertical distribution than other species of Pacific salmon (e.g., Walker et al. 2007). In general, high seas catch data indicate that all life stages of steelhead in the open ocean are distributed primarily in the hyponeuston, just under the surface, and upper epipelagic layer, 0–20 m below the surface (Burgner et al. 1992). The surface orientation of feeding behavior during all marine life stages is supported by the presence of neustonic organisms and floating debris in the stomach contents of steelhead (see *Feeding and Growth*). Nevertheless, limited data from tagging experiments indicate that steelhead make frequent vertical movements. For example, estimated vertical movements from a single maturing data storage (temperature) tagged steelhead in the Gulf of Alaska in summer indicated that the fish made frequent dives during the day to waters 3–5°C cooler than the surface (40–60 m deep), and remained at on near the surface at night (Walker et al. 2000b) (Figure 10). Six adult steelhead tracked in a British Columbia fjord by ultrasonic telemetry (21.0–49.8 h/fish) spent most (average 72%) of the time in surface waters (top 1 m of the water column) with frequent 5-m dives to the halocline (9 min median time between dives) (Ruggerone et al. 1990). Two Ninilchik River (Cook Inlet) kelt steelhead tagged with temperature-depth recording data storage tags in 2002 and recovered in 2004 after 16 months also exhibited diving behavior at sea, but spent 97% of their time near the ocean surface (<6 m depth during day and night, most frequently at depths of 3–4 m) (Nielsen et al. 2011).

Orientation.—Quinn (2005) provides a thorough historical review of competing hypotheses to explain salmon orientation on the high seas. The most compelling evidence suggests that mechanisms of orientation involve a magnetic sensory system that enables true navigation, genetic control, and learned behavior (imprinting) along migration routes. Experimental evidence for Rainbow Trout shows behavioral and electrophysiological responses to magnetic field intensity, and has identified candidate (magnetite-based) receptor cells in the nose (lamina propria of the olfactory epithelium) and sensory pathways to the brain associated with a learned response to magnetic fields (Walker et al. 1997). The hypothesis of magnetite-based receptors is supported at the molecular level by evidence from gene expression in the brains of Rainbow Trout exposed to a magnetic pulse known to disrupt magnetic orientation behavior (Fitak et al. 2017). As indicated for other species (e.g., Putman et al. 2011, 2013), an inherited sense of direction may enable steelhead smolts to successfully navigate to open ocean feeding grounds for the first time.

Acoustic tagging experiments provide some evidence supporting genetic control of direction of movement of steelhead smolts in coastal marine waters. In a coastal fjord in British Columbia, acoustic-tagged steelhead smolts did not appear to use coastline cues for navigation during nearshore migration (Melnychuk et al. 2007, 2013). Intra-population variation in migration direction of individual acoustic-tagged steelhead smolts was documented in the Strait of Georgia (Melnychuk et al. 2010). Acoustic-tagged steelhead smolts off the mouth of the Columbia River in spring 2010 were rarely detected migrating northward, with the majority migrating southward or directly offshore (McMichael et al. 2011). Acoustic-tagged hybrids (steelhead × Cutthroat) in Hood Canal (Puget Sound), Washington, exhibited behaviors (residence times and meandering of migration routes) intermediate to those of either species, indicating additive genetic control over early marine migration behavior (Moore et al. 2010b).

Evidence from high-seas tagging experiments has long indicated that open-ocean orientation of Pacific salmonids is not random, and involves sophisticated orientation or true navigation (e.g., Quinn 1991). As in loggerhead sea turtles (Light et al. 1993), steelhead and other salmonids may use inherited geomagnetic compass directions and angles of inclination and anomalies of the earth's magnetic field to navigate during their extensive open-ocean migrations. Although transplantation experiments with tagged steelhead have not been conducted in the open ocean, tagging and transplantation experiments with Atlantic Salmon *Salmo salar* demonstrated stock-specific patterns of migration and orientation in the open ocean (Kallio-Nyberg and Ikonen 1992; Hansen et al. 1993). Stock-specific patterns may result from natural selection of fish migrating by the shortest possible route to open-ocean feeding areas sufficient for growth and reproduction, and intra-stock variation in migration patterns may be related to biological and environmental factors (Kallio-Nyberg and Ikonen 1992). Experimental evidence shows that juvenile steelhead reared in a natural magnetic field orient in the direction of their seasonal oceanic feeding grounds when exposed in the laboratory to magnetic fields occurring at the northern (southeast orientation) and southern (northwest orientation) limits of their known oceanic range (Putman et al. 2014b). In contrast, juvenile steelhead reared in a magnetic field disrupted by building materials commonly used in hatcheries (iron pipes and steel-rebar reinforced concrete) showed random orientation that could influence marine survival and homing ability (Putman et al. 2014b).

Direction of homeward migration of salmonids from offshore waters also seems to involve an inherited crude compass sense of direction (Hansen et al. 1993) or geomagnetic imprinting at out-migration or both. Tagging and tracking studies show that movements of individual adult Pacific salmonids returning from offshore to coastal waters are rapid and direct (e.g., Ogura and Ishida 1995). During out-migration, steelhead smolts may imprint on the magnetic field of their natal streams and later use this information to direct natal homing from the open ocean (Lohmann et al. 2008). An investigation of the geomagnetic imprinting hypothesis using computer modeling indicates that salmon migrating from the open ocean can use simple behaviors incorporating the difference between local and imprinted fields to approach their home river in a narrow migration corridor along a magnetic field isoline, and that either magnetic field inclination angle or magnetic field intensity are sufficient to direct fish to the river mouth from a wide oceanic region (Bracis and Anderson 2012). The first empirical evidence of geomagnetic imprinting in Pacific salmon suggests geomagnetic models can be used to forecast ocean migration routes (Putman et al. 2013). As shown for Fraser River, B.C., Sockeye and Pink Salmon, geomagnetic imprinting (drift of the magnetic field) accounts for more of the variation in long-distance homing migration routes than olfactory imprinting (ocean circulation) or sea surface temperature (Putman et al. 2014a). Nevertheless, future models of orientation and migration need to capture population-specific strategies and responses of fish to variable oceanographic conditions at appropriate scales (Byron and Burke 2014; Hayes and Kocik 2014).

Homing and Straying

Little is known about homing and straying of steelhead during the ocean life history phase, and empirical studies are needed. However, the ability of wild adult steelhead to home to their natal streams using olfactory cues during the freshwater phase of their spawning migration is well established (Dittman and Quinn 1996), and is an important adaptation for maintaining natural spawning populations. In addition, wild adult steelhead can stray to nonnatal streams (e.g., Shapovalov and Taft 1954; see review by Keefer and Caudill 2014). Straying is a natural behavior that enables steelhead to avoid unfavorable environmental conditions and to colonize new habitats (Quinn 1993; see reviews by Keefer and Caudill 2012, 2014). Keefer and Caudill (2014) estimated the mean donor stray rate for studies they reviewed (13.8%, combined summer and winter steelhead), although there was considerable variability in research methods and life history traits of the populations in these studies. Summer-run steelhead, entering streams 6–10 months prior to spawning, may have reduced olfactory sensitivity (Keefer and Caudill 2014). Increases in straying of adult steelhead from adjacent streams have been observed after natural disasters such as volcanic eruptions (e.g., Leider 1989). Climate and ocean conditions likely affect homing and straying proportions in steelhead populations, however, this has not been investigated.

Straying of hatchery steelhead is a concern because of potential genetic and ecological effects on wild steelhead populations (Keefer and Caudill 2014). Documented straying between Coastal Oregon steelhead Distinct Population Segments, which were based in part on differences northward- or southward ocean migration patterns, suggests that some hatchery steelhead migrate past their release basin and enter an adjacent Distinct Population Segment basin or that ocean migration patterns are more variable than previously indicated (Schroeder et al. 2001). Straying sometimes may be overestimated because steelhead may enter nonnatal streams along their homeward migration route. Locally-adapted hatchery steelhead stray less than transplanted populations, however, straying of hatchery releases can potentially affect wild steelhead over a large geographic area (Schroeder et al. 2001). A genetic study indicated that local steelhead populations have higher reproductive success than strays from nonlocal populations (Narum et al. 2006). A numerical model of steelhead straying in the Snake River showed that even at low (~1%) stray rates large donor hatchery populations could numerically overwhelm small recipient native populations (Keefer and Caudill 2012).

Timing of Entry into Freshwater for Spawning

Timing of steelhead entry into freshwater for spawning is a highly diverse adaptive trait (Table 15). Steelhead enter rivers throughout the year at various stages of sexual maturity from completely immature to completely mature, however, the overall pattern is generally classified into two opposite categories—stream-maturing or ocean-maturing (Table 1; Burgner et al. 1992). Stream-maturing steelhead are immature at freshwater entry, typically entering rivers in summer and fall (commonly called summer or summer-run steelhead), where they overwinter and spawn the following spring. Ocean-maturing steelhead (commonly called winter-run steelhead) are sexually mature at freshwater entry, typically entering rivers in winter and spring and spawning shortly thereafter. Genetic data do not support the hypothesis that ocean- and stream-maturing fish are separate monophyletic units (see review by Busby et al. 1996); that is, when both ocean- and stream-maturing steelhead occur in the same river system, they are genetically more similar to each other than to populations with similar run timing in adjacent systems. An investigation of steelhead returning to the Kalama River, Washington, found that stream-maturing and ocean-maturing steelhead can be differentiated by levels of stored (somatic) lipids (twice as high in stream-maturing fish) but not by marine trophic position and location, as indexed by stable isotopes of N and C (Lamperth et al. 2017). Perhaps this might be a useful technique to distinguish seasonal ecotypes of steelhead on the high seas.

In western Kamchatka, most steelhead are stream-maturing, commonly called the hiemal (fall) race (Table 1) because they enter rivers in September and October, as well as under the ice in November, and spawn in May–June (Table 15; Savvaitova et al. 1973, 1999, 2007; Maksimov 1976; Kuzishchin et al. 2008). However, small numbers of ocean-maturing (vernal race or spring-run) steelhead enter western Kamchatka rivers in early May, e.g., the Bolshaya River (Maksimov 1976), Utkholok River (Savvaitova et al. 1973), and the Kekhta River, and spawn immediately thereafter (Savvaitova et al. 2007). Kamchatka fishermen have also re-

Table 15. Months of adult freshwater entry (shaded), spawning (s), and peak spawning (P) timing for selected natural populations of steelhead. Run types of steelhead are indicated by (O) = ocean-maturing and (S) = stream-maturing. Months: March (3), April (4), May (5), June (6), July (7), August (8), September (9), October (10), November (11), December (12). Source: Updated from Busby et al. 1996 with addition of data on Kamchatka populations (Savvaitova et al. 1973, 1999, 2007; Maksimov 1976; Kuzishchin et al. 2008).

Region	Month of adult freshwater entry																
Stock (run)	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7
Western Kamchatka																	
Snatolvayam (S)							▨	▨	▨								
Kvachina (S)							▨	▨									
Utkholok (S)							▨	▨	▨						S	S	
Utkholok (O)															▨		
Kol (S)															S	S	
Utka (S)						▨	▨	▨	▨					S	S	S	
Bolshaya (S)						▨								S	S		
Bolshaya (O)														▨ S	▨ S		
Southcentral Alaska																	
Karluk (S)						▨	▨	▨									
Anchor (S)						▨	▨	▨									
Southeast Alaska																	
Situk (S)						▨	▨	▨	▨	▨ P	▨ P	▨	▨				
Situk (O)												▨	▨	▨	▨	▨	
Sitkoh (O)														▨	▨	▨	
Karta (O)														▨	▨	▨	
Puget Sound, Washington																	
Nooksack (O)									▨	▨	▨	▨ S	▨ S	▨ S	▨ P	S	
Samish (O)									▨	▨	▨	▨ S	▨ S	P	S		
Skagit (O)									▨	▨	▨	▨	▨ S	▨ S	P	S	
Sauk (S)					▨	▨	▨	▨					S	S			
Cascade (S)			▨	▨	▨	▨	▨	▨			S	S	S	S			
Stillaguamish (O)									▨	▨	▨	▨	▨ S	▨ S	P	S	
Deer (S)					▨	▨	▨	▨						S	S		
SF Stillaguamish (S)			▨	▨	▨	▨	▨	▨			S	S	S	S			
Snohomish (O)									▨	▨	▨	▨	▨ S	▨ P	S	S	
NF Skykomish (S)					▨	▨	▨	▨									
L. Washington (O)										▨	▨	▨	▨	▨	▨		
Green (O)										▨	▨	▨	▨ S	▨ P	▨ P	S	
Puyallup (O)										▨	▨	▨	▨ S	▨ P	▨ P	S	
Nisqually (O)											▨	▨	▨ S	▨ P	▨ P	S	
Deschutes (O)									▨	▨	▨ S	▨ P	▨ S	S			
South Sound Inlets (O)										▨	▨	▨ S	▨ P	P			
Tahuya (O)										▨	▨	▨ S	▨ S	P	S		
Skokomish (O)										▨	▨	▨ S	▨ S	P	S	S	
Dewatto (O)										▨	▨	▨ S	▨ S	P	S		
Discovery Bay (O)										▨	▨	▨ S	▨ S	P	S	S	
Dungeness(O)										▨	▨	▨	▨ S	S	P	S	
Morse (O)										▨	▨	▨ S	▨ S	P	S	S	

Table 15. Continued.

Region	Month of adult freshwater entry																
Stock (run)	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7
Olympic Peninsula, Washington																	
Pysht (O)										▨	▨	S	S	P	S	S	
Hoko (O)									▨	▨	▨	S	S	P	S	S	
Quillayute (O)										▨	▨	S	S	P	P	S	
Quillayute (S)			▨	▨	▨	▨	▨	▨									
Hoh (O)										▨	▨	S	S	P	P	S	
Hoh (S)			▨	▨	▨	▨	▨	▨									
Queets (O)									▨	▨	▨	S	S	P	P	S	
Queets (S)			▨	▨	▨	▨	▨	▨									
Quinault (O)									▨	▨	▨	S	S	P	P	S	
Quinault (S)			▨	▨	▨	▨	▨	▨									
Moclips (O)									▨	▨	S	S	S	P	P	S	
Copalis (O)									▨	▨	▨	S	S	S	S	S	
Southwest Washington																	
Humptulips (O)										▨	▨	S	S	P	P	S	
Humptulips (S)			▨	▨	▨	▨	▨	▨									
Hoquiam (O)										▨	▨	S	S	P	P	S	
Wishkah (O)										▨	▨	S	S	P	P	S	
Wynoochee (O)										▨	▨	S	S	P	P	S	
Satsop (O)										▨	▨	S	S	P	P	S	
Chehalis (O)										▨	▨	S	S	P	P	S	
Skookumchuck (O)										▨	▨	S	S	P	P	S	
Willapa Bay (O)										▨	▨	S	S	P	P		
Columbia River Basin, Washington																	
Grays (O)										▨	▨	▨	S	S	S	S	
Elochoman (O)										▨	▨	▨	S	P	P	S	
Mill, WA (O)										▨	▨	▨	S	P	P	S	
Abernathy, WA (O)										▨	▨	▨	S	P	P	S	
Germany Ck, WA (O)										▨	▨	▨	S	P	P	S	
Columbia River Basin (CRB)																	
FW entry (S)	▨	▨	▨	▨	▨	▨	▨	▨									
Lower Columbia River																	
Cowlitz, WA (O)										▨	▨	▨	S	S	S	S	
Toutle, WA (O)										▨	▨	▨	S	P	P	S	
Coweeman, WA (O)										▨	▨	▨	S	S	S	S	
Kalama, WA (O)										▨	▨	▨	S	P	P	S	
Kalama, WA (S)				▨	▨	▨	▨	▨			S	S	S	S			
Lewis, WA (S)			▨	▨	▨	▨	▨	▨	▨				S	S	S	S	
Willamette, OR (O)														▨	S	P	S
Clackamas, OR (O)													▨	▨	S	P	P
Washougal, WA (S)			▨	▨	▨	▨	▨	▨	▨				S	S	S	S	
Wind, WA (S)			▨	▨	▨	▨	▨	▨	▨				S	S	S		
White Salmon, WA (S)			▨	▨	▨	▨	▨	▨	▨				S	S	S		
Middle Columbia River																	
Klickitat, WA (S)			▨	▨	▨	▨	▨	▨	▨				S	S	S		
Fifteenmile, OR (O)												▨	S	S			
Deschutes, OR (S)				▨	▨	▨	▨	▨	▨	▨		S	S	S	S		
John Day, OR (S)						▨	▨	▨	▨	▨	▨	▨	S	S	S		

Table 15. Continued.

Region	Month of adult freshwater entry																
Stock (run)	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7
Rock, OR (S)			▨	▨	▨	▨	▨	▨	▨				S	S	S		
Walla Walla, WA (S)								▨	▨	▨	▨	▨	▨ S	S	S		
Touchet, WA (S)										▨	▨	▨	▨ S	P	P		
Yakima, WA (S)							▨	▨	▨	▨	▨	▨ S	▨ S	▨ P	▨ S		
Upper Columbia River																	
Wenatchee, WA (S)					▨	▨	▨	▨	▨	▨	▨	▨	▨ S	▨ S	P	S	S
Entiat, WA (S)							▨	▨	▨	▨	▨	▨	▨ S	▨ S	P	S	S
Methow, WA (S)					▨	▨	▨	▨	▨	▨	▨	▨	▨ S	▨ S	▨ S	▨ S	S
Okanogan, WA (S)					▨	▨	▨	▨	▨	▨	▨	▨	▨ S	▨ S	▨ S	▨ S	S
Snake River Basin																	
A-run FW entry (S)				▨	▨	▨											
B-run FW entry (S)						▨	▨	▨									
Tucannon, WA (S)								▨	▨	▨	▨	▨	▨ S	P	P		
Asotin, WA (S)								▨	▨	▨	▨	▨	▨ S	P	P		
Grande Ronde, OR (S)						▨	▨	▨	▨	▨	▨	▨	▨ S	S	S		
Oregon Coast																	
Yaquina (O)								▨	▨	▨ S	▨ S	▨ S	▨ S	S			
Rogue (S)			▨	▨	▨	▨	▨				P	P	S	S			
Klamath Mountains Province																	
Smith, CA (O)										▨	▨ S	▨ P	▨ S	▨ S			
Smith, CA (S)					▨	▨	▨	▨		S	P	S					
Klamath, CA (O)							▨	▨	▨	▨	▨ S	▨ S	▨ S	▨ P	▨ S	▨ S	
Klamath, CA (S)		▨	▨	▨	▨	▨	▨	▨		S	P	S					
Trinity, CA (O)							▨	▨	▨ S	▨ P	▨ P	▨ P	▨ P	▨ S	▨	▨	
Trinity, CA (S)			▨	▨						S	P	S					
Northern California																	
Redwood (O)									▨	▨ S	▨ P	▨ S	▨ S				
Redwood (S)		▨	▨	▨	▨												
Mad (O)							▨	▨	▨	▨	▨ S	▨ P	▨ P	▨ S			
Mad (S)		▨	▨	▨													
Jacoby (O)										▨ S	▨ S	▨ P	▨ P	▨ S	▨		
Freshwater (O)										▨ S	▨ S	▨ P	▨ P	▨ S	▨		
Eel (O)							▨	▨	▨ S	▨ S	▨ P	▨ P	▨ S	▨ S	▨	▨	
Eel (S)	▨	▨	▨	▨	▨	▨	▨	▨		S	P	S	S				
Pudding (O)									▨	▨ S	▨ P	▨ P	S				
Casper (O)										▨	▨	▨ S	▨ P	▨ S	▨	▨	
Gualala (O)									▨	▨	▨ S	▨ P	▨ S				
California Central Valley																	
Sacramento Basin																	
Early run (O)						▨	▨	▨	▨	▨ S	▨ S	▨ P					
Late run (O)									▨	▨ S	▨ P	▨ P	▨ S	S			
American (O)								▨	▨	▨ S	▨ P	▨ P	▨ S	▨ S	▨ S		
Feather (O)							▨	▨	▨ S	▨ S	▨ P	▨ P	▨ S	▨ S	▨ S	▨ S	
Mokelumne (O)								▨	▨	▨ S	▨ S	▨ P	▨ S	▨ S	S		

Table 15. Continued.

Region	Month of adult freshwater entry																
Stock (run)	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7
Central California Coast																	
Russian (O)								▨	▨	▨ S	▨ P	▨ P	▨ P	▨ S	S		
San Gregorio (O)										▨ S	▨ S	▨ P	▨ S	▨			
Waddell (O)									▨	▨ S	▨ P	▨ P	▨ P	▨ S	▨ S		
Scott (O)									▨	▨ S	▨ P	▨ P	▨ P	▨ S	▨ S	▨	
South Central California Coast																	
San Lorenzo (O)									▨	▨ S	▨ S	▨ P	▨ S	▨			
Carmel (O)											▨ S	▨ P	▨ P	▨ S			
Southern California																	
Santa Ynez (O)									▨	▨ S	▨ S	▨ P	▨ P	▨ S	▨ S	S	
Ventura (O)							▨	▨	▨	▨	▨ S	▨ P	▨ P	▨ S	▨ S	▨ S	
Santa Clara (O)									▨	▨ S	▨ S	▨ P	▨ P	▨ S	▨ S	▨ S	
Malibu (O)										▨	▨ S	▨ P	▨ P		S		

ported that small numbers of ocean-maturing steelhead enter the Opala River in spring (Savvaitova et al. 2007). Although precise migration dates for ocean-maturing Kamchatka steelhead are not known, the open-ocean migration model proposed by Kovalenko et al. (2005) does not preclude the possibility of an early (May–June) run of ocean-maturing steelhead to western Kamchatka (see *Seasonal Migration Model of Major Stocks*).

Busby et al. (1996) compiled data on timing of freshwater entry of natural populations of steelhead in Alaska and along the U.S. West Coast (Table 15). Ocean-maturing steelhead have the broadest geographic distribution, occurring in nearly all coastal rivers of Washington, Oregon, and California, south to Malibu Creek. Stream-maturing steelhead are less common. However, in the Columbia River Basin all inland steelhead are stream maturing. There is a high degree of overlap in timing of freshwater entry among populations with the same ocean- or stream-maturing run type and, among all populations, in spawn timing regardless of run type. Nevertheless, California populations spawn earlier (December) than populations farther to the north, e.g., most Washington steelhead begin spawning in February or March. In the Columbia River, inland populations spawn later than lower river populations. In southeast Alaska, the dominant run type is ocean-maturing (March to early June entry timing) in all river systems except rivers with headwaters in Canada (called transboundary rivers). Stream-maturing steelhead have been documented as a relatively minor component of total returns to 36 streams in southeast Alaska (Alaska Department of Fish and Game, unpublished data). In contrast, stream-maturing steelhead (August–October entry timing) are the dominant run type in southcentral Alaska. In both southeast and southcentral Alaska, steelhead spawn in spring (mid April–early June).

Factors Affecting Ocean Distribution and Migration Timing

Sea temperature.—The preponderance of evidence from field research indicates that sea temperature is the primary physical factor influencing the distribution of steelhead in the open ocean. In general, steelhead in the open ocean are distributed between the 15°C isotherm (southern boundary) and 5°C isotherm (northern boundary), and shifts in distribution are associated with seasonal changes in sea surface temperature (SST) (Sutherland 1973). For example, in the central North Pacific Ocean and Gulf of Alaska (170°E–145°W), the distribution of steelhead (all age/maturity groups combined), as indicated by Japanese research vessel catch data (1981–1989), shifts northward with respect to SSTs from late spring to summer (Burgner et al. 1992; peak CPUEs at 7.0–7.9°C in May, 8.0–8.9°C in June, 9.0–9.9°C in July). As a result, the main body of feeding-migrating steelhead in this region is located well north of the subarctic boundary (vertical 34.0 isohaline, Favorite et al. 1976) and south of the Aleutian Islands.

Similarly, the northwestward extent of distribution of steelhead in the western North Pacific Ocean (Figure 7) appears to be related to seasonal warming of sea surface temperatures (SST) (Kovalenko et al. 2003, 2005). In the vicinity of the Kuril Islands during 1996–2002, no steelhead were caught in surface gillnet surveys during May and most of June at SSTs < 5.4°C. During late June and early July, steelhead were distributed south of 46°N at SSTs of 5.5–7.8°C. As temperatures near the Kuril Islands increased in July and August (up to 7–10°C), steelhead occurred throughout the area to as far north as 50°30'N, and began entering the southern Okhotsk Sea by the end of July. The majority of steelhead in this region were caught at SSTs of 7–11.0°C.

Field-based evidence from high seas research vessel surveys (1956–1996) suggests that steelhead respond behaviorally to upper and lower temperature thresholds that limit latitudinal distribution across most of the width of the North Pacific (Welch et al. 1998). Lower thermal limits of steelhead, however, are not well defined due to the lack of winter data. The upper thermal limits of distribution of steelhead (all age and maturity groups combined) from winter to early summer were at sea surface temperatures (SSTs) of about 11°C, and increased to 12–15.5°C by August. Thermal limits of steelhead distribution were largely stable over four decades (1956–1996), however, upper thermal limits showed statistically significant fine-scale differences between oceanic regions (<2°C) and between decades (<0.5°C). In winter and spring, the latitudinal ranges of upper and lower SST limits and freshwater spawning distribution of North American steelhead were roughly matched, suggesting that thermal requirements of steelhead at ocean entry might drive freshwater distribution (Welch et al. 1998).

Climate-driven change in oceanographic conditions in open-ocean feeding areas and along migratory routes of Asian and North American salmon can result in predictable changes in the thermal habitats of steelhead (Welch et al. 1998; Abdul-Aziz et al. 2011). Estimated thermal habitats of steelhead in the North Pacific Ocean and adjacent seas in the 1980s, based on published reference sea surface temperatures of steelhead habitat (6–12.5°C in spring–fall and 5–11°C in winter), were 10.2 million km^2 (2.5 million km^2 in the Gulf of Alaska) in July and 8.3 million km^2 (4.0 million km^2 in the Gulf of Alaska) in December (Abdul-Aziz et al. 2011). Warming of ocean temperatures associated with greenhouse gas emissions may reduce thermal habitats of steelhead in the North Pacific Ocean, possibly resulting in a northward shift in steelhead distribution. As temperatures warm in the Bering Sea, conditions may be more favorable for steelhead in eastern Kamchatka and western Alaska streams that currently host only resident Rainbow Trout (Abdul-Aziz et al. 2011).

Due to bioenergetic constraints, older age-maturity groups of steelhead may have lower thermal preferences in the open ocean than juvenile (ocean age 0) steelhead. For example, bioenergetic model simulations using field-based (1991–2008) input data indicated that optimal temperatures for growth in the open ocean were 14°C for juvenile steelhead and 12°C for older (ocean age-1) steelhead (Atcheson et al. 2012a). Off the coasts of Oregon and Washington, the mean sea surface temperature was 13.4°C (SD 1.4) in the area of highest abundance of juvenile steelhead (37.2–46.3 km offshore) in May–July (Pearcy et al. 1990). During summer trawl surveys in the southward-flowing California Current from central California to southern Oregon, all juvenile steelhead were caught at SSTs less than 14.3°C (Hayes et al. 2016). Hayes et al. (2016) speculated that the half-pounder life history strategy (Table 1), which is relatively common in steelhead of the Klamath region of Northern California, may result from the consistently cool (< 14°C) summer SSTs that persist until fall, when warm (> 14°C) SSTs effectively block migratory pathways to the open ocean, forcing steelhead juveniles to return to cooler natal rivers for overwintering. In the central Gulf of Alaska during June–July 1993–2000, research gillnet sampling found juvenile steelhead distributed at all latitudes sampled from 49°N to 56°N (8–13°C SST), and juveniles were most frequent in catches at 52°N (10°C SST)(Myers et al. 2001). The observed distribution of juvenile steelhead at less than optimal temperatures for growth suggests that when temperatures are within the range of thermal tolerance other factors may play an important role in open-ocean distribution of steelhead.

The extent of offshore distribution of North American steelhead during their second year at sea may be influenced by sea surface temperatures (SSTs) experienced during the first year in the Gulf of Alaska (GOA). For example, first-year ocean growth of ocean age-1 steelhead distributed in the Central Subarctic North Pacific (CNP) during 1991–2009 was positively correlated with GOA SSTs lagged to year of ocean growth, while growth of steelhead that remained in the GOA was not significantly related to GOA SSTs (Atcheson 2010). In addition, in most years ocean age-1 steelhead distributed in the CNP had larger initial (except 1997) and final (except 2001) body weights (estimated from scale growth increments) during their first year at sea than steelhead remaining in the GOA (Atcheson et al. 2012a). This suggests that growth of large juveniles entering the GOA was positively influenced by warm GOA SSTs, and larger fish migrated farther westward (to the CNP or beyond) than smaller fish.

Salinity.—Little is known about the effects of salinity on distribution of steelhead in the North Pacific Ocean. Off the coasts of Oregon and Washington, low mean surface salinity (28.6‰) in the area of highest abundance of juvenile steelhead (37.2–46.3 km offshore in May–July) indicated the influence of freshwater, frequently the Columbia River plume (Pearcy et al. 1990). In the western North Pacific Ocean, research vessel observations indicate that the southern range of Pacific salmon in winter and spring is limited by the upper salinity (halo) limit (Azumaya et al. 2007). While halo limits in the western North Pacific Ocean appear to be species specific, steelhead were not included in analyses by Azumaya et al. (2007). The upper halo limit of Pacific salmon often corresponds to the location of salinity fronts in the North Pacific (Azumaya et al. 2007). The Subarctic Boundary (34.0‰ at 0 m) (Favorite et al. 1976) generally defines the southern limit of salmonid distribution in the Central North Pacific Ocean, and can be considered the upper halo limit of steelhead in the western North Pacific Ocean in winter and spring until more precise information is available.

Current.—The ocean range of steelhead encompasses the five major current systems in the Subarctic Pacific. These current systems include the Okhotsk-Kuril system in the Sea of Okhotsk; the Subarctic Current System, which originates in the Sea of Okhotsk and extends eastward across the Pacific Ocean; the California Current System, located off the U.S. West Coast; the Alaska Current system, which sometimes originates as far south as the mouth of the Columbia River, flows around the perimeter of the Gulf of Alaska and extends westward along the Aleutian-Commander Island Arc and northward into the Bering Sea; and the cyclonically (counterclockwise) flowing Bering Current system (Favorite et al. 1976; McKinnell et al. 2010). While these major current systems likely play an important role in ocean distribution and migration timing, steelhead have never been the focus of research on this topic. The two major gyres in the subarctic North Pacific, the Western Subarctic Gyre and the Gulf of Alaska Gyre likely provide the most productive feeding habitats for steelhead. In the California Current, the recovery of coded-wire tagged juvenile steelhead far to the south of ocean entry locations may be related to advection of surface waters during the upwelling season (Pearcy et al. 1990). In the central Gulf of Alaska gyre, persistent mesoscale (200–300 km) and small (<200 km) eddies may influence primary productivity and the associated distribution of juvenile steelhead trout and their prey (primarily small fish and squid) (Onishi et al. 2000; Myers et al. 2001). Spin up (increased circulation) of the gyre will produce more upwelling and increased production (W. Pearcy, Oregon State University, personal communication).

The effects of tidal currents on the distribution and migration timing of steelhead in river estuaries and inland coastal waters have been investigated to a limited extent by acoustic tagging and tracking studies. In British Columbia inland coastal waters, acoustic-tagged adult steelhead drifted with the tidal currents at night, however, during the day tidal stage and direction of flow did not significantly affect travel rates or orientation (Ruggerone et al. 1990). There were no apparent effects of currents on direction of migration of acoustic-tagged steelhead smolts through the Strait of Georgia, British Columbia (Melnychuk et al. 2010). However, Furey et al. (2015) proposed that observed counterclockwise movements of acoustic-tagged steelhead smolts during outmigration through the Strait of Georgia may be due to counterclockwise tidal and wind-driven surface currents in the region. During high tides and on ebbing (outgoing) flows smolts (e.g., McMichael et al. 2011; Clements et al. 2012) and kelts (Nielsen et al. 2011) moved downstream and entered the ocean. Adult steelhead typically enter rivers from the ocean on high tides and flooding (incoming) flows.

