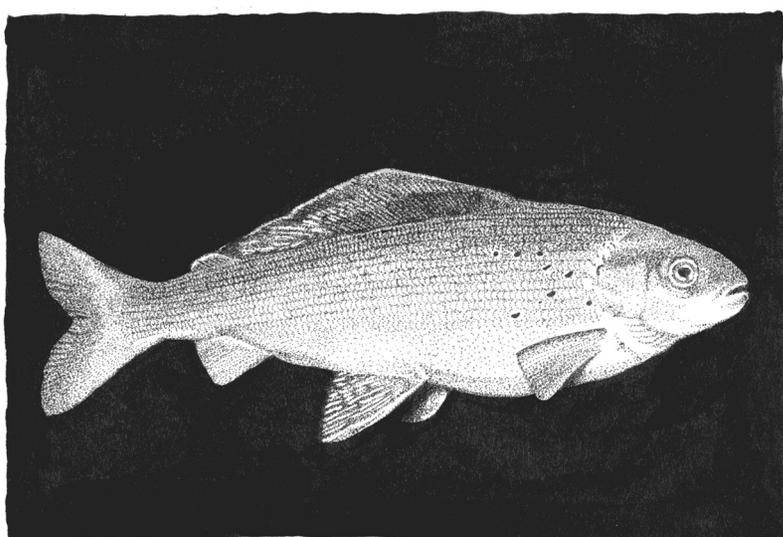


From Macro- to Micro- Evolution

Tempo and Mode in
Salmonid Evolution

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Arctic grayling

7

What are the salient features of salmonid evolution? “Diversity” is perhaps the most obvious, as evidenced by many of the contributions to this book. Moreover, an appreciation of the prevalence and importance of salmonid diversity is reflected in the emphasis placed on protection and management at subspecific levels (Waples 1991a; Ford 2003—*this volume*). However, diversity without pattern can give the impression of chaotic evolution. The aim of this chapter is therefore to interpret the great diversity of salmonids in the context of the evolutionary patterns and processes through which it is generated. This is the domain of tempo (i.e., rate) and mode (i.e., pattern) in salmonid evolution.

G.G. Simpson’s *Tempo and Mode in Evolution* (Simpson 1944) provided the inspiration for this chapter’s title and subject. Although investigations of rate and pattern preceded Simpson’s treatise, his integration of paleontological patterns with genetic principles was a landmark exploration of evolutionary patterns and their driving mechanisms. Simpson, as a paleontologist, focused heavily on apparent discontinuities at higher taxonomic levels (e.g., orders), which he referred to as mega-evolution. Most subsequent studies of tempo and mode have retained this focus on higher taxonomic levels and paleontological data (e.g., Fitch and Ayala 1995). A similar approach is not as tractable for salmon and their closest kin, owing to their taxonomic level (within the family Salmonidae or subfamily Salmoninae) and poor fossil record. Our chapter will therefore focus on lower phylogenetic scales (genera, species, and populations) and on extant evolutionary patterns and processes.

For the sake of expedience, we restrict much of our discussion to Atlantic and Pacific salmon, as well as their closest kin. Like Simpson, our approach is descriptive and logical, as opposed to formally analytical, although we are now afforded with insights drawn from modern methods unavailable in Simpson’s time. We first provide background information on some theoretical aspects of tempo and mode. We next consider a phylogenetic history of salmonids from the standpoint of tempo and mode. We then examine the evolution of intraspecific variation since the last major glaciation, particularly with regard to the diversity of life histories. Finally, we consider contemporary evolution and its relevance to larger phylogenetic and temporal scales.

