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# Variation in Salmonid Life Histories: Patterns and Perspectives

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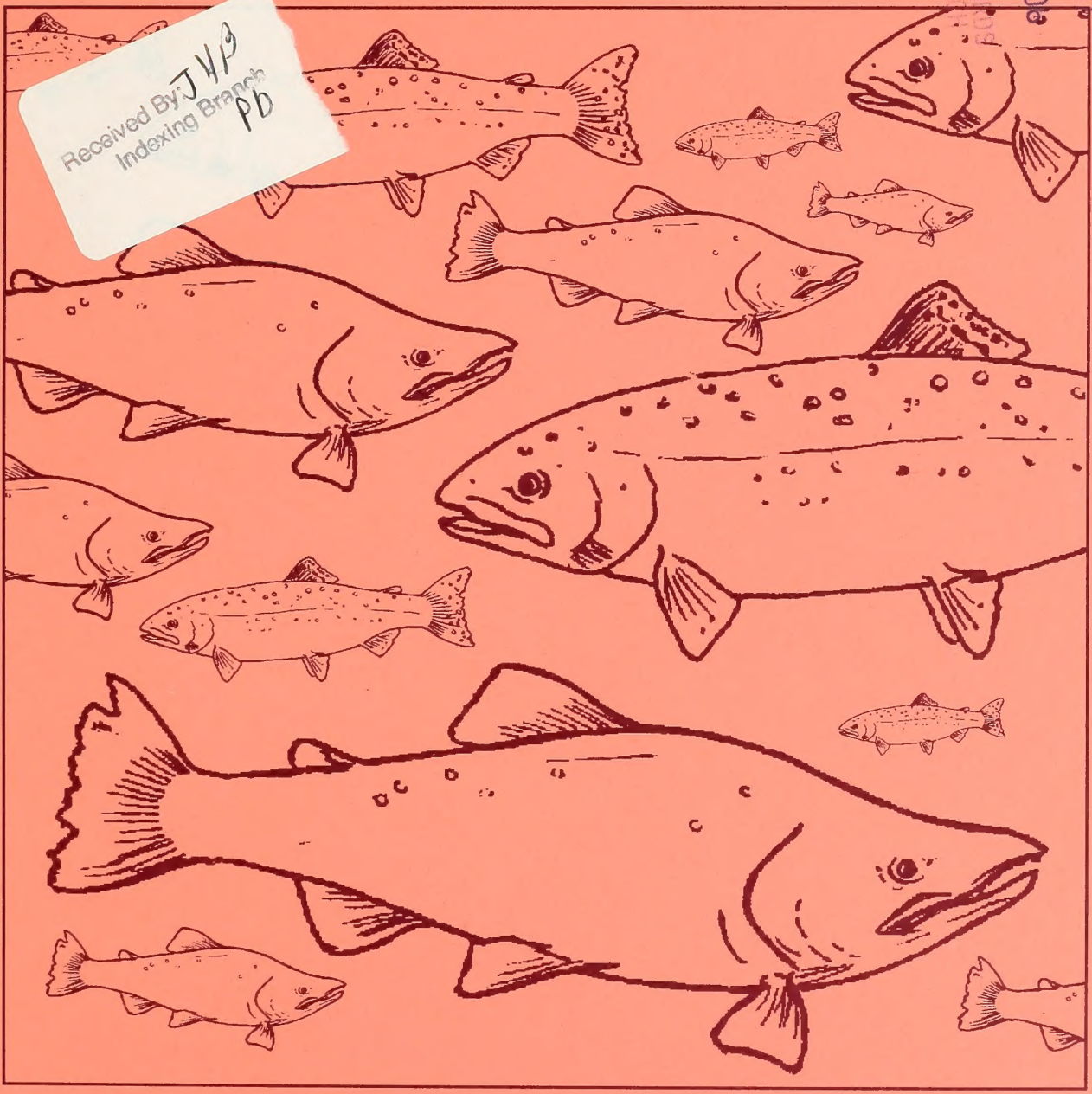
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## Abstract

Salmonid fishes differ in degree of anadromy, age of maturation, frequency of reproduction, body size and fecundity, sexual dimorphism, breeding season, morphology, and, to a lesser degree, parental care. Patterns of variation and their possible significance for ecology and evolution and for resource management are the focus of this review.

Keywords: Salmon, char, *Oncorhynchus*, *Salmo, Salvelinus*, life history, sexual dimorphism, age of maturation, semelparity, anadromy, phenology, phenotypic variation, parental care, speciation.

## Summary

Salmonid fishes differ in degree of anadromy, age of maturation, frequency of reproduction, body size and fecundity, sexual dimorphism, breeding season, morphology, and to a lesser degree, parental care. The advantages of large body size in reproductive competition probably favored the evolution of ocean foraging, and the advantages of safe breeding sites probably favored freshwater spawning. Both long-distance migrations and reproductive competition may have favored the evolution of semelparity. Reproductive competition has favored the evolution of secondary sexual characters, alternative mating tactics, and probably nest-defense behavior. Salmonids provide good examples of character divergence in response to ecological release and of parallel evolution. The great phenotypic plasticity of these fishes may facilitate speciation. Patterns of variation and the processes that generate them are valuable tools for foresighted management practices, predicting the outcomes of anthopogenic changes, managing to maintain biodiversity or particular populations of wildlife consumers, and maintaining the viability of fish populations.

# Contents

## Introduction

"Few fishes, except possibly the Atlantic cod and the Atlantic herring, have had as large an impact on man, and of man on them, as have the five Pacific salmons..." (Scott and Crossman 1973:146). Prehistoric human settlement patterns on the west coast of North America (especially after about 3000 years ago; Maxwell 1995) were greatly determined by the seasonal abundance of salmon, and a salmon-based economy is still critical to many coastal communities. Human harvest has so profoundly affected the perception of salmon populations that breeding-population size is customarily referred to as "escapement." This term emphasizes that population size is seen principally as the number of individuals that escape specifically from humans. All animals are subject to natural mortality from predators and parasites, but we do not refer to the populations of adult sticklebacks or other noncommercial fishes as escapements.

Because of the huge natural variations in the abundance of salmon from year to year and place to place, much of the human attention to these species has been prompted by an interest in reducing the variation and simultaneously maintaining or raising the mean abundance. In contrast, the importance of salmon and their relatives to the ecology of other species dependent on them and to the ecology of riparian ecosystems has scarcely been noticed (Willson and Halupka 1995). When Evermann said that "the most important family of all the fishes of the world is the Salmonidae...", he may have been referring to their economic importance, in part, but he also noted that "no group of fishes provides better material for study" (quoted in Donaldson 1982).

Only a small fraction of the salmonid literature focuses on evolutionary processes and patterns. The augmentation of stocks by hatchery releases and fertilization of rearing ponds and lakes and severe habitat disruption by logging, road building, and dams have undoubtedly altered the biology of the remaining natural stocks, thus removing the natural settings for evolutionary studies (e.g., Larkin 1977). Furthermore, harvests commonly remove huge fractions of the adult population, often size-selectively. For instance, an estimated average of 77 percent of the coho salmon returning to the Berners River in southeast Alaska were harvested in the 8 years for which data are available, but the take ranged as high as 93 percent of the returning population (Halupka and others 1996b; scientific names of all salmonid species are shown in table 1). As much as 80 percent of certain sockeye runs may be taken in 24 hours (Rogers 1987). Some evolutionary lessons nevertheless can be drawn from patterns of variation in the salmonids, which still offer many opportunities for studies of the dynamics of evolutionary processes (see Frank and Leggett 1994). Furthermore, the relevance of evolutionary processes to harvest management has seldom received adequate attention.

A salient feature of salmonid biology is a remarkable array of variation at all levels, among congeners, among conspecific populations, and within populations (Miller and Brannon 1982, Taylor 1991, Thorpe 1986). Life histories differ in almost every aspect, including the presence and degree of anadromy, the age of first reproduction, the frequency of reproduction in a lifetime, the phenology of reproduction, body size and the body-size/fecundity relation, sexual dimorphism, and parental care. Many of the species exhibit a great range of variation in morphology and coloration as well.

**Table 1—Scientific and common names, and spawning habitats, of salmonids in North America[a]**

| Scientific name | Common name | Spawning habitats |
|---|---|---|
| Coregoninae: | | |
|    *Stenodus* | Inconnu, sheefish | Streams |
|    *Prosopium* | Whitefish | Lakes, streams |
|    *Coregonus* | Whitefish, cisco | Lakes, streams |
| Thymallinae: | | |
|    *Thymallus* | Grayling | Streams |
| Salmoninae: | | |
|    *Salvelinus alpinus* (Linnaeus) | Arctic char | Lakes, river pools |
|    *S. confluentus* (Suckley) | Bull char or trout | Streams |
|    *S. malma* (Walbaum) | Dolly Varden char | Streams |
|    *S. fontinalis* (Mitchill) | Brook char or trout | Streams, shoreline reefs |
|    *S. namaycush* (Walbaum) | Lake char or trout | Lakes, streams |
|    *Salmo salar* Linnaeus | Atlantic salmon | Streams |
|    *Oncorhynchus mykiss* (Walbaum) | Rainbow trout, steelhead (sea-run) | Streams, lakes |
|    *O. clarki* (Richardson) | Cutthroat trout | Streams, lakes |
|    *O. tshawytscha* (Walbaum) | Chinook or king salmon | Streams |
|    *O. kisutch* (Walbaum) | Coho or silver salmon | Streams |
|    *O. nerka* (Walbaum) | Sockeye or red salmon | Streams, lake shores |
| | Kokanee (fresh water) | Streams, lake shores |
|    *O. keta* (Walbaum) | Chum or dog salmon | Streams, intertidal |
|    *O. gorbuscha* (Walbaum) | Pink or humpback salmon | Streams, intertidal |

[a] Only the genus name is presented for nonsalmonines. Principal spawning habitats are listed first.

I review patterns of variation in selected aspects of salmonid biology, emphasizing species found in North America. Patterns of variation, at several levels, often offer intellectual windows into the evolutionary biology of a taxon (Thompson 1988). In addition, knowledge of variation and evolutionary processes is essential to the conservation of biological diversity in the taxon and to its evolutionary future (Balon 1993, Behnke 1992, Frank and Leggett 1994, Gresswell and others 1994). The conservation of genetic diversity in salmonids poses many problems for current and future land and fisheries management (Behnke 1992; Gross 1991; Mangel 1994a, 1994b).

The goals of this review were to summarize variation in salmonid life history, with an emphasis on the salmonine lineage, and to suggest some ecological, evolutionary, and management implications. Other members of the family are included, in less detail, to provide perspective and a phylogenetic setting. The literature on salmonid biology is voluminous; this review therefore is intended to be illustrative rather than exhaustive. Furthermore, I focused principally on selected, often related, aspects of life history and did not attempt to cover every aspect of salmonid biology. Although my emphasis was simply on the *extent* of variation, an adaptive landscape showing the distribution of fitness consequences of variation ultimately is desirable. The initial motivation for this review was autodidactic, but I hope that bringing together this material, with this particular perspective, will encourage others to increasingly mine salmonid biology for its potentially vast intellectual and practical interest.

## Background on Salmonidae

Salmonids have a Holarctic distribution throughout much of Eurasia and North America (Scott and Crossman 1973). Many species in the family have relatively broad distributions, and much variation, both phenotypic and genetic, occurs among and within populations (e.g., Behnke 1972, Kato 1991, Khan and Qadri 1971, Lindsey 1964, Thorpe 1986). Much of the variation within populations and species may be of relatively recent origin, reflecting events of glacial and post-glacial times (op. cit.).