Food availability.—Food availability is likely the primary biological factor affecting distribution of steelhead in the ocean. However, most of the preferred prey consumed by steelhead in the ocean make extensive diel vertical migrations or are distributed in the neuston, and are difficult to sample using conventional plankton nets or fishing gear. Because of the difficulty of synoptic sampling of steelhead and their preferred prey at sea (e.g., Pearcy et al. 1988), the effects of food availability on steelhead distribution are largely speculative. The potential effects of food availability on steelhead growth, survival, and carrying capacity are discussed below (see *Feeding and Growth* and *Survival*).

Interspecific interaction.—Community structure analysis of ocean catch data indicates that juvenile Pacific salmon species tend to co-occur in the ocean (e.g., Brodeur et al. 2004). In the Gulf of Alaska, high overlap in diets of steelhead and other species of Pacific salmon except Chum Salmon (Pearcy et al. 1988), indicates the potential for interspecific interactions if prey resources, especially the gonatid squid *Berryteuthis anonychus*, are limited. While there is no direct evidence on the effects of interspecific interactions on ocean distribution, juvenile (ocean age-0) steelhead are distributed farther offshore than juveniles of other species of Pacific salmon (e.g., Pearcy and Masuda 1982, 1987; Hartt and Dell 1986; Pearcy et al. 1990). The unique behavioral strategies of juvenile steelhead, e.g., rapid offshore migration to the open ocean and distribution at or near the ocean surface, may have evolved to reduce interspecific interactions with more abundant Pacific salmon species. Similarly, the largely dissimilar ocean distribution patterns and ecology of steelhead and Cutthroat Trout (Pearcy et al. 1990) likely evolved to reduce interspecific interactions. The potential growth and survival effects of interactions of steelhead with other species of Pacific salmon, as well as ecological interactions with other species of prey, competitors, and predators, are discussed below (see *Feeding and Growth* and *Survival*).

Feeding and Growth

Food Habits and Feeding Ecology

Information on feeding ecology, that is, what organisms are consumed (food habits), how food is obtained (foraging habits), and where food is located (habitat), is key to understanding the productivity of steelhead. Steelhead are facultative predators able to consume a wide variety of prey and forage in diverse (freshwater, estuarine, coastal marine, and open ocean) habitats. In freshwater habitats, steelhead smolts typically consume small invertebrate or fish prey species that often differ between rivers (e.g., McCabe et al. 1983), depending on prey availability. For example, in the Columbia River, benthic, tube dwelling gammarid amphipods (*Corophium* species) are the dominant prey of steelhead smolts passing the lowermost dam (Bonneville) before entering the estuary (Muir and Emmett 1988). In contrast, steelhead smolts in the Utkholok River in western Kamchatka feed mainly on Chum Salmon parr (Savvaitova et al. 1973).

Generally, steelhead smolts migrate rapidly through river estuaries (see above, T*iming of Entry into Seawater*), and frequently have empty or only partially full stomachs (e.g., Sasaki 1966; Dawley et al. 1986; Daly et al. 2014). Stomach contents commonly include prey obtained in freshwater habitats, also suggesting rapid movement. For example, common invertebrate prey found in the stomachs of steelhead smolts in estuaries include the largely freshwater (salinity <0.1‰) gammarid amphipod *Corophium salmonis*, larval and adult insects (e.g., hymenoptera), and the freshwater benthic Asiatic clam *Corbicula manilensis* (Sasaki 1966; Loch 1982; McCabe et al. 1983; Bottom et al. 1984; Dawley et al. 1986; Bottom and Jones 1990). Juvenile steelhead consume increasing amounts of food as they enter the ocean and migrate offshore (Daly et al. 2014).

In coastal and inland marine habitats, juvenile (ocean age-0) steelhead feed primarily on small fish and zooplankton. Most prey are heavily pigmented and relatively large, revealing the highly visual foraging behavior of juvenile steelhead (Brodeur 1989). In inland waters of Puget Sound, Washington, juvenile steelhead diets are dominated by fish, e.g., Northern Anchovy *Engraulis mordax*, juvenile Chinook Salmon, and smelt (Fresh et al. 1981). In coastal marine habitats off Oregon, the dominant prey of juvenile steelhead varies interannually between euphausiids, which may be abundant during years of strong upwelling (Brodeur 1986; Pearcy et al. 1990), and larval and juvenile fish (Brodeur 1990b; Miller and Brodeur 2007). In some years, Dungeness crab (*Cancer magister*) megalopae are also a dominant prey of juvenile steelhead in coastal waters off Oregon and Washington (Daly et al. 2014). Some prey (insects, barnacle larvae, Cancer spp. megalops larvae, and some fish taxa, e.g., rockfishes, hexagrammids, and anchovy), are commonly associated with the neustonic (surface) layer (Brodeur et al. 1987; Shenker 1988), indicating the surface-foraging behavior of steelhead (Brodeur 1989; Pearcy et al. 1990). There is no apparent relationship between juvenile steelhead size and the size of fish prey in their diets (Pearcy et al. 1990), although the maximum girth of whole fish and squid prey is probably limited by gape width (space between the open jaws) of individual steelhead. That *O. mykiss* is a highly facultative species is demonstrated by anadromy in a population of introduced Rainbow Trout that is now well established in the Atlantic Patagonian shelf habitats, where young steelhead feed primarily on amphipods (Pascual et al. 2001; Ciancio et al. 2008, 2010).

In open-ocean habitats beyond the continental shelf, juvenile (ocean age-0) steelhead in the Gulf of Alaska (GOA) feed primarily on larval and juvenile fish and small gonatid squid (e.g., Myers et al. 2001; Atcheson et al. 2012a, 2012b; Figure 11). The prey of juvenile steelhead includes significantly higher proportions of fish and amphipods than the prey of older age groups (ocean age-1, -2, and -3) of steelhead. Interannual variation in the dominant prey

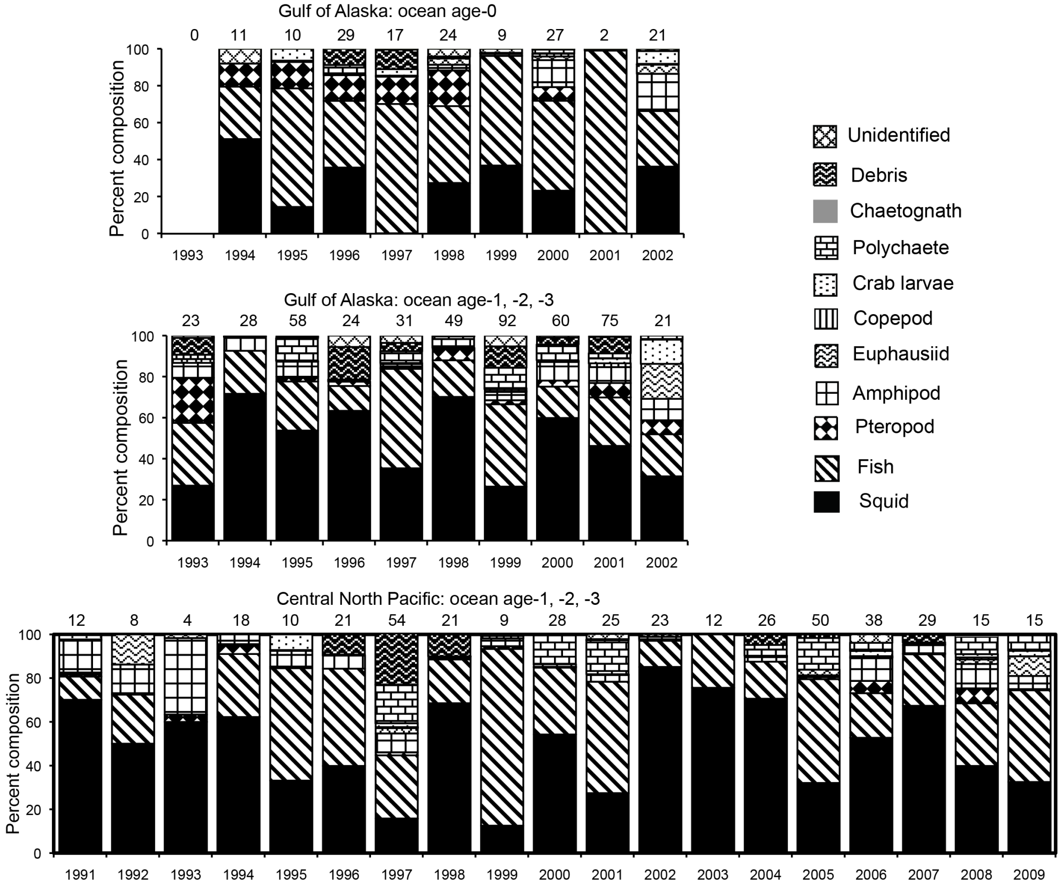

Figure 11. Prey composition (percent volume) of summer diets of steelhead, showing mean diets for ocean age-0 fish in the Gulf of Alaska, 1994–2002 (top), ocean age-1, -2, and -3 fish in the Gulf of Alaska, 1993–2002 (middle), and ocean age-1, -2, and -3 fish in the Central North Pacific, 1991–2009 (bottom). Numbers above the columns are sample sizes. Source: Atcheson et al. 2012b.

of juvenile steelhead (Figure 11) is likely related to changes in prey abundance or distribution with respect to environmental conditions.

Immature, maturing, and adult steelhead are capable of consuming a large variety of prey species in coastal and open ocean marine habitats (e.g., Light 1985; Pearcy et al. 1988; Kovalenko et al. 2005; Atcheson et al. 2012a, 2012b). Thus, Pearcy et al. (1988) categorized steelhead as opportunistic foragers, lacking specialized diets in the open ocean. Food habits data, however, indicate that steelhead in the open ocean specialize to at least to some degree on relatively few species of highly visable micronekton, including cephalopods (especially *Berryteuthis anonychus*), small mesopelagic fish (Myctophids), juveniles of epipelagic fish, crustaceans (adult euphausiids, pelagic decapods, amphipods), pelagic mollusks (pteropods), and pelagic polychaetes (Taylor and LeBrasseur 1957; LeBrasseur 1966; Manzer 1968; Light 1985; Pearcy et al. 1988; Brodeur 1990a; Tadokoro et al. 1996; Kaeriyama et al. 2004; Kovalenko et al. 2005; Atcheson et al. 2012a, 2012b; Qin and Kaeriyama 2016). The stomachs of individual steelhead in open-ocean habitats typically contain only a few species (Burgner et al. 1992). All steelhead caught in the same net haul may have empty stomachs or a high abundance of one prey species, leading Burgner et al. (1992) to speculate that individuals either selectively consume evenly-distributed prey or feed opportunistically on patchily-distributed prey (Burgner et al. 1992). Gelatinous zooplankton, which often comprise the majority of the plankton biomass in the North Pacific Ocean, are not found in steelhead diets (Brodeur 1990a) (Figure 11). Thus, foraging behavior of steelhead in the ocean appears to involve both opportunistic and selective strategies.

Food habits data show considerable spatiotemporal variation in the dominant prey (epipelagic and mesopelagic fish or squid) in diets of immature, maturing, and adult steelhead in the North Pacific Ocean (e.g., Light 1985; Pearcy et al. 1988; Kaeriyama et al. 2004; Kovalenko et al. 2005; Atcheson et al. 2012b; Qin and Kaeriyama 2016). Peak feeding occurs in late spring or early summer (Light 1985), and fish distributed the farthest offshore, particularly south of the Subarctic Boundary, tend to have fuller stomachs and fewer empty stomachs (Light 1985; Pearcy et al. 1988). In pelagic habitats near or over the continental shelf (average depth of about 200 m), steelhead diets are often dominated by fish (especially Atka Mackerel *Pleurogrammus monopterygius*, Threespine Sticklebacks *Gasterosteus aculeatus*, and Northern Lampfish *Stenobrachius leucopsarus*), while gonatid squids often dominate diets in pelagic habitats over the deep western, central, and eastern North Pacific basins (average depth of about 4,000 m). In the central North Pacific and Gulf of Alaska (GOA), gonatid squid (*Berryteuthis anonychus*) are the most important prey consumed by steelhead, contributing to high stomach fullness and prey energy density (Atcheson et al. 2012b). In the eastern North Pacific and GOA, there is a strong latitudinal trend in summer diets of steelhead with an abrupt change near the Subarctic Boundary; the major prey are pelagic fish and polychaetes north of the boundary and gonatid squids south of the boundary (Pearcy et al. 1988; Kaeriyama et al. 2004). These two distinct feeding zones are associated with the July latitudinal sea surface temperature minimum (Aydin et al. 2000). In a two-year study of steelhead diets in the western North Pacific, the dominant prey were squid in the first year and fish in the second year (Light 1985). Longer time series of food habits data show significant interannual variation in primary prey (Figure 11), as well as stomach fullness, average prey energy density, and percentage of steelhead with empty stomachs, and higher interannual variation in regions farther offshore in the CNP than in the GOA (Atcheson et al. 2012b). Interannual variability in steelhead diets probably reflects changes in prey availability, although differences in sample time and location may contribute to observed differences in steelhead diets (Burgner et al. 1992). As facultative predators, steelhead can switch their prey. When prey abundance is low, steelhead may feed nonselectively on prey of various sizes and species, while selection of a single species of large prey and high diet overlap with other species may occur at high prey densities.

Taylor and LeBrasseur (1957) were the first to speculate that steelhead in the open ocean feed at the surface, based on the presence of bird feathers in steelhead stomach contents. Many subsequent food habit studies have supported surface-foraging behavior, for example, showing that steelhead consume plastic and other floating debris, as well as pelagic invertebrate species such as pteropods and polychaetes that swarm in large numbers at the surface (e.g., Atcheson et al. 2012b). Although surface-feeding behavior of steelhead has not been directly observed in the open ocean, high seas catch data suggest that steelhead remain in the near-surface (upper 20 m) layer (Burgner et al. 1992). In the Great Lakes, where *O. mykiss* is an introduced species, steelhead feed very close to the surface under scum lines of insects and debris concentrated by thermal fronts (Haynes et al. 1986; Aultman and Haynes 1993; Höök et al. 2004). Thermal fronts in the North Pacific Ocean are well known as productive feeding habitats for pelagic fishes, but steelhead feeding behavior along thermal fronts in the open ocean has not been investigated.

In the open ocean, immature, maturing, and adult steelhead (ocean age-1 and older) are active pelagic predators (Kovalenko et al. 2003), and probably feed continuously over a 24-h period. Diel variations in feeding habits of Pacific salmon in the Gulf of Alaska indicate a dietary shift from squids, fishes, and amphipods during the day to bioluminescent organisms that migrate vertically to the surface at night, e.g., euphausiids and myctophids, forming dense aggregations readily exploited by steelhead at very low light levels (Pearcy et al. 1984). Comparisons of stomach contents and midwater trawl catches also indicate that steelhead forage at the surface at night (Pearcy et al. 1988). In general, this hypothesis is supported by limited information from data storage tags. For example, a data storage tag record (temperature) from one maturing steelhead in the open ocean (Gulf of Alaska) indicated that at night the fish was located primarily at the surface but made periodic dives to 40–60 m below the surface throughout full 24-h periods (Walker et al. 2000a, 2000b) (Figure 10). Data storage tag records (temperature and depth) from two steelhead kelts (16 months at sea) showed that the fish spent 97% of time (both day and night) near the ocean surface (Nielsen et al. 2011).

The food habits of steelhead in stream, estuary, and ocean habitats reveal an ontogenetic (developmental) shift similar to patterns in other salmonids (Keeley and Grant 2001), i.e., young, small steelhead feed primarily on small fish and invertebrates and older, larger (>40 cm FL) steelhead feed primarily on larger (2–10 cm) actively swimming micronekton (e.g., squid, fish, and euphausiids; Figure 11). This ontogenetic shift is a key feature of steelhead feeding ecology, independent of their native habitats, as demonstrated by exotic steelhead in Patagonia, where young steelhead in coastal marine habitats feed primarily on macrozooplankton (amphipods) and older steelhead in offshore habitats feed primarily on euphausiids, fish, and squid (Ciancio et al. 2008, 2010).

Scientific data on the food habits of adult and kelt steelhead in coastal and inland marine waters are scarce, although anecdotal evidence from saltwater anglers indicates that they feed primarily on small pelagic fish (e.g., herring, anchovy, sandlance, and smelt) in these habitats. There is limited evidence that adult steelhead do not feed in river estuaries (e.g., Sasaki 1966). Steelhead adults and kelts are known to feed in freshwater, however, published scientific data are scarce. In the Snake River, a relatively high percentage (38%) of emigrating steelhead kelts, particularly those in good condition, had food or fecal matter in the gastrointestinal tract (Penney and Moffitt 2014b). An experimental steelhead kelt reconditioning project (i.e., freshwater culture of postspawning fish during the period when they reinitiate feeding and gonad development) indicated more aggressive feeding and better health and survival when kelts were fed a natural marine diet (euphausiids, fish, squid) rather than pelletized feed (D. Hatch, Columbia River Inter-Tribal Fish Commission, personal communication).

Age, Body Size, and Growth of Juvenile, Immature, and Maturing Fish in the Ocean

As in most ectotherms (animals dependent on external sources of body heat), growth of steelhead is regulated by food availability and metabolic rate, which is strongly influenced by water temperature. Accelerated growth under artificial rearing conditions enables release of most hatchery steelhead smolts after only one year of freshwater rearing. Nevertheless, experimental evidence indicates that rearing hatchery steelhead for an additional year before release results in larger smolts and improves out-migration survival and travel times (Tatara et al. 2017). Wild juvenile steelhead have been documented to rear in freshwater for 0–7 years (typically, 2 years) before smoltification and ocean entry (Table 9). Steelhead populations rearing in freshwater habitats with sub-optimal conditions for growth, e.g., high elevations or latitudes (Alaska, British Columbia), low-productivity streams, or interior headwater streams (Columbia and Fraser River basins) tend to smolt at age 3 or older (Withler 1966; Narver 1969; Sanders 1985; Burgner et al. 1992; Harding and Coyle 2011). Smoltification of juvenile steelhead is less related to age than to body size (e.g., Conte and Wagner 1965; Fessler and Wagner 1969) (see above, *Timing of Entry into Seawater*, for additional discussion).

The freshwater age composition of steelhead in the open ocean is uncertain because most studies have used scales rather than otoliths for age determination (Burgner et al. 1992). Juvenile steelhead can experience high scale loss, and replacement (regenerated) scales usually cannot be used to accurately determine freshwater age; see Davis and Light (1985) for steelhead scale and otolith age determination techniques. In addition, accurate determination of freshwater age of steelhead in mixed-stock samples of unmarked hatchery and wild steelhead is difficult. The major difficulties are that scales of freshwater age-1 hatchery steelhead are similar in size to the scales of freshwater age-2 or older wild fish and may have growth checks (bands of closely spaced or broken circuli) that can be misinterpreted as freshwater annuli (Figure 12) (Davis and Light 1985; Bernard and Myers 1996). Estimated proportions of freshwater age-1 steelhead in high seas samples collected during the 1980s (Figure 13) were lower than expected given the high abundance of North American hatchery steelhead (Table 2); however, they were substantially higher than in the 1950s and 1960s when hatcheries were less widespread and less successful (Burgner et al. 1992).

The results of experiments in which two steelhead populations, one from Northern California Central Valley (Upper Sacramento River basin) and one from Coastal Central California (Scott Creek) were reared in a common laboratory environment, showed population-specific differences in size thresholds for smolting, and indicated that the condition of fish soon after emergence may significantly affect whether steelhead adopt a freshwater resident or smolt life history strategy (Beakes et al. 2010). The approximate size threshold for marine survival of steelhead smolts is 15 cm (Ward and Slaney 1988; Bond et al. 2008; Hayes et al. 2011). At the southern extent of their North American range (Southern California Distinct Population Segment region; Table 3) both resident and anadromous *O. mykiss* in Topanga

Figure 12. Examples of the freshwater and early marine portions of steelhead scales. Left panel: scale from a freshwater age-1 male hatchery steelhead (510 mm fork length). Right panel: scale from a freshwater age-2 female wild steelhead (690 mm fork length). Both fish were sampled at Priest Rapids Dam, Columbia River, Washington, on September 18, 1990. The arrows indicate the transition between freshwater and marine growth. Source: Bernard and Myers 1995.

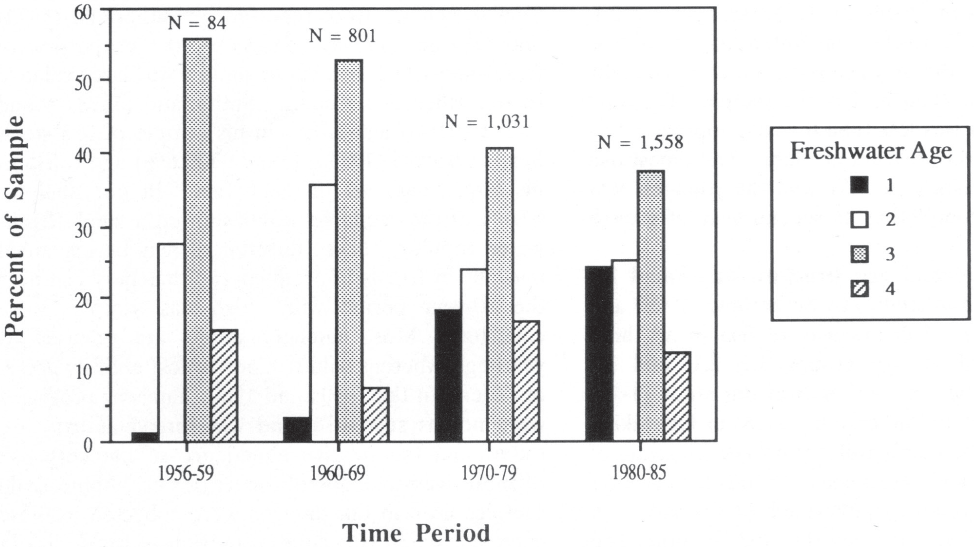

Figure 13. Trends in freshwater age composition of high-seas steelhead samples, 1956–1985 (N = 3,475 fish). Source: Figure 7, Burgner et al. 1992.

Creek, Los Angeles County, California, grow throughout the year, even when summer water temperatures are high (daily maximum >23°C), and smolts reach a large size (>17 cm) at age 2 associated with high (>10%) marine survival in northern populations (Bell et al. 2011).

Few studies have reported growth rates of juvenile steelhead in coastal marine waters. Juvenile steelhead distributed in the California Current region (off the Oregon and Washington coast) in May and June, 1981–1985, had mean back-calculated fork lengths (FL) at ocean entry of 19.9 cm (SD = 29 mm FL, n = 84 fish) and the estimated average growth rate was 1 mm/d (Pearcy et al. 1990). The range of lengths of juvenile steelhead in purse seine catches was broad, perhaps due to variable size and age at ocean entry or variable growth rates among stocks in mixed-stock ocean samples (Pearcy et al. 1990). As indicated by genetic stock identification, juvenile steelhead distributed in the California Current region (off California and Oregon) in June and August 2000 included only stocks from rivers located south of Cape Blanco, i.e., the Rogue River and nearby Oregon coastal streams (53%), Sacramento and San Joaquin rivers (14%), northern California coastal rivers (10%), and central and southern California coastal rivers (3%), although the stock origins of approximately 19% of the fish were unknown due to incomplete genetic baseline data (Brodeur et al. 2004). In the Oregon-Washington coastal region in 2006, estimated mean size of juveniles at ocean entrance was larger for hatchery fish (22.4 cm FL, SD = 24.6 mm, n = 16) than wild fish (21.1 cm FL, SD = 46.3 mm, n = 5 fish), while marine growth rates were similar (0.33 mm/d hatchery, 0.30 mm/d wild)(Daly et al. 2014). Variation in early marine growth rate of steelhead smolts migrating through the Columbia River estuary can be partially explained by population-specific variation in body size and timing at ocean entry (Weitkamp et al. 2015).

Burgner et al. (1992) analyzed long-term (1955–1985) field data on body size and growth of juvenile (ocean age 0), immature, and maturing steelhead in the open ocean. Despite significant statistical differences in body size of steelhead caught by various types of fishing gear (purse seines, gillnets, and longlines), data were pooled over all gear types and years to obtain a full range of body sizes for growth analyses. Juvenile steelhead were poorly represented in these data because of selectivity of fishing gear for larger fish. Statistical differences between sexes in ocean age-specific body sizes of steelhead were not considered to be biologically significant. Mean monthly fork lengths indicated rapid and continuous growth of steelhead, especially during the first two years at sea (Figure 14). The body length-weight relationship of steelhead in these samples (Figure 15) was similar to relationships for both ocean- and stream-maturing steelhead derived using back-calculation procedures from adult steelhead scales (e.g., Hooton et al. 1987; Pearcy et al. 1990).

Information on ocean growth rates of maturing and kelt steelhead is sparse. The estimated growth rate of a maturing steelhead (445 mm FL) tagged and released near the mouth of the Columbia River and recovered 79 d later in the Columbia River was 0.63 mm/d (Pearcy et al. 1990). Body lengths of repeat-spawning steelhead in Forks Creek, Washington, were shorter than those of first-time spawners of the same age, reflecting reduced growth associated with spawning (Quinn et al. 2011).

Age at Maturity and Repeat Spawning

Steelhead typically spend 1–3 years in the ocean before returning to spawn for the first time (e.g., Savvaitova et al. 1973; Okazaki 1984a; Burgner et al. 1992; Busby et al. 1996). Attempts to determine the maturity composition of steelhead at sea have been largely unsuccessful because most ocean sampling is done in April–September, well before most ocean-matur-

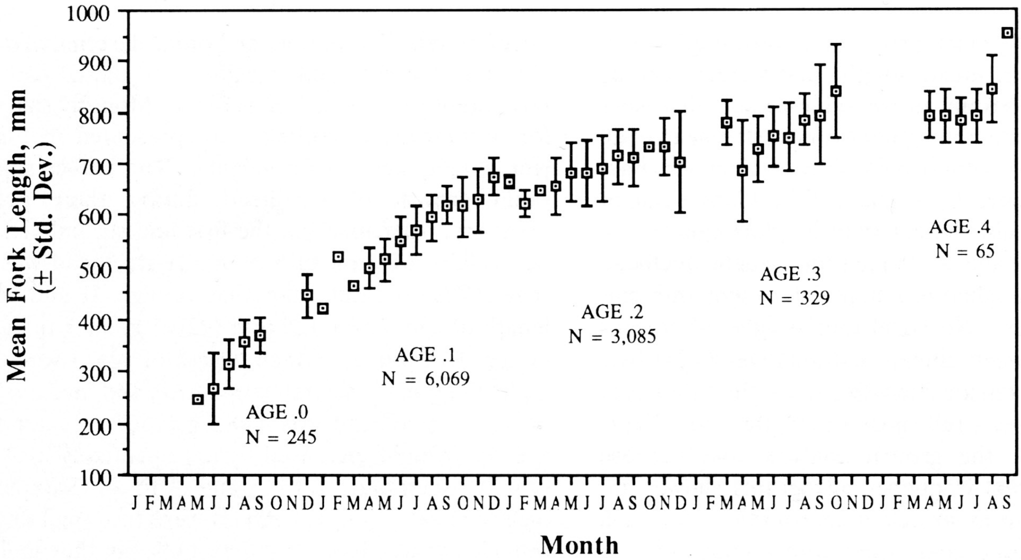

Figure 14. Mean monthly lengths of ocean-caught steelhead by ocean age group, 1955–1985 (*N* = 9,824 fish). Apparent decreases in mean length between age groups likely reflects migration of larger, maturing individuals to freshwater (Source: Burgner et al. 1992).

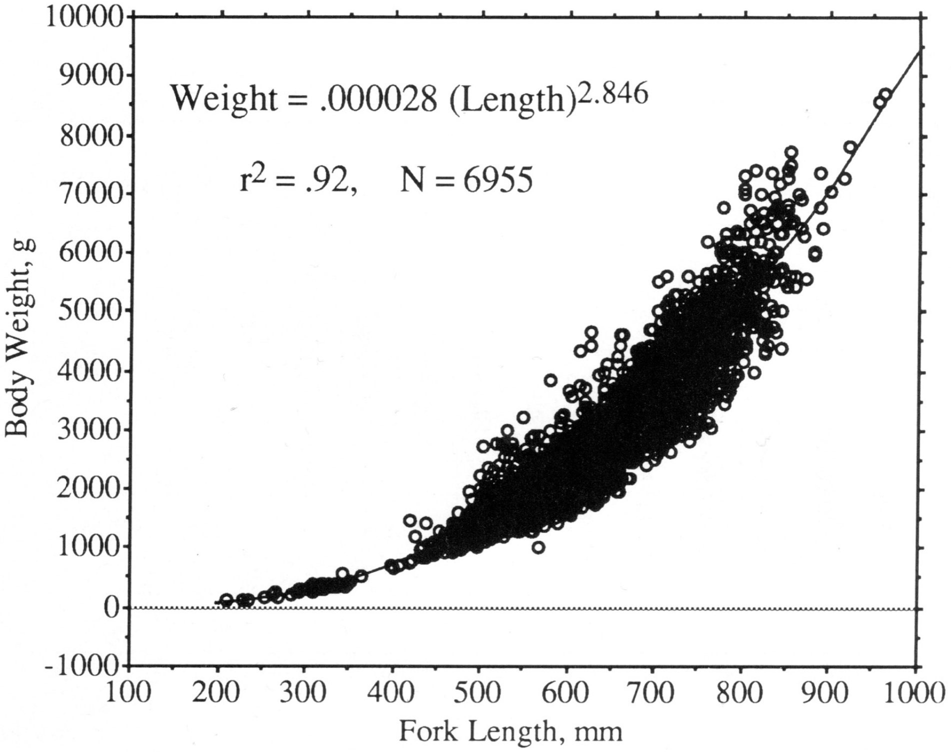

Figure 15. Length-weight relationship for ocean-caught steelhead (*N* = 6,955 fish). Source: Burgner et al. 1992.

Table 16. Ocean age at maturity. Values are age frequency at river entry for first-time spawning migrations for selected Russian (Western Kamchatka) and North American steelhead populations. Modal values are presented in bold font. Populations are generally arranged from north to south. Data are the number of ocean annuli counted on adult steelhead scales. Run type: stream-maturing (S); ocean-maturing (O) steelhead. For stream-maturing steelhead, the data generally do not include the additional time spent in freshwater prior to spawning. Ck. = creek; D. = dam, L. = lower, M. F. = middle fork. Sample size: n/a = sample size not reported in reference. Source: Updated from Busby et al. (1996) by addition of data for western Kamchatka steelhead (Savvaitova et al. 1973; Maksimov 1976).

		Ocean age at river entry							
Population	Run type	0	1	2	3	4	5	Sample size	Reference
Western Kamchatka									
Snatolvayam	S^a	--	0.08	**0.47**	0.28	0.17	--	53	Savvaitova et al. 1973
Kvachina	S^a	--	0.07	**0.58**	0.30	0.04	0.01	217	Savvaitova et al. 1973
Utkholok	S^a	--	0.16	**0.55**	0.23	0.06	--	64	Savvaitova et al. 1973
Utka	S^a	--	0.31	**0.43**	0.22	0.03	0.01	68	Savvaitova et al. 1973
Bol'shaya	S^a	--	0.05	**0.56**	0.39	--	--	18	Maksimov 1976
Southcentral Alaska									
Karluk	S	--	0.18	**0.79**	0.03	--	--	62	Sanders 1985
Anchor	S	--	0.26	**0.74**	--	--	--	80	Sanders 1985
Upper Copper	S	--	0.17	**0.77**	0.06	--	--	30	Sanders 1985
Southeast Alaska									
Situk	S/O	--	--	**0.57**	0.43	--	--	211	Sanders 1985
Sitkoh	O	--	--	**0.59**	0.41	--	--	497	Sanders 1985
Karta	O	--	<0.01	**0.72**	0.27	--	--	542	Sanders 1985
British Columbia (mainland)									
Babine	S	--	0.10	**0.72**	0.18	--	--	100	Narver 1969
Cheakamus	O	--	--	**0.52**	0.40	0.08	--	64	Withler 1966
Capilano	O	--	--	**0.67**	0.33	--	--	70	Withler 1966
Capilano	S	--	0.01	**0.56**	0.42	0.01	--	86	Withler 1966
Seymour	O	--	0.07	**0.57**	0.34	0.02	--	58	Withler 1966
Seymour	S	--	--	**0.64**	0.36	--	--	25	Withler 1966

Table 16. Continued.