1. Theory: Tempo and Mode in Evolution

How do differences among species, genera, or families, arise? Are they the result of gradual divergence among lineages accumulating micro-evolutionary changes, or are they the result of dramatic evolutionary innovations during periods of punctuated evolution? The former scenario is expected to reflect natural selection acting on mutations of small effect, and the latter, genetic innovations or dramatic changes in the selective environment. Although arguments in favor of one or the other viewpoint have received considerable attention (e.g., Gould and Eldredge 1977; Stanley 1979; Charlesworth et al. 1982), most evolutionary biologists would now concede elements of both. Adherents to the modern synthesis have built a compelling body of theory and empirical evidence linking the

origin of species (i.e., macro-evolution), to underlying micro-evolutionary mechanisms (e.g., Charlesworth et al. 1982; Schluter 2000). However, a parallel body of literature has added credence to punctuational mechanisms through the evolution of developmental pathways, genes of major effect, and dramatic environmental events (e.g., Schwartz 1999; Jablonski 2000).

Are patterns of evolutionary diversification repeatable? In one scenario, similar selective regimes generate similar evolutionary outcomes (i.e., determinism). In the alternative, a rewinding and replaying of the “tape of life” (Gould 1989) would generate dramatically different outcomes owing to historical contingency. Given the obvious role of chance events in setting the evolutionary stage, a replay of life would certainly not produce an identical result. Still, there can be no doubt that determinism is also very important, as evidenced by numerous cases of parallel and convergent evolution (Losos et al. 1998; Taylor 1999; Schluter 2000; Taylor and McPhail 2000; Gilchrist et al. 2001). Arguments as to which scenario is more important are perhaps akin to arguments of whether the glass is half full or half empty. For example, even the classic examples of convergent and parallel evolution are likely contingent on historical events that exposed organisms with similar evolutionary potential to similar selective factors. In general, we expect that deterministic patterns should be stronger at shallower phylogenetic scales (e.g., populations, species, and genera), where genetic backgrounds and ecological niches are likely more similar. This prediction forms the rationale for our emphasis on convergence, parallelism, and continuity of evolutionary patterns in salmonids, a recently divergent and closely related set of taxa.

In recent years, interest has grown in the observation and experimental study of evolution over contemporary time scales (reviews: Hendry and Kinnison 1999; Kinnison and Hendry 2001; Bone and Farres 2001; Stockwell et al. 2003). Early observations indicated that evolutionary rates over such scales are much greater than those over longer time frames, particularly as revealed in the fossil record (e.g., Reznick et al. 1997). Such observations in turn fostered a renewed interest in the analytical basis for evolutionary rate inferences, and the significance of contemporary evolution to macro-evolution. Hendry and Kinnison (1999) reviewed the use of two evolutionary rate metrics, *darwins* and *haldanes*, for use in studies of contemporary evolution.

$$\text{darwins} = \frac{(\log_p \bar{X}_2 - \log_e \bar{X}_1)}{t}$$

where $\log_e \bar{X}$ is the natural logarithm of the mean trait value at time 1 and time 2 (in the case of a time series for one population, i.e., allochronic) or in population 1 and population 2 (in the case of divergence from a common ancestor, i.e., synchronic), and t is the time interval in millions of years (Haldane 1949).

$$\text{haldanes} = \frac{(\bar{X}_2/S_p) - (\bar{X}_1/S_p)}{g}$$

where \bar{X} is the mean trait value at time 1 and time 2 (or population 1 and population 2), S_P is the pooled standard deviation, and g is the number of generations (Gingerich 1993; see also D'_H in Lynch 1990). When trait variation is expected to scale with the mean, raw data are \log_e transformed to standardize variances.

Hendry and Kinnison (1999) concluded that haldanes are of greater utility to studies of contemporary evolution because: (1) they are dimension-independent, (2) they are applicable to a wider range of data types, (3) they express evolutionary change in generations (which facilitates comparisons among organisms with different reproductive schedules), and (4) they are equivalent to quantitative genetic predictions of evolutionary change. These benefits come at the cost of more parameters to estimate. Generation length can be particularly difficult to estimate but can at least be approximated in most extant organisms (Kinnison and Hendry 2001).