The Family Salmonidae is thought to have arisen by an autopolyploidization event (Allendorf and Thorgaard 1984). Although polyploidization is recorded for various fishes at the species level, the salmonids are one of only two families that apparently have arisen by this means (Allendorf and Thorgaard 1984). Polyploidy in the salmonids may have facilitated their "unparalleled anadromous success" by permitting the expression of different duplicated genes in freshwater and saltwater phases of the life history (Allendorf and Thorgaard 1984).

The three subfamilies (table 1) appear to have diverged 25 to 100 million years ago (Allendorf and Thorgaard 1984). Salmonine and thymalline subfamilies are thought to be more closely related to each other than to coregonines (Kendall and Behnke 1984). Within the salmonines, there seems to be general agreement that the Old World *Brachymystax* and *Hucho* are related to *Salvelinus*, and that *Salmo* and *Oncorhynchus* are near neighbors in the phylogenetic tree (Kendall and Behnke 1984, Phillips and Pleyte 1991). Within *Oncorhynchus*, rainbow and cutthroat trout can hybridize and are probably closely related to each other, as are chinook and coho salmon (Behnke 1988, 1992; Phillips and Pleyte 1991; Smith and Stearley 1989; Stearley 1992; Thomas and others 1986). Chum, pink, and sockeye salmon are commonly seen as closely related. The Asian masu salmon (*O. masou* (Brevoort)) and the closely related amago salmon (*O. rhodurus* (Jordan and McGregor)) have been placed in various taxonomic relations. The precise arrangement of the tree can be debated (Pearcy 1992, Phillips and Pleyte 1991, Smith and Stearley 1989, Stearley 1992), and new species are still being discovered (Skopets 1992).

## Patterns and Extent of Variation
### Anadromy

Anadromy occurs in several families of Salmoniformes; the ability to use both fresh-water and oceanic habitats is ancestral in the order (McDowall 1987, 1988; Nelson 1984). In large part because of the reproductive dependence on fresh water, the family Salmonidae has generally been thought to have originated there (Hoar 1976, McDowall 1988, Stearley 1992; but see Thorpe 1982, 1994). Within the family, evolutionary trends seem to go both toward greater dependence on marine habitats and reduction of the freshwater phase (especially seen in pink and chum salmon) and toward complete absence of the marine phase (in several species; McDowall 1988, Smith and Stearley 1989, Thorpe 1987), thereby emphasizing the tremendous evolutionary flexibility of this group of fishes.

Passage between habitats (fresh or salt water) can be seen as an extension of migratory movements within habitats (Gross 1987). The three subfamilies of salmonids in North America exhibit a range of variation in migratory behavior. In the whitefish lineage, the three species of *Prosopium* live almost exclusively in fresh water and make seasonal migrations within stream systems; one species sometimes moves to brackish water (Scott and Crossman 1973). About half of the 14 species of *Coregonus* in North America appear to be strictly freshwater; the remainder are at least partly anadromous (Behnke 1972, Scott and Crossman 1973). *Stenodus* has some strictly freshwater populations and some that are anadromous, but these move only to brackish water in estuaries (Alt 1969, Dymond 1943). Grayling sometimes make extensive seasonal movements within fresh water, but seldom enter the sea (except perhaps some Asian populations; Armstrong 1986, Scott and Crossman 1973).

The salmonine lineage makes the most use of the marine environment, although in the Old World, *Brachymystax* and most populations of *Hucho* occupy fresh water. Most anadromous char (*Salvelinus*) make relatively short seasonal visits to salt water and typically do not make long-distance migrations in the ocean (e.g., references in Stearley 1992), but some populations of Arctic char are more seagoing (Johnson 1980). Three species of *Salvelinus* (Arctic, Dolly Varden, brook char) in North America have anadromous populations as well as some totally freshwater populations (McDowall 1988, Meehan and Bjornn 1991, Scott and Crossman 1973). The lake char (which is sufficiently distinct to be classified as a separate genus, sometimes; Lindsey 1964, Rounsefell 1958) is found almost exclusively in fresh water, but some populations occasionally may enter salt (or at least brackish) water. The bull char also is primarily an interior species, seldom reaching coastal waters (Haas and McPhail 1991). *Salmo salar*, the only member of this genus (as presently constituted) native to North America, is mostly anadromous, making extensive oceanic migrations (Rounsefell 1958, Scott and Crossman 1973). Atlantic salmon have some landlocked populations and at least one known nonanadromous stream population (Behnke 1972, Mills 1989, Thorpe 1987).

The seven principal species of *Oncorhynchus* that occur in North America (table 1) all have anadromous populations. Five of these seven species are chiefly anadromous (Behnke 1992, Groot and Margolis 1991, McDowall 1988, Scott and Crossman 1973), and the anadromous populations make extensive sea voyages (Groot and Margolis 1991, Healey 1986, Rounsefell 1958). Many steelhead populations also make long ocean migrations (Burgner and others 1992, Johnston 1982, Rounsefell 1958). Chum and chinook salmon exhibit extreme variation in their use of fresh water for spawning and in the length of freshwater migration. Most populations spawn in fresh water, a few making prodigious upriver journeys far into the interior, but some populations spawn intertidally or in tidally influenced segments of rivers (Halupka and others 1995a, 1996a; Salo 1991). Cutthroats are partly anadromous, but they usually do not venture into the sea very far or for very long.

Strictly freshwater natural populations of *Oncorhynchus* are known for four (cutthroat, rainbow, sockeye, coho) of the seven principal species that occur in North America (although freshwater populations of coho occur in Asia; Behnke 1992, Burgner 1991, Ricker 1972, Sandercock 1991). The only fully freshwater species in the genus are landlocked derivatives of the rainbow-cutthroat lineages in the American southwest (such as the apache and gila trout, *O. apache* (Miller) and *O. giliae* (Miller), respectively).

All the anadromous species except Pacific salmon are capable of making repeated trips between fresh and salt water, although not all individuals do so. Many populations of char and cutthroat and some populations of steelhead are technically "amphidromous," in that individuals often return seasonally to fresh water as juveniles, sometimes for several years, before returning to spawn (Burgner and others 1992; Johnston 1982; McDowall 1987, 1988).

Among the anadromous stocks, the length of freshwater residency differs (Groot and Margolis 1991, Jones 1977, Randall and others 1987, Rounsefell 1958). Two major life-history variants of chinook salmon are defined by the length of juvenile residence in fresh water and geographic distribution: juveniles of "ocean-type" chinooks spend only 2 to 3 months in fresh water and occur chiefly in coastal streams in the southern part of the species' range, although some Alaska populations have ocean-type life histories (Johnson and others 1992); juveniles of "stream-type" chinooks spend 1+ years in fresh water and are more common in the northern (and Asian) part of the range and in interior regions in the southern part of the range (Healey 1991; Taylor 1990a, 1990b). Although the juveniles of most sockeye populations rear in fresh water, sometimes for several years, those of a few populations go directly to salt water (Eiler and others 1992, Heifetz and others 1989, Rice and others 1994, Wood and others 1987). Juveniles of some populations of coho also go to sea directly but may return to fresh water to spend the winter (Halupka and others 1996b). Steelhead stocks, often in the same stream system, differ in the length of time spent in fresh water as adults, before spawning: they enter fresh water in summer, winter, or spring (in some southeast Alaska streams), but all spawn in late winter or spring (Burgner and others 1992, Lohr 1996, Withler 1966). Some of such variation is phenotypic; for example, supplemental feeding has led to decreased freshwater residency in several salmonids (Nordeng 1983, Randall and others 1987).

The ability to use fresh water for the entire life cycle is commonly present in a species, even if it is not often expressed. Chinook, pink, and coho salmon have been successfully transplanted to fresh water (Burgner 1991, Healey 1991, Meehan and Bjornn 1991, Sandercock 1991); chinook and chum salmon can be reared to sexual maturity in fresh water in captivity[1] (Salo 1991); and at least one individual chum salmon has been recorded as resident in fresh water (Peden and Edwards 1976). Pink salmon generally are thought to be the least dependent on fresh water of all Pacific salmon, because the young go to sea almost immediately and, in fact, some spawning is intertidal. The life history is sufficiently plastic, however, that at least one introduction to a completely freshwater system (the Great Lakes) was successful (although unplanned; Kwain 1987). Similarly, some normally nonanadromous species or populations retain the ability to become anadromous (e.g., Arctic char, Atlantic salmon, kokanee; Behnke 1972, Eriksson and others 1987, McDowall 1988, Myers 1984, Nordeng 1983, Rounsefell 1958).

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[1] Personal communication, 1996, T. P. Quinn, School of Fisheries, University of Washington, Seattle WA 98195.

The occurrence of anadromy also varies within populations of some salmonine species. So-called "residual" individuals, in populations that are characteristically sea-run, never go to sea. "Residuals" typically mature earlier and at a smaller size than anadromous individuals, often even as parr. The offspring of typically anadromous parents, they are recorded for Arctic, Dolly Varden, and brook char, Atlantic salmon, and sockeye, chinook, coho, and steelhead (Armstrong and Morrow 1980, Foote and others 1991, Groot and Margolis 1991, Jonsson and Hindar 1982, Myers 1984, Saunders and Schom 1985, Thorpe 1987). Sexual maturation as parr seems to have a significant cost in survival (Foote and others 1991, Lundqvist and others 1988, Myers 1984), although some go to sea and can return as full adults (references in Foote and others 1991). In general, males are more likely than females to exhibit this form of life history, but there are female residuals in some freshwater systems (Bain 1974; Balon 1980; Behnke 1992; Groot and Margolis 1991; McDowall 1988; Mills 1989; Thorpe 1986, 1987). There is great variation among populations in the probability of reproduction by parr (Myers and others 1986, Taylor 1989, Thorpe 1987).

**Age of Maturation**

Age at maturity is so highly variable within species that it is difficult to sort out differences among species. In almost every species whose range encompasses a variety of habitat types or latitudes, the age of maturation is greater in habitats with poorer food supplies, shorter growing seasons, and lower temperatures. Geographic variation in growth rate is extensive and often correlated negatively with age of maturation (Hutchings 1994). In Atlantic salmon (Nicieza and others 1994) and other fishes (references in Gotthard and Nylin 1995), fish from northern populations grow faster than those from southern populations, under identical conditions; northern fish thus are able to compensate at least partly for the short growing season. Phenotypic plasticity is often well developed also (e.g., Eriksson and others 1987); for example, brook char introduced to a cold lake with a poor prey base grew slowly and lived six times as long as individuals in the source population (Behnke 1992). Other factors, such as fishing pressure (especially size-selective harvests) and the option of going to sea and becoming larger, also play a role in determining age of maturation (Gross 1991).

In the whitefish lineage, females of several species are reported to mature later, live longer, and get bigger than males (Alt 1969, Scott and Crossman 1973), although only males reached ages >10 years in *Coregonus pidschian* (Gmelin) (Alt 1979). Ages of maturation range from 2 to 14 years, depending on the species and location (Alt 1969, Carlander 1969, Mann 1974, Scott and Crossman 1973). Even within any species, age at maturity can range from 1 to 10 years (e.g., *C. clupeiformis* (Mitchill); Carlander 1969). Grayling mature at ages 2 to 22 years, and females may mature a year later and live a bit longer than males (Beauchamp 1982, Craig and Poulin 1974, Scott and Crossman 1973, Tripp and McCart 1974; although Armstrong 1986 found no evidence of differential maturation).