Population	Run type	Ocean age at river entry						Sample size	Reference
		0	1	2	3	4	5		
British Columbia (Fraser River Basin)									
Coquitlam	O	--	0.01	**0.73**	0.23	0.03	--	146	Withler 1966
Alouette	O	--	--	**0.50**	0.46	0.04	--	131	Withler 1966
Chilliwack	O	--	<0.01	**0.50**	0.49	<0.01	--	770	Maher and Larkin 1955
Chehalis	O	--	--	0.50	0.50	<0.01	--	111	Withler 1966
Coquihalla	O	--	0.05	**0.64**	0.31	--	--	39	Withler 1966
Coquihalla	S	--	0.12	**0.83**	0.05	--	--	150	Withler 1966
British Columbia (Vancouver Island)									
Keough	O	--	0.01	**0.65**	0.34	<0.01	--	1,391	Ward and Slaney 1988
Nanaimo	?	0.01	**0.68**	0.31	--	--	--	228	Narver and Withler 1974
Nahmint	S	--	0.05	**0.91**	0.03	--	--	58	Narver 1974
Puget Sound, Washington									
Skagit	O	--	--	**0.57**	0.42	0.01	--	n/a[b]	WDFW 1994
Deer Ck	S	--	1.00	--	--	--	--	n/a	WDF et al. 1993
Snohomish	O	--	--	**0.57**	0.42	0.01	--	n/a	WDF et al. 1993
Green	O	0.02	0.07	**0.66**	0.25	--	--	100	Pautzke and Meigs 1941
Puyallup	O	--	--	**0.70**	0.30	--	--	n/a	WDFW 1994
Nisqually	O	--	--	**0.63**	0.36	0.01	--	n/a	WDFW 1994
Olympic Peninsula, Washington									
Quillayute	O	--	--	**0.53**	0.45	0.02	--	n/a	WDF 1994
Hoh	O	--	0.02	**0.81**	0.17	--	--	n/a	Larson and Ward 1954
Southwest Washington									
Chehalis	O	--	0.07	**0.72**	0.20	0.01	--	n/a	Larson and Ward 1954
Lower Columbia River (Washington)									
Toutle	O	--	0.08	**0.81**	0.11	--	--	37	Howell et al. 1985
Cowlitz	O	--	--	**0.64**	0.34	0.02	--	56	Howell et al. 1985
Kalama	O	--	0.04	**0.76**	0.20	--	--	1,363	Howell et al. 1985
Kalama	S	--	0.20	**0.74**	0.06	--	--	909	Howell et al. 1985
Washougal	S	--	0.14	**0.71**	0.14	--	--	7	Howell et al. 1985

Table 16. Continued.

Population	Run type	Ocean age at river entry						Sample size	Reference
		0	1	2	3	4	5		
Lower Columbia River (Oregon)									
Willamette	O	--	--	**1.00**	--	--	--	141	Howell et al. 1985
Middle Columbia River (Washington)									
Klickitat	S	--	0.16	**0.79**	0.05	--	--	148	Howell et al. 1985
Yakima	S	--	**0.51**	0.47	0.02	--	--	64	BPA 1992
Middle Columbia River (Oregon)									
Deschutes	S	--	**0.53**	0.47	0.02	--	--	100	Howell et al. 1985
John Day	S	--	**0.51**	0.44	0.04	--	--	115	Howell et al. 1985
Upper Columbia River (Washington)									
Wenatchee	S	--	**0.76**	0.18	0.06	--	--	17	Howell et al. 1985
Entiat	S	--	**0.88**	0.12	--	--	--	8	Howell et al. 1985
Above Wells	S	--	0.30	**0.70**	--	--	--	349	Mullan et al. 1992
Snake River Basin (Washington)									
L. Granite D.	S	--	0.29	**0.55**	0.16	--	--	100	Hassemer 1992
Snake River Basin (Idaho)									
Clearwater	S	--	**0.61**	0.38	0.01	--	--	510	Whitt 1954
S.F. Salmon	S	--	--	0.20	0.80	--	--	65	BPA 1992
Lemhi	S	--	0.09	**0.86**	0.05	--	--	353	BPA 1992
Oregon (coastal)									
Nehalem	O	--	0.07	**0.84**	0.08	--	--	310	Weber and Knispel 1977
Alsea	O	--	0.05	**0.66**	0.26	0.03	--	978	Chapman1958
Siuslaw	O	--	--	**0.82**	0.17	0.01	--	125	Lindsay et al. 1991
Rogue[b]	O	--	0.14	**0.86**	--	--	--	547	ODFW 1990
Klamath Mountains Province (Oregon and northern California)									
Klamath	S	--	**0.78**	0.22	<0.01	--	--	391	Kesner and Barnhart 1972

Table 16. Continued.

Population	Run type	Ocean age at river entry						Sample size	Reference
		0	1	2	3	4	5		
Northern California									
Mad	O	--	0.28	**0.69**	0.03	--	--	35	Forsgren 1979
Jacoby Ck	O	--	0.35	**0.63**	0.02	--	--	109	Harper 1980
Van Duzen	S	--	0.09	**0.62**	0.29	--	--	58	Puckett 1975
M. F. Eel	S	--	**0.56**	0.42	0.02	--	--	82	Puckett 1975
California Central Valley									
Sacramento	O	--	**0.57**	0.43	--	--	--	83	Hallock 1989
Central California Coast									
Waddell Ck	O	--	**0.60**	0.40	<0.01	--	--	3,888	Shapovalov and Taft 1954

[a] Includes only "typically marine" (not "coastal") life history type.

[b] Adults with half-pounder life history (spawning migrants, ODFW 1990) are included as age-2-ocean; these comprise 26% of the sample size.

ing (winter-run) steelhead have begun to mature, and because stream-maturing (summer-run) steelhead are sexually immature at river entry. Ocean age 2 is the modal age at maturity for most populations of Asian and North American steelhead (Table 16). Some precocious male steelhead may mature in freshwater and spawn prior to their first ocean migration (e.g., Shapovalov and Taft 1954; Seamons et al. 2004; McMillan et al. 2012). Steelhead age at maturity appears to be at least partially heritable and partially related to saltwater environment (Tipping 1991).

There is evidence indicating an inverse relationship between growth or size at age and age at maturity (Quinn et al. 2011). Age at maturity of steelhead may reflect variation in marine processes controlling trade-offs between egg size and fecundity. For example, the length of hatchery steelhead in Forks Creek, Washington, is positively correlated with egg size and fecundity, but younger (age 1.2) females have smaller eggs for their size than older (1.3) fish, suggesting an effect of growth rate at sea. As determined by scale measurements of Forks Creek steelhead, however, smolt size and size after the first year of ocean growth were not related to egg size or egg number after adjustment for length.

Steelhead display a relatively high potential for iteroparous reproduction (Narum et al. 2008a); that is, an individual fish can spawn more than once during its lifetime. The majority of kelts (repeat-spawning steelhead) are female (e.g., Busby et al. 1996; Lohr and Bryant 1999; Savvaitova et al. 2003; Wertheimer and Evans 2005; Keefer et al. 2008). Spawning events can be identified from scale patterns, which reveal that some kelts spawn in consecutive years while others skip a year between spawning events (e.g., Davis and Light 1985; Keefer et al. 2008). Elevated levels of maturation-indicating hormone (estradiol) and protein (vitellogenin) in the blood of female post-spawning summer-run steelhead kelts, held captive and reconditioned in the Yakima River, Washington, indicated that the decision to re-mature (consecutive spawning) or not (presumed skip spawning) occurs relatively soon (June-August) after spawning in spring (Pierce et al. 2017). The frequency of repeat spawning is highly variable within and among populations (Busby et al. 1996; Table 17). Most coastal populations of North American steelhead have higher levels of iteroparity than inland populations (Busby et al. 1996). Repeat spawning is relatively common in California and Oregon steelhead populations, although more than two spawning events is unusual. The largest number of spawning events reported by Busby et al. (1996) was five, from the Siuslaw River, Oregon (Bali 1959). Kamchatka (stream-maturing) steelhead can rarely exhibit up to seven spawning events (Berejikian and Myers 1996). In Alaska, kelts return to spawn from mid-May through June, and 65–80% of kelts are female (Harding and Coyle 2011). Ocean-maturing (winter-run) stocks in Southeast Alaska appear to have a greater proportion of kelts than summer-run stocks (Lohr and Bryant 1999). While Busby et al. (1996) reported that repeat-spawning of North American steelhead was highest in southern populations, she did not report data for southeast Alaska ocean-maturing populations, which may have a higher percentage of repeat spawners—typically 20–30% of a run and ranging from 10% to 50%, than other North American steelhead (Lohr and Bryant 1999; Harding and Coyle 2011). Long-term (30-year) observations indicate that percentages of repeat spawners in steelhead populations undergo periodic changes; for example, when population size is low the number of repeat spawners is high (Savvaitova et al. 2003). In the Columbia River Basin, annual repeat migration estimates of summer-run steelhead kelts are related to river distance traveled (higher for kelts traveling a shorter distance to the ocean)—likely due to the negative effect of dam passage (Keefer et al. 2008). In the Snake River Basin of Washington, Oregon, and Idaho, summer-run steelhead

Table 17. Repeat spawning frequency for selected Russian (Western Kamchatka) and North American steelhead populations. Data were collected from scale samples. Numbers indicate the proportion of steelhead collected in each study during a given spawning migration; for example, 31% of the steelhead collected by Savvaitova et al. (2003) in the Snatolvayam River were on their first spawning migration. Modal values are indicated in bold font. Populations are generally arranged from north to south. Run type: O = ocean maturing; S = stream maturing. A value of 0.00 indicates a percentage of <0.01. Source: updated from Busby et al. (1996) by addition of data for Kamchatka steelhead (Savvaitova et al. 2003) and Alaska steelhead (Lohr and Bryant 1999).

		Spawning migration					Sample	
Population	Run type[a]	1	2	3	4	5	size	Reference
Western Kamchatka								
Snatolvayam	S	0.31	**0.41**	0.24	0.04	--	n/a[a]	Savvaitova et al. 2003[b]
Kvachina	S	0.30	**0.35**	0.10	0.10	0.10	n/a[a]	Savvaitova et al. 2003[b]
Utkholok	S	**0.45**	0.30	0.23	0.02	--	n/a[a]	Savvaitova et al. 2003[b]
Sopochnaya	S	**0.44**	0.30	0.23	0.03	--	n/a[a]	Savvaitova et al. 2003[b]
Southcentral Alaska								
Karluk	S	**0.85**	0.13	0.02	--	--	2,506	Lohr and Bryant 1999
Anchor	S	**0.79**	0.18	0.03	--	--	814	Lohr and Bryant 1999
Southeast Alaska								
Situk	O	**0.71**	0.20	0.07	0.02	--	471	Lohr and Bryant 1999
Sitkoh	O	**0.66**	0.26	0.07	0.01	0.00	1,261	Lohr and Bryant 1999
Peterson	O	**0.54**	0.33	0.10	0.03	0.00	455	Lohr and Bryant 1999
Petersburg	O	**0.61**	0.26	0.09	0.03	0.00	1,408	Lohr and Bryant 1999
Karta	O	**0.62**	0.28	0.08	0.02	0.00	1,777	Lohr and Bryant 1999
British Columbia (mainland)								
Babine River	S	**0.97**	0.03	--	--	--	121	Narver 1969
Cheakamus River	O	**0.69**	0.26	0.05	--	--	64	Withler 1966
Capilano River	S	**0.94**	0.06	--	--	--	99	Withler 1966
Seymour River	O	**0.95**	0.05	--	--	--	41	Withler 1966
Seymour River	S	**0.96**	0.04	--	--	--	45	Withler 1966
British Columbia (Fraser River Basin)								
Coquitlam River	O	**0.95**	0.03	0.02	--	--	148	Withler 1966
Coquihalla River	O	**0.94**	0.03	0.03	--	--	31	Withler 1966
Coquihalla River	S	**0.94**	0.06	<0.01	--	--	158	Withler 1966

Table 17. Continued.

Population	Run type[a]	Spawning migration 1	2	3	4	5	Sample size	Reference
Puget Sound, Washington								
Skagit River	O	**0.92**	0.07	0.01	--	--	n/a[a]	WDFW 1994
Snohomish River	O	**0.92**	0.06	0.01	--	--	n/a	WDFW 1994
Green River	O	**0.93**	0.07	<0.01	--	--	n/a	WDFW 1994
Puyallup River	O	**0.89**	0.10	<0.01	--	--	n/a	WDFW 1994
Nisqually River	O	**0.93**	0.06	0.01	--	--	n/a	WDFW 1994
Olympic Peninsula, Washington								
Quillayute River	O	**0.91**	0.07	0.01	--	--	n/a	WDFW 1994
Lower Columbia River (Washington)								
Cowlitz River	O	**0.96**	0.04	--	--	--	56	Howell et al. 1985
Toutle River	O	**0.89**	0.05	0.05	--	--	37	Howell et al. 1985
Kalama River	O	**0.93**	0.06	<0.01	<0.01	--	1,363	Howell et al. 1985
Kalama River	S	**0.94**	0.06	<0.01	--	--	909	Howell et al. 1985
Middle Columbia River (Washington)								
Klickitat River	S	**0.97**	0.02	0.01	--	--	148	Howell et al. 1985
Oregon Coast								
Alsea River	O	**0.89**	0.09	0.02	--	--	1,223	Chapman 1958
Siuslaw River	O	**0.86**	0.11	0.02	--	0.01	125	Lindsay et al. 1991
Rogue River	S	**0.79**	0.17	0.04	--	--	4,058	ODFW 1994
Northern California								
Mad River	O	**0.77**	0.17	0.06	--	--	35	Forsgren 1979
Jacoby Creek	O	**0.83**	0.17	--	--	--	109	Harper 1980
California Central Valley								
Sacramento River	O	**0.83**	0.14	0.02	0.01	--	n/a	Hallock 1989
Central California Central								
Waddell Creek	O	**0.83**	0.15	0.02	<0.01	--	3,888	Shapovalov and Taft 1954

[a] Sample size not indicated in reference.

[b] Data are from samples collected in 2001.

kelts exhibited extensive energy (lipid) depletion between upstream migration (September) and kelt emigration (June), and this lipid depletion probably limits post-spawning survival (Penney and Moffitt 2014a, 2014b, 2015). While repeat-spawning is clearly a bet-hedging evolutionary strategy (Wilbur and Rudolf 2006) against reproductive failure, little is known about how ocean conditions affect the frequency of repeat-spawning steelhead.

Feeding Rate and Growth

Bioenergetics model simulations using field-based input data indicate that steelhead growth in the open ocean is highly variable depending on prey quality, consumption rates, total consumption, and thermal experience (Atcheson et al. 2012a). Juvenile (ocean age 0) steelhead in the Gulf of Alaska consume relatively high-energy diets (annual average 4,967 J/g) at relatively moderate feeding rates (48.5%) (Atcheson et al. 2012a), compared with low-energy (2,800 J/g) and high-energy (5,000 J/g) diets of other species of ocean age-0 (10–100 g) salmon feeding at high rates (50–100% C_{max}) in epipelagic coastal and shelf waters (Beauchamp et al. 2007). Higher feeding rates can sometimes compensate for low-energy diets. Growth is higher in years when thermal experience is close to optimal, and optimal temperature is higher for juvenile (ocean age-0) steelhead than for older, larger fish. Significant declines in growth occur when thermal experience deviates substantially from the optimum. In the open ocean steelhead appear to have a narrow temperature window in which to achieve optimal growth (Atcheson et al. 2012a). Vertical migrations do not appear to significantly alter temperature effects on growth. For example, thirty-day bioenergetic simulations of steelhead growth using field-based temperatures from a data storage tagged steelhead in the GOA found that final body weights of steelhead modeled with constant actual SST at the release site (10.9°C) versus daily range of data storage tag temperatures (6.4°C–15.6°C) were 1.5% less (Walker et al. 2000a).

Trophic Interactions

There are fundamental differences between steelhead and other species of Pacific salmon in trophic strategies during the first ocean year. Community structure analyses of diets and trophic relationships among dominant marine nekton within the northern California Current ecosystem indicate that during the coastal marine phase juvenile (ocean age-0) steelhead form a trophic cluster in some years (2002) with other juvenile salmon species that consume fish as their primary prey, e.g., Chinook, Coho, and Chum Salmon, but not in other years (2000) (Miller and Brodeur 2007). Juvenile steelhead diets also overlapped with diets of other pelagic fishes such as Jack Mackerel *Trachurus symmetricus*, Pacific Herring *Clupea pallasii*, and smelt due to consumption of adult euphausiids (Miller and Brodeur 2007; Miller et al 2010). These dietary overlaps indicate the potential for interspecific trophic interactions during the coastal marine juvenile phase (Miller et al. 2010). However, while Chinook, Coho, and Chum Salmon spend most or all of their first ocean summer foraging in productive coastal and continental shelf habitats, ocean age-0 steelhead leave predator- and prey-dense marine coastal and shelf habitats for less productive epipelagic waters over the deep ocean basin (Burgner et al. 1992; Atcheson et al. 2012b).

Species-specific differences in stomach anatomy suggest divergence in Pacific salmon species that serves to reduce interspecific trophic interactions in the open ocean (Welch

1997). For example, steelhead have a long, thin, tubular stomach, consistent with their ocean diet of large, high energy prey (fish and squid), while Chum Salmon have a large stomach that can hold 3.5 times more food volume than Pink Salmon, the most abundant species (Welch 1997). Nevertheless, stable isotope analyses indicate that steelhead and other species of Pacific salmon feed at similar trophic levels in the Central Subarctic North Pacific (CNP) and Gulf of Alaska (GOA) (Kaeriyama et al. 2004; Atcheson et al. 2012b; Qin and Kaeriyama 2016; Figure 16). Thus, there is potential for trophic interactions among these species that may affect growth and survival. While open-ocean GOA habitats are less productive than coastal habitats, by consuming high-energy prey (fish and squid) juvenile (ocean age 0) steelhead are able to gain final body weights not achieved by other species of Pacific salmon until the second ocean year (Atcheson et al. 2012a). These interspecific differences in size-at-age might increase the potential for competitive interactions between juvenile (ocean age-0) steelhead and older age groups of other more abundant salmon species, particularly maturing Pink Salmon. Trophic interactions between steelhead and older age groups of salmon distributed in the same open-ocean habitats might be avoided at least in part by spatial (vertical) partitioning of foraging habitats, as steelhead appear to feed at or closer to the surface than other species of Pacific salmon. However, hatchery salmonids may be conditioned or domesticated to feed at the surface by hatchery feeding practices (Reinhardt 2001), increasing the potential for trophic interactions between hatchery steelhead and salmon at sea.

Density-dependence

In marine habitats, intraspecific density-dependent effects on growth and survival would most likely occur at juvenile and immature stages when abundance and densities are highest. The greatest potential for interactions is likely between large-scale releases of hatchery steelhead and depleted populations of natural (wild) steelhead in inland and coastal marine habitats along the west coast of North America. In both the Columbia River estuary and coastal ocean off Oregon and Washington, natural-origin steelhead smolts had higher feeding intensities, fewer empty stomachs, better condition, and slightly higher growth than hatchery fish (Daly et al. 2014). For hatchery and wild steelhead adults returning to Forks Creek, Washington, stable isotope analysis indicates that wild steelhead feed at a somewhat higher trophic level with more reliance on nearshore sources of carbon than hatchery fish (Quinn et al. 2012). Differences in isotopic patterns between wild and hatchery Forks Creek steelhead appeared to be related to differences in ecological processes (foraging behavior or feeding location) rather than a size or growth effect. Intraspecific density-dependent effects on growth of steelhead in the open ocean may be unlikely given that steelhead are solitary predators and their abundance in open ocean habitats is low.

The availability of micronekton (squid and fish) and crustacean resources to salmonids in the Central Subarctic North Pacific Ocean (CNP) may be limited during years of high Pink Salmon abundance (Tadokoro et al. 1996). Tadokoro et al. (1996) speculated, however, that steelhead might not be affected by food limitations because there was little overlap in distribution with Pink Salmon along a 180°-longitude survey transect in the CNP (June–July 1991–1992). Atcheson et al. (2012b) found that indicators of good steelhead diets (high proportions of squid and high prey energy density) along the same CNP survey transect (June–July 1991–2009) were negatively correlated with the abundance of wild populations of eastern Ka-

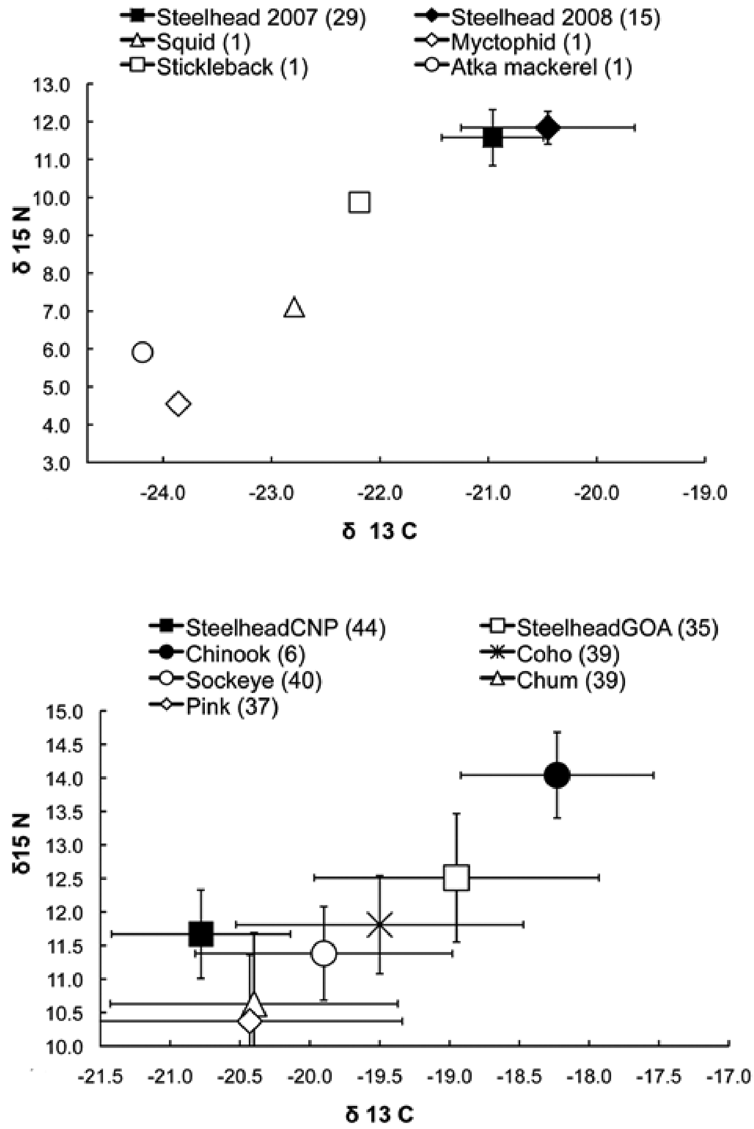

Figure 16. Mean levels of carbon (δ13C) and nitrogen (δ15N) stable isotopes of steelhead and the four most abundant prey of steelhead in the Central North Pacific (CNP) in 2007 and 2008 (top), and relationship between δ13C and δ15N of steelhead in the CNP (this study) and published (Kaeriyama et al., 2004) values for six species of Pacific salmon in the Gulf of Alaska (GOA) (bottom). Sample sizes are shown in the legends. Error bars are standard deviations. Source: Atcheson et al. 2012b.

mchatka Pink Salmon. While steelhead and Pink Salmon distribution may not directly overlap in time and space, large runs of adult Pink Salmon may deplete prey resources throughout a broad oceanic region. In the Gulf of Alaska, however, there was no evidence for competition between steelhead and North American Pink Salmon (Atcheson et al. 2012b). North American Pink Salmon are typically 20–30% less abundant than eastern Kamchatka Pink Salmon (Ruggerone et al. 2010a, 2010b).

When adult steelhead returns are low, density-dependent processes (growth and survival of juveniles) can deplete marine-derived nutrients from freshwater habitats (Moore et al. 2011). Iteroparous steelhead export (as kelts and smolts) the majority of the amount of marine-derived nutrients that they import (as adults), importing only 1.6 times more than exporting, compared to semelparous species, e.g. Chinook (8.3 times) and Coho (10.4 times) (Moore et al. 2011).

Other Causes of Ocean Growth Variation

Climate-driven changes in ocean conditions can affect diets and growth of steelhead migrating in the North Pacific Ocean. For example, during the 1997–1999 ENSO event there was a large decrease in squid in the summer diets of steelhead in the Gulf of Alaska (GOA) (Kaeriyama et al. 2004; Atcheson et at. 2012b; Qin and Kaeriyama 2016). The decrease in dietary squid was even larger in the Central Subarctic North Pacific (CNP) than in the GOA during 1997 and 1999, and steelhead diets in the CNP in 1997 contained the highest proportion of marine debris, including potentially toxic plastic, observed over a 19-year time series (Atcheson et al. 2012b).

In the 1990s and 2000s, summer sea surface temperatures (SSTs) did not reach optimal temperatures for open-ocean steelhead growth except during the 1997 El Niño event (Atcheson et al. 2012a). Ward et al. (1989) observed higher smolt-to-adult survival of smaller size classes of Keogh River, British Columbia, steelhead smolts during the 1982–1983 El Niño event compared with other (non-El Niño) years. Modeled growth potential of steelhead under future SST scenarios showed reduced growth as temperatures warm beyond the optimum growth temperature for a given feeding rate and body mass of steelhead (Figure 17; Atcheson et al. 2012a). Daily growth curves show that the combined reduction in physiological maximum feeding rate and increasing metabolic costs prevent any potential increases in steelhead feeding rate or energetic prey quality from sustaining historical growth rates for temperatures beyond 14°C for ocean age-0 steelhead and 12.2–12.5°C for ocean age-1 steelhead. The resulting growth decline might become a strong selective force in shifting the geographic distribution of steelhead in the ocean and perhaps in freshwater (Atcheson et al. 2012a).

Survival

Trends in Abundance

No quantitative data on trends in abundance of western Kamchatka steelhead are available. Kamchatka steelhead were included in, “The Red Book of Russia” of 1983 (Pavlov et al. 1999), a state document that lists rare and endangered wild species, because abundance levels were thought to be low—apparently due to illegal freshwater fishing activities (poaching). Incidental catches by Asian high seas driftnet fisheries targeting more abundant species of Pacific salmon and squid likely also had a significant impact on Kamchatka steelhead abundance up to the early 1990s when the high seas driftnet fisheries were terminated. In the 2000s, most populations of Kamchatka steelhead appeared to be relatively healthy and increasing in abundance (P. W. Soverel, Kamchatka Steelhead Project, Wild Salmon Center, personal communication).

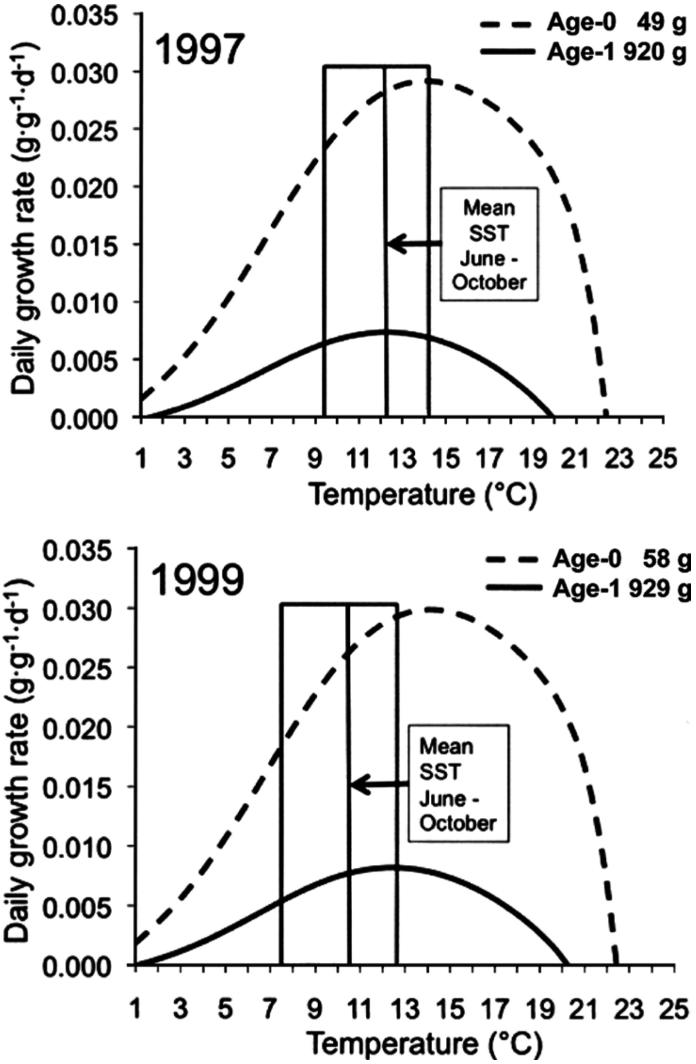

Figure 17. Temperature-dependent daily growth responses for steelhead of two different body masses (smolt and ocean age 1) using field-based prey energy density and estimated consumption rates for the Gulf of Alaska (GOA) in 1997 (top panel: 4,420 J/g diet, 55% C_{max}) and 1999 (bottom panel: 5,582 J/g, 46% C_{max}). The rectangle enclosing the GOA mean sea surface temperature (SST) line (12.2°C) includes the minimum–maximum range of GOA monthly mean SSTs during 1997 (9.4–14.2°C) and 1999 (7.4–12.6°C). Source: Atcheson et al. 2012a.

In North America, the abundance of wild steelhead has been declining in most major production regions since the late 1800s. Although estimates of historical peak run sizes are not available for many U.S. West Coast steelhead Distinct Population Segments (Table 3), abundance may have been highest in the Central Valley of California (Sacramento-San Joaquin and Klamath-Trinity River basins), where run size may have approached 1–2 million adults annually in the late 1800s, and declined to <40,000 adults in the 2000s (McEwan 2001). In the inland waters of Puget Sound, Washington, estimated total abundance of winter-run steelhead during the year of peak commercial catch (1895) was 622,000 fish (range 485,000–930,000 fish) (Gayeski et al. 2011). Historical abundance of wild steelhead was also high in the Columbia River, where estimated catches during the 5-year peak fishing period (1892–1896) averaged 382,000 steelhead per year, and then rapidly declined due to overfishing and degradation of freshwater habitats (Chapman 1986). During the 1980s and 1990s, trends in abundance of adult hatchery and wild steelhead populations along the Pacific Coast of North America were often similar, indicating that the climate-driven (Aleutian Low, El Niño/La Niña events) changes in the ocean environment (e.g., sea level height, sea temperature, coastal upwelling, strength of the California Current, circulation in the Subarctic Gyre, nutrient and zooplankton concentrations, predator distribution and abundance) played a major role in determining abundance trends (Cooper and Johnson 1992; Fisher and Pearcy 1994). In general, abundance was low during the early 1980s, peaked during 1985–1988 run years, and declined into the 1990s. A comparison of adult abundance trends for 20 Washington State populations of wild steelhead between the 1980s (1980-1989) and 2000s (2000-2009) showed that all populations had declined except for two Lower Columbia River populations (mean percent change: Puget Sound = –53%, n = 7 populations; Strait of Juan de Fuca = –34%, n = 3; Washington Coast = –22%, n = 5; Lower Columbia River = –13%, n = 5) (Kendall et al. 2017).