The significance of contemporary evolution can be assessed in the context of several broad questions, listed here in order of increasing complexity. First, do human-induced perturbations, such as translocations or selective harvest, cause substantial evolutionary change in wild populations? Second, are patterns of contemporary evolution consistent with variation among long-established indigenous populations, such as those established after the last glaciation? Third, in what fashion do rates and trends of contemporary evolution contribute to broader scales of diversification? We consider each of these three questions near the end of the following section.

2. Empirical Evaluations of the Theory

2.1. The Phylogeny of Salmon—Intergeneric Scale

The phylogeny of salmonid fishes has been extensively studied using morphological, allozyme, karyological, mitochondrial, and nuclear DNA characteristics, but nonetheless still engenders debates at both shallow (i.e., sister species) and deeper (i.e., sister genera) scales. This uncertainty reflects the group's rich evolutionary history and provides an interesting case study in elucidating pattern and process in taxonomic radiation. A brief review of the generic relations of salmon and their closest relatives (i.e., the subfamily Salmoninae within the family Salmonidae) provides some interesting insights into factors impacting the tempo and mode of evolution. A detailed history of salmonid (Salmonidae) and salmonine (Salmoninae) classification is provided by Stearley and Smith (1993) and Oakley and Phillips (1999) and a table of scientific and common names of the taxa discussed here is provided in Table 7.1. The trees presented in Figures 7.1 and 7.2 represent hypothesized phylogenies based largely on Phillips and Oakley (1997) and Oakley and Phillips (1999) but incorporate considerations from other studies of morphological (Stearley and Smith 1993), allozyme (Osinov and Lebedev 2000), mitochondrial (McVeigh and Davidson 1991), ribosomal (Phillips et al. 1992), and nuclear DNA (Murata et al. 1993) variation.

Table 7.1. Members of the Salmonidae discussed in this chapter, including scientific names, common names, geographic range, and notes on taxonomy and life history (see Stearns and Hendry 2003—*this volume* for a more extensive list).

Scientific name	Common name	Range	Notes ^a
Coregoninae	Whitefishes, ciscoes	N. temperate/polar	Mostly fresh water
Thymallinae	Graylings	Circumpolar	Fresh water only
<i>Thymallus</i> <i>thymallus</i>	European grayling	N. Europe and Asia	
Salmoninae	Salmon, trout, charr, and kin	Circumpolar	Most species capable of tolerating or using marine conditions
<i>Brachymystax</i> <i>Hucho</i>	Lenoks Danube salmon, Taimen, Huchen	Russia E. Europe and Asia	Fresh water only Fresh water only; Huchen perhaps in own genus <i>Parahucho</i>
<i>Salvelinus</i>	Charrs	Circumpolar	Most species capable of diadromy
<i>Salmo</i> <i>S. trutta</i> <i>S. salar</i>	Brown trout Atlantic salmon	Europe N. Atlantic	Often diadromous Usually anadromous
<i>Oncorhynchus</i> <i>O. clarki</i>	Cutthroat trout	W. North America	Diadromous subspecies (<i>O. c. clarki</i>); other subspecies use inland rivers and lakes
<i>O. mykiss</i>	Rainbow trout, steelhead	N. Pacific	Steelhead anadromous; some freshwater forms considered distinct subspecies or species
<i>O. masou</i>	Masu, yamame, or amago salmon	N.W. Pacific	Anadromous individuals are semelparous
<i>O. kisutch</i>	Coho salmon	N. Pacific	Anadromous and semelparous
<i>O. tshawytscha</i>	Chinook salmon	N. Pacific	Anadromous and semelparous
<i>O. nerka</i>	Sockeye salmon	N. Pacific	Anadromous and semelparous, fry rear in lakes
<i>O. keta</i>	Chum salmon	N. Pacific and Arctic Ocean	Anadromous and semelparous, fry migrate immediately to sea
<i>O. gorbuscha</i>	Pink salmon	N. Pacific and Arctic	Anadromous and semelparous, fry migrate immediately to sea

^a Species iteroparous unless otherwise stated.