The age of maturation differs tremendously in the salmonines as well (table 2). Anadromous forms commonly mature later than nonanadromous relatives, and males of many populations normally mature about a year earlier than females. Maturity is often achieved by individuals with very different life histories, in terms of time spent in fresh water and salt water, and the range of variation in age structure at maturity differs enormously within and among species (e.g., reviewed in Halupka and others 1995a, 1996a, 1996b). For example, among the species of *Oncorhynchus*, sockeye exhibit 22 different age categories at maturity, ranging from 0.2 (no years in fresh water, 2 years in salt water) to 4.3 (4 years in fresh water, 3 years in salt water) (Healey 1986). Chinook (16 age categories), coho (12), and chum (6) are less variable (Healey 1986). Steelhead mature in 18 different age categories in southeast Alaska alone (Lohr 1996). In contrast, pink salmon normally show almost no variation in age at maturity, as they typically mature as 2 year olds (Healey 1986). However, 1-year-old and 3-year-old pinks occur occasionally in natural populations (Anas 1959, Foster and others 1981, Turner and Bilton 1968) and in the introduced populations of the Great Lakes (Kwain 1987).

Disruptive selection on reproductive tactics has led to two principal life-history variants: "normal" adults that develop secondary sexual characteristics and high levels of aggression during spawning, and "precocious" adults that mature early, exhibit few or no secondary sexual traits, and spawn by sneaking into the nests of spawning females (Gross 1985, Fleming and Gross 1994, Montgomery and others 1987). Normal males adopt various mating tactics, depending on their dominance status: subordinate males often occupy satellite positions near a spawning pair of dominant individuals and may spawn by quietly joining the mating pair. Precocious maturation after less than a year at sea is known for males ("jacks") of many anadromous species and, less commonly, females ("jills") of a few species (table 2). Among the species in North America, the Atlantic salmon illustrates the wide range of variation that is possible. Many individuals mature after 2 to 4 years at sea. A few males migrate to sea but return early, maturing as jacks at a smaller size, and some spend 1 year at sea ("grilse"). Some males mature as parr (age 1 to 5 years) in fresh water, breeding once or sometimes more (Mills 1989, Montgomery and others 1987, Myers 1984, Saunders and Schom 1985). The frequency of precocious individuals, and of associated alternative mating tactics, differs greatly among Atlantic salmon stocks, ranging from close to zero to as high as 100 percent of males in a population (e.g., Myers 1984, Myers and others 1986). Precocious male parr have been reported for several species of *Oncorhynchus* as well (Montgomery and others 1987, Thorpe 1987, Tsiger and others 1994).

Along with alternative mating tactics may come other differences; for example, Asian Dolly Varden males that use alternative mating behavior also cannibalize eggs in the nest of the female with which they are attempting to spawn, but this behavior has not been seen in Alaska populations (Maekawa 1983; Maekawa and Hino 1986, 1987, 1990). Egg-eating is also known in postspawning parr of Atlantic and chinook salmon, possibly as a means of recovering some of the costs of spawning (Montgomery and others 1987).

Table 2—Variation in age of maturation and the occurrence of precocious reproduction in North American salmonines

| Species | Range of variation (Years) | Patterns | Precocious | Additional references[a] |
|---|---|---|---|---|
| Arctic char | 2-22 | Anad. 1 to 2 yr later than nonanad. | Males, females | Bain 1974, Glova and McCart 1974, Johnson 1980, Vøllestad and L'Abée-Lund 1994 |
| Lake char | 4-19 | Fish-eaters later than plankton-eaters; later in north | — | Martin and Olver 1980 |
| Dolly Varden: | | | | |
| North | Nonanad.: 2-6 Anad.: 7-9 | | Males | Armstrong and Morrow 1980 |
| South | Nonanad.: 1-4 Anad.: 3-8 | | | |
| Bull char | 4-10 | | — | Bjornn 1991 |
| Brook char: | | | Males | Power 1980 |
| North | 3-7 | Anad. 1 to 2 yr later than nonanad. | | |
| South | 1-2 | | | |
| Atlantic salmon | 1-8+ | | Males, females | Mills 1989, Myers 1984, Saunders and Schom 1985, |
| Steelhead, rainbow | Steelhead: 2-9 Rainbow: 1-10 | Later in north Later in north | Males | Burgner and others 1992, Jones and Bentz 1994, Lohr 1995, Pearcy 1992, Russell 1977, Withler 1966 |
| Cutthroat | 2-7 | Anad. later than non-anad., later in large than small rivers | N.d. | Thurow and others 1988, Trotter 1989 |
| Coho | 1-5 | Later in north | Males (esp. in south) | Crone and Bond 1976, Drucker 1972, Gross 1991, Sandercock 1991 |
| Chinook | Stream: 1-8 Ocean: 1-5 | | Males, females | Foote and others 1991, |
| Sockeye | Anad.: 2-7 Kokanee: 2-8 | | — Males, females | Halupka and others 1996a, Healey 1991, Major and others 1978 Burgner 1991, Foerster 1968, |
| Chum | 1-6 | Later in north | | Salo 1991 |
| Pink | 1-3 (almost always 2) | Age 4 in some lab populations; age 3 relatively common in Great Lakes | | Heard 1991 |

N.d. = no data.
[a] General references include Healey 1986, McPhail and Lindsey 1970, Montgomery and others 1987, Myers 1984, Randall and others 1987, Scott and Crossman 1973, Stolz and Schnell 1991.

**Frequency of Reproduction**

The life histories of salmoniforms range from regularly iteroparous to spectacularly semelparous, and the full range of variation is seen within the Salmonidae. Lifespan, and the degree of iteroparity, are phenotypically very plastic in many species (Behnke 1992). For example, supplemental enrichment of the prey supply can extend the life and increase the growth rate of brown trout (*Salmo trutta* Linnaeus) nearing the end of their expected lifespan. Plasticity in frequency of reproduction is less evident in Pacific salmon, which normally breed only once in a lifetime. The frequency of iteroparity in species that can breed more than once is commonly less in males than in females.

Grayling and whitefishes are typically iteroparous, although reproduction does not occur every year for some individuals and populations (Alt 1969, Carlander 1969, Scott and Crossman 1973). Within the salmonines, variation occurs not only among species, but between sexes and geographic locations. Chars are fundamentally itero-parous (averaging 10 to 20 percent mortality after first spawning, in anadromous populations [Stearley 1992]; but sometimes exceeding 50 to 80 percent [Armstrong and Morrow 1980, Johnson 1991]). There is great variation in the breeding interval, particularly for females (Balon 1980, Behnke 1992, Scott and Crossman 1973). Dolly Varden sometimes reproduce annually, but both anadromous and freshwater individuals often reproduce at 2-year intervals, especially in the northern part of the range. Females are more likely to be iteroparous than males (Armstrong 1974). Lifespan is as much as 18 to 20 years, but more commonly 10 to 12 years (Armstrong and Morrow 1980, Scott and Crossman 1973). Bull char sometimes spawn two or three times in a lifetime but often skip a year between breeding attempts (Bjornn 1991). Breeding is annual in some populations of Arctic char (mostly freshwater, one anadromous population), but for most anadromous individuals, the interval between breeding is 2 to 4 years, especially in the north (Dutil 1984, Johnson 1980, ). Lifespan is potentially long, up to 40 years (Scott and Crossman 1973) but more often about 15 years (Johnson 1991). Male brook char often reproduce annually, but females in some populations only breed at 2- to 3-year intervals. This species tends to be short lived, with a maximum lifespan of less than 12 years; females tend to live longer than males (Carlander 1969). Where piscine or human predators are active, brook char often live only 3 or 4 years (Power 1980, Scott and Crossman 1973), perhaps reproducing only once. Lake char females commonly breed in alternate years, especially in the north. These fish are potentially long lived (>25 years), and individuals may reproduce many times if maturity is not long delayed (Carlander 1969, Martin and Olver 1980).

*Salmo* reproductive patterns are mixed: Although many Atlantic salmon die after spawning (perhaps 70 to 95 percent; Stearley 1992), iteroparity (up to five or six times) also occurs. The interval between breeding differs, however, with the length (Schaffer and Elson 1975) or stream discharge (Jonsson and others 1991) of the river used for spawning. Repeat spawning is more common in females than males (Carlander 1969, Mills 1989).

*Oncorhynchus* species are principally semelparous. Individuals (both anadromous and freshwater) of the five North American species of Pacific salmon typically die after spawning (but there are occasional exceptions; e.g., in chinook salmon; Healey 1991, Ricker 1972, Stearley 1992). Average postspawning mortality is so high in anadromous cutthroats (50 to 60 percent) and steelhead (50 to 95 percent; Lohr 1996, Stearley 1992) that one-time spawning is common (Behnke 1992, Withler 1966). Repeat spawning (up to five times) does occur, however, particularly in downriver freshwater populations, although the interval between spawnings and the probability of repeating varies greatly (Behnke 1992, Carlander 1969, Jones 1977, Liknes and Graham 1988, Lohr 1996, Thurow and others 1988, Withler 1966). Females repeat-spawn more often than males (Burgner and others 1992, Carlander 1969, Lohr 1996). The frequency of iteroparity in steelhead ranged from 5 to 53 percent of the breeding populations assessed. Males of summer-run steelhead are more likely to spawn repeatedly than are winter-run males (Lohr 1996). Withler (1966) reports a latitudinal trend of increasing semelparity in steelhead from Oregon northward, although a California population also was highly semelparous.

**Body Size and Fecundity**

All salmonid species exhibit variation among populations in average body size at maturity (Bain 1974, Bakkala 1970, Balon 1980, Behnke 1992, Blackett 1973, Blair and others 1993, Carlander 1969, Groot and Margolis 1991, Liknes and Graham 1988, Maekawa 1984, Maekawa and Onozato 1986, McPhail and Lindsey 1970, Meehan and Bjornn 1991, Morrow 1980, Thurow and others 1988, Scott and Crossman 1973, Ward 1932). Several trends are apparent: (1) Larger bodies of water commonly support larger fish. Thus, sea-run individuals usually achieve larger size than freshwater individuals (e.g., rainbows, cutthroat, sockeye, Atlantic salmon, brook char, Arctic char, Dolly Varden). Ocean-type chinooks differ little in size from stream-type conspecifics (Roni and Quinn 1995), but their oceanic migrations are less extensive (Healey 1991). Individuals living in lakes commonly become bigger than stream dwellers (e.g., cutthroat, steelhead, brook char, Asian form of Dolly Varden) and those in large streams are bigger than those in small streams (e.g., cutthroat, brook char, pinks). There are, however, some notable exceptions in this trend (Hutchings and Morris 1985); for example, grilse differ little from older Atlantic salmon in size (Mills 1989), and individuals of any freshwater population living in unproductive lakes can be quite small. (2) Diet can affect body size at maturity. Individuals in populations preying on fishes reach larger sizes than those depending on invertebrate prey (e.g., Dolly Varden, Arctic char, lake char, cutthroat, rainbow). In some cases, diet differences are correlated with habitat differences. In addition, improved feeding conditions in fresh water also can permit a higher proportion of juveniles to grow quickly and mature at a small size in fresh water (Thorpe 1987). (3) Body size often decreases with increasing latitude (e.g., several Pacific salmon). (4) Sea-run populations appear to differ less in body size than freshwater populations (data from Carlander 1969), perhaps reflecting differences in feeding conditions or predation risks; for example, landlocked populations of Atlantic salmon differ as much as 15-fold in average body size at the same age, but sea-run populations typically differ less than threefold. Kokanee populations differ as much as tenfold in average body size, but sea-run sockeye stocks appear to differ only about twofold. In general, populations of sea-run species of salmonids differ less in adult size (usually less than threefold) than populations of species with chiefly freshwater life-histories (up to 30-fold in brook char, up to 50-fold in some whitefishes, but only fourfold to sixfold in lake char, twofold to fourfold in grayling, and fourfold to fivefold in inconnu).