More information is needed on steelhead stock status and trends throughout Alaska (Marston 2010, 2012). During the 2000s, adult escapements of wild steelhead populations in Alaska were considered stable and higher than in the late 1990s, although some populations had not increased from depressed levels in the late 1980s and early 1990s. During the mid 2000s, adult steelhead abundance trends (long-term median counts, 1992–2011 in index populations) were at an all time high in southeast Alaska and below average in southcentral Alaska. During the late 2000s and early 2010s, these geographic trends were somewhat reversed, with southeast populations at or below the long-term median and southcentral populations at or above the long-term median (late 2000s) or mixed (early 2010s). Primary threats to steelhead in Alaska are habitat degradation (roads, hydroelectric projects, timber harvest management, mining projects) and undocumented harvest in commercial and subsistence fisheries (Marston 2010, 2012).

In British Columbia (B.C.), landscape approaches that estimate maximum fry, parr, smolt or adult capacity in freshwater habitats (e.g., Tautz et al. 1992; Riley et al. 1998), and estimates derived from adult stock and recruitment relationships (Lill 2002), combined with estimates of current abundance fry or adult abundance, have been used to assess status of steelhead stocks. A provincial review of the status of 580 steelhead stocks in 2000 listed 29% of stocks as an "extreme conservation concern" (i.e., there is probability that the stock could be extirpated), 23% as a "conservation concern," that is, the stock is over-fished, and 48% as ”healthy“ (BCMWLAP 2002). Decreases in abundance of southern B.C. stocks in the 2000s were largely attributed to environmental change, rather than over-fishing (BCMWLAP 2002).

During the 2000s, the abundance of steelhead was low in the southern third of B.C., relatively high along the west coast of Vancouver Island, and even higher in the northern two thirds of B.C. (Bison 2008). However, there was evidence of a downward trend or shift in abundance of major runs in northern B.C. (e.g., Dean, Skeena, and Nass) during or starting in the mid 2000s. These broad trends were generally considered to reflect latitudinal variation in marine survival. In the early 2010s, survival of some southern B.C. (Georgia Basin) stocks improved, particularly coastal summer- and winter-run steelhead stocks on Vancouver Island and southern mainland areas (Pollard and Beere 2012). However, Keogh River and interior summer-run Fraser stocks continued to experience record low abundances, perhaps related to low freshwater productivity and low nearshore ocean survival (Pollard and Beere 2012).

Along the U.S. West Coast during the 2000s, total adult run sizes of wild steelhead in coastal Distinct Population Segments (Table 3) in Washington State (Puget Sound, Olympic Peninsula, Southwest Washington, and Lower Columbia River) declined, while inland Distinct Population Segments (Middle and Upper Columbia River) increased (Scott and Gill 2008; Anderson 2010; Ford 2011; Marshall and Leland 2012). Gayeski et al. (2011) estimated that the current abundance of Puget Sound winter steelhead is likely only 1–4% of what it was in the late 1800s (mode of 622,000 fish), and concluded that without an extraordinary decline in productivity in freshwater and/or the ocean, loss of freshwater habitat alone could not account for this reduction in abundance. Smolt-to-adult returns of wild Snake River steelhead increased between 1977 and 1987, and then decreased beginning in the late 1980s to low levels seen previously only in 1973, 1977, and 1981 (Williams et al. 2001). A standardized quantitative status and risk assessment for wild steelhead in the Lower Columbia River (12 stocks), Middle Columbia River (28 stocks), and Upper Columbia River and Snake River (7 stocks) Distinct Population Segments (Table 3) showed long-term (1965–2000) declining trends throughout the Columbia River Basin (McClure et al. 2003). Under the assumption that hatchery-reared spawners were straying to natural spawning grounds and reproducing, thus masking trends in natural populations, natural reproduction and survival of Columbia River Basin steelhead was extremely low. The long-term outlook was poor, with an estimated probability of >25% that steelhead Distinct Population Segments would be only one-tenth of current levels in 50 years. Nevertheless, in the 2000s, abundance of hatchery and wild Idaho steelhead (inland populations of the Snake River Basin Distinct Population Segment) increased—reversing the 30-year decline, and the 2009–2010 run was the largest on record at 312,430 steelhead (42,100 wild steelhead) (Byrne 2010). During the 1960s, prior to construction of four major dams and reservoirs on the lower Snake River, however, most steelhead returning to Idaho were wild, and runs averaged about 70,000 fish.

In Oregon, the abundance of the Columbia River Distinct Population Segments (Mid-Columbia, Lower Columbia, Upper Willamette DPSs) during the 2000s was low or continued to decline, however, abundance increased in the late 2000s and early 2010s (Goodson 2010, 2012). There were no apparent declining trends in abundance of the Oregon Coast or Klamath Mountains Province Distinct Population Segments during the 2000s.

In California, monitoring has been inadequate to detect trends in abundance, but the abundance status of most wild steelhead stocks during the 2000s was considered to be low and stable (Jackson 2010; Nelson 2012). However, if present trends in climate change, reduced supply of fresh water, habitat degradation, and adverse effects of hatchery production continue most California steelhead could be extinct or extirpated within the next 100 years (Katz et al. 2012). The abundance of populations in most watersheds in the Southern California Distinct Population Segment (U.S. Endangered Species Act-listed as endangered, Table 3), however, likely continued to decline in the 2000s (http://www.swr.noaa.gov/recovery/Steelhead_SCS.htm). Wild populations of Southern California Distinct Population Segment steelhead were considered extirpated in over half of the 46 watersheds where they spawned historically, and estimated total annual runs declined from 55,000 to less than 500 adult steelhead. Run sizes in the four largest watersheds (Santa Maria, Santa Ynez, Ventura, and Santa Clara Rivers) in the northern portion of the Distinct Population Segment declined by 90% or more. Since the original U.S. Endangered Species Act (ESA) listing, steelhead were documented in only three watersheds in the southern California range extension (from Malibu to the USA–Mexico border).

Ocean Mortalities of Juvenile, Immature and Maturing Fish

Survival and abundance of steelhead is determined by the cumulative effects of mortality factors across all life stages and habitats (e.g., Bisbal and McConnaha 1998). Until recently, however, life stage specific estimates of ocean mortalities of wild steelhead were seldom available. Estimates of smolt-to-adult return survival, which include components of downstream mortality of smolts and upstream mortality of adults, are often used as a proxy for marine survival. A synopsis of estimates of smolt-to-adult return survival of British Columbia and U.S. steelhead (mostly hatchery) populations showed a broad range of values (0–18%) (Bley and Moring 1988). Extensive hatchery programs can obscure trends in abundance of wild populations. Availability and quality of freshwater habitat are frequently considered primary factors in observed declines in steelhead abundance (Kope and Wainwright 1998). Some of the most detailed studies of life stage specific survival have focused on Columbia River steelhead populations. The survival of steelhead smolts (hatchery and wild) migrating downstream through the Snake River and Columbia River, estimated using data from passive integrated transponder (PIT)-tagged fish, was higher in the 1990s than in the 1970s (Muir et al. 2001). Nevertheless, there was no improvement in adult steelhead return rates, indicating the importance of ocean survival and probable effects of poor ocean conditions.

To evaluate whether declines in abundance of Snake River and Columbia River steelhead might be related to ocean conditions, McClure et al. (2003) compared long-term population growth rates during two periods: (1) 1980–2000, when hydropower conditions were stable and ocean conditions were generally regarded as poor, and (2) a longer period (1965–2000) with both favorable and poor ocean conditions. The results showed no significant decline in population growth rates between the two periods for Columbia River steelhead Distinct Population Segments, however, estimated population growth rates for the Snake River Distinct Population Segment were significantly lower during the longer period, perhaps due to unstable hydropower conditions, i.e., dam construction on the Snake River during the 1960s and 1970s.

Smolt-to-adult returns (SARs) of wild Snake River steelhead, estimated using counts of smolts and adults at the uppermost dam and published estimates of wild smolt abundance, averaged 7.3% in the 1960s, 3.5% during the 1970s and 1980s and 2.3% during 1990–2005 (Petrosky and Schaller 2010). Estimated survival during the first ocean year showed a similar declining trend, averaging 21.1% in the 1960s, 11.0% during 1970–1984, and 2.7% during 1990–2005. Low SARs and first-year ocean survival rates were statistically related to both in-river conditions (warmer water temperature, slower river velocity) during smolt out-migration and early ocean conditions (warmer nearshore sea surface temperature and reduced upwelling in the spring), indicating that freshwater and ocean survival rates are not independent. PIT-tag estimates of SARs for wild Snake River steelhead during the late 2000s and early 2010s continued well below the Northwest Power and Conservation Council (NPCC) SAR objectives of a 4% average and 2% minimum for recovery of this ESA-listed population (Tuomikoski et al. 2012).

Estimates of SARs and spatial covariation in SARs for 33 populations of steelhead from Oregon, Washington, and B.C. showed annual values ranging from <0.1% to 35% (mean 4%), large variation and declining trends over time for most populations, greater similarity among geographically proximate populations than among distant populations, and an estimated spatial scale of synchrony in SARs at 248 km (Kendall et al. 2017). The relatively small spatial scale of synchrony in estimated SARs suggested that factors important to survival occur early in the marine life of steelhead, before populations intermix on the high seas (Kendall et al. 2017). However, because steelhead abundance data (smolt and adult) are usually collected in fresh water, SAR estimates may conflate potential effects of freshwater and ocean conditions at multiple life stages.

Acoustic telemetry studies have revealed that early marine survival of hatchery steelhead is often lower than that of wild fish (Goetz et al. 2015; Moore et al. 2015). An investigation in Hood Canal (Puget Sound), Washington, indicated that poor hatchery practices (high rearing density and associated issues with rearing fish in large rectangular raceways) reduced early marine survival of hatchery steelhead smolts (Moore et al. 2012). An investigation of possible causes of low SARs (~0.5%) of Seymour River (North Vancouver, B.C.) hatchery steelhead, which compared the migration and survival of numerous different experimental groups within each study year (2006–2009), showed no significant effects of race (summer- vs. winter-run fish), time of day (night vs. day), and date of release (groups released 10 days apart) on survival (Balfrey et al. 2011). However, there was a significant improvement in early marine survival (from 2% to 32%) for groups of hatchery fish released directly into the ocean compared to conventional (freshwater) release groups (Balfrey et al. 2011). Mark-recapture models of acoustic-tagged hatchery and wild steelhead smolts in Puget Sound indicated substantial variation in survival probabilities by hatchery/wild rearing type, as well as by year (2006–2009), release date, population, and migration segment (Moore et al. 2015). Another investigation tracked acoustic-tagged hatchery steelhead smolts during outmigration in coastal British Columbia, and found that survival after release was lowest in the river and first marine inlet located along the monitored migratory route, while survival of a second group of smolts released beyond the first marine inlet increased by a factor of two (Healy et al. 2017).

The results of acoustic telemetry investigations indicate substantial spatial and temporal variation in marine survival of steelhead (also see above—*Timing of entry into seawater*). In British Columbia, Keogh River (northeast Vancouver Island) steelhead smolts migrating from the river mouth through Queen Charlotte Strait (~23–34 km) experienced relatively low early marine mortality (≤45%), suggesting that this might not be the most critical stage for determining steelhead recruitment (Welch et al. 2004). In contrast, Cheakamus River (B.C. Mainland) steelhead smolts experienced high daily (5–10%) and total (65–73%) mortality as they migrated downstream and through Howe Sound and the Strait of Georgia (406–422 km) (Melnychuk et al. 2007). Total marine survival of Cheakamus steelhead was about 5–10%, therefore, estimated mortality during the remaining 1–3 years of ocean life was 17–22% (Melnychuk et al. 2007). In Puget Sound, Washington, hatchery and wild steelhead smolts had high daily (3%) and total (72%) mortality rates as they migrated from river mouths to the Strait of Juan de Fuca (~160–210 km), and daily mortality rates in the open ocean would have had to decrease substantially (0.43–0.28%) to achieve 2–5% SARs (Moore et al. 2010a). In two coastal Oregon streams, reach-specific estimates of survival of acoustic-tagged steelhead varied among years, generally decreased as smolts moved from freshwater and through the estuary to the ocean, and were lowest in the estuary-ocean transition reach at the river mouth (Nehalem River: 59% in 2001, 77% in 2002, 64% in 2009; Alsea River: 39% in 2007, 58% in 2009)(Romer et al. 2012). Reach-specific survivals of acoustic-tagged Central California Coast native steelhead smolts were 70% in the initial 30-km reach (Napa River), highest in the estuary (San Pablo Bay, 89%; San Francisco Bay, 96%), and lowest in the coastal ocean (60%)(Sandstrom et al. 2013b). A reciprocal acoustic tagging experiment tracked steelhead smolts from two Puget Sound populations (Nisqually River, Duwamish-Green River) released into both natal and non-natal rivers, and found that a short (64 km) difference between release sites (river mouths) in the initial marine migration route accounted for most of the difference in early marine survival through Puget Sound (6% for the longer route; 17% for the shorter route) (Moore and Berejikian 2017). While there are many potential sources of bias in survival estimates derived from acoustic telemetry data (see review by Klimley et al. 2013; see below—*Predation*), the results suggest that levels of mortality sufficient to affect SARs can occur during both early and later marine life-history stages.

Critical Period

The first summer in the ocean is considered the most critical period for ocean survival of Pacific salmon (e.g., Hartt 1980; Hartt and Dell 1986; Beamish and Mahnken 2001; Farley et al. 2007). In general, mortality appears to be highest when juveniles are distributed in river estuary, inland marine, and open-coast continental shelf regions. The critical size and critical period hypothesis identified two distinct critical periods of early ocean mortality of Pacific salmon (Beamish and Mahnken 2001). The first period occurs immediately after ocean entry when predation mortality is likely high, and the second occurs during late fall and winter when size-selective mortality is likely high. Size-selective mortality of steelhead during all marine life stages may be driven by overall growth rates established during early freshwater life stages (Thompson and Beauchamp 2014).

As discussed in the previous section, evidence from survival studies suggests that ocean mortality of steelhead sufficient to affect the number of adult returns can occur during both early and later marine life history phases. For example, the post-ocean entry growth of juvenile Columbia River steelhead distributed on the continental shelf off Oregon and Washington in May was positively correlated with adult returns (Jacobson et al. 2012). Estimated survival during the initial marine period in inland waters (~1 month) for acoustic-tagged southern British Columbia steelhead and Sockeye Salmon populations was large (approximately one in six juveniles surviving to exit the Salish Sea) compared to smolt-to-adult survival determined by other methods (approximately one in 25–100 migrants) (Welch et al. 2011).

Winter may be the most critical period for density-dependent salmonid growth in the open ocean, even though growth is slower in winter than in summer (Aydin 2000). Exploratory ECOSIM models indicate that regime-scale (1976–1977) changes in salmon biomass are related more to shifting of winter trophic pathways between plankton and salmon rather than a shift in plankton themselves (Aydin et al. 2003). Russian research vessel surveys in the western subarctic North Pacific (winter–spring 1986–1992 and 2009–2011, and summer 2004–2014) discovered intensive winter foraging of other salmonid species (Pink, Chum, and Coho Salmon) that was not significantly different than in other seasons (Naydenko et al. 2016). Research on steelhead and salmon during their first winter in the North Pacific Ocean would provide useful information for further testing the critical period hypothesis with respect to the second critical phase (Myers et al. 2016).

Diseases and Parasites

The importance of pathogens to ocean survival of steelhead is difficult to determine, particularly in population time series data, because the effects of pathogens often occur at a local scale while larger-scale factors, e.g., climate and ocean conditions, also influence overall population dynamics (Fujiwara et al. 2011). A practical limitation is the difficulty of assessing fish health at sea. Marine ectoparasites, however, can often be observed with the naked eye. For example, the salmon louse *Lepeophtheirus salmonis* is a copepod ectoparasite that feeds on the skin of salmonids. Salmon lice frequently occur in clusters near the anal fin and cause lesions that can become infected by bacterial or fungal diseases, and may cause osmoregulatory failure in severe cases (Wooten et al. 1982; Nagasawa 1987). Annual (1991–1997) monitoring of the population size of salmon lice on six species of *Oncorhynchus*, caught by surface longline in offshore waters of the North Pacific Ocean and Bering Sea, indicated that steelhead, Pink Salmon, and Chinook Salmon consistently had the highest prevalence, mean intensity, and abundance of infection (Nagasawa 2001). Due to low abundance of steelhead, however, the species consistently hosted only a small percentage of the total *L. salmonis* population (Nagasawa 2001). Salmon lice are probably transmitted from adult to juvenile salmonids during periods of overlapping distribution in coastal marine waters (Ho and Nagasawa 2001; Beamish et al. 2007). For steelhead, adult-to-juvenile transmission of salmon lice might also occur in the open ocean, because juvenile steelhead migrate offshore during their first summer at sea, where their distribution overlaps with adult (kelt) steelhead. The natural ocean mortality of steelhead caused by salmon lice has not been investigated.

Health status of steelhead before entering the ocean likely affects disease resistance and subsequent ocean survival. Specific measures of external condition (e.g., body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations) are significantly correlated with both the presence of selected pathogens, detected by histopathology and polymerase chain reaction analyses, and out-migration survival of ocean age-0 steelhead (Hostetter et al. 2011). Adverse responses to anthropogenic factors during out-migration may vary among salmonid species, making them more or less susceptible to pathogens. For example, before and after measures of stress (increased plasma cortisol and glucose concentrations and decreased plasma chloride concentrations) indicated that steelhead were less stressed by barge transport around dams than Chinook Salmon (Congleton et al. 2000). In polluted rivers and estuaries, immunosuppressive organochlorine compounds are accumulated by juvenile salmonids (Arkoosh et al. 1998), which might increase susceptibility of steelhead to marine pathogens (Macdonald et al. 2003).

Romer et al. (2012) examined steelhead smolts for parasite loads in two coastal Oregon Rivers (Nehalem River and Alsea River). They found that parasite loads, especially a trematode parasite (*Nanophyetus salmincola*) associated with early ocean mortality of Coho Salmon (Jacobson et al. 2008), differed significantly between rivers. Survival of infected smolts could not be evaluated because of lethal sampling, however, estimated estuarine survivals of acoustic-tagged fish released during the same study were not significantly different between rivers (Romer et al. 2012).

Pathogens may frequently be present without any symptoms of disease. Disease challenge experiments indicate that *Oncorhynchus* spp., including steelhead, are highly resistant to infectious salmon anemia virus compared to Atlantic Salmon (Rolland and Winton 2003). Given a sufficient number of markers, molecular genetic technologies can be used to produce genetic maps for steelhead to identify quantitative/qualitative trait loci affecting phenotypic variation in disease resistance (Rexroad and Vallejo 2009). Early marine survival of hatchery steelhead may be enhanced vaccinating fish against common fish diseases (vibriosis, furunculosis) (Balfry et al. 2011). Once released into the natural environment, however, survival of hatchery-reared fish is seldom as high as that of wild conspecifics (Thorpe 2004). Hatcheries can be successful in rearing pathogen-free steelhead, but hatchery fish can rapidly acquire a diverse profile of infectious agents once released into the natural environment (Halpenny and Gross 2008). Pathogens, e.g., *Myxobolus cerebralis*—the causal agent of whirling disease, may be spread from enzootic freshwater regions by infected adult hatchery steelhead that stray on their return migration routes (Zielinski et al. 2010).

Predation

As steelhead smolts pass through river estuaries to the ocean, avian predation can be high (e.g., Roby et al. 2003; Ryan et al. 2003). For example, Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*) were estimated to consume more than 50,000 juvenile salmon and steelhead trout, as indicated by PIT tags found at a single colony on a man-made island (East Sand Island) in the Columbia River estuary (Collis et al. 2001). Juvenile steelhead appear to be more susceptible than other salmonid species (except subyearling Chinook Salmon; Sebring et al. 2013) to avian predation in the Columbia River estuary, perhaps because they are larger and migrate closer to the surface than other species (Collis et al. 2001; Antolos et al. 2005; McMichael et al. 2011; Harnish et al. 2012). Those at higher risk of avian (Caspian tern) predation had low gill NA^+, K^+ ATPase activity level and early migration timing that increased the predator–prey overlap period (estimated mortality of ~250,000 steelhead in April; ~500,000 in May; ~250,000 in June), and predation risk was not related to steelhead length, rearing type (hatchery or wild), or year (Kennedy et al. 2007). Estimated minimum predation rates of PIT-tagged juvenile salmonids by Caspian terns and double-crested cormorants nesting on East Sand Island were highest (16.0%) for Snake River steelhead (Evans et al. 2012). Poor external body condition and fork length (up to 202 mm), as well as river conditions and rearing environment (decrease water discharge, water clarity), were related to increased predation of Snake River steelhead smolts by Caspian terns and double-crested cormorants in the Columbia River estuary (Hostetter et al. 2012). Survival models for Columbia River and Snake River steelhead indicate that explanatory variables for smolt condition (body injuries, fin damage, and disease) are important predictors of adult survival (Evans et al. 2014). Seabird predation by common murres (*Uria aalge*) and sooty shearwaters (*Puffinis griseus*) is also a direct cause of mortality of juvenile steelhead in coastal marine waters off the mouth of the Columbia River (Jacobson et al. 2012). Multi-year studies have shown that avian predation rates are highly variable among years. For example, in two small coastal California estuaries (short shallow sandbar channels at the river mouths) estimated ranges of median avian predation rates of steelhead smolts, primarily by western gulls (*Larus occidentalis*), were 0.08–0.67 (7 years) in Scott Creek and 0.11–0.82 (4 years) in Waddell Creek (Osterback et al. 2013).

In coastal marine areas outmigrating juvenile steelhead may concentrate at river plume frontal regions (De Robertis et al. 2005). The sharp boundary between turbid and clear water in plume fronts may provide both quick protection from predators and productive feeding for juvenile steelhead, as they are surface-feeding visual predators. Nevertheless, simulations of within-season variation in the size and location of the Columbia River plume compared with smolt-to-adult return rates (SARs) of barged steelhead indicate that the plume environment provides only a narrow window of survival benefit at ocean entry, assisting rapid offshore movements away from coastal predators (Burla et al. 2010). The Columbia River plume did not provide any survival benefit to steelhead in years when large-scale ocean conditions were poor, i.e., warm phase of the Pacific Decadal Oscillation (PDO) (Burla et al. 2010).

The decline in many steelhead populations in the Pacific Northwest coincides with the increase in abundance of pinniped populations, e.g., California sea lion *Zalophus californicus*, Steller sea lion *Eumetopias jubatus*, and Pacific harbor seal *Phoca vitulina*, after the passage of the Marine Mammal Protection Act in 1972 (Naughton et al. 2011). Pinniped predation on migrating smolt and adult steelhead can be exacerbated by human activities and development. For example, in Puget Sound, a floating bridge (Hood Canal Bridge) forms a partial barrier that delays steelhead smolt migration, and higher mortality of acoustic-tagged smolts at the bridge than at other monitored locations is likely due to the attraction of pinniped predators to dense aggregations of smolts (Moore et al. 2013). California sea lions consumed as much as 65% of total annual adult steelhead returns at the Ballard Locks in Seattle, Washington, a man-made barrier to fish migration (Scordino and Pfeifer 1993). In the Columbia River at Bonneville dam, 44% of adult steelhead examined over a 7-years period sustained pinniped-caused injuries that likely occurred in the nearshore ocean or estuary, however, radio tag studies showed fish with and without injuries had similar survival to tributaries (Naughton et al. 2011). Pinnipeds are frequently observed feeding on steelhead caught by recreational hook and line fishing or commercial net fishing. In general, efforts to reduce pinniped predation such as harassment and non-lethal or lethal removal of predators have had only limited or short-term effectiveness.

Acoustic tags used to track juvenile steelhead outmigrations have revealed movement patterns suggestive of tags inside predator (unidentified marine mammal or fish) stomachs or stationary tags assumed to have been consumed and defecated by predators (e.g., Moore et al. 2013; Melnychuk et al. 2013). The ultrasound frequency pulses (pings) emitted by acoustic tags can be detected by marine mammal predators (e.g., Cunningham et al. 2014), and laboratory experiments have shown that marine mammals can learn to use the pings from acoustic tags to enhance foraging success, called a dinner-bell effect (Stansbury et al. 2015). This complicates the use of acoustic tags to estimate survivorship of migrating steelhead smolts. Acoustic receivers mounted on Pacific harbor seals and Global Positioning System (GPS) loggers were used to infer seal predation on steelhead smolts with delayed (no pinging for 10 days) or continuously pinging acoustic tags migrating through Puget Sound, Washington (Berijikian et al. 2016). The investigators found no statistical evidence for a dinner-bell effect, but concluded that a more robust experiment with larger sample sizes was needed (Berijikian et al. 2016). An acoustic tag has been developed to detect and signal when a tagged fish has been consumed by a predator (Schultz et al. 2017). If this and other acoustic tagging technologies can be perfected in concert with remote sensing capabilities, they may be useful for investigating predator-prey interactions in the open ocean.

Ecological Interactions

The complex ecological interactions of steelhead and their predators, prey, competitors in the open ocean have been investigated to a limited extent by exploratory quantitative food web and ecosystem models (Figure 18) (Aydin et al. 2003). Open ocean diets of steelhead in the Eastern Subarctic Pacific Gyre region (ESA; north of 40°N and east of 170°W, excluding the continental shelf) were most similar to those of Coho and Chinook Salmon and Northern right whale dolphins *Lissodelphis borealis*, with major shared prey being pelagic

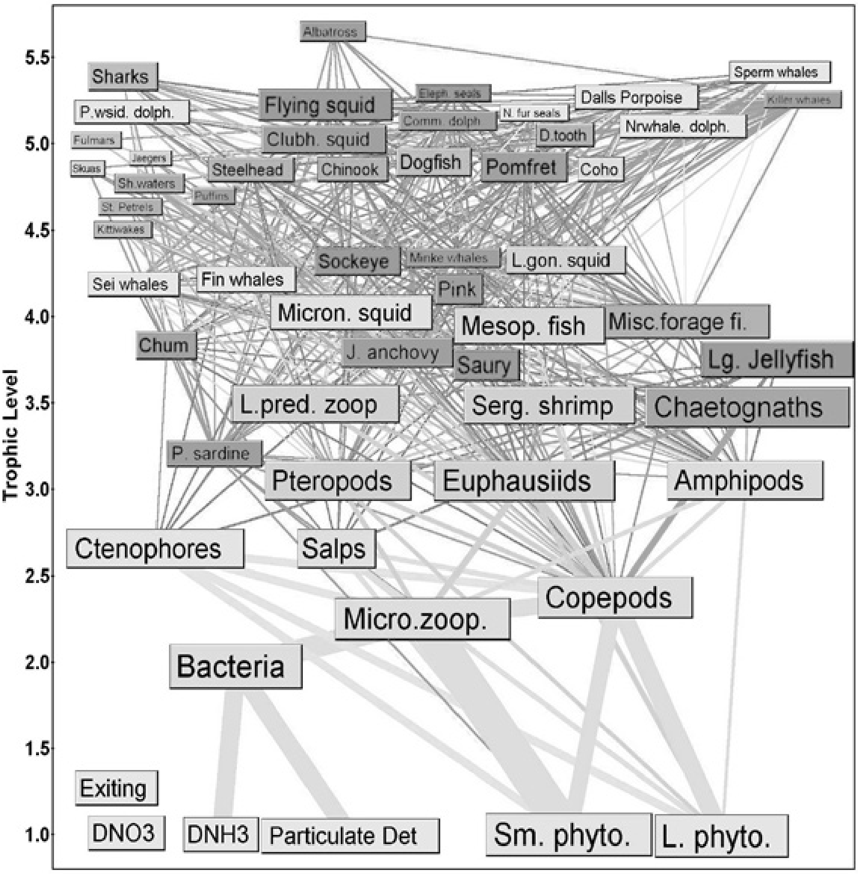

Figure 18. A combined quantitative food web of the Eastern and Western Pacific Subarctic Gyres constructed from data assembled at the March 2001 BASS/MODEL workshop and presented at the PICES Tenth Annual Meeting. Species in both the Western and Eastern Gyres are shown. The area of each compartment is proportional to log of average biomass density (t/km^2), and the width of each connecting flow is proportional to the square root of the averaged yearly flow volume (t/km^2/year).
Source: Figure E1, Aydin et al. 2003.

and mesopelagic fish (particularly myctophids or lanternfish) and micronektonic (gonatid) squid. In the western subarctic gyre (WSA; north of 40°N and west of 170°W, excluding the continental shelf) steelhead diets were most similar to those of Coho and Chinook Salmon, Pacific pomfret *Brama japonica*, boreal clubhook squid *Onychoteuthis borealijaponica*, Northern fulmar *Fulmarus glacialis*, and Leach's Storm-Petrel *Oceanodroma leucorhoa*, with micronektonic squid being the major shared prey (Aydin et al. 2003). Predatory zooplankton such as euphausiids, pteropods, and amphipods function as both prey and competitors of steelhead.

Relatively little is known about the ecological interactions between hatchery and wild steelhead in the marine environment. Recreational catches of adult Washington State steelhead have long indicated a negative influence of increased hatchery smolt abundance on wild fish, i.e., a smaller proportion of wild smolts survive as hatchery release numbers increase

(Peterman 1978). In the 1980s, increased releases of hatchery steelhead during years of low ocean productivity might have increased competition and decreased survival of both hatchery and wild steelhead (Cooper and Johnson 1992). Distribution and diets of hatchery and wild steelhead in the open ocean do not appear to differ (K. Myers, unpublished data), suggesting that feeding competition is likely to occur if prey resources are limited. The potential for density-dependent growth effects due to hatchery and wild steelhead interactions in the ocean has not been evaluated, and is an important topic for future research. However, Atcheson (2010) found that the second year of ocean growth of steelhead migrating far offshore in the central subarctic North Pacific was significantly less in odd-year cycles when adult returns of wild Asian Pink Salmon were high. In addition, large-scale releases of hatchery salmon, particularly Pink and Chum Salmon, around the Pacific Rim increase the potential for feeding competition among all species of salmonids in the open ocean (Ruggerone et al. 2010a, 2010b).

Climate Effects

Since the 1980s, numerous studies have addressed the effects of climate and ocean conditions on the abundance and survival of Pacific salmon (e.g., Rogers 1984; Francis and Sibley 1991; Mantua et al. 1997; Hare et al. 1999, Mueter et al. 2002; Francis and Mantua 2003; and many others—see Beamish et al. 2010). Few climate-effect studies, however, have focused on steelhead. Cooper and Johnson (1992) identified climate-related low productivity in the Gulf of Alaska as one of several possible causes of low steelhead returns along the Pacific Coast of North America in the early 1990s. Fisher and Pearcy (1994) hypothesized that three major interrelated processes, including El Niño events (1982–1983, 1991–1993), coastal conditions, and large-scale fluctuations of ocean climate, were the probable cause of similar trends in the abundance of steelhead from northern California to British Columbia during the 1980s and 1990s. Analysis of coded-wire-tagged (CWT) recovery data indicated that ocean conditions, rather than disease, genetic changes, or location or length of hatchery operation, were responsible for declines in survival rates of CWT hatchery steelhead in the Pacific Northwest in the 1970s–1990s (Coronado-Hernandez 1995). Coronado-Hernandez (1995) speculated that density-dependent mortality might also be an important factor, but this hypothesis was confounded by ocean changes, and was not tested in her study.

Welch et al. (2000) hypothesized that overall recruitment trends in British Columbia (B.C.) steelhead are primarily influenced by changes in marine (not freshwater) survival associated with climate shifts. Recruitment trends of steelhead migrating to the ocean in 1963–1990 were consistent across all regions of B.C., increasing after the 1977 regime shift. An abrupt shift in 1990 to different regional patterns, decreasing in southern regions (Smith and Ward 2000) and increasing in northern regions, might have been related to decreased ocean productivity in southern coastal B.C. (Welch et al. 2000).