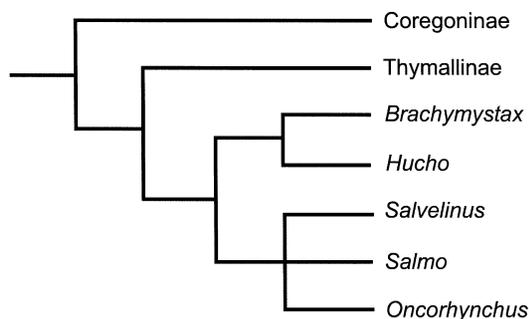


Figure 7.1. Hypothesized family and generic relations of the Salmonidae. Tree based primarily on Oakley and Phillips (1999), Osinov and Lebedev (2000), and Crespi and Fulton (see phylogeny in Stearns and Hendry 2003—*this volume*). The relationship between *Salmo*, *Oncorhynchus*, and *Salvelinus* is drawn as polytomy given that recent work does not support the traditional grouping of *Salmo* and *Oncorhynchus* as sister taxa (instead favoring *Oncorhynchus* and *Salvelinus* as sister taxa).

Total evidence DNA phylogenies are currently being developed (B. Crespi and M. Fulton unpublished), and these should be consulted for the most recent interpretations.

Although formal classification of Atlantic salmon (*S. salar*) and brown trout (*S. trutta*) to the genus *Salmo* dates from Linnaeus, Pacific salmon (*O. gorbuscha*, *O. nerka*, *O. keta*, *O. kisutch*, *O. tshawytscha* and *O. masou*) were only formally renamed to a separate genus (*Oncorhynchus*) in the mid-1800s (Stearley and Smith 1993). Pacific trouts (e.g., *O. mykiss*, *O. clarki*, and others) remained classified in *Salmo* until 1988 when they were reclassified into *Oncorhynchus* in accord with a review by Smith and Stearley (1989). This affinity previously had been recognized by a number of other investigators (e.g., Regan 1914; Rounsefell 1962; Behnke et al. 1962; Tsuyuki and Roberts 1966). Several taxa of uncertain standing, at times referred to as “archaic trouts,” have been problematic and variously included in *Salmo* or separate genera (i.e., *Platysalmo*, *Salmothymus* and *Acantholingua*).

Affinities of the commonly regarded “salmon” clades, *Oncorhynchus* and *Salmo*, relative to other genera of the Salmoninae are also contentious. Until recently, most salmonid biologists would have aligned *Oncorhynchus* and *Salmo* as sister taxa, more distantly related in turn to *Salvelinus* (charr), *Hucho* (huchen and taimen) and *Brachymystax* (lenok). Indeed, a consensus view on the sibling status of *Salmo* and *Oncorhynchus* was likely greater than for any other generic relationship in the Salmoninae. However, this pairing, based initially on multiple morphological analyses, has not been universally upheld by recent molecular analyses. Parsimony analyses of growth hormone introns, ITS1, ITS2, 18s and cytochrome b sequences have provided comparable or greater support for phylogenies pairing *Salvelinus* with *Oncorhynchus* (McVeigh and Davidson 1991; Oakley and Phillips 1999; Crespi and Fulton unpublished, see phylogeny in Stearns and Hendry 2003—*this volume*).