As for many biological traits, there are both genotypic and phenotypic sources of variation in body size and fecundity (e.g., Smoker and others 1994). For example, fecundity can be increased by artificial selection at least in some species (e.g., Carlander 1969, Martin and Olver 1980). On the other hand, experimental supplemental feeding increased fecundity in a population of lake char (Martin and Olver 1980), and starved trout have low fecundity (Behnke 1992, Bromage and others 1992).

Larger body size usually is associated with greater fecundity in female salmonids, as in most fishes. Therefore, as a rule, females maturing precociously at small sizes have much lower fecundity than "normal" females. The slope of fecundity on body size seems to be lower for sockeye and chinooks than for other salmonids (Burgner 1991; Healey 1987, 1991; Healey and Heard 1984); moreover, the slope of the regression differs among populations in many species (e.g., grayling, Atlantic salmon, lake char, Dolly Varden, brook char, cutthroats, sockeye, chinooks, and some whitefish; e.g., Gresswell and others 1994, Mann 1974, Tripp and McCart 1974). In a few populations of some species, the typical correlation is insignificant or absent, possibly indicating some general biological constraint (such as extreme food limitation or strong countervailing selection pressures).

**Sexual Dimorphism**

Sexual dimorphism in the whitefish lineage is minimal (Carlander 1969, McPhail and Lindsey 1970). The inconnu exhibits little external difference between the sexes, although females can be slightly bigger than same-age males. Whitefish males commonly develop breeding tubercles, especially on the flanks, but tubercles are less well developed and rarer on females. Grayling males are brighter than females, sometimes larger, and have longer dorsal and pelvic fins (Carlander 1969, McPhail and Lindsey 1970).

In *Salmo*, most *Salvelinus*, and most *Oncorhynchus*, a major sexual difference is found in the development, in normal breeding individuals, of elongated, hooked jaws with enlarged teeth. An upturned lower jaw is technically called a kype; an enlarged and often distorted upper jaw is termed a snout (Morton 1965). Kype and snout development differs not only among individuals but also among species and conspecific populations: it is generally greater in stream-dwelling and anadromous forms than in lake-spawning or strictly freshwater forms (Morton 1965). Kypes and snouts are best developed in males, although females of some species also develop smaller ones. Male lake char are capable of developing a kype, but they almost never do (Morton 1965). Another secondary sexual trait is a hump anterior to the dorsal fin, found especially in males. Male pink salmon normally develop a pronounced hump, but males adopting a satellite-male mating tactic have only a small hump (Keenleyside and Dupuis 1988, Noltie 1990). Hump size in sockeyes differs greatly among populations (Blair and others 1993, Halupka and others 1995c). Male mating success within some sockeye populations is positively correlated with hump size (Quinn and Foote 1994).

Other secondary sexual characteristics also are probably related to competition among males or female mating preferences, or both. For example, female chum salmon respond less to small, striped males than to large, barred males (Schroder 1981), and the relative size of the adipose fin in male Atlantic salmon contributed to mating preferences of females in a laboratory setting (Järvi 1990). Male breeding colors are often brighter or more intense than in females (e.g., Morrow 1980). Male lake char may be more iridescent than females, sport a black lateral stripe, or develop (in some populations) breeding tubercles, but generally they show less sexual dimorphism than other char do. Pectoral and pelvic fins are longer in male than female brook char.

Breeding males may be a little larger than females (e.g., sockeye, chum, Dolly Varden), or a little smaller (e.g., coho, steelhead), on average, but size differences generally are not marked. In fact, the direction and magnitude of size dimorphism in several species (e.g., Arctic char, coho, sockeye, masu) are highly variable, indicating population differences in selection pressures and constraints (Bain 1974; Halupka and others 1995a, 1996a; Holtby and Healey 1990; Kato 1991; Sandercock 1991). Mating preferences of females (and of males, Foote 1988) are sometimes size-selective (e.g., Foote and Larkin 1988, Maekawa and others 1993, Schroder 1981, Sigurjónsdóttir and Gunnarsson 1989), but the range of available choices obviously differs among populations.

**Parental Care**

Parental care is absent in coregonids and lake char. Egg-burial (grayling) is a simple form of parental care. Preparation and defense of a nest site for egg deposition and protection of embryos, characteristic of most char and salmon, are a bigger investment in parental care, but even this is reported to differ: sockeye salmon in certain populations apparently do not build redds but drop their eggs among algae-covered boulders (Foerster 1968). The success of such behavior is unrecorded, but poorly buried eggs in coarse rocks can be successful (Olsen 1968). Arctic char females may defend the nest briefly, unlike brook char (Johnson 1980). Postspawning females of Pacific salmon also commonly guard their nests for several days (up to 3 weeks by coho) before they die (Quinn and Foote 1994; Scott and Crossman 1973; Stearley 1992; van den Berghe and Gross 1986, 1989). In contrast, female steelhead reportedly do not nest-guard (Burgner and others 1992). Instream life varies both within season and among years and streams for several species of salmon (Dangel and Jones 1988, Groot and Margolis 1991). Instream lifespan, and concomitant ability to defend nests, varied with female body size in coho (van den Berghe and Gross 1986) but not in a beach-spawning population of sockeye (Quinn and Foote 1994).

**Breeding Season**

The Family Salmonidae includes species that breed at all times of the year. Grayling spawn chiefly in spring and summer (March through July), but most whitefish spawn in fall (but inconnu in summer and early fall and some species of *Coregonus* in summer or winter) (Carlander 1969, Scott and Crossman 1973). *Salmo* and most char are fall breeders, although a few populations of Arctic char breed in spring (Johnson 1980). Among the species of *Oncorhynchus*, the salmon are typically late-summer spawners (the exact timing differing among locations and years), although some southern chinook populations breed in spring (Healey 1991), and some coho populations breed in late winter (Halupka and others 1996b). In contrast, rainbows (including steelhead) and cutthroats characteristically breed in late winter, spring, and summer, although a few populations of both species in warm rivers breed in fall (Behnke 1992). The difference between spring and fall spawning is sometimes considered to be a major point of divergence in the course of salmonid evolution (e.g., Miller and Brannon 1982), but the existence of intraspecific variation in several species argues against such a proposition. Conspecific spawning stocks of *Oncorhynchus* and other salmonines with differing phenology sometimes breed in the same body of water (Behnke 1972, Groot and Margolis 1991, Johnston 1982, Withler 1966), although spawning times often differ less than timing of the migration (e.g., Healey 1991, Withler 1966). Interbreeding between stocks of differing phenology is generally thought to be slight (Behnke 1972, Leider and others 1984).

Selection and "common garden" experiments clearly show a genetic component to breeding phenology and run timing in some cases (e.g., Ricker 1972). Timing also differs in response to environmental factors, including streamflow, stream size and length, latitude (usually earlier in the north), substrate and water temperature, length of the season for juvenile rearing (for certain species) and population density (Balon 1980, Behnke 1992, Burger and others 1985, Frost 1965, Groot and Margolis 1991, Johnston 1982, Meehan and Bjornn 1991, Siitonen and Gall 1989, and others).

**Morphology**

Many salmonids exhibit extensive variation among conspecific populations in morphology, including body proportions, fin size, jaw characteristics, as well as life-history features (e.g., Blair and others 1993, Dymond 1943, Nehlsen and others 1991, and others). Furthermore, differentiation of lacustrine and fluvial morphs within fresh water is known for rainbows, cutthroats, Atlantic salmon, and grayling (Behnke 1972, Mills 1989) and perhaps others in North America, as well as brown trout and Japanese populations of Dolly Varden (Maekawa 1984). There also is geographic variation in body shape and fins in coho (Sandercock 1991) and other stream breeders, generally in relation to stream characteristics (Vøllestad and L'Abée-Lund 1994). Morphological difference within fish populations often is associated with differences in foraging and habitat (e.g., Ehlinger 1990; Meyer 1987,1990), so it seems highly probable that some of these differences among salmonid populations also have concomitant differences in ecology.

A very common form of differentiation of sympatric populations is the existence of "normal" and "dwarf" forms of a single species. This situation is found in Arctic char, rainbows, some whitefish, Dolly Varden, and brook char, among others (Armstrong and Morrow 1980, Behnke 1972, Cavender 1980, Mann 1974, Scott and Crossman 1973, Robinson and Wilson 1994). Dwarfing is generally thought to have arisen independently many times in different drainages; the closest relative of the dwarf forms is usually the normal form (Balon 1984, Behnke 1972). Dwarfs and normals may interbreed: dwarf males sneak in to spawn at nests of normal females, in addition to spawning with dwarf females (Jonsson and Hinder 1982). Moreover, like the precocious males of some chars and salmon (see above), they also eat eggs (Sigurjónsdóttir and Gunnarsson 1989). Females often are aggressive against small males, whose success is thought to be correspondingly low (Sigurjónsdóttir and Gunnarsson 1989). Dwarf forms, as well as precociously maturing individuals, are generally less sexually dimorphic than their "normal" relatives (Jonsson and Hinder 1984).

Some *Salvelinus*, *Salmo*, and *Oncorhynchus* diversify into multiple, sympatric, or occasionally parapatric morphs, distinguished by their trophic morphology, body size, and life history (Vøllestad and L'Abée-Lund 1994, Skúlason and Smith 1995). The Arctic char is a classic example of such remarkable polymorphism. As many as four distinct morphs of Arctic char may coexist in a lake (Behnke 1972, Riget and others 1986, Sandlund and others 1992). The morphs in any one lake are typically very closely related to each other (Behnke 1984, Hindar and others 1986, Sandlund and others 1992), and in some cases, they may belong to the same gene pool, as individuals can sometimes shift from one morph to another during a lifetime (Nordeng 1983). The morphs also may have some genetic basis, perhaps with maternal effects (Skúlason and others 1989), and Behnke (1984) suggests that the morphological part of the genome has differentiated much more than the metabolic part. Much of the diversification of Arctic char appears, however, to result principally from developmental plasticity rather than being under direct genetic control (Nordeng 1983, Vrijenhoek and others 1987). Levels of food abundance influence the relative frequency of different morphs. They are specialized to different habitats and foraging habits and have different reproductive phenology, ontogeny and growth patterns, life history, and parasite faunas (e.g., Barbour 1984, Curtis 1984, Dick 1984, Hammar 1984, Malmquist and others 1992, Sandlund and others 1992).

Sympatric conspecific forms in fresh water also are known for (at least) sockeye salmon, rainbow trout, brook char, Dolly Varden, lake char, *Coregonus*, and *Prosopium* (Armstrong 1996, Behnke 1972, Dymond 1943, Heintz 1987, Lindsey and others 1970, McCart 1970, Nikolsky and Reshetnikov 1970, Skúlason and others 1989, Skúlason and Smith 1995).