The warm (positive) phase of the Pacific Decadal Oscillation (PDO; Mantua et al. 1997) was negatively associated with Snake River steelhead ocean-adult survival during 1964–2006 (survival from downstream smolt passage of the lowermost dam, Bonneville, in the Columbia River to upstream adult passage of the lowermost dam, Lower Granite, in the Snake River) and smolt-to-adult returns (SAR) (Petrosky and Schaller 2010; Haeseker et al. 2012), while the effects of April–June upwelling on ocean-adult mortality rates and SARs were generally weak or inconsistent (Haeseker et al. 2012).

The decrease in ocean productivity associated with global climate change will likely increase marine mortality of steelhead (Beamish et al. 1997). Whitney and Freeland (1999) outlined the steps of the plausible mechanism linking observed changes in climate and ocean conditions and productivity of some fish stocks in the northeastern Pacific, which is the primary rearing area for North American stocks of steelhead: (1) “increased frequency of El Niños or warm events leads to a persistent warming of surface waters in Alaskan Gyre;” (2) “increased buoyancy of waters in winter limits the depth of mixing and the resupply of nutrients to the euphotic zone;” (3) “reduced macronutrient supply leads to broader areas of nitrate depletion in summer, which decreases new production over substantial areas;” (4) “reduced levels of new production and/or a shift to smaller phytoplankton would affect the structure of the zooplankton community;” and (5) “changes to zooplankton communities would affect the productivity of fish populations which mature in the open ocean.”

During 2003–2008, the eastern North Pacific experienced increased climatic and environmental variability (McKinnell et al. 2010). For example, “within a span of three years, the annual average ocean surface temperature in the Gulf of Alaska went from one of the warmest in the last 100 years (2005) to one of the coldest (2008). In contrast, the surface layer of the Western Subarctic Gyre was warmer in 2008 than most of the last century” (McKinnell et al. 2010). The results of field-based bioenergetic models suggested that cool summer temperatures in the open ocean, i.e., temperatures below the optimum for growth of ocean age-0 (14°C) and ocean age-1 (12°C) steelhead, are unfavorable to survival (Atcheson et al. 2012a). The bioenergetic effects of increased variability and east-west trends in sea surface temperatures with respect to optimum growth temperatures have not been evaluated for steelhead.

Forecasted changes by the middle of the 21st century under an equilibrium climate change scenario with doubled atmospheric CO_2 concentrations indicated a substantial reduction in open ocean thermal habitat of steelhead (Welch et al. 1998). Forecasted reductions in potential open-ocean thermal habit of steelhead in summer under a medium (A1B) Intergovernmental Panel of Climate Change (IPCC) scenario emissions scenario included a northward shift and east–west contraction in the southern (warmest) thermal boundary, particularly in the Subarctic North Pacific, Okhotsk Sea, and Gulf of Alaska by the 2040s and substantial reductions in these regions by the 2080s (Figure 19) (Abdul-Aziz et al. 2011). In the 1980s, estimated potential thermal habitat of steelhead during winter covered a relatively narrow east–west band, including most of the Gulf of Alaska and Subarctic North Pacific and part of the Bering Sea; however, the Okhotsk Sea and Arctic Ocean did not provide any potential thermal habitat suitable for steelhead during winter (Figure 20). Forecasted changes in potential winter thermal habitat by the 2040s and 2080s, included a northward shift of the northern (coldest) boundary in most of the Bering Sea and Okhotsk Sea; however, these habitat gains were almost completely offset by almost equal losses due to the northward shift of the southern (warmest) boundary. Thus, the total area of potential winter habitat in future periods was similar to the past or reduced only slightly (1–2%), which was less than the 7% coefficient of variation in 1980s potential habitat.

Ocean Carrying Capacity

As defined by the U.S. Global Ocean Ecosystem Dynamics (GLOBEC) research program, “carrying capacity is a measure of the biomass of a population that can be supported by the eco-

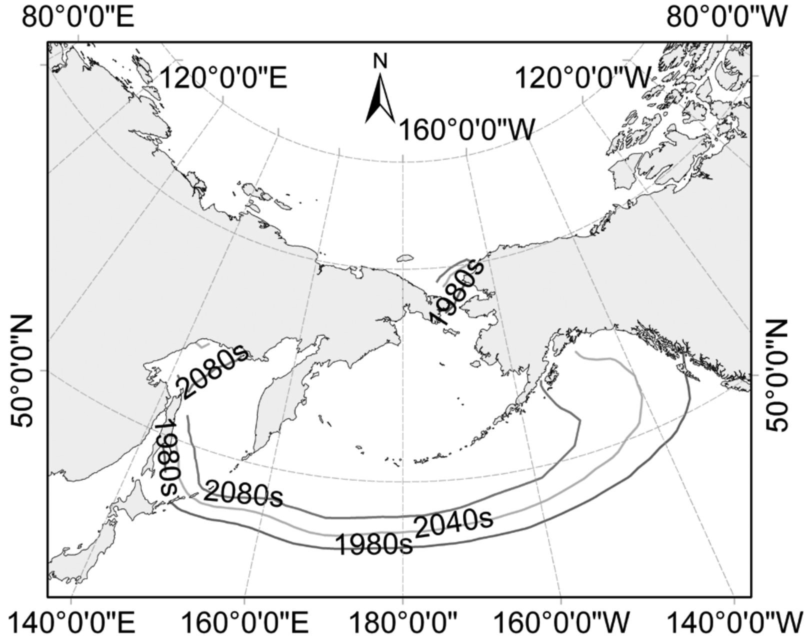

Figure 19. Reference summer (July) thermal habitat ranges in 1980s, 2040s, and 2080s for steelhead under an IPCC A1B (medium) greenhouse gas emissions scenario. Source: Abdul-Aziz et al. 2011.

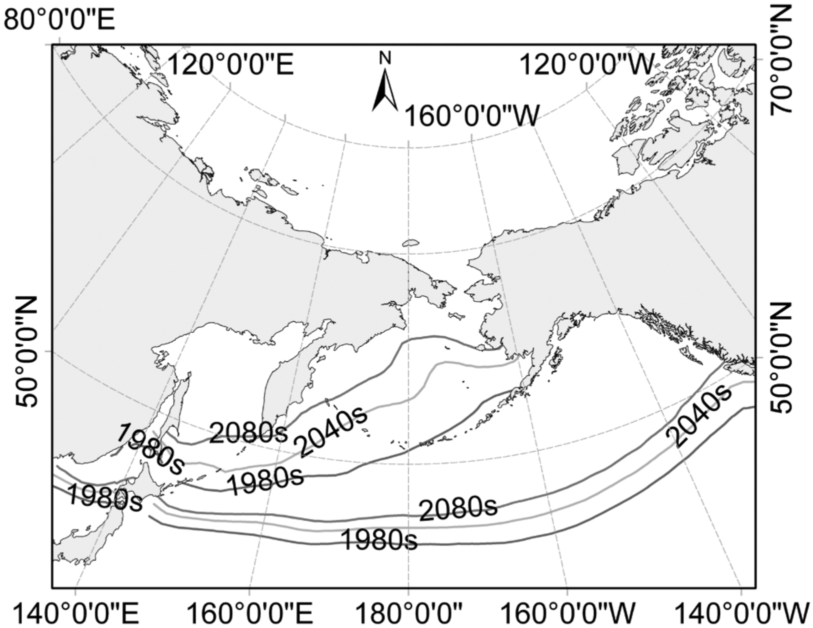

Figure 20. Reference winter (December) thermal habitat ranges in 1980s, 2040s, and 2080s for steelhead under an IPCC A1B (medium) greenhouse gas emissions scenario. Source: Abdul-Aziz et al. 2011.

system. The carrying capacity changes over time with the abundance of predators and supply of food. The food supply is a function of the productivity of the prey populations and competition for that food from other predators. Changes in the biotic environment affect the distributions and productivity of all populations involved" (Hargreaves 1996). In addition, "changes in the abiotic environment can affect the distributions and productivity of populations at all trophic levels" (Hollowed 1996). Thus, the carrying capacity of steelhead in the North Pacific Ocean is dynamic and limited by a complex biological community of interacting organisms and the physical environment. Field-based evidence indicates that abundance of Asian Pink Salmon, availability of micronectonic (gonatid) squid prey, and climate are important potential drivers of carrying capacity or productivity of steelhead in the open ocean (Atcheson et al. 2012b).

In mass-balance food web and ecosystem models, carrying capacity of salmonids in the open ocean is considered to be set by the energy available for somatic growth, because abundance appears to be determined largely by coastal ocean processes at juvenile life stages (Aydin et al. 2003). Pacific salmonids, including steelhead, and squid tend to have the highest trophic uncertainty in marine pelagic food-web models, because of high uncertainty in predation mortality of middle trophic levels (Aydin et al. 2003). Exploratory manipulations of Ecopath with Ecosim models (Christensen et al. 2000) for the Eastern Subarctic Pacific Gyre region (ESA) and Western Subarctic Pacific Gyre region (WSA) theoretically showed increased production of steelhead from: (1) a general 20% increase in longterm (year-30) biomass for all species, including steelhead, as a result of the 20% increase in long-term primary production in both the ESA and WSA; (2) complete removal of neon flying squid *Ommastrephes bartramii*, which reduces predation pressure on forage fish and increases ability of steelhead to obtain food, resulted in substantial (>100%) increase in long term steelhead biomass in the ESA but not in the WSA (baseline biomass of neon flying squid is an order of magnitude higher in the ESA than in the WSA); (3) removal of boreal clubhook squid increased (~25%) long term steelhead biomass in the WSA (likely by reducing predation pressure on micronektonic squid) but not in the ESA (increases biomass of micronektonic squid, which outcompete other forage species consumed by steelhead); (4) removal of all salmonids (or only Pink Salmon, which are the most abundant species) showed that salmonids are not an important group in the ESA (low biomass relative to the rest of the species), however, Pink Salmon are an important competitor controlling the system in the WSA; and (5) removal of sharks resulted in a classic trophic cascade (Paine 1980) in both the ESA and WSA (all shark prey species, including salmonids and squid, increased and their prey decreased) (Aydin et al. 2003). The sensitivity of the WSA to Pink Salmon biomass fluctuations has important implications for the influence of coastal mechanisms, including hatchery salmon production, on open ocean gyre dynamics (Aydin et al. 2003).

Linked nutrient-phytoplankton–zooplankton (NPZ/NEMURO), food web (Ecopath/Ecosim), and bioenergetics models have been used to explore relationships between seasonal zooplankton dynamics and annual food web productive potential for salmon in the Alaskan subarctic gyre ecosystem (Aydin et al. 2005). The results demonstrated the importance of lipid-rich forage species, especially the gonatid squid *Berryteuthis anonychus*, that connect zooplankton to upper trophic level production in the subarctic North Pacific. Thus, bioenergetic models need to account for seasonal and ontogenetic prey switching of salmonids from zooplankton to squid and the lower energetic cost of foraging in spring, when zooplankton are concentrated by shallowing of pelagic mixed-layer depth. While carrying capacity of salmonids is often assumed to be limited by density-dependent interactions in freshwater, density-dependent interactions in the ocean also may limit salmonid abundance. For example, density-dependent coastal processes that have a relatively minor effect on salmonid growth can delay seasonal timing of ontogenetic diet shifts, e.g., from zooplankton to larger squid prey, and thus magnify the effect on overall salmonid growth rates (Aydin et al. 2005). Scientific understanding of ocean carrying capacity effects on survival of salmonids, including steelhead, will continue to advance with the development of fully coupled planktonic ecosystem and fisheries food web models for the North Pacific pelagic ecosystem (Kearney et al. 2012).

Fishing Effects

Burgner et al. (1992) reviewed historical harvests of steelhead in Asian high seas driftnet fisheries. Because of their low abundance compared to other species of Pacific salmon, steelhead were never a target species of Asian high seas driftnet fisheries. Reported incidental catches of steelhead by the Japanese landbased salmon driftnet fishery (concentrated in the western North Pacific Ocean between 42°N and 46°N, 165°E and 175°E) were relatively low (see Myers et al. 1993 review of the fishery), ranging from 29,000 steelhead in 1983 to 3,000 steelhead in 1989. Incidental catches of steelhead by the Japanese mothership salmon driftnet fishery and the large-scale Asian high seas driftnet fisheries for flying squid *Ommastrephes bartrami* were also relatively low, as fishery times and areas generally did not overlap the spatiotemporal distribution of steelhead on the high seas (Burgner et al. 1992). However, direct biological information on steelhead in squid driftnet catches was limited to a few fish sampled by observers in 1990 (Myers and Bernard 1993). Large-scale removals of flying squid and other competitors and predators by these fisheries may have benefitted steelhead growth and survival. Nevertheless, Cooper and Johnson (1992) identified interceptions by the high seas squid driftnet fisheries as one of several possible causes of low steelhead returns along the Pacific Coast of North America in the early 1990s. Illegal catches by the Asian high seas driftnet fisheries operating in high seas areas closed to salmon fishing during the 1980s and early 1990s (Pella et al. 1993) may have had a significant impact on steelhead in both Kamchatka and North America. The last year of operation of the Japanese high seas salmon driftnet fisheries was in 1991, and the Asian high seas driftnet fisheries for squid were terminated at the end of 1992. The effect of termination of the high seas driftnet fisheries on the abundance and biological characteristics of steelhead in North America and Asia has never been evaluated.

The combination of comparatively low adult steelhead returns and highly abundant returns of other Pacific salmon species can increase the difficulty of managing coastal marine and estuarine commercial salmon fisheries to maintain or restore steelhead abundance and biodiversity. For example, in the late 1980s and early 1990s many believed that the decline in wild summer-run steelhead escapements in the Skeena River in west-central British Columbia was due to incidental harvests by marine commercial net fisheries targeting Sockeye and Pink Salmon in Alaska and Canada (Wood 2001). A management policy to reduce steelhead harvest in coastal marine net fisheries by 50% was considered somewhat successful in Canada but not in Alaska because of fishery management difficulties under the Canada–USA treaty (Wood 2001). Nevertheless, changes in time and location of Skeena River salmon fishery openings have not been sufficient to reduce steelhead bycatch (Walters et al. 2008). As a result, Canadian fishery managers have implemented experimental methods for avoiding steelhead interception by commercial net fisheries for salmon, e.g., weed lines, which lower gillnets to about 1 m below the surface, short-duration gillnet sets, on-board fish resuscitation, and live release of captured steelhead; however, the use of these methods has not been adequately monitored or enforced (Walters et al. 2008). The major difficulty in addressing whether recruitment overfishing caused the decline is the lack of long-term data on abundance trends of adult steelhead in the Skeena River (Walters et al. 2008). During the 2010s, incidental harvests of small, early-run steelhead stocks by commercial salmon fisheries continue to be a conservation concern for Skeena River steelhead (Pollard and Beere 2012). In general, incidental marine and estuarine harvests of steelhead by nontarget commercial fisheries and illegal harvests in most regions of North America are considered to be low, but total illegal and incidental harvest numbers are not known.

Other Causes of Ocean Mortalities

Small initial body size at ocean emigration may be an important cause of ocean mortality of steelhead. For example, studies using scale back-calculation procedures indicate smolt (ocean age-0)-to-adult survival of Keogh River, B.C., steelhead was positively correlated with smolt size (Ward and Slaney 1988; Ward et al. 1989). Starting in 1990, however, Keogh River steelhead experienced a sharp drop in smolt-to-adult survival from an average of 15–16% to 4% and marine survival of Keogh River steelhead was no longer strongly related to smolt size (Welch et al. 2000). Further analysis indicated that a sustained period of postsmolt growth (first summer-fall at sea) contributed to marine survival patterns of Keogh River steelhead during 1977–1999, and adult return rates were negatively correlated with SSTs in assumed postsmolt ocean rearing habitats (Friedland et al. 2014). During the 1990s–2000s, sea surface temperatures (SSTs) in the Gulf of Alaska during most years were cool relative to the estimated threshold for optimum growth of postsmolt (ocean age-0) steelhead (Atcheson et al. 2012a). Cool SSTs and associated growth reductions might increase size-selective mortality of steelhead, particularly during the first summer-fall in the ocean, as bioenergetic models indicate that the optimal temperature for steelhead growth decreases with increasing body size (Atcheson et al. 2012a).

The delayed-mortality hypothesis is that stress experienced by salmonid smolts during out-migration causes delayed or latent mortality in the ocean (see Budy et al. 2002 for a review of evidence supporting the hypothesis)). For example, freshwater and marine mortality rates and overall smolt-to-adult returns (SARs) of Snake River steelhead and wild spring/summer Chinook Salmon, estimated by detecting Passive Integrated Transponder (PIT)-tagged smolts and adult returns as they migrated through the Snake and Columbia River hydrosystem (a series of eight dams and reservoirs), were positively correlated (Haeseker et al. 2012). These results supported the delayed-mortality hypothesis that the cumulative stress of shared environmental factors (river flow spilled over dams and water transit time) during out-migration influenced both freshwater and marine mortality of both species (Haeseker et al. 2012).

An emerging issue related to ocean mortality is the consumption of plastic marine debris (pellets, foam, and sheets) by steelhead in international waters (Myers et al. 2013). Types and forms of plastic debris found in steelhead stomachs include plastic fragments, foam, sheets, monofilament, pellets, oil, tar, and rubber. Potential mechanisms of mortality due to ingestion of marine plastic debris may be direct, such as lethal mechanical injury or toxicity, or delayed, such as heritable alterations in gene expression (epigenetic) affecting early marine survival of progeny. Research that directly addresses this potentially important anthropogenic source of ocean mortality of steelhead is needed.

Concluding Remarks

Summary

While much has been learned about the marine life history and ecology of steelhead over the past 60 years, there are still many important gaps in our knowledge. Abundance data for naturally spawning (wild) populations of steelhead are insufficient throughout most of their range. Harvest data are incomplete for most major production regions. The general biology and marine life history of steelhead is complex because there are thousands of stocks (discrete, reproductively isolated populations) that include diverse phenotypic adaptations. This natural diversity is key to survival of the species in a constantly changing environment.

Stock-specific models of seasonal ocean distribution and migration patterns of steelhead remain highly speculative due to the lack of comprehensive genetic baselines and quantitative estimates of stock proportions in ocean mixture samples. Almost nothing is known about late autumn and winter distribution and migration patterns of steelhead in the open ocean (see review by Myers et al. 2016). Sea temperature and food availability are considered to be the primary factors influencing the distribution of steelhead in the open ocean. However, little is known about the effects of salinity, currents, interspecific interactions, and many other abiotic and biotic factors on distribution and migration timing.

Steelhead growth in the open ocean is continuous throughout the year, but highly variable depending on prey quality, consumption rates, total consumption, and thermal experience. Steelhead have a narrow temperature window in which to achieve optimal growth. Steelhead are surface-oriented feeders, and diel vertical migrations do not appear to significantly alter sea surface temperature effects on bioenergetics and growth. Stable isotope analyses indicate that steelhead and other species of Pacific salmon feed at similar trophic levels. Thus, there is potential for interspecific trophic and density-dependent interactions that may affect steelhead growth and survival. Ecosystem models indicate that winter is the most critical period for density-dependent salmonid growth in the open ocean, even though growth is slower in winter than in summer, due to shifting pathways of energy transfer between upper and lower trophic levels. Nevertheless, by consuming high-energy prey (fish and squid), juvenile (ocean age 0) steelhead gain final body weights not achieved by other species of Pacific salmon until the second ocean year. Large body size of steelhead in the first ocean summer, however, can also be attributed large body size at ocean emigration, compared to most species of Pacific salmon.

The factors affecting ocean survival of steelhead are largely a mystery, and information on trends in overall abundance are lacking. No quantitative data on trends in abundance of western Kamchatka steelhead are available. In North America, abundance of wild steelhead has been declining in most major production regions since the late 1800s. Many wild populations of steelhead, particularly U.S. West Coast populations, are considered threatened, endangered, or extinct. While human activities in freshwater (habitat, hydrosystem, hatchery, and harvest) are generally considered to be the primary causes of these declines, there is increasing awareness of the importance of climate and ocean effects on steelhead productivity. Life stage specific estimates of ocean mortalities of wild steelhead, however, are seldom available, and extensive hatchery programs can obscure trends in abundance of wild populations. Nevertheless, evidence from survival studies suggests that ocean mortality of steelhead sufficient to affect the number of adult returns can occur during both early and later marine life history phases.

The carrying capacity of steelhead in the North Pacific Ocean is dynamic and limited by a complex biological community of interacting organisms and the physical environment. Field-based evidence indicates that abundance of Asian Pink Salmon, availability of micronectonic (gonatid) squid prey, and climate are important potential drivers of carrying capacity or productivity of steelhead in the open ocean. Projected reductions in summer thermal habitats of steelhead due to greenhouse gas emissions by the 2080s are substantial and need further investigation. More information is needed on the distribution and biomass of gonatid squid, which are a major steelhead prey. Ecosystem models indicate that Pink Salmon, the most abundant species of Pacific salmon, are an important competitor controlling the system in the western North Pacific but not in the eastern North Pacific. This has important implications for the influence of coastal mechanisms, including hatchery salmon production, on carrying capacity of steelhead in the open ocean.

Future Research

The continuation of coastal and open ocean (high seas) field research and monitoring of steelhead and the factors that might affect their growth and survival is needed to improve our understanding of both long- and short-term fluctuations in steelhead abundance and biomass. In particular, we need stock-specific information on the distribution, growth, and feeding ecology of steelhead during winter months (to test the critical period hypothesis) and the availability and relative abundance and biomass of the major prey species of steelhead during all seasons. This effort will require development of comprehensive genetic baselines and applications for stock identification of steelhead in high seas mixture samples of steelhead. Multispecies models of trophic and ecological interactions would be improved by collection of time-series data on biomass or relative biomass trends and diet data (prey identified to the lowest taxonomic group possible, and number and volume of each prey item) for as many pelagic species as possible (Aydin et al. 2003). In particular, data for competitors and predators of steelhead such as flying squid, pomfret, and sharks, and collection of seasonal data, particularly during transition periods, are needed for development of integrative models to examine the effects of shifting fronts and currents and linkages (energy transfer) between coastal, marginal sea, and open ocean (gyre) habitats (Aydin et al. 2003). Future tagging research on the marine behavior and ocean survival of steelhead could incorporate important potential drivers such as ocean conditions, tagging and handling effects, physiology, predation, disease, pollutants, and hatchery/wild interactions (e.g., Drenner et al. 2012).

Pelagic trawls have become the fishing gear of choice for ocean surveys of Pacific salmon species. However, steelhead are seldom captured using surface trawl configuration and deployment techniques successful at catching other species of Pacific salmon. New pelagic trawling methods effective at sampling steelhead need to be developed. Techniques for quantitatively reliable sampling of steelhead prey, particularly gonatid squid and neustonic species, need to be developed. While shipboard research is expensive, costs of ocean research and monitoring can be reduced through greater use of remote sensing technologies, satellite and archival tags, mobile acoustic telemetry technologies, existing government and private vessel infrastructure and platforms of opportunity, increased collaboration and data sharing among the scientific community, and cost sharing among governments, universities, and foundations (e.g., Hayes et al. 2013; Hayes and Kocik 2014).

A basic tenant of conservation biology is the need to maintain species and population diversity. For example, diversity in *O. mykiss* life history can reduce fluctuations in population abundances and biomass and mediate the effects of environmental change (Moore et al. 2014). Freshwater maturing forms of *O. mykiss* can moderate the effects of poor ocean productivity on population structure and genetics (Christie et al. 2011; see review by Sloat et al. 2014). Molecular ecology is a rapidly advancing field, and sequencing of the *O. mykiss* genome, which is the first published genome of a salmonid, has been completed (Berthelot et al. 2014). Investigations of the *O. mykiss* genome and development of future genetic tools will increase the ability to identify the genes and molecular pathways related to diversity in steelhead. In addition, the application of new genetic stock identification methods for steelhead, e.g., assembly of a TaqMan-based panel of single-nucleotide polymorphism markers for population genetics analysis (Hansen et al. 2011), to historical high seas collections of steelhead biological samples (scales) might be a cost-effective approach to gaining a long-term perspective on stock-specific distribution, migration patterns, growth, and survival of steelhead in open ocean habitats.

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References

Abadía-Cardoso, A., J. C. Garza, R. L. Mayden, and F. J. García de León. 2015. Genetic structure of Pacific trout at the extreme southern end of their native range. PLoS ONE 10(10): e0141775. https://doi.org/10.1371/journal.pone.0141775.

Abdul-Aziz, O. I., N. J. Mantua, and K. W. Myers. 2011. Potential climate change impacts on thermal habitats of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and adjacent seas. Canadian Journal of Fisheries and Aquatic Sciences 68:1660–1680.

Adams, B. L., W. S. Zaugg, and L. R. McLain. 1975. Inhibition of saltwater survival and Na-K-ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Transactions of the American Fisheries Society 104:766–769.

Allendorf, F. W., D. M. Esperlund, and D. T. Scow. 1980. Coexistence of native and introduced Rainbow Trout in the Kootenai River drainage. Proceedings of the Montana Academy of Sciences 39:28–36.

Alt, K. T. 1986. Annual performance report for western Alaska Rainbow Trout studies. Volume 27, Project F-10–1, Study T, Alaska Department of Fish and Game, Division of Sport Fish, Anchorage. Available: http://www.sf.adfg.state.ak.us/FedAidPDFs/FREDf-10–1%2827%29T-6–1.pdf. (October 2017).

Anderson, J. 2010. Washington State steelhead status review. Pages 4–5 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the Twelfth Pacific coast steelhead management meeting, March 9–11, 2010, Eagle Crest Resort, Redmond Oregon. Available: http://www.psmfc.org/steelhead/past-2010.html. (October 2017).

Antolos, M., D. D. Roby, D. E. Lyons, K. Collis, A. F. Evans, M. Hawbecker, and B. A. Ryan. 2005. Caspian tern predation on juvenile salmonids in the mid-Columbia River. Transactions of the American Fisheries Society 134:466–480.

Araki, H., R. S. Waples, W. R. Ardren, B. Cooper, and M. S. Blouin. 2007. Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life history forms. Molecular Ecology 16:953–966.

Arkoosh, M. R., E. Casillas, E. Clemons, A. N. Kagley, R. Olson, P. Reno, and J. E. Stein. 1998. Effect of pollution on fish diseases: potential impacts on salmonid populations. Journal of Aquatic Animal Health 10:182–190.

Atcheson, M. 2010. Interannual variation in steelhead trout (*Oncorhynchus mykiss*) diet, growth and consumption in North Pacific marine ecosystems. Master's thesis. University of Washington, Seattle. Available: http://fish.washington.edu/research/publications/ms_phd/Atcheson_M_MS_Sp10.pdf. (March 2015).

Atcheson, M. E., K. W. Myers, D. A. Beauchamp, and N. J. Mantua. 2012a. Bioenergetic response by steelhead to variation in diet, thermal habitat, and climate in the North Pacific Ocean. Transactions of the American Fisheries Society 141:1081–1096.

Atcheson, M. E., K. W. Myers, N. D. Davis, and N. J. Mantua. 2012b. Potential trophodynamic and environmental drivers of steelhead (*Oncorhynchus mykiss*) productivity in the North Pacific Ocean. Fisheries Oceanography 21:321–335.

Augerot, X. 2005. Atlas of Pacific salmon: the first map-based status assessment of salmon in the North Pacific. University of California Press, Berkeley.

Aultman, D. C., and J. M. Haynes. 1993. Spring thermal fronts and salmonine sport catches in Lake Ontario. North American Journal of Fisheries Management 13:502–510.

Aydin, K. Y. 2000. Trophic feedback and carrying capacity of Pacific salmon (*Oncorhynchus* spp.) on the high seas of the Gulf of Alaska. Doctoral dissertation. University of Washington, Seattle.

Aydin, K. Y., K. W. Myers, and R. V. Walker. 2000. Variations in summer distribution of the prey of Pacific salmon (*Oncorhynchus* spp.) in the offshore Gulf of Alaska in relation to oceanographic conditions, 1994–98. North Pacific Anadromous Fish Commission Bulletin 2: 43–54. Available: http://www.npafc.org/new/publications/Bulletin/BulletinNo.2/pages43–54(Aydin).PDF. (October 2017).

Aydin, K. Y., G.A. McFarlane, J. R. King, and B. A. Megrey. 2003. The BASS/MODEL report on trophic models of the Subarctic Pacific Basin ecosystems. PICES Scientific Report 25. Available: https://www.pices.int/publications/scientific_reports/Report25/default.aspx. (October 2017).

Aydin, K. Y., G. A. McFarlane, J. R. King, B. A. Megrey, and K. W. Myers. 2005. Linking oceanic food webs to coastal production and growth rates of Pacific salmon (*Oncorhynchus* spp.), using models on three scales. Deep-Sea Research II 52:757–780.

Azumaya, T., T. Nagasawa, O. S. Temnykh, and G. V. Khen. 2007. Regional and seasonal differences in temperature and salinity limitations of Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 4:179–187. Available: http://www.npafc.org/new/publications/Bulletin/BulletinNo.4/179–187Azumaya.pdf. (October 2017).

Balfry, S., D. W. Welch, J. Atkinson, A. Lill, and S. Vincent. 2011. The effect of hatchery release strategy on marine migratory behaviour and apparent survival of Seymour River steelhead smolts (*Oncorhynchus mykiss*). PLOS ONE 6. DOI: 10.1371/journal.pone.0014779.

Bali, J. M. 1959. Scale analyses of steelhead trout, *Salmo gairdnerii gairdnerii* Richardson, from various coastal watersheds of Oregon. Master's thesis. Oregon State College, Corvallis.

(BCMWLAP) British Columbia Ministry of Water, Land, and Air Protection. 2002. Environmental trends in British Columbia. Strategic Planning, Policy and Intergovernmental Relations Branch, British Columbia Ministry of Water, Land, and Air Protection, Victoria, B.C. Available: http://www.env.gov.bc.ca/soe/archive/reports/et02/ET2002_report.pdf. (October 2017).

Beakes, M. P., W. H. Satterthwaite, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. Transactions of the American Fisheries Society 139:1263–1275.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Beamish, R. J., M. Henderson, and H. A. Regier. 1997. Impacts of climate change on the fisheries of British Columbia. Pages 12.1–12.16 *in* E. M. Taylor and B. G. Taylor, editors. Responding to global climate change in British Columbia and the Yukon. Volume 1 of the Canada country study: climate impacts and adaptation. Aquatic Sciences and Atmospheric Division, Environment Canada, Pacific and Yukon Region, and the Air Resources Branch, British Columbia Ministry of Environment, Lands and Parks, Vancouver, B.C. Available: http://www.climateaccess.org/sites/default/files/Taylor_Responding%20to%20Global%20Climate%20Change%20in%20BC.pdf. (October 2017).

Beamish, R. J., G. A. McFarlane, and J. R. King. 2005. Migratory patterns of pelagic fishes and possible linkages between open ocean and coastal ecosystems off the Pacific coast of North America. Deep-Sea Research II 52(5–6):739–755.

Beamish, R. J., C. M. Neville, R. M. Sweeting, S. R. M. Jones, N. Ambers, E. K. Gordon, K. L. Hunter, and T. E. McDonald. 2007. A proposed life history strategy for the salmon louse, *Lepeophtheirus salmonis* in the subarctic Pacific. Aquaculture 264:428–440.

Beamish, R. J., K. L. Lange, B. E. Riddell, and S. Urawa, editors. 2010. Climate impacts on Pacific salmon: bibliography. North Pacific Anadromous Fish Commission Special Publication 2:168 pp. Available: http://www.npafc.org/new/pub_special.html. (October 2017).

Beauchamp, D. A., A. D. Cross, J. L. Armstrong, K.W. Myers, J. H. Moss, J. L. Boldt, and L. J. Haldorson. 2007. Bioenergetic responses by Pacific salmon to climate and ecosystem variation. North Pacific Anadromous Fish Commission Bulletin 4:257–269. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%204/257–269Beauchamp.pdf. (October 2017).

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society Monograph 6.

Behnke, R. J. 2002. Trout and salmon of North America. The Free Press, New York.

Bell, E., S. M. Albers, J. M. Krug, and R. Dagit. 2011. Juvenile growth in a population of southern California steelhead (*Oncorhynchus mykiss*). California Fish and Game 97:25–35.