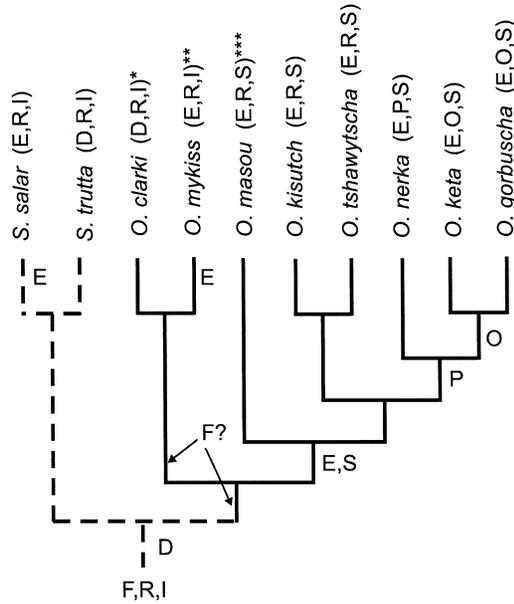


Figure 7.2. Phylogeny and life history of salmon and their congeners. The hypothesized phylogeny is based largely on relationships described in Stearley and Smith (1993), Oakley and Phillips (1999), and Osinov and Lebedev (2000). The dashed branch connecting *Salmo* and *Oncorhynchus* indicates questionable sister taxon status. Life history classifications shown in parentheses next to species names are for populations with access to marine environments and are written in the following order: diadromy type, juvenile habitat, and parity. Abbreviations mapped onto branches indicate hypothesized evolution of life history synapomorphies. Abbreviations: F = freshwater resident, D = facultative diadromy or amphidromy, E = extensive anadromy (with long migration), R = riverine juveniles (territorial), P = pelagic shoaling, O = immediate ocean shoaling, I = iteroparity (potential in all individuals), S = semelparity (in diadromous individuals). Hypothesized life history of the salmonid ancestor is inferred from an outgroup consisting of other Salmoninae (*Brachymystax* and *Hucho*) along with Thymallinae and Coregoninae. Several Pacific trouts (*Oncorhynchus* spp.), regarded as morphologically plesiomorphic, are not shown but are all freshwater resident. Uncertainty about the phylogenetic position of these forms (basal to *O. mykiss*, basal to all Pacific trouts, basal to all *Oncorhynchus*?), and whether their freshwater dependence is vicariant or secondarily evolved, leads to uncertainty about a possible freshwater resident ancestry to all modern Pacific trouts or *Oncorhynchus* (reflected by “F?” on phylogeny). * The life history is for diadromous subspecies *O. c. clarki* (other subspecies restricted to inland freshwater habitats—diadromy in *O. c. clarki* thus possibly secondary). ** The life history is for the “steelhead” form. *** The life history is for diadromous individuals or populations (freshwater resident individuals or populations tend to be iteroparous).

Why have generic relations of the Salmoninae proven so difficult to resolve and what insights may be inferred regarding pattern and process at this scale? First, convergent evolution of form and life history, presumably a deterministic process, may occur even on this scale, thus resulting in a lack of concordance

between some elements of phenotypic and molecular phylogenies. But why have even the molecular phylogenies been so variable and contentious? One possibility is that the Salmonidae (including Salmoninae) experienced a rapid radiation 25–100 million years ago (precise dating is difficult due a poor fossil record). Rapid radiations tend to result in star-shaped phylogenies and “hard” polytomies that are nearly insurmountable for phylogenetic reconstruction (Hoelzer and Melnick 1994). Such phylogenies are known for other taxa that have undergone rapid radiations (e.g., African cichlids—Kornfield and Smith 2000). If this scenario is true, the next logical question is, what evolutionary factors might favor a punctuated radiation of forms?

A tetraploid event (duplication of a diploid genome) that occurred in the ancestors of all Salmonidae has been hypothesized as a factor promoting their diversification (Allendorf and Thorgaard 1984). Tetraploidy is still detectable in the form of duplicate loci for many genes in salmonids, such as growth hormone introns. Under some conditions, duplication of a genome could theoretically allow for an increase in genetic variation and adaptive potential, opening the door for a rapid radiation (Otto and Whitton 2000). Polyploid events are common in plants and may also have contributed to the radiation of all vertebrates and of teleosts (Otto and Whitton 2000). On a scale more comparable to salmonids, polyploidy may underlie the diversity of catostomids (suckers and their relatives, Ferris 1984). However, the sizeable radiations within the subfamilies Salmoninae and Coregoninae (roughly 30 extant species each) have not been mirrored by a similar radiation in their tetraploid kin, the Thymallinae (only a few species). This would suggest that tetraploidy is not the only factor contributing to rapid diversification.

