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Ecology of Salmonids in Estuaries around the World

Adaptations, Habitats, and Conservation

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The following web-based supplemental materials can be accessed at: http://hdl.handle.net/2429/57062.

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Why a Focus on Salmonids and Estuaries?

Throughout history, both estuaries and salmonids have played an important role in human civilization. River mouths linked interior and coastal peoples, especially after the dawn of maritime trade. Salmon were a link between the ocean and rivers, providing a steady supply of protein-rich food to estuary dwellers, who could catch the fish with little effort in the constricted river mouths. Salmonid carcasses in river watersheds and lakes brought marine nutrients (nitrates and phosphates) to a variety of ecosystems, including the estuaries of short rivers. Subsistence fisheries for salmonids were widespread in the Northern Hemisphere, which, until the nineteenth century, was the only place in the world where these anadromous species were found. Consequently, the history of humans in the Northern Hemisphere is closely linked with salmonids in estuaries. Salmonids were introduced to the Southern Hemisphere in the 1800s and are now sought by recreational fishers in that part of the globe.

Historically, Vikings, Inuit, Beothuk, Mi'kmaq, and Mohicans harvested Atlantic salmonids at river mouths, while Aleuts, Haida, Salish, Ainu, and numerous other First Nations gathered Pacific salmon species. Estuarine fishing weirs capable of catching salmonids have been found in 5,000-year-old sites in Alaska (Tveskov and Erlandson 2003). The Kaspi people netted salmonids in the numerous estuaries around the Caspian Sea. In medieval times, salmonid fishing in European estuaries was conducted as far south as the Douro River estuary in Portugal. As the European fishing industry developed more formal marketing and distribution methods, salmonid processing plants and canneries were built at the mouths of larger rivers (Hoffmann 2005). In the early 1900s, there were hundreds of canneries in estuaries on both the northwest and northeast Pacific coasts (Bottom 1997). In Japan, commercial harvesting of salmon began as early as the 1600s (Nagata and Kaeriyama 2003).

Salmonids as a Cultural Icon

Salmonid stories or celebrations have featured in numerous cultures around the world. For example, from Victorian England:

> In every stage of their existence, salmon are surrounded by enemies innumerable, and it is really wonderful that they do not become extinct. They are, however, so prolific, that when care is bestowed upon them, and their enemies kept under as much as possible, they increase in numbers and size in a most wonderful manner. (Buckland 1880, 289)

From Scandinavia/Iceland at the time of the Norse Sagas:

> Skallagrim also had his men go up the rivers looking for salmon, and settled Odd the Lone-dweller at the Gljufur River where he attended to the salmon-fishing. (Byock 2001, 29)

From West Coast First Nations in Canada:

> Raven and a friend were invited to dinner at the village of the fish. Two children, a boy and a girl, were sent into the water, and shortly after, Raven was given his salmon dinner. Raven ate his meal, but instead of putting all the bones on his plate, he kept a small bone from the salmon's head in his mouth. The bones were gathered up and thrown back into the water, where they changed back into little children. The boy was okay, but the little girl couldn't open her eyes. The parents knew that a bone had not been put on the plate and began to look for it. They searched all over. Suddenly, Raven pulled the bone out of his mouth and remarked, "Maybe this is the one!" They told the little girl to go back into the water and then threw the missing bone in after her. When she came out, she was whole again. That is why you must always throw the salmon bones back into the ocean. (D. Kennedy and Bouchard 1983, 26)

And from contemporary Japan:

> On the island of Hokkaido, Japan, an Ainu ceremony called the *Ashiri Cheppu Nomi* is held every year in September on the Toyohira-gawa River plain in Sapporo to invoke the new run of salmon. (City of Sapporo 2015)

Importance of Salmonids around the World

Today, as they have been for centuries, salmonids are an iconic fish, especially in the northern temperate region. For example, in the northeast Pacific region, they are an indicator of ecosystem health for 130 species of fish and wildlife, and salmonid life history characteristics relate strongly to local ecosystem processes such as productivity (Cederholm et al. 2000). For a long time, salmonids have also been of significant interest to evolutionary biologists, including Darwin (1871). They are highly prized for providing ecosystem services related to food provision, culture, recreation, and industry. However, countries around the world, especially those affected by globalization and industrial development, often have conflicting goals within management agencies for salmonids and their estuarine habitats. Many estuaries have major habitat degradation and water quality problems with nutrient enrichment from farms and cities in the catchment basins of rivers. Compared with other fishes, salmonids are vulnerable to local extinction due to a variety of life history factors, including relatively low fecundity (Powles et al. 2000); habitat sensitivity associated with the complexity of the freshwater/estuary/marine habitats used in their life cycle, and with their ocean range, which extends across national boundaries and exclusive economic zones; and susceptibility of populations to bycatch in mixed-stock fisheries.