**Evolutionary
Ecology of
Variation**
**Anadromy**

The habit of reproducing in fresh water, so common among salmonids, exploits a set of habitats thought to be relatively unproductive of both prey and predators (Gross 1987, McDowall 1988, Miller and Brannon 1982, Thorpe 1987). On the other hand, occupation of marine habitats in the temperate zone is associated with rich food resources, rapid growth, and achievement of large body size—and great hazards (Beamish and Neville 1995, Gross 1987, Gross and others 1988, McDowall 1988, Miller and Brannon 1982, Roff 1988, Thorpe 1987). The evolution of anadromy therefore involves balancing the benefits of each habitat type against the costs of getting there (Gross 1987). If the rich foraging found in marine habitats is a general condition, then the maintenance of strictly freshwater populations (or individuals), or of prolonged freshwater existence, neither of which take full advantage of the rich marine resources, requires particular explanation (e.g., Taylor 1990a). In some cases, freshwater populations are landlocked—prevented from reaching the sea by physical or physiological barriers (e.g., Arctic char in alpine lakes in Europe and lakes in eastern Canada [Johnson 1980], kokanee in many lakes [Burgner 1991], many populations of rainbows, cutthroats, Dolly Varden, and lake char [e.g., Behnke 1992, Martin and Olver 1980, Wright[2]]). In other cases, sheer distance from a marine environment may favor freshwater living (Taylor 1990a) or there may be biological barriers such as predators or parasites (Behnke 1972, Fraser and others 1995, Nordeng 1983) that alter the balance between benefits and costs of anadromy. The length of freshwater residence by some species is associated with different migration routes in the ocean (Randall and others 1987). Length of residence in fresh water has obvious potential consequences for the incidence of certain kinds of parasites (e.g., Dick 1984), exposure to particular predators and competitors, and diet and growth rates. When only certain individuals within a population stay in fresh water, the usual explanation is that selection has favored an alternative life history (usually for males especially) as a means of circumventing intense reproductive competition among "normal" individuals (Gross 1984, 1985, 1991, 1996). The complex patterns of maturation in masu and amago salmon (Kato 1991) are especially intriguing for further evolutionary analysis.

The reverse situation, the extreme reduction of the freshwater phase, is much less common, but some populations of pink and chum salmon spawn in the intertidal zone, and some populations of chinook, sockeye, and possibly coho, have very short juvenile periods in fresh water. In theory, assuming that the pattern is adaptive, the hypothetically safe sites for nests and rearing of juveniles in freshwater habitats may have been sacrificed for some other, unknown, gain. Alternatively, if one argues that the intertidal and inshore zones might be as safe as fresh water, the theory ceases to account for the typical return to fresh water. In some locations, freshwater habitats may simply be inaccessible to returning fish, which must then use intertidal areas or go elsewhere.

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The anadromous habit may facilitate colonization of new areas (McDowall 1988). Movement to the ocean, to exploit the rich resources, may be followed by exploration of new regions, invasion of new breeding areas, followed by further straying and colonization. The ranges of Arctic and brook char, especially the anadromous populations, are presumed to have expanded as the Pleistocene ice sheets retreated (Johnson 1980, McDowall 1988), thereby exposing unoccupied freshwater breeding habitats. Many other anadromous species apparently have expanded their ranges, as well. The nonanadromous lake char also has expanded to fresh waters over much of boreal North America (Martin and Olver 1980, Scott and Crossman 1973), probably from multiple glacial refugia (Lindsey 1964, Khan and Qadri 1971). It is possible that lake char once ventured into salt water in sufficient numbers to spread quickly to new regions, and indeed they apparently have made sea crossings in parts of the Canadian Arctic (Lindsey 1964). The usual assumption nevertheless seems to be that their range expanded as the last glaciers retreated, which created suitable freshwater habitats and colonization routes (Ihssen and others 1988, Lindsey 1964, Stearley 1992), in the absence of regular anadromy.

Balon (1984) considered that the dwarf forms found in many freshwater salmonid populations are more generalized than the normal forms and therefore are better invaders of new habitats and better able to survive environmental perturbations. In parallel, the freshwater form of the brown trout is considered to be less specialized than the sea-run form. By this argument, the jacks and jills of *Oncorhynchus* also are juvenilized generalists, as are freshwater cutthroats and rainbows and their close relatives (Balon 1984). Jacks, however, do not appear to stray more than adults (Labelle 1992, Quinn 1993, Quinn and Fresh 1984, Unwin and Quinn 1993), which contradicts Balon's idea. Balon envisioned *Salmo* as the most specialized representative of one line of salmonid evolution, and *Oncorhynchus* as the most specialized of another. Pink salmon, in this scenario, are the most specialized of all the Pacific salmon; however, pink salmon (and the closely related chum and sockeye) have very broad ranges, which seems to argue for considerable powers of colonization (or survival of Pleistocene perturbations) of these supposedly specialized forms.

Latitudinal gradients in the frequency of anadromy have been described for teleosts in general (McDowall 1987, 1988); both the number and proportion of species that are anadromous are greatest in cool temperate regions. For North America, the number of anadromous species changes very little from about 40° N. lat. northward, but the proportion is highest at high latitudes because the total number of fish species there is low (McDowall 1988). The pattern for North American salmonids generally follows that for all anadromous fishes (McDowall 1988). Latitudinal variation in the development of anadromy also is seen within some salmonine species. Anadromy is more prevalent in northern populations of Arctic and brook char (as well as brown trout and masu) than in southern populations (and most North American whitefish with anadromous populations are found in Arctic or subarctic waters; McDowall 1988, Rounsefell 1958, Scott and Crossman 1973). Such trends are not apparent, however, in steelhead, cutthroat, Atlantic salmon, or Dolly Varden (Balon 1980, Groot and Margolis 1991, McDowall 1988, Trotter 1989, Withler 1966). It is not clear if latitudinal patterns in the frequency of anadromy are related to the relative advantages of marine and freshwater living, to habitat accessibility, or to the time available for local evolutionary changes.

**Age of Maturation**

Age at maturity is an important transition point in the life cycle (reviewed in Bernardo 1993). Among-population variation is expected, theoretically, to be related (not necessarily linearly) to the relative levels of adult and juvenile survivorship. For example, precocious maturation may be favored by long and arduous migrations and by high harvest levels of returning fish (e.g., Myers 1984, Taylor 1989, Thorpe 1987). In the proximate sense, variation also may reflect foraging conditions: later maturation in many high-latitude populations is related to the short foraging season available for accumulating the nutrients needed to achieve competitive size and breeding condition.

Females commonly, but not always, mature about a year later than males (except in pink salmon, with a 2-year life cycle). If the extra year results in larger body size, females may gain both greater fecundity and greater competitive ability (Fleming and Gross 1989, van den Berghe and Gross 1989). Males also gain competitive ability by increased body size (Fleming and Gross 1994, Quinn and Foote 1994), but either males can grow faster per unit time or the potential gain is less than that for females. I have not found any comparisons of the relative strength of selection on body size in males and females.

Precocious maturation is a conspicuous life-history variant within salmonid species. Although the frequency of early maturation may be determined, in part, genetically (Iwamoto and others 1984), it is largely a conditional strategy in which a "decision" reflects the physiological and behavioral status of the individual (Gross 1991, 1996; Thorpe 1994; Thorpe and others 1992). For example, fast-growing juveniles are more likely to mature early in several species (e.g., Gross 1996, Hutchings 1993, Thorpe 1987), and such individuals are likely to be of high status in the population of juveniles (Gross 1996, Thorpe and others 1992). The average fitness consequences of the alternatives within a conditional strategy may differ, but fitness at the "switchpoint" or point of "decision" would be equal (and status-dependent)(Gross 1996). Males using alternative mating tactics are commonly presumed to achieve lower reproductive success than "normal" males, but variation in their relative success is expected and potentially may even include greater success in some cases (Gross 1996). The ability of some Atlantic salmon individuals to reproduce both precociously and as "normal" adults after some time at sea then represents a particularly complex case, with two switchpoints. There is an open field for investigation in this arena, relating variation in switchpoints to variation in environmental and population variables and to the fitness consequences.

**Frequency of Reproduction**

There is a broad correlation in salmonids between the degree of anadromy and semelparity, perhaps because of the energy expenditure needed to travel between oceanic feeding grounds and freshwater breeding grounds (Bell 1980, Fleming and Gross 1989, Miller and Brannon 1982, Rounsefell 1958, Stearley 1992). Two partially iteroparous species (steelhead, Atlantic salmon) make extensive sea voyages; the frequency of iteroparity in steelhead varies inversely with freshwater migration distance (Behnke 1992, Meehan and Bjornn 1991). Repeat-spawning steelhead females have less extensive patterns of ocean migration than individuals that have not spawned previously (Burgner and others 1992).

Costs of migration can be high. For example, sockeye migrating up the Fraser River in British Columbia allocated an estimated 59 to 70 percent of their expended fat stores and up to 49 percent of their protein stores to swimming and basal metabolic costs (calculated from Gilhousen 1980). The remainder was allocated to enlargement of gonads and spawning activity. The costs of migration should be much less for coastal spawners, such as most populations of pink salmon and many populations of chum salmon.

On top of the migratory expenditure comes a cost of reproduction. Females, in general, allocate more resources to gonadal development than males do: sockeye salmon females allocated up to 19 times as much of their fat reserves to gonad enlargement as did males (calculated from Gilhousen 1980). The gonads of female sockeye were developed during upstream migration, when feeding had ceased; male gonadal development occurred chiefly before upstream migration began (Gilhousen 1980). Males, on the other hand, often expend more resources than females on spawning activity (up to 2.2 times as much of the fat reserves in sockeye; calculated from Gilhousen 1980). There may be survival costs as well as energetic costs, for iteroparous species: Hutchings (1994) estimated that reproduction of nonmigratory female brook char decreased the probability of survival by as much as about 90 percent.

Female reproductive costs that relate to the "choice" between iteroparity and semelparity may lie more in the intensity of competition for nest sites than in building eggs, despite the energetic costs of egg development, because the average ratio of clutch weight to body weight is not greater for semelparous than iteroparous females (Bell 1980). For males, the principal cost of reproduction probably is related to the intensity of competition for mates. It seems likely that the costs of reproductive competition are commonly higher for males than for females and that this contributes to the lower probability of iteroparity in males. A high intensity of male-male competition is suggested by high energy costs of spawning activity and by the greater development of secondary sexual traits in males than in females. Furthermore, instream time of males during the spawning season is commonly longer than that of females, at least in some species (e.g., Lohr 1996, Salo 1991, Schroder 1981; but with some variation, see Dangel and Jones 1988), perhaps increasing male reproductive costs.

Although females tend to be more iteroparous than males (and tend to mature later), iteroparous females are more likely than iteroparous males to skip a year between spawnings. Alternate-year spawning suggests that some costs of reproduction may be greater for females than for males. These costs may include those incurred by constructing nutrient-rich eggs, which are more costly to produce than male gametes. Alternatively, repeat-spawning males and females might undergo different migratory behavior.

For several species of salmon, the duration of instream life decreased through the season for both males and females (Dangel and Jones 1988, Groot and Margolis 1991). Instream life also may differ annually and among streams, in relation to predation by bears and water levels (Burgner 1991, Dangel and Jones 1988). At this point, one cannot say, however, whether seasonally diminishing the duration of instream life decreases the cost of competition or perhaps increases the intensity of competition and thus increases the cost. Some careful modeling of mixed life-history strategies (as has been done for alternative male mating strategies) would be appropriate.

Costs of migration are relatively low for coastal spawners and for kokanee, which are neither anadromous nor highly migratory. Nevertheless, individuals in such populations are semelparous, suggesting that there may be no necessary link between migration and semelparity. The semelparous habit could simply be retained, evolutionarily, from ancestral forms, although the tremendous variability in the salmonids suggests that such constraints are few. Alternatively, the intensity of reproductive competition may be sufficient in these cases to maintain the semelparous habit. It is clear that much more information is needed on the energetics of migration and reproduction for males and females in different populations, to assess the possible role of migratory and reproductive costs in the evolution of semelparity.