Berejikian, B. A., and K. W. Myers. 1996. The 1994 joint U.S.-Russian Kamchatka steelhead expedition. Final report to National Marine Fisheries Service Contract No. 50ABNF400001. FRI-UW-9609, Fisheries Research Institute, University of Washington. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4229. (October 2017).

Berejikian, B. A., M. E. Moore, and S. J. Jeffries. 2016. Predator-prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry. Marine Ecology Progress Series 543:21–35

Berg, L. S. 1948. Freshwater fishes of the USSR and contiguous countries. Part I. Moscow-Leningrad.

Bernard, R. L., and K. W. Myers. 1996. The performance of quantitative scale pattern analysis in the identification of hatchery and wild steelhead (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 53:1727–1735.

Berthelot, C., F. Brunet, D. Chalopin, A. Juanchich, M. Bernard, B. Noël, P. Bento, C. Dasilva, K. Labadie, A. Alberti, J-M. Aury, A. Louis, P. Dehais, P. Bardou, J. Montfort, C. Klopp, C. Cabau, C. Gaspin, G. H. Thorgaard, M. Boussaha, E. Quillet, R. Guyomard, D. Galiana, J. Bobe, J-N. Volff, C. Genêt, P. Wincker, O. Jaillon, H. Roest Crollius, and Y. Guiguen. 2014. The Rainbow Trout genome provides novel insights into evolution after whole-genome duplication in vertebrates. Nature Communications 5:3657.

Bisbal, G. A., and W. E. McConnaha. 1998. Consideration of ocean conditions in the management of salmon. Canadian Journal of Fisheries and Aquatic Sciences 55:2178–2186.

Bison, R. 2008. A status review of steelhead. Pages 8–10 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the eleventh Pacific coast steelhead management meeting, March 4–6, 2008, Oxford Suites, Boise, Idaho. 41 pp. Available: http://www.psmfc.org/steelhead/past-2008.html. (October 2017).

Bley, P. W., and J. R. Moring. 1988. Freshwater and ocean survival of Atlantic Salmon and steelhead: a synopsis. U.S. Fish Wildlife Service Biological Report 88:1–22.

Bond, M. H. 2006. Importance of estuarine rearing to central California steelhead (*Oncorhynchus mykiss*) growth and marine survival. Master's thesis. University of California Santa Cruz, Santa Cruz.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242–2252.

Bottom, D. L., and K. K. Jones. 1990. Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River estuary. Progress in Oceanography 25:243–270.

Bottom, D. L., K. K. Jones, and M. J. Herring. 1984. Fishes of the Columbia River estuary. Final Report, Columbia River Estuary Data Development Program, Oregon Department of Fish and Wildlife, Portland.

Boughton, D. A., H. Fish, K. Pipal, J. Goin, F. Watson, J. Casagrande, J. Casagrande, and M. Stoecker. 2005. Contraction of the southern range limit for anadromous *Oncorhynchus mykiss*. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFSC-380, Southwest Fisheries Science Center, La Jolla, California. 21 pp. Available: https://swfsc.noaa.gov/publications/TM/SWFSC/NOAA-TM-NMFS-SWFSC-380.PDF. (October 2017).

Boughton, D. A., P. B. Adams, E. Anderson, C. Fusaro, E. Keller, E. Kelley, L. Lentsch, J. Nielsen, K. Perry, H. Regan, J. Smith, C. Swift, and L. Thompson. 2007. Viability criteria for steelhead of the south-central and southern California coast. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFSC-407, Southwest Fisheries Science Center, La Jolla, California. Available: https://swfsc.noaa.gov/publications/TM/SWFSC/NOAA-TM-NMFS-SWFSC-407.PDF. (October 2017).

(BPA) Bonneville Power Administration. 1992. Stock summary reports for Columbia River anadromous salmonids, 5 volumes. Columbia River Coordinated Information System (CIS). Available: Bonneville Power Administration, Portland, Oregon.

Bracis C., and J. J. Anderson. 2012. An investigation of the geomagnetic imprinting hypothesis for salmon. Fisheries Oceanography 21:170–181.

Brodeur. R. D. 1986. Northward displacement of the euphausiid *Nyctiphanes simplex* Hansen to Oregon and Washington waters following the El Niño event of 1982–83. Journal of Crustacean Biology 6:686–692.

Brodeur, R. D. 1989. Neustonic feeding by juvenile salmonids in coastal waters of the northeast Pacific. Canadian Journal of Zoology 67:1995–2007.

Brodeur, R. D. 1990a. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific. International North Pacific Fisheries Commission Document, FRI-UW-9016, Fisheries Research Institute, University of Washington, Seattle. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4138. (October 2017).

Brodeur, R. D. 1990b. Feeding ecology of and food consumption by juvenile Pacific salmon in coastal waters with implications for early ocean survival. Doctoral dissertation, University of Washington, Seattle.

Brodeur. R. D., W. G. Pearcy, B. C. Mundy, and R. W. Wisseman. 1987. The neustonic fauna in coastal waters of the northeast Pacific: abundance, distribution, and utilization by juvenile salmonids. Oregon Sea Grant College Program Publication ORESU-T-87–001, Oregon State University, Corvallis.

Brodeur, R. D., K. W. Myers, and J. H. Helle. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 3:89–131. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%203/Pages%2089-132%20%28USAReview%29.pdf. (October 2017).

Brodeur, R. D., J. P. Fisher, D. J. Teel, R. L. Emmett, E. Casillas, and T. W. Miller. 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the northern California current. U.S. National Marine Fisheries Service Fishery Bulletin 102:25–46.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35–51.

Burger, C. M., M. Scott, M. Small, and W. Potterville. 1983. Overwintering and spawning areas of steelhead trout in tributaries of the Upper Copper River, Alaska. U.S. Fish and Wildlife Service, Final Report, National Fisheries Research Center, Anchorage, Alaska.

Burgner, R. L., J. T. Light, L. Margolis, T. Okazaki, A. Tautz, and S. Ito. 1992. Distribution and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the North Pacific Ocean. International North Pacific Fisheries Commission Bulletin 51. Available: http://www.npafc.org/new/inpfc/INPFC%20Bulletin/Bull%20No.51/Bulletin51.pdf. (October 2017).

Burla, M., A. M. Baptista, E. Casillas, J. G. Williams, and D. M. Marsh. 2010. The influence of the Columbia River plume on the survival of steelhead (*Oncorhynchus mykiss*) and Chinook Salmon (*Oncorhynchus tshawytscha*): a numerical exploration. Canadian Journal of Fisheries and Aquatic Sciences 67:1671–1684.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status Review of West Coast steelhead from Washington, Idaho, Oregon, and California. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum, NMFS-NWFSC-27, Northwest Fisheries Science Center, Seattle, Washington. Available: http://www.nwfsc.noaa.gov/publications/techmemos/tm27/tm27.htm. (October 2017).

Byrne, A. 2010. Steelhead status in Idaho. Pages 4–5 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. 2010. Summary of the twelfth Pacific coast steelhead management meeting, March 9–11, 2010, Eagle Crest Resort, Redmond Oregon. Available: http://www.psmfc.org/steelhead/past-2010.html. (October 2017).

Byron, C. J., and B. J. Burke. 2014. Salmon ocean migration models suggest a variety of population-specific strategies. Reviews in Fish Biology and Fisheries 24:737–756.

(California HSRG). California Hatchery Scientific Review Group. 2012. California Hatchery Review Report. Prepared for the U.S. Fish and Wildlife Service and Pacific States Marine Fisheries Commission. Available: http://cahatcheryreview.com/reports/. (October 2017).

Chapman, D. W. 1958. Studies on the life history of Alsea River steelhead. Journal of Wildlife Management 22:123–134.

Chapman, D. W. 1986. Salmon and Steelhead Abundance in the Columbia River in the Nineteenth Century. Transactions of the American Fisheries Society 115:662–670.

Chapman, E. D., A. R. Hearn, C. J. Michel, A. J. Ammann, S. T. Lindley, M. J. Thomas, P. T. Sandstrom, G. P. Singer, M. L. Peterson, R. B. MacFarlane, and A. P. Klimley. 2013. Diel movements of out-migrating Chinook Salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) smolts in the Sacramento/San Joaquin watershed. Environmental Biology of Fishes 96:273–286.

Chapman, E. D., A. R. Hearn, G. P. Singer, W. N. Brostoff, P. E. LaCivita, and A. P. Klimley. 2015. Movements of steelhead (*Oncorhynchus mykiss*) smolts migrating through the San Francisco Bay Estuary. Environmental Biology of Fishes 98:1069–1080.

Chereshnev, I. A., V. V. Volobuev, A. V. Shestakov, and S. V. Frolov. 2002. Salmonoidei of the Northeast of Russia. Dal'nauka, Vladivostok. (In Russian).

Christensen, V., C. J. Walters, and D. Pauly. 2000. ECOPATH with ECOSIM: a Users Guide, October 2000 Edition. Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia.

Christie, M. R., M. L. Marine, and M. S. Blouin. 2011. Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Molecular Ecology 20:1263–1276.

Ciancio, J. E., M. A. Pascual, F. Botto, E. Frere, and O. Iribarne. 2008. Trophic relationships of exotic anadromous salmonids in the southern Patagonian Shelf as inferred from stable isotopes. Limnology and Oceanography 53:788–798.

Ciancio, J., D. A. Beauchamp, and M. Pascual. 2010. Marine effect of introduced salmonids: prey consumption by exotic steelhead and anadromous brown trout in the Patagonian continental shelf. Limnology and Oceanography 55:2181–2192.

Clements, S., T. Stahl, and C. B. Schreck. 2012. A comparison of the behavior and survival of juvenile Coho Salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) in a small estuary system. Aquaculture 362–363:148–157.

Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: vulnerability of different salmonid species, stocks, and rearing types. Transactions of the American Fisheries Society 130:385–396.

Congleton, J. L., W. J. LaVoie, C. B. Schreck, and L. E. Davis. 2000. Stress indices in migrating juvenile Chinook Salmon and steelhead of wild and hatchery origin before and after barge transportation. Transactions of the American Fisheries Society 129:946–961.

Conte, F. P., and H. H. Wagner. 1965. Development of osmotic and ionic regulation in juvenile steelhead trout, *Salmo gairdneri*. Comparative Biochemistry and Physiology 14:603–620.

Cooper, R., and T. H. Johnson. 1992. Trends in steelhead abundance in Washington and along the Pacific coast of North America. Washington Department of Wildlife, Fisheries Management Division Report 92–20. Available: http://docs.streamnetlibrary.org/Washington/DFW/wdfw92-20.pdf. (October 2017).

Coronado-Hernandez, M. C. 1995. Spatial and temporal factors affecting survival of hatchery-reared Chinook, coho and steelhead in the Pacific Northwest. Doctoral dissertation. School of Fisheries, University of Washington, Seattle.

Courter, I. I., D. B. Child, J. A. Hobbs, T. M. Garrison, J. J. G. Glessner, and S. Duery. 2013. Resident Rainbow Trout produce anadromous offspring in a large interior watershed. Canadian Journal of Fisheries and Aquatic Sciences 70:701–710.

Cunningham, K. A., S. A. Hayes, A. M. W. Rub, and C. Reichmuth 2014. Auditory detection of ultrasonic coded transmitters by seals and sea lions. The Journal of the Acoustical Society of America 135:1978−1985.

Dalton, T. 1991. Variation in prevalence of *Nanophyetus salmincola*, a parasite tag indicating U.S. Northwest origin, in steelhead trout (*Oncorhynchus mykiss*) caught in the central North Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 48:1104–1108.

Daly, E. A., J. A. Scheurer, R. D. Brodeur, L. A. Weitkamp, B. R. Beckman, and J. A. Miller. 2014.. Juvenile steelhead distribution, migration, feeding, and growth in the Columbia River estuary, plume, and coastal waters. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 6:62–80. Available: http://www.tandfonline.com/doi/pdf/10.1080/19425120.2013.869284. (October 2017).

Davis, N. D., and J. T. Light. 1985. Steelhead age determination techniques. International North Pacific Fisheries Commission Document. Fisheries Research Institute, University of Washington, Seattle. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4047. (October 2017).

Davis, N. D., K. W. Myers, R. V. Walker, and C. K. Harris. 1990. The Fisheries Research Institute's high-seas salmonid tagging program and methodology for scale pattern analysis. American Fisheries Society Symposium 7:863–879.

Dawley, E. M., R. D. Lederwood, T. H. Blam, C. W. Sims, J. T. Durkin, R. A. Kirn, A. E. Rankin, G. E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966–1983. Unpublished report by National Marine Fisheries Service, Seattle, Washington.

Del Real, S. C., M. Workman, and J. Merz. 2012. Migration characteristics of hatchery and natural-origin *Oncorhynchus mykiss* from the lower Mokelumne River, California. Environmental Biology of Fish 94:363–375.

De Robertis, A., C. A. Morgan, R. Schabetsberger, R. W. Zabel, R. D. Brodeur, R. L. Emmett, C. M. Knight, G. K. Krutzikowsky, and E. Casillas. 2005. Columbia River plume fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon. Marine Ecology Progress Series 299:33–44.

Dittman, A.H., and T. P. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. Journal of Experimental Biology 199:83–91.

Docker, M., and D. Heath. 2003. Genetic comparison between sympatric anadromous steelhead and freshwater resident Rainbow Trout in British Columbia, Canada. Conservation Genetics 4:227–231.

Doctor, K., B. Berejikian, J. J. Hard, and D. Van Doornik. 2014. Growth-mediated life history traits of steelhead reveal phenotypic divergence and plastic response to temperature. Transactions of the American Fisheries Society 143:317–333.

Drenner, S. M., T. D. Clark, C. K. Whitney, E. G. Martins, S. J. Cooke, and S. G. Hinch. 2012. A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. PLoS ONE 7(3): e31311. doi:10.1371/journal.pone.0031311.

Eaton, D. M., and F. J. Adams. 1995. The effects of global warming on the distribution of steelhead trout populations on the Alaska Peninsula, Alaska. Alaska Fisheries Technical Report 33, U.S. Fish and Wildlife Service, King Salmon, Alaska. Available: alaska.fws.gov/fisheries/fish/Technical_Reports/t_1995_33.pdf. (October 2017).

Evans, A. F., N. J. Hostetter, K. Collis, D. D. Roby, and F. J. Loge. 2014. Relationship between juvenile fish condition and survival to adulthood in steelhead, Transactions of the American Fisheries Society 143:899-909.

Evans, A. F., N. J. Hostetter, D. D. Roby, K. Collis, D. E. Lyons, B. P. Sandford, R. D. Ledgerwood, and S. Sebring. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Transactions of the American Fisheries Society 141:975–989.

Farley, E. V., J. H. Moss, and R. J. Beamish. 2007. A review of the critical size, critical period hypothesis for juvenile Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 4:311–317. http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%204/311-317Farley.pdf. (October 2017).

Favorite, F., A. J. Dodimead, and K. Nasu. 1976. Oceanography of the subarctic Pacific Region, 1960–71. International North Pacific Fisheries Commission Bulletin 33. Available: http://www.npafc.org/new/inpfc/INPFC%20Bulletin/Bull%20No.33/Bulletin%2033.pdf. (October 2017).

Fessler, J. L., and H. H. Wagner. 1969. Some morphological and biochemical changes in steelhead trout during the parr–smolt transformation. Journal of the Fisheries Research Board of Canada 26:2823–2841.

Fisher, J. P., and W. G. Pearcy. 1994. Interannual trends in steelhead abundance and in ocean conditions. Report prepared for the Association of O and C Counties, under sub-contract to S. P. Cramer and Associates, Gresham, Oregon. Available: http://ir.library.oregonstate.edu/xmlui/handle/1957/13854. (October 2017).

Fitak, R. R., B. R. Wheeler, D. A. Ernst, K. J. Lohmann, and S. Johnsen. 2017. Candidate genes mediating magnetoreception in Rainbow Trout (*Oncorhynchus mykiss*). Biology Letters 13:20170142.

Ford, M. J., editor. 2011. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. U.S. Department of Commerce National Oceanic and Atmospheric Administration Technical Memorandum NMFS-NWFSC-113, Northwest Fisheries Science Center, Seattle, Washington.

Forsgren, H. L. 1979. Age, growth, origin and repeat spawning of winter steelhead (*Salmo gairdneri*) in Mad River, California. Master's thesis, Humboldt State University, Arcata, California.

Francis, R. C., and N. J. Mantua. 2003. Climatic influences on salmon populations in the Northeast Pacific. Pages 37–76 *in* A. D. MacCall and T. C. Wainwright, editors. Assessing extinction risk for West Coast salmon. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum NMFS-NWFSC-56, Northwest Fisheries Science Center, Seattle, Washington. Available: http://www.nwfsc.noaa.gov/assets/25/5393_06162004_130044_tm56.pdf. (October 2017).

Francis, R. C., and T. H. Sibley. 1991. Climate change and fisheries: what are the real issues? Northwest Environmental Journal 7:295–307.

Freese, J. L. 1982. Selected aspects of the ecology of adult summer steelhead in the Trinity River, California. Master's thesis. Humboldt State University, Arcata, California.

Fresh, K. L., R. D. Cardwell, and R. R. Koons. 1981. Food habits of Pacific salmon, baitfish, and their potential competitors and predators in the marine waters of Washington, August 1978 to September 1979. Washington Department of Fisheries, Progress Report 145, Olympia.

Friedland, K. D., B. R. Ward, D. W. Welch, and S. A. Hayes. 2014, The effects of postsmolt growth and thermal regime on the marine survival of steelhead trout (*Oncorhynchus mykiss*) from the Keogh River, British Columbia. Marine and Coastal Fisheries 6:1–11. Available: http://www.tandfonline.com/doi/pdf/10.1080/19425120.2013.860065. (October 2017).

Fujiwara, M., M. S. Mohr, A. Greenberg, J. S. Foott, and J. L. Bartholomew. 2011. Effects of Ceratomyxosis on population dynamics of Klamath fall-run Chinook Salmon. Transactions of the American Fisheries Society 140:1380–1391.

Fukuwaka, M., S. Sato, S. Imai, N. D. Davis, K. W. Myers, R. V. Walker, J. M. Murphy, K. Cieciel, J. Moss, V. I. Karpenko, A. V. Bugaev, and S. F. Zolotukhin. 2007. Recoveries of high-seas tags in 006–2007, and tag releases and recoveries of fin-clipped salmon in 2007 from Japanese research vessel surveys in the North Pacific Ocean. North Pacific Anadromous Fish Commission Document 1042. Available: http://www.npafc.org/new/publications/Documents/PDF 2007/1042%28Japan%29.pdf. (October 2017).

Furey, N. B., S. P. Vincent, S. G. Hinch, and D. W. Welch. 2015. Variability in migration routes influences early marine survival of juvenile salmon smolts. PLoS ONE 10(10):e0139269. doi:10.1371/journal. pone.0139269.

Gayeski, N., B. McMillan, and P. Trotter. 2011. Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data. Canadian Journal of Fisheries and Aquatic Sciences 68:498–510.

Goetz, F. A., E. Jeanes, M. E. Moore, and T. P. Quinn. 2015. Comparative migratory behavior an survival of wild and hatchery steelhead (*Oncorhynchus mykiss*) smolts in riverine, estuarine, and marine habitats of Puget Sound, Washington. Environmental Biology of Fishes 98:357–375.

Good, T. P., R. S. Waples, and P. Adams, editors. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum, NMFS-NWFSC-66, Northwest Fisheries Science Center, Seattle, Washington. Available: http://swfsc.noaa.gov/publications/fed/00749.pdf. (October 2017).

Goodson, K. 2010. Status of steelhead in Oregon. Page 4 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the twelfth Pacific coast steelhead management meeting, March 9–11, 2010, Eagle Crest Resort, Redmond Oregon. Available: http://www.psmfc.org/steelhead. (October 2017).

Goodson, K. 2012. Status of steelhead in Oregon. Page 4 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the Thirteenth Pacific Coast Steelhead Management Meeting, March 13–15, 2012, Fort Worden, Port Townsend, Washington. Available: http://www.psmfc.org/steelhead/2012/2012_Steelhead_Summary_FINAL.pdf. (October 2017).

Gustafson, R., R. S. Waples, J. M. Myers, J. J. Hard, G. J. Bryant, O. W. Johnson, and L. A. Weitkamp. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21:1009–1020.

Haeseker, S. L., J. A. McCann, J. Tuomikoski, and B. Chockley. 2012. Assessing freshwater and marine environmental influences on life stage-specific survival rates of Snake River spring–summer Chinook Salmon and steelhead. Transactions of the American Fisheries Society 141:121–138.

Hallock, R. J. 1989. Upper Sacramento River steelhead, *Oncorhynchus mykiss*, 1952–1988. A report prepared for the U.S. Fish and Wildlife Service, Red Bluff, California.

Halpenny, C., and M. R. Gross. 2008. Macro- and microparasite infection profiles of hatchery fish before and after release from a conservation hatchery (steelhead trout, *Oncorhynchus mykiss*). Ecoscience 15:417–422.

Hansen, L. P., N. Jonsson, and B. Jonsson. 1993. Oceanic migration in homing Atlantic Salmon. Animal Behaviour 45:927–941.

Hansen, M. H. H., S. Young, H. B. H. Jorgensen, C. Pascal, M. Henryon, and J. Seeb. 2011. Assembling a dual purpose TaqMan-based panel of single-nucleotide polymorphism markers in Rainbow Trout and steelhead (*Oncorhynchus mykiss*) for association mapping and population genetics analysis. Molecular Ecology Resources 11 (Supplement 1):67–70.

Harding, R. D., and C. L. Coyle. 2011. Southeast Alaska steelhead, trout, and Dolly Varden management. Alaska Department of Fish and Game, Special Publication 11–17, Anchorage. Available: http://www.adfg.alaska.gov/FedAidpdfs/SP11–17. (October 2017).

Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries 24:6–14.

Hargreaves, N. B., editor. 1996. Science Plan, Implementation Plan (Report of the PICES-GLOBEC International Program on Climate Change and Carrying Capacity). North Pacific PICES Scientific Report No. 4, North Pacific Marine Science Organization (PICES), Sidney, B.C., Canada. Available: http://www.pices.int/publications/scientific_reports/. (October 2017).

Harnish, R. A., G. E. Johnson, G. A. McMichael, M. S. Hughes, and B. D. Ebberts. 2012. Effect of migration pathway on travel time and survival of acoustic-tagged juvenile salmonids in the Columbia River estuary. Transactions of the American Fisheries Society 141:507–519.

Harper, W. G. 1980. Age, growth, and migration of coho salmon and steelhead trout in Jacoby Creek, California. Master's thesis, Humboldt State University, Arcata, California.

Hartt, A. C. 1980. Juvenile salmonids in the oceanic ecosystem-the critical first summer. Pages 25–57 *in* W. McNeil and D. Himsworth, editors. Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis.

Hartt, A. C., and M. B. Dell. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. International North Pacific Fisheries Commission Bulletin 46. Available: http://www.npafc.org/new/inpfc/INPFC%20Bulletin/Bull%20No.46/Bulletin46%28Hartt+Dell%29.PDF. (October 2017).

Hassemer, P. F. 1992. Run composition of 1991–92 run-year Snake River summer steelhead measured at Lower Granite Dam. Report to the National Oceanic and Atmospheric Administration, Award NA90AA-D-IJ718. Idaho Fish and Game, Boise.

Hayes, S. A., and J. F. Kocik. 2014. Comparative estuarine and marine migration ecology of Atlantic salmon and steelhead: blue highways and open plains. Reviews in Fish Biology and Fisheries 24:757–780.

Hayes, S. A., A. J. Ammann, J. A. Harding, J. L. Hassrick, L. deWitt, and C. A. Morgan. 2016. Observations of steelhead in the California Current lead to a marine-based hypothesis for the "half-pounder" life history, with climate change implications for anadromy. North Pacific Anadromous Fish Commission Bulletin 6:97–105.

Hayes, S. A., M. H. Bond, C. V. Hanson, A. W. Jones, A. J. Ammann, J. A. Harding, A. L. Collins, J. Perez, and R. B. MacFarlane. 2011. Down, up, down and "smolting" twice? Seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. Canadian Journal of Fisheries and Aquatic Sciences 68:1341–1350.

Hayes, S. A., M. H. Bond, B. K. Wells, C. V. Hanson, A. W. Jones, and R. B. MacFarlane. 2012a. Using archival tags to infer habitat use of central California steelhead and coho salmon. Pages 471–492 *in* J. McKenzie, B. Parsons, A. Seitz, R. Kopf, M. Mesa, and Q. Phelps, editors. Advances in fish tagging and marking technology. American Fisheries Society Symposium 76, Bethesda, Maryland.

Hayes, S. A., C. V. Hanson, D. E. Pearse, M. H. Bond, J. C. Garza, and R. B. MacFarlane. 2012b. Should I Stay or Should I Go? The influence of genetic origin on emigration behavior and physiology of resident and anadromous juvenile *Oncorhynchus mykiss*. North American Journal of Fisheries Management 32:772–780.

Hayes, S. A., N. M. Teutschel, C. J. Michel, C. Champagne, P. W. Robinson, M. Fowler, T. Yack, D. K. Mellinger, S. Simmons, D. P. Costa, and R. B. MacFarlane. 2013. Mobile receivers: releasing the mooring to 'see' where fish go. Environmental Biology of Fishes 96:189–201.

Haynes, J. M., D. C. Nettles, K. M. Parnell, M. P. Voiland, R. A. Olson, and J. D. Winter. 1986. Movements of Rainbow steelhead trout (*Salmo gairdneri*) in Lake Ontario and a hypothesis for the influence of spring thermal structure. Journal of Great Lakes Research 12:304–313.

Healy, S. J., S. G. Hinch, A. D. Porter, E. L Rechisky, D. W. Welch, E. J. Eliason, A. G. Lotto, and N. B. Furey. 2017. Route-specific movements and survival during early marine migration of hatchery steelhead (*Oncorhynchus mykiss*) smolts in coastal British Columbia. Marine Ecology Progress Series 577:131–147.

Hendrickson, D. A., H. Espinosa P´erez, L. T. Findley, W. F. Joseph, R. Tomelleri, R. L. Mayden, J. L. Nielsen, B. Jensen, G. Ruiz Campos, A. Varela Romero, A. van der Heiden, F. Camarena, and F. J. García de León. 2002. Mexican native trouts: a review of their history and current systematic and conservation status. Reviews in Fish Biology and Fisheries 12:273–316.

Ho, J., and K. Nagasawa. 2001. Why infestation by *Lepeophtheirus salmonis* (Copepoda: Caligidae) is not a problem in the Coho Salmon farming industry in Japan. Journal of Crustacean Biology 21:954–960.

Hoar, W. S. 1988. The physiology of smolting salmonids. Pages 275–343 *in* W. W. Hoar and D. J. Randall, editors. Fish physiology, Vol. XIB, Academic Press, New York.

Hollowed, A., editor. 1996. Report on climate change and carrying capacity of the North Pacific Ecosystem. U.S. Global Ocean Ecosystems Dynamics Report Number 15. U.S. GLOBEC Scientific Steering Committee Coordinating Office Department of Integrative Biology, University of California, Berkeley. Available: http://www.usglobec.org/reports/pdf/rep15.pdf. (October 2017).

Höök, T. O., E. S. Rutherford, S. J. Brines, D. J. Schwab, and M. J. McCormick. 2004. Relationship between surface water temperature and steelhead distributions in Lake Michigan. North American Journal of Fisheries Management 24:211–221.

Hooton, R. S., B. R. Ward, V. A. Lewynsky, M. G. Lirette, and A. R. Facchin. 1987. Age and growth of steelhead in Vancouver Island populations. B.C. Ministry of Environment and Parks, Fisheries. Technical Circular 77.

Hostetter, N. J., A. F. Evans, D. D. Roby, K. Collis, M. Hawbecker, B. P. Sandford, D. E. Thompson, and F. J. Loge. 2011. Relationship of external fish condition to pathogen prevalence and out-migration survival in juvenile steelhead. Transactions of the American Fisheries Society 140:1158–1171.

Hostetter, N. J., A. F. Evans , D. D. Roby, and K. Collis. 2012. Susceptibility of juvenile steelhead to avian predation: the influence of individual fish characteristics and river conditions. Transactions of the American Fisheries Society 141:1586–1599.

Howell, P., K. Jones, D. Scarnecchia, L. LaVoy, W. Kendra, and D. Ortmann. 1985. Stock assessment of Columbia River anadromous salmonids Volume II: Steelhead stock summaries stock transfer guidelines—information needs. Final Report to Bonneville Power Administration, Contract DE-AI79–84BP12737, Project 83–335. Available: https://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=12737-2. (October 2017).

Jackson, T. A. 2007. California steelhead fishing report-restoration card, a report to the legislature. California Department of Fish & Game, Fisheries Branch, Sacramento. Available: www.dfg.ca.gov/fish/Resources/Reports/By_Year.asp. (October 2017).

Jackson, T. 2010. California steelhead stock status and management efforts. Pages 3–4 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the twelfth Pacific Coast steelhead management meeting, March 9–11, 2010, Eagle Crest Resort, Redmond Oregon. Available: http://www.psmfc.org/steelhead/past-2010.html. (October 2017).

Jacobson, K., B. Peterson, M. Trudel, J. Ferguson, C. Morgan, D. Welch, A. Baptista, B. Beckman, R. Brodeur, E. Casillas, R. Emmett, J. Miller, D. Teel, T. Wainwright, L. Weitkamp, J. Zamon, and K. Fresh. 2012. The marine ecology of juvenile Columbia River Basin salmonids: a synthesis of research 1998–2011. U.S. National Marine Fisheries Service, Fisheries and Oceans Canada, Kintama Research Services, Ltd., and Oregon State University to Northwest Power and Conservation Council, Portland, Oregon. Available: http://www.nwcouncil.org/library/report.asp?docid=664. (October 2017).

Jacobson, K. C., D. Teel, D. M. Van Doornik, and E. Castillas. 2008. Parasite-associated mortality of juvenile Pacific salmon caused by the trematode *Nanophyetus salmincola* during early marine residence. Marine Ecology Progress Series 354:235–244.

Johnson, S. L., J. H. Power, D. R. Wilson, and J. Ray. 2010. A comparison of the survival and migratory behavior of hatchery-reared and naturally reared steelhead smolts in the Alsea River and Estuary, Oregon, using acoustic telemetry. North American Journal of Fisheries Management 30:55–71.

Kaeriyama, M., M. Nakamura, R. Edpalina, J. R. Bower, H. Yamaguchi, R. V. Walker, and K. W. Myers. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. Fisheries Oceanography 13:197–2004.

Kaganovski, A. G. 1949. On the presence of *Salmo penshinensis Pallas* in the Amur River estuary. Izvestia of the Pacific Research Institute of Fisheries and Oceanography (TINRO), Volume 31, Vladivostok. (In Russian.)

Kallio-Nyberg, I., and E. Ikonen. 1992. Migration pattern of two salmon stocks in the Baltic Sea. ICES Journal of Marine Science 49:191–198.

Katz, J., P. B. Moyle, R. M. Quiñones, J. Israel, and S. Purdy. 2012. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. Environmental Biology of Fishes 96:1169–1186.

Kearney, K. A., C. Stock, K. Aydin, and J. L. Sarmiento. 2012. Coupling planktonic ecosystem and fisheries food web models for a pelagic ecosystem: description and validation for the subarctic Pacific. Ecological Modelling 237–238:43–62.

Keefer, M. L., and C. C. Caudill. 2012. A review of adult salmon and steelhead straying with emphasis on Columbia River populations. Department of Fish and Wildlife Resources, University of Idaho, Technical Report 2012–6, U.S. Army Corps of Engineers, Walla Walla District. Available http://www.dfw.state.or.us/fish/OHRC/docs/2013/pubs/steelhead_and_salmon_straying.pdf. (October 2017).

Keefer, M. L., and C. C. Caudill. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24:333–368.

Keefer, M. L., R. H. Wertheimer, A. F. Evans, C. T. Boggs, and C. A. Peery. 2008. Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): implications for conservation. Canadian Journal of Fisheries and Aquatic Sciences 65:2592–2605.