Estuarine Profile in Salmonid Evolution

How salmonids may have evolved their complex patterns of freshwater, estuarine, and ocean habitat use has intrigued evolutionary ecologists. A brief description of the salmonid life cycle is required before we turn to an overview of their findings. The family Salmonidae, which in turn includes the four anadromous genera I discuss, includes the subfamily Salmoninae (Nelson 1994). Anadromous salmonids are hatched from eggs spawned in fresh water, move to the ocean, where they attain sexual maturity, and then move back to fresh water to reproduce. They move to and from the ocean via the estuary. Anadromous salmonids display two forms of reproduction, which determine the degree of estuarine use. *Semelparous* species migrate from the ocean to spawn in fresh water and then die. *Iteroparous* species spawn in rivers and overwinter in rivers or estuaries, but repeatedly migrate into estuaries or adjacent coastal waters during summer to feed. They eventually die in the river after a final spawning. These species obviously spend more of their lives in estuaries than semelparous species. The two basic patterns are shown schematically in Figure 1.

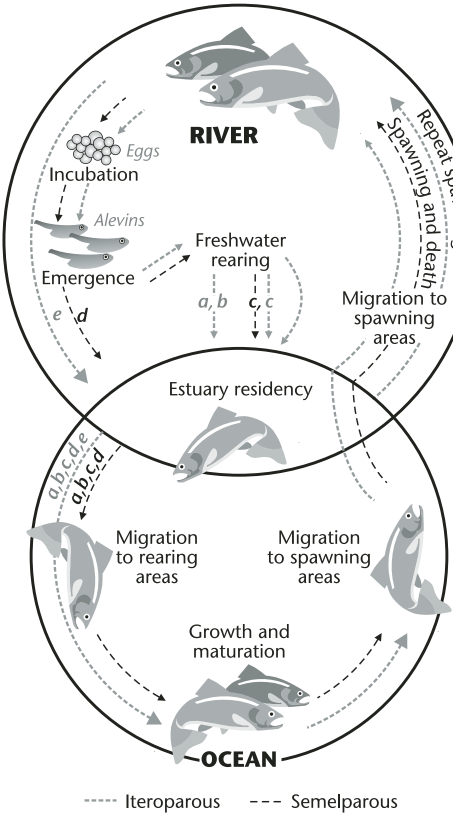

Figure 1 Generalized life history of iteroparous and semelparous anadromous salmonids, showing the central role of the estuary as a transition between the freshwater and ocean phases of the life cycle.

Notes: a – subyearling migrants, midsummer; b – subyearling migrants, autumn; c – yearling smolts; d – early spring migrants (fry or repeat migrants); e – kelts or returning veterans.

Source: Modified from Nicholas and Hankin 1988.

Most anadromous salmonids are generally considered freshwater fish that have evolved to live in the ocean, but this view is not held by all evolutionary ecologists (McPhail 2007). Most of the discussion of salmonid evolution focuses on reproductive success, which tends to emphasize the freshwater and ocean parts of the life cycle (e.g., Fleming 1998; Kinnison, Unwin, and Quinn 2008). However, the estuary has figured in the thinking about the evolution of anadromous salmonids. According to Tchernavin (1939 in Hoar 1976), sometime during the glacial period less than 1 million years ago (approximately the Pleistocene era) in the Northern Hemisphere, particularly Siberia, when "conditions of life in freshwater were unfavourable and food scarce ... some of the Salmonidae (for example, the genus *Salmo*) acquired habits of descending to the sea from the exhausted rivers to feed" (Hoar 1976, 1236). Furthermore, the type ancestor of semelparous Pacific salmonids (genus