The development of semelparity may have favored the evolution of strong homing tendencies, assuming local adaptation to home-stream conditions, because semelparous individuals have only one chance to reproduce (Miller and Brannon 1982). If so, we should expect to find the best developed capacity for homing in semelparous *Oncorhynchus*, less homing capacity in anadromous but limitedly iteroparous cutthroats, steelhead, and char, and still less in whitefish and inconnu. Similarly, homing would be expected to be more precise in males than in females, and more precise in species with little flexibility in spawning habitat. Data appear to be inadequate to examine these propositions (Quinn 1993).

**Body Size and Fecundity**     Body size has many important ecological implications, including locomotor ability, prey size, susceptibility to predators, fecundity, and life history (Claytor and others 1991, Fleming and Gross 1989, Schaffer and Elson 1975, Stearley 1992, Taylor and McPhail 1985, Williams 1966). Variation in slope of the regression between fecundity and body size implies that life-history tradeoffs differ among species and conspecific populations. For instance, the cost of reproduction in brook char was greater at small body sizes (and greater ages), with some variation among populations and sexes (Hutchings 1994). In contrast, large Arctic char and brown trout females allocate more energy to reproduction than small females and have a lower probability of subsequent breeding (Dutil 1984, Jonsson and others 1991). Such variations within and among species offer opportunities to explore the ecological basis of differing life-history tradeoffs.

Constraints on egg size can limit variability in fecundity and the relation between body size and fecundity, if there are tradeoffs between egg size and number. Within species, egg size often varies with female body size (Bain 1974, Hankin and McKelvey 1985, van den Berghe and Gross 1989, Winemiller and Rose 1992) and commonly determines the size and survival probabilities of juveniles (e.g., Bain 1974, Bradford and Peterman 1987, Chadwick 1987, Chapman 1962, Neave 1948, Taylor 1980). The advantages to a parent of producing large (but perhaps fewer) eggs are expected to differ with environmental patchiness in terms of environmental conditions for egg and juvenile survival, including the metabolic costs of dealing with different temperature regimes and relative risks of predation, both within and among populations (Fleming and Gross 1990, Quinn and others 1995, Winemiller and Rose 1993). If large females, with large eggs, have better access to prime spawning sites, the distribution of egg sizes across females would differ with the distribution of gravel sizes across nesting sites (Fleming and Gross 1990). Alternatively, large females may be better able to invest resources in both egg size and egg numbers (Quinn and others 1995). Egg size and numbers may differ with intensity of breeding competition and

arduousness of migration, both of which can affect body size (Fleming and Gross 1989; but see also Blair and others 1993, Roni and Quinn 1995). Thus, the potential tradeoff between egg size and egg number, expected in theory and often observed, could differ among females and influence the relation between body size and fecundity both within and among populations.

Body size has additional fitness consequences for intraspecific competitive ability in both males and females; intensity of competition generally increases the advantages of large body size (and the pressure to use alternative mating tactics, as well). Large males generally dominate small males in competition for access to spawning females and often may be preferred as mates by females, but subordinate males adopt alternative strategies to achieve breeding success (e.g., Beacham and Murray 1985, Foote 1989, Hanson and Smith 1967, Hino et al 1990, Järvi 1990, Keenleyside and Dupuis 1988, Quinn and Foote 1994, Schroder 1981,), even in the tiny gila trout (Rinne 1991). Large coho females are better able to acquire and defend a good nest site, although factors other than size also are important (Fleming and Gross 1994; van den Berghe and Gross 1986, 1989). Similar advantages were suggested for female chinooks and sockeye (Hankin and McKelvey 1985, Healey 1987, Healey and Heard 1984; but compare Holtby and Healey 1986, Schroder 1982). Nevertheless, smaller females may have some advantages (or at least can mitigate their disadvantages) in certain circumstances (Healey and Heard 1985), including the production of smaller eggs in small-grained substrates (Healey 1987, van den Berghe and Gross 1989) or, perhaps, adopting alternative mating strategies (Jonsson and Hindar 1982, van den Berghe and Gross 1989). Northcote (1992) suggests that fitness gains from large size may be greater for females than males, and that this difference could contribute to more extensive migrations by females.

## Sexual Dimorphism

Sexual dimorphism (i.e., in size, hump, or kype) is not associated simply with density at spawning, as many species breed in dense groups. Although life-history theory and empirical evidence show that small-bodied species commonly have higher adult mortality than large-bodied species and therefore are likely to have higher reproductive effort (e.g., Williams 1966) and possibly better developed sexual dimorphism, this pattern is not clearly evident in the salmonines. The sexually dimorphic grayling is small, the Pacific salmon are intermediate to large in size and strongly dimorphic, and the nondimorphic inconnu is large. Life-history theory also suggests that semelparous species are likely to have higher reproductive effort than iteroparous species, and that sexual dimorphism is better developed in semelparous species than in closely related iteroparous ones (Williams 1966, reviewed in Andersson 1994). Although grayling, chars, and Atlantic salmon are commonly iteroparous and sexually dimorphic, the extremes of sexual dimorphism in the salmonines are found in the semelparous Pacific salmon.

In general, the kype is better developed in stream-dwelling anadromous forms than in lake-spawning, nonanadromous salmonines (Maekawa 1984, Morton 1965), and fish spawning in freshwater streams are reported to be more aggressive than their relatives in salt water or lakes (references in Taylor 1990b). Furthermore, stream-spawning salmonines differ in the degree of kype and snout development, for reasons not yet clear: Some, all of rather small body size, have little or no kype (golden trout [*O. aguabonita* (Jordan)], Mexican golden trout [*O. chrysogaster* Needham and Gard], freshwater cutthroat and rainbows, brook char). Kype development is intermediate,

for reasons undetermined, in the remaining anadromous chars, steelhead and sea-run cutthroats, and Atlantic and chinook salmon. Extreme kypes are seen in normal pinks, chum, sockeye, and coho, but not in precociously maturing males[3] (e.g., Wydoski and Whitney 1979, Stolz and Schnell 1991). Male kokanee can develop a pronounced kype, but they do not in some populations (see footnotes 2 and 3). The cost of developing secondary sexual characteristics is unknown, but Gilhousen (1980) suggests a significant protein cost for males.

Differences in spawning habitat go hand in hand with differences in spawning behavior and, broadly, with sexual dimorphism. Inconnu, whitefish, and lake char typically spawn in groups in open water (although some lake char spawn in streams; Martin and Olver 1980). Although several males may accompany each spawning female (Morrow 1980), there is little or no defense of territory or females, no nest is built, and sexual dimorphism is little developed or absent. Grayling males are territorial; females visit the territory to spawn (Morrow 1980). The longer fins and brighter colors of the males are presumably used in aggressive or courtship displays. Arctic char males reportedly set up territories, in which the females place their nests (Johnson 1980), and coho salmon males sometimes do so as well (Healey and Prince 1995). These two species thus appear to differ somewhat from the other stream-spawning chars and salmon, in which females choose the nest sites and males compete intensely to mate with nest-holding females. The strong kype serves as a weapon for defense of mating opportunities. With the shift to egg-burial comes intensified sexual selection (Stearley 1992), setting the stage for the evolution of greater sexual dimorphism and alternative male strategies. Commonly, a dominant male guards a female, several subordinate or satellite males (including both those that matured precociously and "normal" but small individuals) station themselves nearby or cruise from nest to nest and spawn by sneaking into the nest when the dominant pair is spawning (Fleming and Gross 1994, Groot and Margolis 1991, Healey and Prince 1995, Morrow 1980).

The degree of sexual dimorphism commonly varies within a species (Burgner 1991, Carlander 1969, Kato 1991, McPhail and Lindsey 1970, Morrow 1980), indicating that costs and benefits differ among individuals, between sexes, and among populations (e.g., Holtby and Healey 1990). In particular, the relative development of secondary sexual characteristics are likely to differ with the intensity of breeding competition, size- and sex-specific predation levels, and the costs of locomotion in different waters. Females sometimes also develop kypes: the degree of development of breeding color and of kype in female coho was correlated with average levels of competition in different populations (Fleming and Gross 1989). Secondary sexual traits such as kypes and snouts are more likely to be well developed in larger individuals within a species (e.g., Stolz and Schnell 1991): normal morphs more than dwarfs, anadromous individuals more than freshwater residents, normal adults more than jacks. Allometric relations between head shape and body size contribute to the better development of secondary sexual characteristics in large individuals, but there is detectable independent, direct selection on male (but not female) snout size in coho (Fleming and Gross 1994) and hump size in sockeye (Quinn and Foote 1994) as well.

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[3] Personal communication, 1996, S. McCurdy, Forestry Sciences Laboratory, 2770 Sherwood Lane, Juneau, AK 99801.

**Parental Care**

Across the salmoniforms, parental care is inversely correlated with egg size (Winemiller and Rose 1992) and relative fecundity. Relative fecundity (mean number of eggs per unit weight of female) tends to be high in whitefish and inconnu (often well over 10,000 eggs/kilogram), intermediate in grayling (about 10,000 eggs/kilogram, but ranging up to 16,000), and low in most char and salmon (<5,000 eggs/kilogram usually) (e.g., Bell 1980, Carlander 1969).

Females of regularly iteroparous species commonly make >1 redd (nest site; perhaps as a means of reducing losses resulting from variable water levels), and extended defense is not feasible (Barlaup and others 1994). High levels of competition among females in *Oncorhynchus* may have provided selection for nest guarding (van den Berghe and Gross 1989) and relinquishing the bet-hedging strategy of multiple nests. Egg guarding is best developed in semelparous species, in which female competition is severe, and each female usually defends a single redd (Barlaup and others 1994, Burgner and others 1992, van den Berghe and Gross 1989). Variation in duration of instream life (of pink salmon; Dangel and Jones 1988) suggests that variation in nest guarding is likely, but it is not clear if this is a response to differing and unpredictable stream conditions that alter female survival or if there are differing levels of selection for female competitive ability.

**Breeding Season**

The balance of ecological factors determining the evolution of migration and spawning time are not fully understood. In some cases, streamflow and accessibility to spawning areas must be involved. Water temperatures and the length of time needed for incubation and juvenile growth are surely critical. But some mysteries remain. Some steelhead spend the summer in fresh water before spawning the following spring, and coho, chinook, and sockeye salmon sometimes enter fresh water several months before spawning; in such cases foraging opportunities have been lost. Arctic char in northern Canada enter fresh water in fall and spend a year there before spawning the following fall (Dutil 1984, Johnson 1991), at the price of missing a summer of feeding in the sea and the resulting increase in body condition. In circumstances where several summers of ocean feeding are needed between spawnings of iteroparous char, the extra summer in fresh water is puzzling.

**A Scenario of Life-History Evolution**

I have tried to synthesize some critical relations into a possible scenario for the pattern of life-history evolution within the salmonines (fig. 1; see also Hutchings and Morris 1985, Miller and Brannon 1982, Stearley 1992). The illustrated relations are simplified and hypothetical, but they serve a purpose in identifying particular links in a chain of interactions, each of which can be examined to explore the basis of intraspecific and interspecific variations in life history.
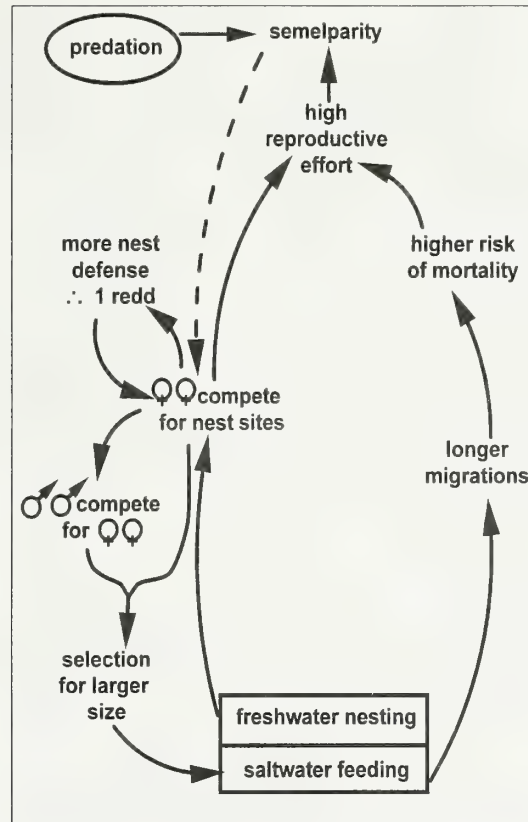
Figure 1—A possible scenario for the evolution of life-history patterns in salmonine fishes, suggesting some relations that might account for salient features of their life history. A high risk of predation to adults in the spawning streams (e.g., by bears) would decrease the probability of spawning more than once in a lifetime and thus favor the evolution of semelparity and associated life-history features.