Keeley, E. R., and J. W. A. Grant. 2001. Prey size of salmonid fishes in streams, lakes, and oceans. Canadian Journal of Fisheries and Aquatic Sciences 58:1122–1132.

Kendall, N. W., G. W. Marston, and M. M. Klungle. 2017. Declining patterns of Pacific Northwest steelhead trout (*Oncorhynchus mykiss*) adult abundance and smolt survival in the ocean. Canadian Journal of Fisheries and Aquatic Sciences 74:1275–1290.

Kendall, N. W., J. R. McMillan, M. R. Sloat, T. W. Buehrens, T. P. Quinn, G. R. Pess, K. V. Kuzishchin, M. M. McClure, and R. W. Zabel. 2015. Anadromy and residency in steelhead and Rainbow Trout (*Oncorhynchus mykiss*): a review of the processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 72:319–342.

Kennedy, B. M., W. L. Gale, and K. G. Ostrand. 2007. Relationship between smolt gill Na+, K+ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. Canadian Journal of Fisheries and Aquatic Sciences 64:1506–1516.

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

Klimley, A. P., R. B. MacFarlane, P. T. Sandstrom, and S. T. Lindley. 2013. A summary of the use of electronic tagging to provide insights into salmon migration and survival. Environmental Biology of Fishes 96:419–428.

Klovach N. V., V. I. Karpenko, A. E. Bobyyrev, A. K. Gruzevich, E. M. Klovach, and S. S. Kozlov. 2002. Atlas of marine distribution of Pacific salmon during the spring-summer feeding and pre-spawning migrations. VNIRO Publishing, Moscow. (In Russian.)

Kope, R.G., and T.C. Wainwright. 1998. Trends in the status of Pacific salmon populations in Washington, Oregon, California and Idaho. North Pacific Anadromous Fish Commission Bulletin 1:1–12. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%201/page%201-5%28Kope%29.PDF. (October 2017).

Kovalenko S. A., and A. O. Shubin. 2000. Distribution and some biological characteristics of mikizha (*Parasalmo mykiss*) in May–August 1996–2000 in the Kuril Island waters of Pacific Ocean and the waters of Okhotsk Sea. North Pacific Anadromous Fish Commission Document 508. Available: http://www.npafc.org/new/publications/Documents/PDF%202000/508%28Russia%29.pdf. (October 2017).

Kovalenko S. A., A. O. Shubin, L. D. Khorevin, V. A. Rudnev, E. V. Tarasyuk, V. M. Chupakhin, I. M. Ivanova, Yu. I. Ignatyev, and I. A. Nemchinova. 2003. Distribution and structure of *Parasalmo mykiss* grouping in the near-Kuril waters of Pacific Ocean and Okhotsk Sea. North Pacific Anadromous Fish Commission Document 667. Available: http://www.npafc.org/new/publications/Documents/PDF%202003/667%28Russia%29.pdf. (October 2017).

Kovalenko, S. A., A. O. Shubin, and I. A. Nemchinova. 2005. Distribution and biological characteristics of Kamchatka steelhead *Parasalmon mykiss* (Salmonidae) in Pacific waters off the Kurils and in the Sea of Okhotsk. Journal of Ichthyology 45:70–80.

Kuzishchin, K. V., SD. Pavlov, M. A. Gruzdeva, and D. S. Pavlov. 2002. Spawning population and reproductive ecology of the freshwater Kamchatka mykiss *Parasalmo mykiss* in the basin of the Zhupanova River Basin (East Kamchatka). Journal of Ichthyology 42:601–614.

Kuzishchin, K.V., A. Y. Mal'tsev, M. A. Gruzdeva, K. A. Savvaitova, D. S. Pavlov, and J. A. Stanford. 2007. On joint spawning of anadromous and resident mykiss *Parasalmo mykiss* in rivers of western Kamchatka. Journal of Ichthyology 47:348–352.

Kuzishchin, K. V., A. Yu. Mal'tsev, M. A. Gruzdeva, K. A. Savvaitova, J. Stanford, and D. S. Pavlov. 2008. Reproduction of mykiss *Parasalmo mykiss* in the Kol River (Western Kamchatka) and its controlling factors. Journal of Ichthyology 48:45–56.

Lamperth, J. S., T. P. Quinn, and M. S. Zimmerman. 2017. Levels of stored energy but not marine foraging patterns differentiate seasonal ecotypes of wild and hatchery steelhead (*Oncorhynchus mykiss*) returning to the Kalama River, Washington. Canadian Journal of Fisheries and Aquatic Sciences 74:157–167.

Larson, R. W., and J. M. Ward. 1954. Management of steelhead trout in the state of Washington. Transactions of the American Fisheries Society 84:261–274.

LeBrasseur, R. J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. Journal of the Fisheries Research Board of Canada 23:85–100.

Ledgerwood, R. D., F. P. Thrower, and E. M. Dawley. 1991. Diel sampling of migratory juvenile salmonids in the Columbia River estuary. U.S. National Marine Fisheries Service Fishery Bulletin 89:69–78.

Leider, S. A. 1989. Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mount St. Helens. Environmental Biology of Fishes 24:219–229.

Light, J. T. 1985. Food and feeding of steelhead trout in the epipelagic waters of the North Pacific. FRI-UW-8507, Fisheries Research Institute, University of Washington, Seattle. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4048. (October 2017).

Light, J. T. 1987. Coastwide abundance of North American steelhead trout. FRI-UW-8710. Fisheries Research Institute, University of Washington, Seattle. 18 pp. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4076. (October 2017).

Light, J. T. 1989. The magnitude of artificial production of steelhead trout along the Pacific Coast of North America. FRI-UW-8913, Fisheries Research Institute, University of Washington, Seattle. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4116. (October 2017).

Light, J. T., S. Fowler, and M. L. Dahlberg. 1988. High seas distribution of North American steelhead as evidenced by recoveries of marked or tagged fish. International North Pacific Fisheries Commission Document, FRI-UW-8816, Fisheries Research Institute, University of Washington, Seattle. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4099. (October 2017).

Light, J. T., C. K. Harris, and R. L. Burgner. 1989. Ocean distribution and migration of steelhead (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*). International North Pacific Fisheries Commission Document, FRI-UW-8912, Fisheries Research Institute, University of Washington, Seattle. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4115. (October 2017).

Light, P., M. Salmon, and K. J. Lohmann. 1993. Geomagnetic orientation of loggerhead sea turtles: Evidence for an inclination compass. Journal of Experimental Biology 182:1–9.

Lill, A. F. 2002. Greater Georgia Basin steelhead recovery action plan. Prepared by A. F. Lill and Associates Limited for the Pacific Salmon Foundation, Vancouver, BC. Available: http://www.bccf.com/steelhead/pdf/Steelheadreport092702.pdf. (October 2017).

Lindsay, R. B., K. R. Kenaston, and R. K. Schroeder. 1991. Steelhead production factors. Annual Progress Report, Oregon Department of Fish and Wildlife, Portland, Oregon.

Loch. J. J. 1982. Juvenile and adult steelhead and sea-run Cutthroat Trout within the Columbia River estuary 1980. Washington Department of Game, Fisheries Management Division, Olympia, Washington.

Lohmann, K. J., Putman, N. F., and C. M. F. Lohmann. 2008. Geomagnetic imprinting: a unifying hypothesis of natal homing in salmon and sea turtles. Proceedings of the National Academy of Sciences 105:19096–19101.

Lohr, S. C., and M. D. Bryant. 1999. Biological characteristics and population status of steelhead (*Oncorhynchus mykiss*) in southeast Alaska. Gen. Tech. Rep. PNW-GTR-407. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Available: www.fs.fed.us/pnw/pubs/gtr_407.pdf. (October 2017).

Macdonald, R. W., B. Morton, and S. C. Johannessen. 2003. A review of marine environmental contaminant issues in the North Pacific: the dangers and how to identify them. Environmental Reviews 11:103–139.

Maher, F. P., and P. A. Larkin. 1955. Life history of the steelhead trout of the Chilliwack River, British Columbia. Transactions of the American Fisheries Society 84:27–38.

Mahnken, C., G. Ruggerone, W. Waknitz, and T. Flagg. 1998. A historical perspective on salmonid production from Pacific Rim hatcheries. North Pacific Anadromous Fish Commission Bulletin 1:38–53. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%201/page%2038-53%28Mahnken%29.PDF. (March 2015).

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

Maksimov, V. A. 1976. The ecology of the Kamchatka trout, *Salmo mykiss*, population from the Bol'shaya River (Western Kamchatka). Journal of Ichthyology 16:12–17.

Mangel, M., and W. H. Satterthwaite. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. Bulletin of Marine Science 83:107–130.

Manning, T., and S. Smith. 2004. Washington State sport catch report 2000. Washington Department of Fish and Wildlife, Fish Program, Science Division, Olympia.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

Manzer, J. I. 1968. Food of Pacific salmon and steelhead trout in the Northeast Pacific Ocean. Journal of the Fisheries Research Board of Canada 25:1085–1089.

Margolis, L. 1998. Are naturally-occurring parasite "tags" stable? An appraisal from four case histories involving Pacific salmonids. North Pacific Anadromous Fish Commission Bulletin 1:205–212. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%201/page%20205-212%28Margolis%29.PDF. (October 2017).

Marshall, A., and B. Leland. 2012. Washington State steelhead status review. Pages 5–6 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the Thirteenth Pacific Coast Steelhead Management Meeting, March 13–15, 2012, Fort Worden, Port Townsend, Washington. Available: http://www.psmfc.org/steelhead/past-2012.html. (March 2015).

Marston, B. 2010. Status of Steelhead in Alaska. Pages 6–7 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the Twelfth Pacific Coast Steelhead Management Meeting, March 9–11, 2010, Eagle Crest Resort, Redmond Oregon. Available: http://www.psmfc.org/steelhead/past-2010.html. (October 2017).

Marston, B. 2012. Status of Steelhead in Alaska. Page 8 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the Thirteenth Pacific Coast Steelhead Management Meeting, March 13–15, 2012, Fort Worden, Port Townsend, Washington. Available: http://www.psmfc.org/steelhead/past-2012.html. (October 2017).

Matsubu, W., C. A. Simenstad, and G. E. Horton. 2017. Juvenile steelhead locate coldwater refugia in an intermittently closed estuary. Transactions of the American Fisheries Society 146:680–695.

McCabe, G. T., Jr., W. D. Muir, R. L. Emmett, and J. T. Durkin. 1983. Interrelationships between juvenile salmonids and nonsalmonid fish in the Columbia River estuary. U.S. National Marine Fisheries Service Fishery Bulletin 81:815–826.

McClure, M. M., E. E. Holmes, B. L. Sanderson, and C. E. Jordan. 2003. A large-scale, multispecies status assessment: anadromous salmonids in the Columbia River basin. Ecological Applications 13:964–989.

McCormick, S. D. 2013. Smolt physiology and endocrinology. Pages 199–251 *in* S. D. McCormick, A. P. Farrell, and C. J. Brauner, editors. Fish Physiology, Volume 32. Elsevier, Amsterdam.

McCusker, M., E. Parkinson, and E. Taylor. 2000. Mitochondrial DNA variation in Rainbow Trout (*Oncorhynchus mykiss*) across its native range: testing biogeographical hypotheses and their relevance to conservation. Molecular Ecology 9:2089–2108.

McDowall, R. M. 1993. A recent marine ancestry for diadromous fishes? Sometimes yes, but mostly no. Environmental Biology of Fishes 37:329–335.

McDowall, R. M. 2002. The origin of the salmonid fishes: marine, freshwater … or neither? Reviews in Fish Biology and Fisheries 11:171–179.

McEwan, D. R. 2001. Central Valley Steelhead. *In* Contributions to the biology of Central Valley salmonids, R. L. Brown, editor. California Department of Fish and Game Fish Bulletin 179:1–44.

McKinnell, S., J. J. Pella, and M. L. Dahlberg. 1997. Population-specific aggregations of steelhead trout (*Oncorhynchus mykiss*) in the North Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 54:2368–2376.

McKinnell, S. M., S. Batten, S. J. Bograd, J. L. Boldt, N. Bond, S. Chiba, M. J. Dagg, M. G. G. Foreman, G. L. Hunt, Jr., J. R. Irvine, O. N. Katugin, V. Lobanov, D. L. Mackas, P. Mundy, V. Radchenko, Y. J. Ro, H. Sugisaki, F. A. Whitney, A. Yatsu, and S. Yoo. 2010. Status and trends of the North Pacific Ocean, 2003–2008. Pages 1–55 *in* S. M. McKinnell and M. J. Dagg, editors. Marine Ecosystems of the North Pacific Ocean, 2003–2008. PICES Special Publication 4. Available: http://www.pices.int/publications/special_publications/NPESR/2010/NPESR_2010.aspx. (October 2017).

McMichael, G. A., R. A. Harnish, J. R. Skalski, K. A. Deters, K. D. Ham, R. L. Townsend, P. S. Titzler, M. S. Hughes, J. Kim, and D. M. Trott. 2011. Migratory behavior and survival of juvenile salmonids in the lower Columbia River, estuary, and plume in 2010. PNNL-20443, Pacific Northwest National Laboratory, Richland, Washington.

McMillan, J. R., S. L. Katz, and G. R. Pess. 2007. Observational evidence of spatial and temporal structure in a sympatric anadromous (winter steelhead) and resident *Oncorhynchus mykiss* mating system on the Olympic Peninsula, Washington State. Transactions of the American Fisheries Society 136:736–748.

McMillan, J. R., J. B. Dunham, G. H. Reeves, J. S. Mills, and C. E. Jordan. 2012. Individual condition and stream temperature influence early maturation of Rainbow and steelhead Trout, *Oncorhynchus mykiss*. Environmental Biology of Fishes 93:343–355.

McPhail, J. D. 1996. The origin and speciation of *Oncorhynchus* revisited. Pages 29–38 *in* D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Bulletin 173, Fisheries Research Board of Canada, Ottawa.

McPhail, J. D., and C. C. Lindsey. 1986. Zoogeography of the freshwater fishes of Cascadia (the Columbia system and rivers north to the Stikine). Pages 615–637 *in* C. H. Hocutt and E. O. Wiley, editors. The zoogeography of North American freshwater fishes. Wiley, New York.

McPhee, M. V., F. Utter, J. A. Stanford, K. V. Kuzishchin, K. A. Savvaitova, D. S. Pavlov, and F. W. Allendorf. 2007. Population structure and partial anadromy in *Oncorhynchus mykiss* from Kamchatka: relevance for conservation strategies around the Pacific Rim. Ecology of Freshwater Fish 16:539–547.

McPhee, M. V., D. C. Whited, K. V. Kuzishchin, and J. A. Stanford. 2014. The effects of riverine physical complexity on anadromy and genetic diversity in steelhead or Rainbow Trout *Oncorhynchus mykiss* around the Pacific Rim. Journal of Fish Biology 85:132–150.

Melnychuk, M. C. 2009. Estimation of survival and detection probabilities for multiple tagged salmon stocks with nested migration routes, using a large-scale telemetry array. Marine and Freshwater Research 60:1231–1243.

Melnychuk, M. C., D. W. Welch, C. J. Walters, and V. Christensen. 2007. Riverine and early ocean migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the Cheakamus River, British Columbia. Hydrobiologia 582:55–65.

Melnychuk, M. C., D. W. Welch, and C. J. Walters. 2010. Spatio-temporal migration patterns of Pacific salmon smolts in rivers and coastal marine waters. PLoS ONE 5(9):e12916. doi:10.1371/journal.pone.0012916.

Melnychuk, M. C., V. Christensen, and C. J. Walters. 2013. Meso-scale movement and mortality patterns of juvenile coho salmon and steelhead trout migrating through a coastal fjord. Environmental Biology of Fishes 96:325–339.

Miller, D. R., J. G. Williams, and C. W. Sims. 1983. Distribution, abundance and growth of juvenile salmonids off the coast of Oregon and Washington, summer 1980. Fisheries Research 2:1–17.

Miller, M. R., J. P. Brunelli, P. A. Wheeler, S. Liu, C. E. Rexroad, III, Y. Palti, C. Q. Doe, and G. H. Thorgaard. 2012. A conserved haplotype controls parallel adaptation in geographically distant salmonid populations. Molecular Ecology 21:237–249.

Miller, T. W., and R. D. Brodeur. 2007. Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. U.S. National Marine Fisheries Service Fishery Bulletin 105:548–559.

Miller, T. W., R. D. Brodeur, G. Rau, and K. Omori. 2010. Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Marine Ecology Progress Series 420:15–26.

Mills, J. S., J. B. Dunham, G. H. Reeves, J. R. McMillan, C. E. Zimmerman, and C. E. Jordan. 2012. Variability in expression of anadromy by female *Oncorhynchus mykiss* within a river network. Environmental Biology of Fishes 93:505–517.

Minckley, W. L., D. A. Hendrickson, and C. E. Bond. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. Pages 519–613 *in* C. H. Hocutt and E. O. Wiley, editors. The zoogeography of North American freshwater fishes. Wiley, New York.

Moore, J. W., S. A. Hayes, W. Duffy, S. Gallagher, C. J. Michel, and D. Wright. 2011. Nutrient fluxes and the recent collapse of coastal California salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 68:1161–1170.

Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. Journal of Animal Ecology 83:1035–1046.

Moore, M. E., and B. A. Berejikian. 2017. Population, habitat, and marine location effects on early marine survival and behavior of Puget Sound steelhead smolts. Ecosphere 8:1–21.

Moore, M. E, B. A. Berejikian, and E. P. Tezak. 2010a. Early marine survival and behavior of steelhead smolts through Hood Canal and the Strait of Juan de Fuca. Transactions of the American Fisheries Society 139:49–61.

Moore, M. E., F. A. Goetz, D. M. Van Doornik, E. P. Tezak, T. P. Quinn, J. J. Reyes-Tomassini, and B. A. Berejikian. 2010b. Early marine migration patterns of wild coastal Cutthroat Trout (*Oncorhyn-*

chus clarki clarki), Steelhead Trout (*Oncorhynchus mykiss*), and their hybrids. PLoS ONE 5(9): e12881. doi:10.1371/journal.pone.0012881.

Moore, M. E., B. A. Berejikian, and E. P. Tezak. 2012. Variation in the early marine survival and behavior of natural and hatchery-reared Hood Canal steelhead. PLoS ONE 7:e49645.

Moore, M. E., B. A. Berejikian, and E. P. Tezak. 2013. A floating bridge disrupts seaward migration and increases mortality of steelhead smolts in Hood Canal, Washington State. PLoS ONE 8:e73427.

Moore, M. E., B. A. Berejikian, F. A. Goetz, A. G. Berger, S. S. Hodgson, E. J. Connor, and T. P. Quinn, 2015. Multi-population analysis of Puget Sound steelhead survival and migration behavior. Marine Ecology Progress Series 537:217–232.

Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 59:456–463.

Muir, W. D., and R. L. Emmett. 1988. Food habits of migrating salmonid smolts passing Bonneville Dam in the Columbia River, 1984. Regulated Rivers: Research and Management 2:1–10.

Muir, W. D., S. G. Smith, J. G. Williams, E. E. Hockersmith, and J. R. Skalski. 2001. Survival estimates for migrant yearling Chinook Salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia Rivers, 1993–1998. North American Journal of Fisheries Management 21:269–282.

Mullan, J. W., K. R. Williams, G. Rhodus, T. W. Hillman, and J. D. McIntyre. 1992. Production and habitat of salmonids in mid-Columbia River tributary streams. Monograph I, U.S. Fish and Wildlife Service, Leavenworth, Washington.

Myers, K.W., and R. L. Bernard. 1993. Biological information on Pacific salmon and steelhead trout in observer samples from the Japanese squid driftnet fishery in 1990. International North Pacific Fisheries Commission Bulletin 53(II):217–238. Available: http://www.npafc.org/new/inpfc/INPFC%20Bulletin/Bull%20No.53/Bulletin53%28II%29.pdf. (March 2015).

Myers K.W., R.V. Walker, S. Fowler, and M.L. Dahlberg. 1990. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1989. International North Pacific Fisheries Commission Document, FRI-UW-9009, Fisheries Research Institute, University Washington, Seattle. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4131. (October 2017).

Myers, K.W., C. K. Harris, Y. Ishida, L. Margolis, and M. Ogura. 1993. Review of the Japanese land-based driftnet salmon fishery in the western North Pacific Ocean and the continent of origin of salmonids in this area. International North Pacific Fisheries Commission Bulletin 52. Available: http://www.npafc.org/new/inpfc/INPFC%20Bulletin/Bull%20No.52/Bulletin%2052.pdf. (October 2017).

Myers, K. W., K. Y. Aydin, R. V. Walker, S. Fowler, and M. L. Dahlberg. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1995. North Pacific Anadromous Fish Commission Document 192. Available: https://digital.lib.washington.edu/researchworks/handle/1773/4234. (October 2017).

Myers, K. W., R. V. Walker, R. L. Burgner, and G. Anma. 2001. Distribution, origins, biology, and ecology of juvenile steelhead (*Oncorhynchus mykiss*) in the Gulf of Alaska in summer 1993–2000. North Pacific Anadromous Fish Commission Technical Report 2:30–31. Available: http://www.npafc.org/new/publications/Technical%20Report/TR2/page30-31%28Myers%29.PDF. (October 2017).

Myers, K. W., N. D. Davis, A. G. Celewycz, E. V. Farley, Jr., J. Morris, M. Trudel, M. Fukuwaka, S. Kovalenko, and A. Shubin. 2005. High seas salmonid coded-wire tag recovery data, 2005. North Pacific Anadromous Fish Commission Doc. 905. Available: http://www.npafc.org/new/publications/Documents/PDF%202005/905%28USA%29.pdf. (March 2015).

Myers, K. W., N. V. Klovach, O. F. Gritsenko, S. Urawa, and T. C. Royer. 2007. Stock specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. North Pacific Anadromous Fish Commission Bulletin 4:159–177. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%204/159-177Myers.pdf. (October 2017).

Myers, K. W., N. D. Davis, R. V. Walker, and M. E. Atcheson. 2013. Potential mechanisms of ocean mortality of juvenile salmon and steelhead due to ingestion of plastic marine debris. North Pacific Anadromous Fish Commission Technical Report 9:169–170. Available: http://www.npafc.org/new/publications/Technical%20Report/TR9/Myers%20et%20al.pdf. (October 2017).

Myers, K. W., J. R. Irvine, E. A. Logerwell, S. Urawa, S. V. Naydenko, A. V. Zavolokin, and N. D. Davis. 2016. Pacific salmon and steelhead: life in a changing winter ocean. North Pacific Anadromous Fish Commission Bulletin 6:113–138.

Nagasawa, K. 1987. Prevalence and abundance of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on high-seas salmon and trout in the North Pacific Ocean. Nippon Suisan Gakkaishi (Bulletin of the Japanese Society of Scientific Fisheries) 53:2151–2156.

Nagasawa, K. 2001. Annual changes in the population size of the salmon louse *Lepeophtheirus salmonis* (Copepoda : Caligidae) on high-seas Pacific salmon (*Oncorhynchus* spp.) and relationship to host abundance. Hydrobiologia 453:411–416.

Narum, S. R., C. Contor, A. Talbot, and M. S. Powell. 2004. Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, USA. Journal of Fish Biology 65:471–488.

Narum, S. R., M. S. Powell, R. Evenson, B. Sharp, and A. J. Talbot. 2006. Microsatellites reveal population substructure of Klickitat River native steelhead and genetic divergence from an introduced stock. North American Journal of Fisheries Management 26:147–155.

Narum, S. R., D. Hatch, A. J. Talbot, P. Moran, and M. S. Powell. 2008a. Iteroparity in complex mating systems of steelhead *Oncorhynchus mykiss* (Walbaum). Journal of Fish Biology 72:45–60.

Narum, S. R., J. S. Zendt, D. Graves, and W. R. Sharp. 2008b. Influence of landscape on resident and anadromous life history types of *Oncorhynchus*. Canadian Journal of Fisheries and Aquatic Sciences 65:1013–1023.

Narver, D. W. 1969. Age and size of steelhead trout in the Babine River, British Columbia. Journal of the Fisheries Research Board of Canada 26:2754–2760.

Narver, D. W. 1974. Age and size of Nahmint River summer steelhead in anglers' catches, 1973. Fisheries Research Board of Canada, Nanaimo Biological Station Circular 97.

Narver, D. W., and F. C. Withler. 1974. Steelhead of the Nanaimo River—aspects of their biology and the fishery from 3 years of anglers' catches. Fisheries Research Board of Canada, Nanaimo Biological Station Circular 99.

Naughton, G. P., M. L. Keefer, T. S. Clabough, M. A. Jepson, S. R. Leee, C. A. Peery, and C. C. Caudill. 2011. Influence of pinniped-caused injuries on the survival of adult Chinook Salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) in the Columbia River Basin. Canadian Journal of Fisheries and Aquatic Sciences 68:1615–1624.

Naydenko, S. V., O. S. Temnykh, and A. L. Figurkin. 2016. Is winter the critical period in the marine life history of Pacific salmon? North Pacific Anadromous Fish Commission Bulletin 6:139–152.

Neave, F. 1958. The origin and speciation of *Oncorhynchus*. Transactions of the Royal Society of Canada 52:25–39.

Needham, P. R. and Gard, R. 1959. Rainbow trout in Mexico and California with notes on the Cutthroat series. University of California Publications in Zoology 67:1–124.

Nelson, J. 2012. California steelhead: management, monitoring and recovery efforts. Page 3 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the Thirteenth Pacific Coast Steelhead Management Meeting, March 13–15, 2012, Fort Worden, Port Townsend, Washington. Available: http://www.psmfc.org/steelhead/past-2012.html. (October 2017).

Nielsen, J. L. 1999. The evolutionary history of steelhead (*Oncorhynchus mykiss*) along the U.S. Pacific Coast: Developing a conservation strategy using genetic diversity. ICES Journal of Marine Science 56:449–458.

Nielsen, J. L., C. A. Gan, J. M. Wright, D. B. Morris, and W. K. Thomas. 1994. Biogeographic distribution of mitochondrial and nuclear markers for southern steelhead. Molecular Marine Biology and Biotechnology 3:281–293.

Nielsen, J. L., M. C. Fountain, J. C. Favela, K. Cobble, and B. J. Jensen. 1998. *Oncorhynchus* at the southern extent of their range: a study of mtDNA control-region sequence with special reference to an undescribed subspecies of *O. mykiss* from Mexico. Environmental Biology of Fishes 51:7–23.

Nielsen, J. L., S. M. Turner, and C. E. Zimmerman. 2011. Electronic tags and genetics explore variation in migrating steelhead kelts (*Oncorhynchus mykiss*), Ninilchik River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 68:1–16.

(NOAA) National Oceanic and Atmospheric Administration. 2005. ESA critical habitat designation regulations for southern California steelhead, 2005 Federal Register notices, 2005–09–02, Northwest Regional Office, Seattle. Available: http://www.nwr.noaa.gov/Publications/FR-Notices/2005/Index.cfm. (October 2017).

North Pacific Anadromous Fish Commission (NPAFC). 2014a. NPAFC Pacific salmonid catch statistics (updated 19 December 2014). North Pacific Anadromous Fish Commission, Vancouver. Available: www.npafc.org. (October 2017).

North Pacific Anadromous Fish Commission (NPAFC). 2014b. NPAFC Pacific salmonid hatchery release statistics (updated 19 December 2014). North Pacific Anadromous Fish Commission, Vancouver. Available: www.npafc.org. (October 2017).

Null, R. E., K. S. Niemela, and S. F. Hamelberg. 2012. Postspawn migrations of hatchery-origin *Oncorhynchus mykiss* kelts in the Central Valley of California. Environmental Biology of Fishes. DOI 10.1007/s10641–012–0075–5.

(ODFW) Oregon Department of Fish and Wildlife. 1990. Effects of Lost Creek Dam on winter steelhead in the Rogue River. Phase II Completion Report. Rogue Basin Fisheries Evaluation Project. U.S. Army Corps of Engineers, Contract DACW57–77-C-0033, Available: http://www.dfw.state.or.us/fish/local_fisheries/rogue_river/docs/StW_phase_II_completion_report.pdf. (October 2017).

(ODFW) Oregon Department of Fish and Wildlife. 1994. Effects of Lost Creek Dam on summer steelhead in the Rogue River. Phase II Completion Report. Rogue Basin Fisheries Evaluation Project. U.S. Army Corps of Engineers, Contract DACW57–77-C-0033. Available: http://www.dfw.state.or.us/fish/local_fisheries/rogue_river/docs/StS_phase_II_completion_report.pdf. (October 2017).

Ogura, M. 1990. Outline of biotelemetry study of salmon by Shin-riasu maru, 1990. International North Pacific Fisheries Commission Document. Fisheries Agency of Japan, National Research Institute of Far Seas Fisheries, Shimizu, Japan.

Ogura, M. 1991. Outline of biotelemetry study of salmon by Shin-riasu maru, 1991. International North Pacific Fisheries Commission. Fisheries Agency of Japan, National Research Institute of Far Seas Fisheries, Shimizu, Japan.

Ogura, M., and N. Arai. 1993. Outline of biotelemetry study by the Shin-riasu maru, 1992. Pages 97–104 *in* Y. Ishida (editor). Reports on the research of salmon resources in the North Pacific Ocean in 1992. North Pacific Anadromous Fish Commission Document 16. Available: http://www.npafc.org/new/publications/Documents/PDF%201993/16%28Japan%29.pdf. (October 2017).

Ogura, M., and Y. Ishida. 1995. Homing behavior and vertical movements of four species of Pacific salmon (*Oncorhynchus* spp.) in the central Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences 52:532–540.

Okazaki, T. 1983. Distribution and seasonal abundance of *Salmo gairdneri* and *Salmo mykiss* in the North Pacific Ocean. Japanese Journal of Ichthyology 30:235–246.

Okazaki, T. 1984a. Age composition, growth, sex ratio, and gonad development of *Salmo gairdneri* and *Salmo mykiss* in the North Pacific. Japanese Journal of Ichthyology 31:23–37.

Okazaki, T. 1984b. Genetic divergence and its zoogeographic implications in closely related species *Salmo gairdneri* and *Salmo mykiss*. Japanese Journal of Ichthyology 31:297–311.

Okazaki, T. 1985. Distribution and migration of *Salmo gairdneri* and *Salmo mykiss* in the North Pacific based on allelic variations of enzymes. Japanese Journal of Ichthyology 32:230–215.

Olsen, J., K. Wuttig, D. Fleming, E. Kretcshmer, and J. Wenburg. 2006. Evidence of partial anadromy and resident-form dispersal bias on a fine scale in populations of *Oncorhynchus mykiss*. Conservation Genetics 7:613–619.

Onishi, H., S. Ohtsuka, and G. Anma. 2000. Anticyclonic, baroclinic eddies along 145°W in the Gulf of Alaska in 1994–1999. Bulletin of the Faculty of Fisheries, Hokkaido University 51:31–43. (In Japanese with English abstract).

Osterback A. -M. K,, D. M. Frechette, A. O. Shelton, S. A. Hayes, M. H. Bond, S. A. Shaffer, and J. W. Moore. 2013. High predation on small populations: avian predation on imperiled salmonids. Ecosphere 4(9):116.

Paine, R. T. 1980. Food webs: linkage, interaction strength, and community infrastructure. Journal of Animal Ecology 49:667–685.

Parkinson, E. A., E. R. Keeley, E. B. Taylor, S. Pollard, and A. F. Tautz. 2005. A population database for defining conservation units for steelhead. Province of British Columbia Fisheries Management Report 119.

Pascual, M., P. Bentzen, C. Riva Rossi, G. Mackey, M. T. Kinnison, and R. Walker. 2001. First documented case of anadromy in a population of introduced Rainbow Trout in Patagonia, Argentina. Transactions of the American Fisheries Society 130: 53–67.

Pautzke, C. F., and R. C. Meigs. 1941. Studies on the life history of the Puget Sound steelhead trout (*Salmo gairdnerii*). Transactions of the American Fisheries Society 70:209–220.