Oncorhynchus) may have lived in estuaries as fry before they were able to live in full-strength seawater. During this period, they would have been confined to brackish estuaries until the smolt transformation evolved (Hoar 1976). Thus, the presence of salinity tolerance may also be the result of selection pressures related to the colonization of new regions during periods of changing glaciation, when fresh water from melting ice was widespread (C.C. Wilson and Hebert 1998). D.R. Montgomery (2000) proposed that the topographic variability of watersheds that occurred due to much earlier changes in geology of northwest North America during the Miocene-Pliocene times (20 to 6 million years ago) led to adaptive radiation of Pacific salmonids. They may have evolved into a variety of species using different freshwater habitats in the northeast Pacific region, and could also have taken advantage of productive ocean habitats. The freshwater changes were likely accompanied by the development of a variety of estuary types within the California-Alaska coastal reach, which the salmonids were obligated to use in their migrations between the river and the ocean. In the northwest Atlantic, these geological changes were not observed, suggesting that evolution of Atlantic salmonids in that region was not on the same trajectory (D.R. Montgomery 2000). On the New York–Newfoundland and Labrador coastline, there were only two species of endemic anadromous salmonids, *Salmo salar* (Atlantic salmon) and *Salvelinus fontinalis* (brook trout). Colonization of the region by *Salvelinus alpinus* (Arctic char) is thought to have occurred as the Pleistocene ice receded, and extant populations are considered to be vestiges of the anadromous populations that lived in the Champlain Sea and the Atlantic Ocean (i.e., glacial relict populations; Doucett et al. 1999). The study of the evolution and adaptations of salmonids to estuaries is clearly a complex and interesting challenge for the evolutionary ecologist.

Under some circumstances, salmonid evolution can occur much more quickly than profiled in the classical geological framework. The issue of short-term phenotypic plasticity in salmonids is relatively new and papers on the topic were uncommon before the 1990s (Hutching 2011). A growing body of empirical evidence shows that inheritable salmonid morphology (body size) and life history features (behaviour, growth, etc.) can shift on relatively rapid time scales when factors influencing the traits are modified (McClure et al. 2008; Hutching 2011). Domestication is a force for some of the changes. One example is the earlier return of wild coho salmon to the estuary and river after being subjected to sixty years of supplementation with early-released hatchery fish (Ford et al.

2006). Another example is the change in colour patterns of wild amago with introgression of hatchery-reared traits occurring within about thirty years (K. Kawamura et al. 2012). Short-term evolution has therefore attracted the attention of applied evolutionary ecologists, but there have been very few studies on estuarine salmonids.

In general, few researchers have explored the ability of freshwater species to establish marine populations or the ability of marine and freshwater species to establish euryhaline populations, the most likely starting point in the evolution of anadromy (Dodson, Laroche, and Lecomte 2009). The evolution of osmoregulation, which enables the removal of excess and toxic salts from the fish's body, is clearly a dominant component of the anadromous salmonid's fitness and survival suite of adaptations. However, additional selective forces in the estuary, particularly food supply and other biotic interactions, such as predation and competition, also likely conditioned the evolution of a variety of life histories, including iteroparity and the diversity of life history strategies that is now seen. As explained in following chapters, the divergence away from the conditions to which the salmonids adapted is the basis for present-day conservation concerns.

Estuarine Salmonids and Conservation Concerns

Four important genera of anadromous salmonids are currently of conservation concern, according to their listing by national or international authorities (e.g., the Red Books of the International Union for Conservation of Nature, or IUCN). Several other genera are listed as threatened or endangered by national conservation offices in some countries (see Appendix Table 1.1 at http://hdl.handle.net/2429/57062). Representatives of the salmonid genera *Salmo, Oncorhynchus, Salvelinus,* and *Hucho* are listed in conservation categories in various catchment basins over their natural range in North America, Europe, and Asia. For example, sea trout and Atlantic salmon are endemic, and now rare, in fifteen of the twenty-three estuaries summarized from the literature of northwestern Europe (M. Elliott and Hemingway 2002). In addition, forty-one of the seventy-six *Salmo, Oncorhynchus,* or *Salvelinus* taxocenes from North America listed as extinct, endangered, threatened, or vulnerable (Jelks et al. 2008) are anadromous and therefore must pass through an estuary as juveniles and adults.