If the abundance and distribution of suitable freshwater spawning sites are limited, females compete for sites. Intense female-female competition may lead to defense of single redd sites. Males compete for territories or for females that have access to good nest sites. Intense male-male competition provides the opportunity for alternative male mating strategies, including both precociously maturing forms and satellite normal males, and greater sexual dimorphism. Meanwhile, selection for rapid growth and achievement of large body size, which are advantageous in breeding competition and in increasing fecundity, favor migration to the sea, to make use of abundant food resources. Once a marine phase is present, exploration in search of ever better food resources leads some populations to make extended ocean voyages. The arduousness and length of extensive oceanic and freshwater migrations increase the risk of adult mortality. High reproductive effort is then favored, leading to semelparity and the allocation of all available body resources to one episode of reproduction, thus further intensifying sexual competition. The relative magnitude of migratory and reproductive costs for males and females, and in different populations, must differ greatly. A quantitative assessment of these costs seems critical to understanding the evolution and maintenance of the semelparous habit.

## Variation and Speciation

The polyploidy event that contributed to the origin of the salmonid family may have several evolutionary consequences. Polyploidy may constrain rates of speciation, because replacement of alleles in a polyploid populations requires more generations than in a diploid population (Allendorf and Thorgaard 1984). Rediploidization of the tetraploid genome in salmonids is incomplete, and therefore the potential restraints on speciation may still be operant. The Salmonidae are not particularly depauperate in species (10 genera, about 68 species), however, in comparison with other (diploid) Holarctic families: Osmeridae (6 genera, about 10 species) and Gasterosteidae (5 genera, about 7 species, although at least one "species" in this family in really a complex of closely related species; Nelson 1984, Schluter and Nagel 1995). The only other known teleost family of polyploid origin, the Catostomidae, has a diploidized genome (Ferris 1984), but the number of genera (12) and species (about 61) is similar to that of the salmonids (Nelson 1984). The effects of possible constraints derived from polyploidy thus are not immediately apparent. Biological diversity in salmonids is far greater than the taxonomic diversity (Behnke 1972, Nelson 1984).

Polyploidy, on the other hand, may facilitate the widespread occurrence of anadromy (Allendorf and Thorgaard 1984) and the colonization of habitat made newly available by disturbances (e.g., deglaciation). The "extra" alleles and a variety of meiotic products contribute to a great range of variation, both directly through genetic effects and perhaps indirectly through phenotypic plasticity (see below). In other words, polyploidy might facilitate diversification, with or without speciation, especially in regions where new opportunities for colonization arise, or where the species diversity of other fishes in the same body of water is low. Distinctive but sympatric populations, reproductively isolated or only partly so, are known for most salmonid genera in North America (Behnke 1972, Taylor and Bentzen 1993).

Extensive variation also is found in other (mostly diploid) fishes. The rainbow smelt (*Osmerus mordax* (Mitchill)), in a family (Osmeridae) closely related to Salmonidae, has anadromous and nonanadromous populations, and "dwarf" and "normal" morphs, often sympatric (Taylor and Bentzen 1993). Different migratory forms occur in other salmoniforms, including the ayu (*Plecoglossus altivelus* Temminck and Schlegel; family Plecoglossidae)(Tsukamoto and others 1987) and in the clupeiform alewife (*Alosa pseudoharengus* (Wilson); Clupeidae). Sympatric pairs of populations, of differing degrees of reproductive isolation, have been reported for *Gasterosteus* (McPhail 1994), a taxon unrelated to salmonids. Furthermore, high levels of phenotypic diversification (probably not speciation) also have been reported for petromyzontids, poeciliids, cichlids, centrarchids, and goodeids ( Kornfield and others 1982; Meyer 1987, 1990; Scott and Crossman 1973; Turner and Grosse 1980; Vrijenhoek and others 1987; Wainwright and others 1991), not in association with polyploidy except in poeciliids. The possible relation of polyploidy and its genetic consequences to speciation and diversification in these fishes thus is not clear.

Among species within *Oncorhynchus*, there is a general association between the length of time spent in freshwater rearing habitat and the tendency to produce strictly freshwater forms (table 3). Indeed, Behnke (1972) considered that sockeyeare "preadapted" to a totally freshwater existence because of the long freshwater rearing period in most populations. In many cases, the freshwater populations have diverged in appearance from each other, and from sea-run relatives, to the extent that they sometimes have been accorded separate taxonomic status. For example, the sunapee and blueback chars of eastern North America were once considered

**Table 3—Range of freshwater residency in anadromous salmonines and occurrence of strictly freshwater conspecific forms**

| Species | Freshwater residency | Natural freshwater populations | Freshwater reproductive individuals |
|---|---|---|---|
| | *Years* | | |
| Arctic char | 1-8 (seasonal) | Many | Residuals |
| Dolly Varden | 2-6 (seasonal) | Many | Residuals |
| Brook char | 1-7 | Many | Residuals |
| Atlantic salmon | 1-8 | Some | Residual parr |
| Coho | 1-4 | Rare | Residuals |
| Steelhead | 1-5 | Many | Residuals |
| Sockeye | <1-3 | Many | Residuals |
| Cutthroat | 1-2+ | Many | N.d. |
| Masu | 1-2+ | Many | Residuals |
| Chinook: | | | |
|   Stream type | 1-2 | None | Residuals |
|   Ocean type | <1 | None | None |
| Chum | 1 | None | None |
| Pink | 1 | None | None |

N.d. = no data.
Sourcres: Groot and Margolis 1991, Jones and Bentz 1994, Mills 1989,
Randall and others 1987, Rounsefell 1958, Stearley 1992.

to be separate species from the related Arctic char, the sebago and ouananiche were once separate species related to Atlantic salmon (Scott and Crossman 1973), and the aurora char was once separated from brook char (Balon 1993, Scott and Crossman 1973). More recent work (Balon 1993, Hutchings and Myers 1985) has shown, however, that in these cases even subspecific status probably is not warranted. Kokanees have arisen many times from sockeye and differ in appearance from the ancestral form (McDowall 1988, Taylor and others 1996). Schluter and Nagel (1995) suggest that kokanee comprise a possible example of incipient parallel speciation, their multiple origins constituting evidence for the role of environmental selection in the origin of species. Similarly, steelhead have arisen independently many times from freshwater populations of rainbows (Behnke 1992); presumably sea-run cutthroats have done the same. Both rainbows and cutthroats have diversified to form several distinct freshwater populations that appear to warrant status as separate species and subspecies (Behnke 1992). The bull trout has been separated taxonomically from the related Dolly Varden (Armstong and Morrow 1980, Haas and McPhail 1991, Meehan and Bjornn 1991) or the Dolly Varden-Arctic char complex (Cavender 1980). In contrast to the above examples, the very widespread lake char apparently has differentiated rather little, except for sympatric forms in the Great Lakes area (Behnke 1972, 1980; Khan and Qadri 1971; Ihssen and others 1988; Scott and Crossman 1973), although its present distribution may have originated from multiple Pleistocene refugia (Khan and Qadri 1971, Lindsey 1964).

Diversification of sympatric trophic morphs is probably related to a low intensity of competition and the availability of otherwise empty niches (Robinson and Wilson 1994). Arctic char generally live in areas of low diversity of fish species (Riget and others 1986, Vrijenhoek and others 1987, Robinson and Wilson 1994) and seem not to be very competitive with other fishes. They are more often lake residents in Siberia, where lake char are absent, than in North America, where lake char are widely distributed (Behnke 1984). If other char move in, they often go extinct or undergo a marked shift in habitat and diet (Behnke 1984, Fraser and Power 1984, Nyman 1984). Arctic char in lakes without other coexisting char species grow faster and mature earlier than those in lakes with other chars (Fraser and Power 1984). The general lack of strong competitive ability, coupled with the existence of multiple morphs especially where other char are few, suggests that "swarms" of morphs occupy niches not otherwise occupied by other species (Hindar and Jonsson 1982, Robinson and Wilson 1994, Sandlund and others 1992, Vrijenhoek and others 1987). It seems only a small step from swarms of morphs to sympatric speciation (as in African cichlids; e.g., Schliewen and others 1994). The possible effects of predation on the opportunity for sympatric divergence apparently have not been studied (Robinson and Wilson 1994), although differential predation has been shown to contribute to divergence of conspecific populations of nonsalmonids in different streams (references in Andersson 1994).

Diversification among salmonids is enhanced by homing mechanisms, which facilitate the evolution of local adaptation, either allopatric or sympatric (Behnke 1972, Taylor 1991), and salmon are famous for their ability to return to their streams of origin. On the other hand, "straying" (returning to a nonhome stream to spawn) reduces the likelihood of local adaptation. Straying (and the ability to diversify) facilitates the occupation of new habitats when environmental changes provide the opportunity. The frequency of straying differs substantially among conspecific populations, possibly with the stability of the streams used for spawning, among other factors (Helle 1966; Labelle 1992; Leider 1989; Quinn 1984, 1993; Quinn and Fresh 1984; Quinn and others 1991; Taylor 1991), but no comprehensive surveys of straying tendencies are available to construct comparisons among species or locations.

There is evidence that many life-history features of salmonids are partly heritable (e.g., Ricker 1972), but phenotypic plasticity also is known to be important. Some features, such as age of maturation or body size-fecundity relations, are plastic in many species whose ranges encompass a wide variety of growth conditions (Stearns and Crandall 1984, Weeks 1993). Phenotypic plasticity itself is a heritable trait that enables organisms to respond to changing conditions (Stearns and Koella 1986, Scheiner 1993, and many others). There are many indications that salmonids are flexible even for traits that do not usually vary; for instance, the occasional development of a kype in male lake char, the 3-year life history of pink salmon and their ability to complete a life cycle entirely in fresh water, or the major increases in expressed body size that occurred in Great Lakes cisco species when larger bodied congeners were extirpated (Scott and Crossman 1973).

A relatively unspecialized general body plan may facilitate moderate phenotypic shifts that are more difficult for highly specialized morphologies (Thorpe 1994). Furthermore, "selection may favor genotypes with enough variation to permit phenotypic shifts back and forth between two alternative stable states..." (Balon 1984). A threshold effect or developmental switch (see Stearns 1989) might alternately produce one phenotype or another, such that there is sympatric diversification, as in the several morphs of Arctic

char (Balon 1984); the forms are not separate evolutionary units initially, but may become so later. West-Eberhard (1986, 1989, 1992) argues that phenotypic plasticity can be extremely important, not only during an organism's lifetime, but also in facilitating divergence and ultimately speciation, by providing the opportunity for the accumulation of genes that modify expressed phenotypic variants. Also, species-level differences may be able to arise by changes in only a few genes of considerable effect (e.g., Bradshaw and others 1995), and the possibility of "adaptive mutations" (Harris and others 1994, reviewed by Thaler 1994) further facilitates divergence. Sexual selection, which is probably intense in many salmonids, could contribute to diversification and speciation (Turner and Burrows 1995).