Pavlov, D. S., and K. Kuzishchin. 1999. Morphobiological and genetic features of Kamchatka steelhead *Parasalmo mykiss* from the Voyampolka River (Western Kamchatka). Journal of Ichthyology 39:713–725.

Pavlov, D. S., and K. A. Savvaitova. 2008. On the problem of ratio of anadromy and residence in salmonids (Salmonidae). Journal of Ichthyology 48:778–791.

Pavlov, D. S., K. A. Savvaitova, and K. V. Kuzishchin. 1999. On the problem of epigenetic life-strategy variations in mikizha *Parasalmo mykiss* (Salmonidae, Salmoniformes), a Red-Book Species. Doklady Rossiiskaia Akademii Nauk 367:709–713 [Doklady Biologii 367:386–390 (1999)]. (In Russian.)

Pavlov, D. S., K. A. Savvaitova, and K. V. Kuzishchin. 2000. On dwarf males and reproductive tactics in Kamchatka mykiss *Parasalmo mykiss* Walb. Doklady Rossiiskaia Akademii Nauk Obshchei Biologii 373:135–138. (In Russian).

Pavlov, D. S., K. A. Savvaitova, K. V. Kuzishchin, M. A. Gruzdeva, S. D. Pavlov, V. M. Mednikov, and S. V. Maksimov. 2001. Pacific true salmon and trout in Asia. Nauchnyi Mir, Moscow. (In Russian).

Pavlov, D. S., K. A. Savvaitova, and K. V. Kuzishchin. 2007. Strategy of preservation of Kamchatka mykiss. The Russian Academy of Sciences Severtsov Institute for Ecology and Evolution (IPEE RAN), Moscow. (In Russian).

Pavlov, D. S., K. A. Savvaitova, K. V. Kuzishchin, M. A. Gruzdeva, A. Yu. Mal'tsev, and J. A. Stanford. 2008. Diversity of life strategies and population structure of Kamchatka mykiss *Parasalmo mykiss* in the ecosystems of small salmon rivers of various types. Journal of Ichthyology 48:37–44.

Pavlov, D. S., E. S. Borisenko, and V. M. Pashin. 2009. Investigations of spawning migration and assessment of abundance of the Kamchatka steelhead (*Parasalmo mykiss*) from the Utkholok River by means of Didson dual-frequency identification sonar. Journal of Ichthyology 49:1042–1064.

Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. Washington Sea Grant Program, University of Washington Press, Seattle.

Pearcy, W. G., and J. P. Fisher. 1990. Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981–1985. NOAA Technical Report NMFS 93:1–83. Available: http://spo.nmfs.noaa.gov/tr93opt.pdf. (October 2017).

Pearcy. W. G., and K. Masuda. 1982. Tagged steelhead trout (*Sa1mo gairdneri* Richardson) collected in the North Pacific by the Oshoro-Maru, 1980–1981. Bulletin of the Faculty of Fisheries Hokkaido University 33:249–254. Available: http://eprints.lib.hokudai.ac.jp/dspace/bitstream/2115/23805/1/33%284%29_P249-254.pdf. (October 2017).

Pearcy, W. G., and K. Masuda. 1987. Tagged steelhead trout (*Sa1mo gairdneri* Richardson) collected in the North Pacific by the Oshoro-Maru, 1982–1985. Bulletin of the Faculty of Fisheries Hokkaido University 38:203–208. Available: http://eprints.lib.hokudai.ac.jp/dspace/bitstream/2115/23954/1/38%283%29_P203-208.pdf. (October 2017).

Pearcy, W., T. Nishiyama, T. Fujii, and K. Masuda. 1984. Diel variations in the feeding habits of Pacific salmon caught in gill nets during a 24-h period in the Gulf of Alaska. U.S. National Marine Fisheries Service Fishery Bulletin 82:391–399.

Pearcy, W. G., R. D. Brodeur, J. M. Shenker, W. W. Smoker, and Y. Endo. 1988. Food habits of Pacific salmon and steelhead trout, midwater trawl catches and oceanographic conditions in the Gulf of Alaska, 1980–1985. Bulletin of the Ocean Research Institute 26(II):29–78.

Pearcy, W. G., R. D. Brodeur, and J. P. Fisher. 1990. Distribution and ecology of juvenile Cutthroat (*Oncorhynchus clarki clarki*) and steelhead trout (*O. mykiss*) in the ocean off Oregon and Washington. U.S. National Marine Fisheries Service Fishery Bulletin 88:697–711.

Pearsons, T., S. Phelps, S. Martin, E. Bartrand, and G. McMichael. 2007. Gene flow between resident and anadromous Rainbow Trout in the Yakima Basin: ecological and genetic evidence. *In* K. Schroeder and J. D. Hall, editors. Proceedings of the inland rainbow trout workshop. Oregon Chapter, American Fisheries Society, Corvallis. Available: http://www.ykfp.org/datawh/YKFPPubsReports/SpeciesInteractions/YSIS%201995–1997,%2064878-6.pdf#page=216. (October 2017).

Pella, J., R. Rumbaugh, L. Simon, M. Dahlberg, S. Pennoyer, and M. Rose. 1993. Incidental and illegal catches of salmonids in North Pacific driftnet fisheries. International North Pacific Fisheries Commission Bulletin 53(III):325–358. Available: http://www.npafc.org/new/inpfc/INPFC%20Bulletin/Bull%20No.53/Bulletin%2053%28III%29.pdf. (October 2017).

Penney, Z. L., and C. M. Moffitt. 2014a. Histological assessment of organs in sexually mature and postspawning steelhead trout and insights into iteroparity. Reviews in Fish Biology and Fisheries 24:781–801.

Penney, Z. L., and C. M. Moffitt. 2014b. Proximate composition and energy density of stream-maturing adult steelhead during upstream migration, sexual maturity, and kelt emigration. Transactions of the American Fisheries Society 143:399–413.

Penney, Z. L., and C. M. Moffitt. 2015. Fatty-acid profiles of white muscle and liver in stream-maturing steelhead trout *Oncorhynchus mykiss* from early migration to kelt emigration. Journal of Fish Biology 86:105–120.

Peterman, R. 1978. Testing for density-dependent marine survival in Pacific salmonids. Journal of the Fisheries Research Board of Canada 35:1434–1450.

Petrosky, C. E., and H. A. Schaller. 2010. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook Salmon and steelhead. Ecology of Freshwater Fish 19:520–536.

Pierce, A. L., J. W. Blodgett, T. D. Cavileer, L. R. Medeiros, J. Boyce, L. K. Caldwell, W. J. Bosch, R. Branstetter, D. E. Fast, D. R. Hatch, and J. J. Nagler. 2017. Reproductive development in captive reconditioned female steelhead kelts: evidence for consecutive and skip spawning life histories. Canadian Journal of Fisheries and Aquatic Sciences 74:1049–1060.

Pevan, C. M., R. R. Whitney, and K. R. Williams. 1994. Age and length of steelhead smolts from the Mid-Columbia River Basin, Washington. North American Journal of Fisheries Management 14:77–86.

Pollard, S., and M. Beere. 2012. Steelhead status update for British Columbia. Pages 6–7 *in* Pacific States Marine Fisheries Commission and U.S. Fish and Wildlife Service, sponsors. Summary of the Thirteenth Pacific Coast Steelhead Management Meeting, March 13–15, 2012, Fort Worden, Port Townsend, Washington. Available: http://www.psmfc.org/steelhead/2012/2012_Steelhead_Summary_FINAL.pdf. (October 2017).

Puckett, L. K. 1975. The status of spring-run (*Salmo gairdneri*) of the Eel River system. California Department of Water Resources and California Department of Fish and Game, Memorandum Report. Available: California Department of Fish and Game, Inland Fisheries Division, Sacramento, California.

Putman, N. F., C. S. Endres, C. M. F. Lohmann, and K. J. Lohmann. 2011. Longitude perception and bicoordinate magnetic maps in sea turtles. Current Biology 21:463–466.

Putman, N. F., K. J. Lohmann, E. M. Putman, T. P. Quinn, A. P. Klimley, and D. L. G. Noakes. 2013. Evidence for geomagnetic imprinting as a homing mechanism in Pacific Salmon. Current Biology 23:312–316.

Putman, N. F., E. D. Jenkins, C. G. J. Michielsens, and D. L. G. Noakes. 2014a. Geomagnetic imprinting predicts spatio- temporal variation in homing migration of Pink and Sockeye Salmon. Journal of the Royal Society Interface 11:20140542.

Putman, N. F., A. M. Meinke, and D. L. G. Noakes. 2014b. Rearing in a distorted magnetic field disrupts the ‘map sense’ of juvenile steelhead trout. Biology Letters 10:20140169.

Qin, Y., and M. Kaeriyama. 2016. Feeding habits and trophic levels of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin 6:469–481.

Quinn, T. P. 1991. Models of Pacific salmon orientation and navigation on the open ocean. Journal of Theoretical Biology 150:539–545.

Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18:29–44.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Maryland in association with University of Washington Press, Seattle.

Quinn, T. P., and K. W. Myers. 2004. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Reviews in Fish Biology and Fisheries 14:421–442.

Quinn, T. P., T. R. Seamons, L. A. Vøllestad, and E. Duffy. 2011. Effects of growth and reproductive history on the egg size-fecundity trade-off in steelhead. Transactions of the American Fisheries Society 140:45–51.

Quinn, T. P., T. R. Seamons, and S. P. Johnson. 2012. Stable isotopes of carbon and nitrogen indicate differences in marine ecology between wild and hatchery-produced steelhead. Transactions of the American Fisheries Society 141:526–532.

Reinhardt, U. 2001. Selection for surface feeding in farmed and sea-ranched masu salmon juveniles. Transactions of the American Fisheries Society 130:155–158.

Rexroad, C. E., III, and R. L. Vallejo. 2009. Estimates of linkage disequilibrium and effective population size in Rainbow Trout. BMC Genetics 10:83.

Richter, A., and S. A. Kolmes. 2005. Maximum temperature limits for Chinook, Coho, and Chum Salmon, and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science 13:23–49.

Riley, S. C., R. L. Haedrich, and R. J. Gibson. 1998. Negative bias in removal estimates of Atlantic Salmon parr relative to stream size. Journal of Freshwater Ecology 8:97–101.

Roby, D. D., D. E. Lyons, D. P. Craig, K. Collis, and G. H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. Canadian Journal of Zoology 81:250–265.

Rogers, D. E. 1984. Trends in abundance of northeastern Pacific stocks of salmon. Pages 100–127 *in* W. G. Pearcy, editor. The influence of ocean conditions on the production of salmonids in the North Pacific. Oregon State University Press, Corvallis.

Rolland, J. B., and J. R. Winton. 2003. Relative resistance of Pacific salmon to infectious salmon anemia virus. Journal of Fish Diseases 26:511–520.

Romer, J. D., C. A. Leblanc, S. Clements, J. A. Ferguson, M. L. Kent, D. Noakes, and C. B. Schreck. 2012. Survival and behavior of juvenile steelhead trout (*Oncorhynchus mykiss*) in two estuaries in Oregon, USA. Environmental Biology of Fishes 96:849–863.

Royce, W. F., L. S. Smith, and A. C. Hartt. 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. U.S. National Marine Fisheries Service Fishery Bulletin 66:441–462.

Ruggerone, G. T., T. P. Quinn, I. A. McGregor, and T. D. Wilkinson. 1990. Horizontal and vertical movements of adult steelhead trout, *Oncorhynchus mykiss*, in the Dean and Fisher channels, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 47:1963–1969.

Ruggerone, G. T., R. M. Peterman, B. Dorner, and K. W. Myers. 2010a. Magnitude and trends in abundance of hatchery and wild Pink, Chum, and Sockeye Salmon in the North Pacific Ocean. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 2:306–328. Available: afsjournals.org/doi/pdf/10.1577/C09–054.1. (October 2017).

Ruggerone, G. T., R. M. Peterman, B. Dorner, K. W. Myers, and N. J. Mantua. 2010b. Abundance of adult hatchery and wild salmon by region of the North Pacific. SAFS-UW-1001, School of Aquatic and Fishery Sciences, University of Washington, Seattle. Available: https://digital.lib.washington.edu/research works/handle/1773/16262. (October 2017).

Ryan, B. A., S. G. Smith, J. M. Butzerin, and J. W. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary 1998–2000. Transactions of the American Fisheries Society 132:275–288.

Sanders, G. 1985. Summary of age, sex, run timing, and length-weight characteristics of Alaska steelhead. Pages 29–49 *in* Alaska Department of Fish and Game, Alaska Steelhead Workshop 1985. Available: National Marine Fisheries Service, Environmental and Technical Services, Portland, Oregon. (October 2017).

Sandstrom, P., A. Ammann, C. Michel, G. Singer, E. Chapman, S. Lindley, R. MacFarlane, and A. Klimley. 2013a. Growth, survival, and tag retention of steelhead trout (*Oncorhynchus mykiss*) and its application to survival estimates. Environmental Biology of Fishes 96:145–164.

Sandstrom, P. T., T. Keegan, and G. Singer. 2013b. Survival and movement patterns of central California coast native steelhead trout (*Oncorhynchus mykiss*) in the Napa River. Environmental Biology of Fishes 96:287–302.

Sasaki, S. 1966. Distribution and food habits of king salmon and steelhead rainbow trout in the Sacramento-San Joaquin Delta. Pages 108–114 *in* J. L. Turner and D.W. Kelley, compilers. Ecological studies of the Sacramento-San Joaquin Delta, Part II: Fishes of the Delta. California Department of Fish and Game, Fish Bulletin 136. Available: http://libraries.ucsd.edu/apps/ceo/fishbull/. (October 2017).

Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2009. Steelhead life history on California's central coast: insights from a state-dependent model. Transactions of the American Fisheries Society 138:532–548.

Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2010. State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. Evolutionary Applications 3:221–243.

Satterthwaite, W. H., S. A. Hayes, J. E. Merz, S. M. Sogard, D. M. Frechette, and M. Mangel. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. Transactions of the American Fisheries Society 141:781–794.

Savvaitova, K. A. 1975. The population structure of *Salmo mykiss* in Kamchatka. Journal of Ichthyology 15:876–888.

Savvaitova, K. A., and V. D. Lebedev. 1966. On the systematic position of *Salmo penshinenesis* Pallas and *Salmo mykiss* Walbaum and their relationship with the American representatives of genus *Salmo*. Voprosy Ikhtiologii 4: 593–608. (In Russian).

Savvaitova K. A., and V. A. Maksimov. 1967. On taxonomy of Kamchatka *Salmo mykiss* Walbaum. MSU Vestnik (Moscow University Biological Sciences Bulletin) 4:14–20. (In Russian).

Savvaitova, K.A., V. A. Maksimov, M. V. Mina, G. G. Novikov, L. V. Kokhmenko, and V. E. Matsuk. 1973. Kamchatka true salmon (systematics, ecology, and prospects of using them as an object of trout cultivation and acclimatization). Voronezhskogo Gosudarstvennogo Universiteta. [In Russian] [Savvaitova, K.A., V. A. Maksimov, M. V. Mina, G. G. Novikov, L. V. Kokhmenko, and V. E. Matsuk. 1973. The noble trouts of Kamchatka (systematics, ecology, and the possibilities of using them as the object of trout-culture and acclimatization). The Voronezh University, Publishers. English translation by L.V. Sagen and G.A. Kautsky. Edited by G.A. Kautsky and J.T. Light. Fisheries Research Institute, University of Washington, Seattle.]

Savvaitova, K. A., K. V. Kuzishchin, and D. S. Pavlov. 1999. Population structure of mykiss *Parasalmo mykiss* from rivers of northwestern Kamchatka and North America. Journal of Ichthyology 39:504–516.

Savvaitova, K. A., K. V. Kuzishchin, M. A. Gruzdeva et al. 2003. Long-term and short-term variations in the population structure of Kamchatka steelhead *Parasalmo mykiss* from Rivers of Western Kamchatka. Journal of Ichthyology 43:757–768.

Savvaitova, K. A., M. A. Gruzdeva, K. V. Kuzishchin, D. S. Pavlov, D. A. Stanford, S. G. Sokolov, and B. Ellis. 2005. Half-Pounders of *Parasalmo mykiss*—a special element of the species structure, on the formation of various life strategies. Journal of Ichthyology 45:768–777.

Savvaitova, K. A., D. S. Pavlov, K. V. Kuzishchin, M. A. Gruzdeva, A. V. Kucheryavyi. 2007. Ecological Analogies in the Pacific Lamprey *Lethenteron camtschaticum* and the mykiss *Parasalmo mykiss* in Kamchatka. Journal of Ichthyology 47:341–347.

Scheuerell, M. D., R. W. Zabel, and B. P. Sandford. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). Journal of Applied Ecology 46:983–990.

Schroeder, R. K., R. B. Lindsay, K. R. Kenaston. 2001. Origin and straying of hatchery winter steelhead in Oregon coastal rivers. Transactions of the American Fisheries Society 130:431–441.

Schultz, A. A., V. B. Afentoulis, C. J. Yip, and M. N. Johnson. 2017. Efficacy of an acoustic tag with predation detection technology. North American Journal of Fisheries Management Vol. 37:574–581.

Scordino, J., and B. Pfeifer. 1993. Sea lion/steelhead conflict at the Ballard Locks. A history of control efforts to date and a bibliography of technical reports. Washington Department of Fish and Wildlife Report. Available: Unites States Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Regional Office, Seattle, Washington.

Scott, J. B., Jr., and W. T. Gill, editors. 2008. *Oncorhynchus mykiss*: assessment of Washington State's anadromous populations and programs. Washington Department of Fish and Wildlife, Olympia. Available: wdfw.wa.gov/publications/00150/wdfw00150.pdf. (October 2017).

Seamons, T., P. Bentzen, and T. Quinn. 2004. The mating system of steelhead, *Oncorhynchus mykiss*, inferred by molecular analysis of parents and progeny. Environmental Biology of Fishes 69:333–344.

Sebring, S. H., M. C. Carper, R. D. Ledgerwood, B. P. Sandford, G. M. Matthews, and A. F. Evans. 2013. Relative vulnerability of PIT-tagged subyearling fall Chinook Salmon to predation by Caspian terns and double-crested cormorants in the Columbia River estuary. Transactions of the American Fisheries Society 142:1321–1334.

Shapovalov, L., and A. C. Taft. 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.

Shenker, J. M. 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon. U.S. National Marine Fisheries Service Fishery Bulletin 86:299–317.

Sheppard, D. 1972. The present status of the steelhead trout stocks along the Pacific coast. Pages 519–556 *in* D. H. Rosenberg, editor. A review of the oceanography and renewable resources of the northern Gulf of Alaska. Institute of Marine Science Report R72–23, Sea Grant Report 73–3, Institute of Marine Science, University of Alaska, Fairbanks.

Sheiko. B. A., and V. V. Fedorov. 2000. Catalog of vertebrates of Kamchatka and adjacent seawater areas. Kamchatskiy Petchatniy Dvor, Petropavlovsk-Kamchatskii. [In Russian].

Sloat, M. R., and G. H. Reeves. 2014. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and Rainbow Trout (*Oncorhynchus mykiss*) life histories. Canadian Journal of Fisheries and Aquatic Sciences 71:491–501.

Sloat, M. R., D. J. Fraser, J. B. Dunham, J. A. Falke, C. E. Jordan, J. R. McMillan, and H. A. Ohms. 2014. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. Reviews in Fish Biology and Fisheries 24:689–707.

Smith, B. D., and B. R. Ward. 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for coastal regions of British Columbia support the variable marine survival hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 57:271–284.

Smith, G. R. 1975. Fishes of the Pliocene Glenns Ferry Formation, Southwest Idaho. Pages 1–68 *in* N. E. Friedland, editor. Papers on Paleontology No. 14, Claude W. Hibbard Memorial Volume 5, The Museum of Paleontology, University of Michigan, Ann Arbor. Available: http://deepblue.lib.umich.edu/handle/2027.42/48614. (October 2017).

Smith, G. R., and R. F. Stearley. 1989. The classification and scientific names of Rainbow and Cutthroat Trouts. Fisheries 14:4–10.

Smith, J. J. 1990. The effects of sandbar formation and inflows on aquatic habitat and fish utilization in Pescadero, San Gregorio, Waddell and Pomponio Creek Estuary/Lagoon systems, 1985–1989. Report prepared under interagency agreement 84–04–324, between Trustees for California State University and the California Department of Parks and Recreation. Available: http://www.casefourenvironment.org/wp-content/pdfs/1990_Smith_Frogs_1.pdf. (October 2017).

Snyder, J. O. 1925. The half-pounder of Eel River, a steelhead trout. California Fish and Game 11:49–55.

Stansbury, A. L., T. Götz, V. B. Deecke, and V. M. Janik. 2015. Grey seals use anthropogenic signals from acoustic tags to locate fish: evidence from a simulated foraging task. Proceedings of the Royal Society B 282:20141595.

Sutherland, D. F. 1973. Distribution, seasonal abundance, and some biological features of steelhead trout, *Salmo gairdneri*, in the North Pacific Ocean. U.S. National Marine Fisheries Service Fishery Bulletin 71:787–826.

Suvorov, E. K. 1912. The Commander Islands and its fur harvest. Tipographiya Kirshbauma, St. Petersburg. [In Russian]

Tadokoro, K., Y. Ishida, N. D. Davis, S. Ueyanagi, and T. Sugimoto. 1996. Change in Chum Salmon (*Oncorhynchus keta*) stomach contents associated with fluctuation of Pink Salmon (*O. gorbuscha*) abundance in the central subarctic Pacific and Bering Sea. Fisheries Oceanography 5:89–99.

Tatara, C. P., M. R. Cooper, W. Gale, B. M. Kennedy, C. R. Pasley, and B. A. Berejikian. 2017. Age and method of release affect migratory performance of hatchery steelhead. North American Journal of Fisheries Management 37:700–713.

Tautz, A. F., B. R. Ward, and R. A. Ptolemy. 1992. Steelhead trout productivity and stream carrying capacity for rivers of the Skeena drainage. Pacific Stock Assessment Review Committee Working Paper S92–6 and 8. Ministry of Environment, Lands and Parks, Fisheries Branch, Fisheries

Research and Development Section, University of British Columbia, Vancouver, B.C. Available: http://www.env.gov.bc.ca/wld/documents/steelhead.PDF. (October 2017).

Taylor, G. T., and R. J. LeBrasseur. 1957. Distribution, age and food of steelhead trout (*Salmo gairdneri*) caught in the northeast Pacific Ocean, 1956. Progress Report Pacific Coast Stations, Nanaimo 109:9–11.

Teo, S. L. H., P. T. Sandstrom, E. D. Chapman, R. E. Null, K. Brown, A. P. Klimley, and B. A. Block. 2013. Archival and acoustic tags reveal the postspawning migrations, diving behavior, and thermal habitat of hatchery-origin Sacramento River steelhead kelts (*Oncorhynchus mykiss*). Environmental Biology of Fishes 96:175–187.

Thompson, J. N., and D. A. Beauchamp. 2014. Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. Transactions of the American Fisheries Society 143:910–925.

Thrower, F. P., J. J. Hard, and J. E. Joyce. 2004. Genetic architecture of growth and early life history transitions in anadromous and derived freshwater populations of steelhead. Journal of Fish Biology 65(s1):286–307.

Tipping, J. M. 1991. Heritability of age at maturity in steelhead. North American Journal of Fisheries Management 11:105–108.

Thorpe, J. E. 2004. Life history responses of fishes to culture. Journal of Fish Biology 65 (Supplement A):263–285.

Tuomikoski, J., J. McCann, B. Chockley, H. Schaller, S. Haeseker, J. Fryer, C. Petrosky, E. Tinus, T. Dalton, and R. Ehlke. 2012. Comparative survival study (CSS) of PIT-tagged spring/summer/fall Chinook, summer steelhead, and Sockeye. 2012 Annual Report to Bonneville Power Administration, Contract #19960200, Fish Passage Center, Portland, Oregon. Available: http://www.fpc.org/documents/CSS.html. (October 2017).

Turek, M. F. 2005. Prince of Wales Island subsistence steelhead harvest and use pattern. Alaska Department of Fish and Game, Division of Subsistence, Technical Paper 293. Available: http://www.subsistence.adfg.state.ak.us/TechPap/tp293%20.pdf. (October 2017).

Wahle, R. J. and R. Z. Smith. 1979. A historical and descriptive account of Pacific coast anadromous salmonid rearing facilities and a summary of their releases by region,1960–1976. National Oceanic and Atmospheric Administration Technical Report NMFS SSRF-736.

Walker, M. M., C. E. Diebel, C. V. Haugh, P. M. Pankhurst, J. C. Montgomery, and C. R. Green. 1997. Structure and function of the vertebrate magnetic sense. Nature 390:371–376.

Walker, R. V., K. W. Myers, N. D. Davis, K. Y. Aydin, and K. D. Friedland. 2000a. Using temperatures from data storage tags in bioenergetic models of hish-seas salmon growth. North Pacific Anadromous Fish Commission Bulletin 2:301–308. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%202/pages%20301-308%28Walker%29.PDF. (October 2017).

Walker, R. V., K. W. Myers, N. D. Davis, K. Y. Aydin, K. D. Friedland, H. R. Carlson, G. W. Boehlert, S. Urawa, Y. Ueno, and G. Anma. 2000b. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. Fisheries Oceanography 9:171–186.

Walker, R. J., V. V. Sviridov, S. Urawa, and T. Azumaya. 2007. Spatio-temporal variation in vertical distributions of Pacific salmon in the ocean. North Pacific Anadromous Fish Commission Bulletin 4:193–201. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%20 4/193–201Walker.pdf. (October 2017).

Walters, C. J., J. A. Lichatowich, R. M. Peterman, and J. D. Reynolds. 2008. Report of the Skeena Independent Science Review Panel. A report to the Canadian Department of Fisheries and Oceans and the British Columbia Ministry of the Environment. May 15, 2008. Available: http://skeenawatershedinitiative.com/library/lib157. (October 2017).

Waples, R. S., R. G. Gustafson, L. A. Weitkamp, J. M. Myers, O. W. Johnson, P. J. Busby, J. J. Hard, G. J. Bryant, F. W. Waknitz, K. Neely, D. Teel, W. S. Grant, G. A. Winans, S. Phelps, A. Marshall, and B. M. Baker. 2001. Characterizing diversity in Pacific salmon. Journal of Fish Biology 59 (Suppl. A):1–41.

Waples, R. S., G. R. Pess, and T. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evolutionary Applications 1:189–206.

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo garirdneri*) and the relation to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 46:1110–1122.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853–1858.

(WDF) Washington Department of Fisheries, Washington Department of Wildlife (WDW), and Western Washington Treaty Indian Tribes (WWTIT). 1993. 1992 Washington State salmon and steelhead stock inventory (SASSI). Washington Department of Fish and Wildlife, Olympia, 212 pp. and 5 regional volumes. Available: http://wdfw.wa.gov/publications/00194/wdfw00194.pdf. (October 2017).

(WDFW) Washington Department of Fish and Wildlife. 1994. Letter to the ESA Administrative Record for west coast steelhead, 27 July 1994, enclosure 15, WDFW Steelhead Resource Inventory Tables (tables updated by WDFW in 1995). Available: U.S. Department of Commerce, National Marine Fisheries Service, Environmental and Technical Services Division, Portland, Oregon.

Weber, W., and W. Knispel. 1977. Nehalem River winter steelhead study. Oregon Department of Fish and Wildlife, Anadromous Fish Conservation Project Final Report AFS 65. Available: Oregon Department of Fish and Wildlife, Portland, Oregon.

Weitkamp, L. A., P. J. Bentley, and M. N. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary, U.S.A. U.S. National Marine Fisheries Service Fishery Bulletin 110:426–450.

Weitkamp, L. A., G. Goulette, J. Hawkes, M. O'Malley, and C. Lipsky. 2014. Juvenile salmon in estuaries: comparisons between North American Atlantic and Pacific salmon populations. Reviews in Fish Biology and Fisheries 24:713–736.

Weitkamp, L. A., D. J. Teel, M. Liermann, S. A. Hinton, D. M. Van Doornik, and P. J. Bentley. 2015. Stock-specific size and timing at ocean entry of Columbia River juvenile Chinook Salmon and steelhead: implications for early ocean growth. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 7:370 –392.

Welch, D. W. 1997. Anatomical specialization in the gut of Pacific salmon (*Oncorhynchus*): evidence for oceanic limits to salmon production? Canadian Journal of Zoology 75:936–942.

Welch, D. W., Y. Ishida, K. Nagasawa, and J. P. Eveson. 1998. Thermal limits on the ocean distribution of steelhead trout (*Oncorhynchus mykiss*). North Pacific Anadromous Fish Commission Bulletin 1:396–404. Available: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%201/page%20396-404%28Welch%29.PDF. (October 2017).

Welch, D. W., B. R. Ward, B. D. Smith, and J. P. Eveson. 2000. Temporal and spatial response of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. Fisheries Oceanography 9:17–32.

Welch, D. W., B. R. Ward, and S. D. Batten. 2004. Early ocean survival and marine movements of hatchery and wild steelhead trout (*Oncorhynchus mykiss*) determined by an acoustic array: Queen Charlotte Strait, British Columbia. Deep-Sea Research Part II, Topical Studies in Oceanography 51:897–909.

Welch, D. W., M. C. Melnychuk, J. C. Payne, E. L. Rechisky, A. D. Porter, G. D. Jackson, B. R. Ward, S. P. Vincent, C. C. Wood, and J. Semmens. 2011. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. Proceedings of the National Academy of Sciences 108:8708–8713.

Wertheimer, R. H., and A. F. Evans. 2005. Downstream passage of steelhead kelts through hydroelectric dams on the lower Snake and Columbia rivers. Transactions of the American Fisheries Society 134:853–865.

Whitney, F. A., and H. J. Freeland. 1999. Variability in upper-ocean water properties in the NE Pacific Ocean. Deep-Sea Research II 46:2351:2370.

Whitt, C. R. 1954. The age, growth, and migration of steelhead trout in the Clearwater River, Idaho. Master's thesis. University of Idaho, Moscow.

Wilbur, H. M., and H. W. Rudolf. 2006. Life history evolution in uncertain environments: bet hedging in time. American Naturalist 168:398–411.

Williams, J. G., S. G. Smith, and W. D. Muir. 2001. Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia Rivers hydropower system, 1966–1980 and 1993–1999. North American Journal of Fisheries Management 21:310–317.

Withler, I. L. 1966. Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific coast of North America. Journal of the Fisheries Research Board of Canada 23:365–393.

Wood, C. C. 2001. Managing biodiversity in Pacific salmon: the evolution of the Skeena River Sockeye Salmon fishery in British Columbia. Paper presented at the international conference Blue Millennium: Managing Global Fisheries for Biodiversity thematic workshop, Victoria, Canada, June 25–27, 2001, funded by the Global Environment Facility (through the United Nations Environmental Program) and International Development Research Centre, Ottawa, ON, Canada. Available: https://www.cbd.int/doc/nbsap/fisheries/Wood.pdf. (October 2017).

Wooten, R., J. W. Smith, and E. A. Needham. 1982. Aspects of the biology of the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongates* on farmed salmonids and their treatment. Proceeding of the Royal Society of Edinburgh 81B:185–197.

Wuttig, K., D. Fleming, and J. Olsen. 2004. Stock status and population biology of the Copper River steelhead, Alaska Department of Fish and Game, Fishery Data Series 04–18, Anchorage.

Zaugg, W. S., and H. H. Wagner. 1973. Gill ATPase activity related to par–smolt transformation and migration in steelhead trout (*Salmo gairdneri*): influence of photoperiod and temperature. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry 45:955–965.

Zielinski, C. M, H. V. Lorz, and J. L. Bartholomew. 2010. Detection of *Myxobolus cerebralis* in the Lower Deschutes River Basin, Oregon. North American Journal of Fisheries Management 30:1032–1040.

Zimmerman, C., and G. Reeves. 2002. Identification of steelhead and resident Rainbow Trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Transactions of the American Fisheries Society 131:986–993.

Zimmerman, C. E., and G. H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidences from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57:2152–2162.