Around the world, estuaries are among the most damaged or threatened habitats and deserve consideration as being critical or essential for salmonids. Compilation of current information on estuarine habitat and ecological functions is therefore vital to conservation efforts that aim

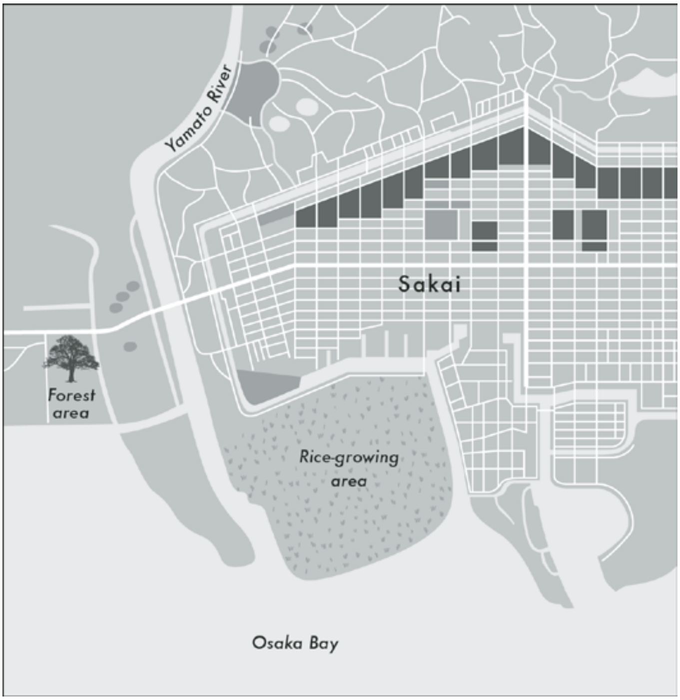

Figure 2 The Yamato River estuary, Japan, from the 18th century, showing how the mouth of the river was straightened for shipping.

Notes: Development of the port is indicated by streets and roads. This estuary is now completely developed and is part of Sakai City, near Osaka.

Source: Redrawn from Japanese Maps of the Tokugawa Era, University British Columbia, Digital Collection, with permission. Adapted from the original by Eric Leinberger. Colour photo in Appendix 5 at http://hdl.handle.net/2429/57062.

to improve survival and develop recovery plans for threatened salmonids. A number of major estuaries where one or more salmonid genera may have been once seasonally dominant organisms are now affected, in varying degrees, by overfishing and industrial or urban disruption, such as the Yamato River estuary in Japan (Luo et al. 2011) (Figure 2), the Petitcodiac River estuary in New Brunswick (Locke et al. 2003), and the Fraser River estuary in British Columbia (Levings 2004). Others have also been affected by water flow alteration, such as the Amu Darya and Syr Darya River estuaries in Uzbekistan and Kazakhstan, on the Aral Sea (Pavlovskaya 1995); by contamination, such as the Puyallup River estuary in Washington state (Stein et al. 1995); or by combinations of these factors, such as the Sacramento–San Joaquin River estuary in California

(Sommer et al. 2007) and northeast Atlantic salmonid estuaries (Limburg and Waldman 2009). In other instances, estuaries are relatively intact, such as the Stikine River estuary in Alaska (Levings 2004), or components of them are being rehabilitated, such as the Rhine River estuary in Germany (Schreiber and Diefenbach 2005) and the Columbia River estuary in Washington and Oregon (Roegner et al. 2010). Except for a few studies in Arctic or Subarctic North America – involving, for example, the Hudson Bay estuaries (Morin and Dodson 1986) and Mackenzie River estuary in the Northwest Territories (Carmack and Macdonald 2002), and the Lena River estuary in Russia (Lambelet et al. 2013) – documentation on the conditions of salmonid estuaries in the North is not extensive. This list excludes, of course, the myriad minor rivers and estuaries with small populations of salmonids that have been totally replaced by infilling to develop towns and cities around the world.

It must be stressed, however, that estuaries are only one of a series of habitats, all of which are essential for survival of wild salmonids. In the broadest sense, these habitats comprise rivers, estuaries, and the ocean (Figure 1). It is very important to realize that negative or positive changes in the estuary ecosystem are part of a continuum of events experienced by anadromous salmonids, with events occurring before (in the river) and after the estuary (in the ocean), perhaps swamping the impacts of factors in the estuary. Under some circumstances, conditions in the estuary may be more important than conditions in the river or the ocean. Most authorities recognize a continuum of ecological conditions between the three macrohabitats (e.g., Attrill and Rundle 2002).