Variability in phylogenetic signal among characters and of rates of evolution among lineages can further complicate phylogenetic reconstruction. The former problem is dramatically exemplified by alternate salmonine growth factor gene introns (GH1C and GH2C). These very closely related genes likely derived from ancestral duplication of a common growth hormone sequence are known to provide different phylogenetic signals (Oakley and Phillips 1999). The latter problem appears in the apparently faster evolution of allozymes in the genus *Oncorhynchus* than in the other genera, violating the assumption of a constant molecular clock. Accordingly, the use of allozymes to calculate genetic distances, assuming constant evolutionary rates, places *Oncorhynchus* at the root of the Salmoninae (Osinov and Lebedev 2000); whereas parsimony analyses of the same data place *Oncorhynchus* as a derived lineage (Osinov and Lebedev 2000).

The challenging intergeneric relations of the Salmoninae suggest potentially complex and intriguing patterns of tempo and mode in their history.

2.2. The Phylogeny of Salmon—Intragenetic Scale

Phylogenies at the intragenetic level of salmon and their closest kin have likewise been extensively debated. However, at this scale we can begin to focus on the evolution of an actual “salmon” life history and the insights it provides into tempo and mode.

Within the subgenus *Oncorhynchus*, *O. masou* have often been considered a sister group to the other Pacific salmon, within which *O. tshawytscha* and *O. kisutch* form one clade, and *O. nerka*, *O. gorbuscha*, and *O. keta* form another (Figure 7.2; Stearley and Smith 1993; Phillips and Oakley 1997). However, *O. masou* are usually neglected in molecular studies and when included occupy variable taxonomic positions (Shed'ko et al., 1996; Oohara et al., 1997; Osinov and Lebedev 2000; Crespi and Fulton unpublished, see phylogeny in Stearns and Hendry 2003—*this volume*). In the following, we adhere to original relationship supported by morphometric and allozyme studies (e.g., Stearley and Smith 1993; Osinov and Lebedev 2000).

The phylogenetic organization of the *O. nerka*, *O. gorbuscha*, and *O. keta* clade has been disputed extensively. Morphological, allozyme, and karyotypic (*O. nerka*, $2N = 56$; *O. gorbuscha*, $2N = 52$; *O. keta*, $2N = 74$) studies usually group *O. nerka* with *O. gorbuscha*, whereas mitochondrial, nuclear, and life history studies suggest an *O. keta* and *O. gorbuscha* sisterhood (Phillips and Oakley 1997; Crespi and Fulton unpublished, see Hendry and Stearns 2003—*this volume*). Observed hybridization between *O. gorbuscha* and *O. keta* led Stearley and Smith (1993) to hypothesize that their mitochondrial affinity may reflect introgressive capture of the mitochondrial genome of one species by the other. Subsequent analyses of additional sequence variation, however, have further supported an *O. gorbuscha/O. keta* clade. Although it may be more parsimonious to conclude that observed hybridization between these species simply reflects their close relatedness, it is worth noting that the introgression hypothesis is not definitively excluded by this outcome. Extensive hybridization could result in similarities in many parts of the genome. Hybridization has also been hypothesized to contributed to the difficulty of phylogenetic reconstruction among charrs of the genus *Salvelinus* (Phillips and Oakley 1997). More generally, hybridization significantly complicates the idealized view of evolution, wherein each species diverges ever further from its sister taxa (Taylor 2003—*this volume*).