Because most of the radiation of morphs or populations within salmonid species is thought to have occurred during or after the Pleistocene (Behnke 1972, Neave 1958, Randall and others 1987, Taylor 1991), these species clearly have an impressive capacity for rapid diversification. In addition, a number of changes are known to have taken place in only a few generations. The existence of numerous local populations can facilitate the evolution of new phenotypes and even the invasion of new adaptive zones (Lande 1980). Chinook salmon, introduced to New Zealand, exhibit interpopulation variation in many traits after only 20 to 25 generations (Quinn and Unwin 1993). Rapid diversification of salmon introduced to the Great Lakes was seen in the origin of an even-year line from the odd-year line of pink salmon, and of a spring-spawning population from a fall-spawning stock of chinooks (Healey and Prince 1995). The phenology of spawning runs in the Columbia River drainage has changed in response to anthropogenic factors in recent historical times (Utter and others 1995). In addition, remarkable variation in body color and markings exists in brook char (Power 1980), Dolly Varden, Arctic char (Maitland and others 1984), rainbows and cutthroat (Behnke 1992, McPhail and Lindsey 1970, Scott and Crossman 1973), sockeye (Burgner 1991), and amago (Kato 1991). The role of body color in mating, concealment from predators, resistance to skin parasites, or other ecological factors apparently has been little studied in salmonines, in contrast to some other fishes.

The huge diversity and plasticity evident in the salmonids facilitates rapid responses to selection (e.g., van Noordwijk 1989) and perhaps rapid speciation (Neave 1958). A remaining question can be asked: Given the impressive array of diversity expressed within any particular salmonid species, why is it still one species and not a species swarm? Some species as presently constituted may be, in fact, species complexes, as yet unrecognized by taxonomists. In addition, most of the salmonid populations occupy recently deglaciated regions, which are not only geologically recent but also somewhat unstable (Bell and Foster 1994, McPhail 1994). As noted by McPhail for sticklebacks, locally adapted populations may flourish and fade; extinction and recolonization may be occurring repeatedly and frequently. Likewise, sockeye populations

that exhibit local adaptation to particular lake systems also may be evolutionary dead-ends; evolutionary and ecological flexibility for the colonization of new habitats or recolonization of depleted habitats may reside principally in the sea and river life-history types (Wood 1995). The salmonids seem to offer good opportunities to examine the evolutionary processes involved in speciation.

**Importance of Variation in Salmonine Ecology, Evolution, and Management**

The idea is dead that variance is just a statistical nuisance or that the biology of a species can inevitably be characterized satisfactorily by constant properties or by the average values of its characteristics (Horne and Schneider 1995; Price 1991; Thompson 1988, 1994). In its place, we have a concept of variation at scales from within to among populations and species. Thompson (1994) emphasizes the importance of encompassing among-population (geographic) variation to understanding ecological and evolutionary patterns and processes. Knowledge of heterogeneity is a critical aid to discerning ecological patterns, which guide the search for mechanisms

and thus the development of ecological theory (Price 1991). Price argues that the weight of evidence determines ecological generalizations; I emphasize (and Price recognizes) that the exceptions, the outliers, are essential too, because they are evidence that we do not know it all—that under some as-yet-not-understood conditions the outcome is different. A better understanding of the "exceptions" readily leads to a better incorporation of heterogeneity into fundamental general concepts of pattern and process, and thence into theory. This clearly indicates the value of comparative studies, which not only provide a legitimate direct basis for expanding our generalizations but also establish where the contrasts lie. By knowing the exceptions that *probe* the rules, we are enabled to seek the processes that underlie the "exceptions" and find still sounder, broader generalizations.

Such thoughts are now widespread in the ecological literature, pertaining to many kinds of organisms, and many fish biologists have long been emphasizing the importance of genetic and ecological diversity in fish stocks (e.g., Behnke 1972, 1992; Larkin 1977). Indeed, the very concept of a "stock" reflects an acknowledgment, at some level, of variation (Nehlsen and others 1991). More recently, an interest in the importance of small-scale ecological variation has become more visible (e.g., Behnke 1995; Gharrett and Smoker 1993a, 1993b; Gresswell and others 1994; Waples 1991, 1995). But, as yet, such considerations have been slow to enter the design of fisheries management, in part because of logistic difficulties in obtaining and assessing the requisite information from mixed-stock fisheries. Although the principles of natural selection have been known for over a century and those of artificial selection for longer still, the notion that selective harvest of certain size classes of salmon could select for different body sizes and ages of maturation came late to the mainstream of fisheries literature (e.g., Ricker 1981; reviewed in Healey 1986). For example, in 1962, one biologist even suggested that the strongly size-selective harvest of male sockeye could be increased still further, without affecting the number of fertilized eggs (Mathisen 1962); this suggestion totally disregards any evolutionary issues. One cannot single out the fisheries managers in this kind of neglect, however, because the same neglect was seen in the evolution of DDT resistance in insect pests and currently is causing a growing human medical problem in the evolution of antibiotic resistance.

Management of salmon harvest has generally been designed for maximum "take," leaving enough spawners to "guarantee" the next generation, to be harvested in due course. This kind of management ignores both ecological and genetic variation, as well as the well-known problem that, when the mating success of individuals is unequal, the number of adults in the population can be much greater than the genetically effective population size (e.g., Baylis 1995). In fact, the "epitaph" for this kind of plan was written two decades ago (Larkin 1977). More recently, means of dealing with population fluctuations have received more attention (Emlen 1995; references

in Frank and Leggett 1994). This is very important, because current management tactics are predicated on prevailing ocean conditions—and, thus, the capacity to support certain population levels and body sizes, although periodic shifts of the Aleutian Low in the North Pacific are probably changing that capacity now (Beamish and Bouillon 1995, Hare and Francis 1995, Pearcy 1992, Ward 1993).

Little consideration has so far been given by fish-harvest managers to local adaptations or the evolutionary processes that control them—or the consequences of changing those processes. A momentary thought provides several examples of variation that have consequences directly relevant to harvest practices. Variation in age of maturation means that generation times differ, as does the possible rate of change in response to selection. Variation in body size among populations suggests that selection pressures and growth opportunities differ, and that selective harvests (e.g., with standard nets) can have different effects on different populations. Variation in life history among populations means that ecological tradeoffs differ, and so the effects of harvest also can be expected to differ. Variation in adult body size and associated instream lifespan can influence the accuracy of population estimates made by certain methods (van den Berghe and Gross 1986). Variation within populations can mean that selective harvests alter the sex ratio, age of maturity, intensity of breeding competition, the phenology of spawning, spawning success, and effective population size. To the extent that fat reserves reflect expected costs of reproduction, alteration of the intensity of breeding competition may change the fat content of the body, which then influences the economic and nutritional value of the harvested fish. Anthropogenic changes of many types alter the selection regimes of most populations and can induce major changes in many aspects of life history (Gross 1991), which can have large effects on harvest yield (Myers 1984).

Not all local variations need be adaptive. In addition to strictly phenotypic responses (e.g., high growth rates in response to temporary resource abundance), genetic drift can produce variant, nonadapted populations under certain circumstances. It thus becomes important to ascertain which variants represent adaptations to local conditions and are thus indicative of specific selection pressures subject to disruption, which are purely phenotypic responses, and which variants exist for genetically based, nonadaptive reasons. Phenotypic responses and nonadaptive variants may produce traits of evolutionary and economic interest, but because the population processes that produce the variants differ, the mechanisms of managing such populations also differ.

Knowledge of local adaptations and ecological plasticity aids managers in several ways (Taylor 1991, Wevers 1993). For instance, the capacity of a stock to adapt to changing conditions (e.g., introduced predators, climate changes) could be estimated (Gross 1991; Mangel 1994a, 1994b). Stocks not well adapted to prevailing conditions, and therefore presumably less resilient to change or harvest, can be identified. The appropriate stock for reintroductions or hybridization attempts (e.g., Hard 1995, Utter and others 1995) can be chosen. Natural genetic variants can contribute important traits to the development of cultured stocks. The development of appropriate theory, encompassing patterns and processes of variation, ultimately aids managers by helping predict the outcome of both natural and anthropogenic changes. Increasing demands for fish protein by escalating human populations will increase the conservation problems for salmonid diversity, however (references in Gharrett and Smoker 1994); huge economic pressure to increase harvests still further will outstrip our ability to determine and use natural variation to our long-term advantage.

Finally, anadromous fishes are a critical seasonal resource for indigenous peoples and many terrestrial wildlife species, but harvest levels are commonly set without regard for the impact of the harvest on the spatial distribution of spawning runs (or smolt emigrations) on the landscape (Mundy and others 1995, Willson and Halupka 1995). Dependence on nutrition derived from anadromous salmon seems to have shifted the breeding season of mink (*Mustela vison*) along the Alaska coast (Ben David 1996), and probably contributes to the large body size attained by coastal brown bears (*Ursus arctos*) and the reproductive success of female bears (Willson and Halupka 1995); other species have not been studied in any detail. Marine-derived nutrients from anadromous fish are moved to terrestrial riparian habitats via feces, discarded carcasses, food caches, and food delivered to nestlings (references in Willson and Halupka 1995; author's personal observations). Marine-derived nutrients can be found in terrestrial riparian vegetation and animals. A major transfer of nutrients from fresh water to land flies in the face of conventional limnological wisdom, judging from an absence of mention in many limnological texts and discussions with several limnologists, and may be detectably significant only in ecosystems in which anadromous fishes provide marine-derived nutrients via freshwater systems. The consequences of such nutrient transfer for the terrestrial food chain have not been explored, although the work of Polis and Hurd (1996) demonstrates that the direct transfer of marine nutrients to terrestrial systems can be significant ecologically. If nutrient transfer from ocean to fresh water to land influences the productivity and population or community biology of organisms in riparian systems, then riparian-zone management practices should incorporate knowledge of the linkage between water and land. Productive riparian zones, for example, might be especially important for the maintenance of local populations of neotropical migrants, and salmon-stream buffer zones, which now are narrow strips of trees sometimes left on the streambanks, might need to be wider to protect terrestrial biodiversity as well. Variation in nutrient input via anadromous fishes could then be a critical element in managing both stream and terrestrial riparian communities.

The dispersion of fish among streams has consequences not only for human subsistence harvesters and terrestrial riparian organisms but also for population viability of the fish. Spatial dispersion can influence variability in performance and therefore susceptibility to fluctuations (Price and Hunter 1995). Streams differ considerably in their vulnerability to anthropogenic disturbances; for example, small streams are more sensitive than large ones to thermal changes induced by removal by tree cover (Halupka and others 1996a). Moreover, a fishery based on mixed stocks, of differing productivity in different streams, will ineluctably impair recovery of less productive stocks and foster overexploitation (Hilborn 1985, Larkin 1977). Thus, the issue of local variations in biology is closely tied to fishery and forestry management practices.

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Salmonid fishes differ in degree of anadromy, age of maturation, frequency of reproduction, body size and fecundity, sexual dimorphism, breeding season, morphology, and, to a lesser degree, parental care. Patterns of variation and their possible significance for ecology and evolution and for resource management are the focus of this review.

Keywords: Salmon, char, *Oncorhynchus*, *Salmo*, *Salvelinus*, life history, sexual dimorphism, age of maturation, semelparity, anadromy, phenology, phenotypic variation, parental care, speciation.

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