Why a Review of Estuarine Salmonid Ecology Is Needed

One of the objectives of this book is to increase the profile of estuaries as rearing areas for juvenile salmonids and highlight the importance of maintaining estuarine ecosystems so that salmonids can successfully complete their life cycle. Some textbooks and papers state that the key importance of estuaries for salmonids is as a migratory corridor between the river and the ocean (e.g., McLusky and Elliott 2004; Lobry et al. 2008). In several review books and papers dealing with salmonids and their habitats, rivers and the coastal and open ocean receive extensive reviews of their importance for salmonids (Cushing, Cummins, and Minshall 2006; Grimes et al. 2007; Brittain et al. 2009), whereas estuaries do not. Major reviews of estuarine fish ecology conducted in areas where salmon are now relatively scarce compared with historical times (e.g., northwestern Europe) focus on nonsalmonids, even though sea trout and Atlantic salmon are part of the estuarine ecosystem in these regions and derive food from estuarine habitats (M. Elliott et al. 2002). Finally, material on the estuarine ecology of salmonids in the Southern Hemisphere, outside of their natural range, is required to complement the papers from this part of the world (e.g., McDowall 2006).

A review and synthesis of the importance of estuaries and how salmonids around the world are adapted to them, in the context of management and conservation strategies, is overdue. Reviews of salmonid use of estuaries are provided by Simenstad and colleagues (1982) (five taxa), Healey (1982) (four taxa), Thorpe (1994) (twelve taxa), and Levings (1994a) (seven taxa), but there has been no comprehensive review of salmonids in estuaries since the early 1990s. Thorpe (1994) and Levings (1994a) dwelt on juvenile salmonids' adaptation to habitat, but did not deal with fitness, assessment and ecosystem aspects, and management problems, or suggest methodology. In this book, I deal with all life history stages of salmonids that use estuaries, including fry, parr, smolts, adults returning to spawn, and those returning to the ocean after reproducing. I provide an overview of salmonids and estuarine ecosystems for citizen scientists and conservationists, including a glossary of terms, which should be useful for these important groups of stakeholders concerned with the salmonid estuary.

The primary ecological advantages of residency for juvenile salmonids in estuaries stem from the opportunity to (1) adjust their osmoregulatory machinery; (2) take advantage of increased food availability in the estuary food web; and (3) postpone an increase in predation or competition risk such as might be encountered in the ocean, as pointed out by Moser and colleagues (1991) and the authors whom they cite. Some of these components are also applicable to adult salmonids, and I discuss this life phase in the estuary as appropriate.

My general approach in describing fitness changes in these three components affecting survival due to human activities in the salmonid estuary is as follows: (1) discuss the component from the viewpoint of mainstream ecology; (2) discuss the baseline condition in the natural estuary, recognizing that data regarding salmonid ecology may have been obtained from partially disrupted areas, and delineate where necessary any problems with methods for determining the baseline; (3) outline methods for estimating survival and point out how inference and context setting are used; (4) describe the typical and important changes that have occurred in salmonid estuaries; and (5) discuss the effects of the change on the component. This comprehensive approach should be useful for a broad audience of researchers and practitioners, and dovetail with the more focused earlier literature on salmonids in the ocean and coastal zone.

This book complements and expands on a number of previous works dealing with the marine and estuarine phases of anadromous salmonids, including Pearcy 1992; Beamish, Pearsall, and Healey 2003; Brodeur, Myers, and Helle 2003; Karpenko 1998 and 2003; and Mayama and Ishida 2003, which reviewed the ecological literature on Pacific salmonids (*Oncorhynchus* spp.) in the marine environment, including the estuary, but mainly for commercially significant species. Klemetsen and colleagues (2003) reviewed the life histories of Atlantic salmon, sea trout, and Arctic char, and sea trout were also discussed by G. Harris and Milner (2006). These authors dealt with broad aspects of the ecology of the species, as did Jonsson and Jonsson (2011), whose review paper compared the habitat ecology of Atlantic salmon and sea trout. Hansen and Quinn (1998) reviewed the marine phase of Atlantic salmon and compared this part of the life history with that of Pacific salmonids. Quinn (2005) reviewed the migrations of Pacific salmonids through estuaries. The estuarine ecology of Atlantic salmon and five species of *Oncorhynchus* were compared by Weitkamp and colleagues (2014). In their book on Atlantic salmon, Aas, Einum, Klemetsen, and Skurdal (2011a) did not specifically discuss the importance of estuaries. In summary, although there have been a number of recent comprehensive reviews on the ecology of anadromous salmonids, the material covered was wide-ranging and did not focus on the estuarine habitat of a range of species.

2
What Salmonids and Estuaries to Consider

There is sometimes confusion in discussions of salmonid taxa in the scientific literature due to a lack of consensus on the nomenclature used, especially for lesser-known species and subspecies that tend to be recognized by local names. The names I use in this book are at the species level, except for two subspecies of the genus *Oncorhynchus* from Asia. For consistency, throughout this book I mainly use the nomenclature found in FishBase (Froese and Pauly 2014), but if a replacement scientific name is mentioned in a paper, I use that name instead of attempting to explain changes in the taxonomic literature.

Salmonids use estuaries on river systems in temperate, subpolar, or polar regions in the Northern and Southern Hemispheres (Figure 3; see Appendix 2). This book includes data from estuaries in nineteen countries in the Northern Hemisphere and six countries or dependencies in the Southern Hemisphere. When I first use a river estuary name from countries other than the United States or Canada, I also give the country, plus additional regional description when helpful for clarifying context.

Salmonids That Utilize Estuaries

Based on the available literature, the eighteen salmonid taxa known to utilize estuaries are as follows: *Hucho perryi* (Sakhalin taimen), *Oncorhynchus clarkii* (cutthroat trout), *Oncorhynchus gorbuscha* (pink salmon), *Oncorhynchus keta* (chum salmon), *Oncorhynchus kisutch* (coho salmon), *Oncorhynchus masou ishikawae* (amago), *Oncorhynchus masou masou* (masu), *Oncorhynchus mykiss* (steelhead), *Oncorhynchus nerka* (sockeye salmon), *Oncorhynchus tshawytscha* (Chinook salmon), *Salmo salar* (Atlantic salmon), *Salmo trutta* (sea trout), *Salvelinus alpinus* (Arctic char), *Salvelinus confluentus* (bull trout), *Salvelinus fontinalis* (brook trout),

Figure 3 Map showing the world oceans and general locations (•) of the estuaries and other water bodies mentioned in the book. See Appendix 2 for names and geographic coordinates.
Source: Adapted from the original by Eric Leinberger

Salvelinus malma (Dolly Varden), *Salvelinus namaycush* (lake trout), and *Salvelinus leucomaenis* (whitespotted char). Many of these taxa are on various conservation lists, but this may be an underestimate of the number that should be conserved owing to insufficient data availability and nomenclature confusion. Because of the extensive movement of salmonids around the world, initially for stock development and more recently for aquaculture purposes, I include taxa that have successfully colonized a river-estuary system or are exploiting in some way natural estuarine habitats outside of their native range.

Given the difficulties in defining a meaningful taxonomic unit at or below the species level, conservation status data in Appendix Table 1.1 (at http://hdl.handle.net/2429/57062) should be considered provisional, giving a minimum number of taxa, and are subject to change. Species and subspecies are usually classified mainly on the basis of their morphological phenotypes – an organism's observable characteristics (e.g., body form, skeletal structure) or other traits (e.g., behaviour) that result from the expression of its genes as well as the influence of environmental factors and the interaction between the two. However, we now know that details of the genotype (the inherited instructions an organism carries within its genetic code) can be used to define meaningful ecological units for classification or conservation purposes. Identification of discrete salmonid populations below the species, subspecies, or life history type level requires complex ecological and genetic analyses. For example, in the United States, the National Marine Fisheries Service defines reproductively isolated groups of salmonids with unique evolutionary legacies (and therefore likely unique genetic backgrounds) as evolutionarily significant units under the Endangered Species Act (see Ruckelshaus et al. 2002).

The degree of estuarine dependence shown by salmonid taxa and their life histories has a genetic basis, a theme introduced here. An early example of a species with strong dependence was revealed by the genetic study by Carl and Healey (1984) for three Chinook salmon populations in the Nanaimo River, British Columbia. Results found an estuary-rearing population, a group that reared in the river for two months and then moved to the estuary, and a stream-rearing population that remained in fresh water over the winter. These populations were coined life history types, an ecological/genetic concept that I elaborate on later in this chapter. The terminology was an expansion of earlier ideas. C.H. Gilbert (1913) proposed two overarching patterns: (1) stream-type Chinook salmon that spend a year in freshwater as juveniles and then migrate to the estuary and the ocean as yearling smolts, and (2) ocean type, which move to the estuary in spring and summer, rear there, and move to the ocean as smolts. Healey (1991) adopted these patterns and proposed that the distribution of the two types were related to latitude. While Healey (1991) concluded that the subvariant life history characteristics of the overarching life history types were inherited and possibly characteristic for major groups of river systems, Brannon and colleagues (2004) concluded that the genetic differences were also mediated by temperature within a region. That is, the life history forms are "more correctly described as a continuum of forms that fall along a temporal cline related to incubation and rearing temperatures that determine spawn timing and juvenile residence patterns" (Brannon et al. 2004, 1). More detailed genetic studies support the inheritance of the life history characteristics (e.g., Rasmussen et al. 2003). Additional data suggest that the patterns may be best named by their temporal patterns of migration to the estuary (e.g., subyearlings, or fish that move to the estuary in their first year of life [Bottom et al. 2005a]) rather than type (Moran et al. 2013).

Where possible, I have restricted my data review to wild or feral fish and have attempted to separate out the characteristics of fish reared in hatcheries. Not all hatchery-reared salmonids are marked, however, so it is possible that some of the field data on salmonids in estuaries are based on hatchery fish.

Scope of Estuaries Used by Salmonids

Historically, each of the salmonid species considered in this book was probably distributed in numerous watersheds, perhaps thousands, and the same number of estuaries. For example, the Atlantic salmon was once found in about 2,600 watersheds in the North Atlantic (World Wildlife Fund 2001). Exceptions might be Sakhalin taimen and lake trout, which are probably found in fewer estuaries given their smaller geographic range (see Appendix Table 1.1 at http://hdl.handle.net/2429/57062). Salmonids are found in a wide variety of estuary sizes. There is a gross and highly variable relationship between salmonid catch (a possible proxy for freshwater productivity) and watershed area and discharge (possible proxies for available freshwater habitat) (Hindar et al. 2007). Watershed area and estuarine marsh area are positively correlated, at least in the northeast Pacific (Hood 2004a). There is a positive correlation between sediment yield and sediment load in rivers worldwide (Milliman and Syvitski 1992), and this in turn must relate to delta or estuary size, as most delta platforms are built by sediment. The situation is complex, because small pocket estuaries are sometimes nested within the freshwater influence of a larger river, as noted for the Skagit River estuary in Puget Sound, Washington (Fresh 2006). The main principles of salmonid use of estuaries can likely be drawn from a small system with a modest population of salmonids, given the complexity of studying the great salmonid estuaries of the world. However, some processes, such as productivity and species diversity, obviously need to be scaled by size. Some large brackish inland seas or lakes (e.g., Puget Sound, the Baltic Sea, and the Bras d'Or Lakes in Nova Scotia) can be classified as estuaries and, where appropriate, I include them. However, the main focus of the book is the landscape at the mouths of rivers.

Terminology for Life History Stages and Types

In this book, I have included all salmonid life history stages that occur in estuaries, but again the nomenclature used in the literature can be confusing. I consider adults to be salmonids in reproductive readiness, migrating through an estuary to a river spawning habitat or seeking a spawning site in an estuary. For iteroparous species, a *kelt* is a spawned-out fish returning to the ocean, but other terms are sometimes used for kelts, such as the *sea-run migrant* for whitespotted char (Morita 2001). The terms *virgin sea run* and *returning veterans* are sometimes used to distinguish adult fish returning to the river for the first time to spawn from those that have had several migrations already (e.g., Morita 2001 for whitespotted char). The terminology for fry, parr, and smolt is more difficult to standardize, because the terms have been used differently in the four genera mentioned in this book. I generally followed Allan and Ritter (1977) in developing operational terms that include these four genera, especially the section of their paper dealing with Atlantic salmon. *Alevins* are the stage from hatching to the end of dependence on the yolk sac as a primary source of nutrition. Alevins are sometimes found in the estuaries of rivers where spawning grounds of salmonids are a short distance above tide water. *Fry* are the stage from independence from the yolk sac as a primary source of nutrition to dispersal from the spawning nest (*redd*), which is a workable definition for the four genera, with the further complexity that some feeding *Oncorhynchus* fry are caught in estuaries with the yolk sac still present. Fry are often defined by size. For example, Chinook salmon fry were defined as fish less than 60 mm in length by Burke (2004), and this size criterion is frequently used for this species to distinguish them from larger juvenile Chinook salmon less than one year old, which are often called *subyearlings*. Definition of a *parr* is more complicated. Allan and Ritter (1977) define this stage as the form after dispersal from the redd to migration down-river as a *smolt,* although for some *Oncorhynchus* species this includes fry, as noted above. As well, the early smolt stages of some *Oncorhynchus* species have parr marks, and these pre-smolts may be found in some estuaries. The darkly pigmented blotches of skin along the lateral line of the fish are the distinguishing feature of parr, and these marks vary between species as well as between populations (Boulding et al. 2008). A smolt is a fully silvered juvenile salmonid migrating to the ocean – that is, leaving the estuary. This definition fits juveniles or first-time migrants of either semelparous and iteroparous species, but does not fit older sea-run migrants or kelts, the adult stages of iteroparous species returning to the sea. Post-smolt is the stage from departure from the estuary until onset of wide annulus formation at the end of the first winter in the ocean, according to Allan and Ritter (1977).

In essence, a variety of terms are used to describe salmonid groupings below the species and subspecies level, often regionally. They include terminology such as "life history type" and "ecotype." "Life history type" is perhaps the most widely used term in this category. In the general ecological sense, it can be thought of as the tactic that enables genetically separate groups of populations to optimize the fitness of individuals within the populations. Alternative patterns of reproduction and the degree to which these are successful in different environmental settings are a widespread demonstration of life history tactics. For example, among species of tropical freshwater fishes, ten variables or tactical features for reproduction were identified (Winemiller 1989). Among salmonids, the tactics are often named according to the region used by a specific life stage or the age of the specific life stage residing in it. For example, a subyearling Chinook salmon is a fish migrating to the estuary when less than one year old, and jacks are precocious one- or two-year-old male Chinook salmon returning to spawn, instead of the normal four- or five-year-old fish (J. Johnson, Johnson, and Copeland 2012). Sometimes the term "ecotype" is used, such as for river- and lake-rearing sockeye salmon (C.C. Wood et al. 2008). An ecotype describes fish that can be described by genetically defined morphological or physiological attributes developed by selection for specific habitats (Gregor 1944). The season that the life history stage appears in the river after ocean life is often used as a descriptor for adults. Thus, the term "fall Chinook salmon" is used to describe fish arriving in the estuary and river in the autumn and spawning within a few weeks, whereas spring Chinook salmon are those that arrive in the spring and stay in the river for several months before spawning in the autumn. Other terms are used for mature and immature estuarine salmonids, and the terminology can be confusing (e.g., "grilse" is a mature Atlantic salmon that has spent only one year in the ocean, but this term is also used to describe post-smolt coho salmon and Chinook salmon in British Columbia). Regional or international guides are often helpful for sorting out these nomenclature and ecosystem-specific terms for estuarine salmonid life history types, stages, or forms.

Conclusions

Although there is sometimes confusion about which particular taxon, stage, or life history type of anadromous salmonids are "officially" listed as a conservation problem, clearly the survival in the wild of almost all species in this group of fishes is threatened over most of their natural range and in a variety of estuary configurations. Many of the endangered salmonid taxa living within their natural range are listed in the Northern Hemisphere south of about 50°N (see Appendix Table 1.1 at http://hdl.handle.net/2429/57062), suggesting either that anthropogenic factors such as human populations are having more effects on estuaries and salmonids in this region or that salmonids in the southern end of their natural range are more susceptible to environmental change. Before discussing adaptations and how natural and human-induced factors affect survival, it is necessary to describe the salmonid estuarine environment.