Given the recent radiation of the Salmoninae and the subtlety of molecular differences that characterize species, the life history and morphological variation within genera is remarkable. As indicated above, Pacific salmon represent a monophyletic lineage more closely related to Pacific trouts and charrs, than to Atlantic salmon. This relationship provides interesting insights into the origins of life histories. Foremost, the appellations “salmon” and “trout” do not delineate natural phylogenetic groups, and the diversity of anadromous and freshwater life histories is clearly convergent within these lineages. Convergence in turn suggests an element of determinism, mediated most likely by a combination of similar genetic backgrounds and parallel selection. In the following, we consider the divergent and convergent evolution of several life history traits: anadromy versus non-anadromy and semelparity versus iteroparity.

Considerable debate has surrounded whether basal salmonids had a freshwater or marine origin. Accordingly, a number of authors have attempted to map diadromy (migrations between fresh water and the ocean) onto salmonid phylogenies (reviews: McDowall 1988; Stearley 1992; McDowall 2002).

Conclusions vary and McDowall (2002) has recently suggested that the ancestral salmonid was already anadromous rather than strictly freshwater or marine. This seems plausible because diadromy is known in the sister families to salmonids (Osmeridae and Galaxiidae). However, regardless of the life history of the ancestral salmonid, several evolutionary transitions between anadromy and non-anadromy, probably in both directions, have occurred within each lineage.

Given our central focus on “salmon”, we will be concerned with the phylogenetic distribution of “extreme” anadromy, wherein salmon begin life in fresh water but then undergo extensive migrations in marine environments after true smoltification (distinct developmental changes in morphologic, physiologic, and behavior—Folmar and Dickhoff 1980). We use the term extreme anadromy to set this life history apart from facultative marine migrations that are short in duration and distance, and may not be accompanied by as distinct a smoltification process. An examination of salmonid phylogeny suggests that extreme anadromy has evolved independently within *Salmo* and *Oncorhynchus*. Supporting evidence includes the prevalence of less diadromous kin within both genera (Figure 7.2), a lack of similarly extreme anadromy in *Salvelinus*, and limited diadromy in the more distant sister taxa (e.g., *Brachymystax*, *Hucho*, Thymallinae and Coregoninae). The parallel evolution of extreme anadromy seems quite palpable given the prevalence of facultative marine migrations in the other species (Gross 1987; McDowall 1988). If the ancestors of Atlantic and Pacific salmon were already diadromous, then the existence of numerous non-anadromous populations within many species (Hendry et al. 2003b—*this volume*) represents further examples of parallel (within species) and convergent (between species) evolution (discussed below).

The evolution of anadromy/non-anadromy within salmonids appears linked with the evolution of other traits. For example, Stearley (1992) noted a phylogenetic association between the social and migratory behavior of juveniles, ranging from species that show juvenile territoriality and perhaps facultative marine migration after years in fresh water (e.g., coastal cutthroat trout) to others that shoal and migrate to the sea immediately after immergence (e.g., pink and chum salmon, Figure 7.2). Atlantic salmon are in many ways more analogous in many of these life history features to steelhead (anadromous *O. mykiss*) than to the generally regarded Pacific salmon. For example, both have a tendency to enter marine environments after multiple territorial years in fresh water and to then migrate extensive distances at sea (brown trout and most other Pacific trouts migrate only short distances in salt water). Most notably, however, they also share a propensity for iteroparity. We will now turn our discussion to parity and its ties to anadromy and other aspects of life history evolution in salmon.

Semelparity may sometimes seem a discrete genetic innovation but we agree with Stearley (1992) that “the reproductive difference between Pacific salmon species and other *Salmo* and *Oncorhynchus* is one of degree and not one of kind.” Semelparity represents one end of a continuum that is bounded at the other end by substantial iteroparity. Semelparous salmon are predominantly anadromous and common ancestry from a semelparous/anadromous forebear may contribute to this association (McDowall 2002; Figure 7.2). However, extensive marine

migrations associated with anadromy may negatively impact survival and residual reproductive value, thus favoring increasing investment into current reproduction at the expense of post-reproductive survival (see also Schaffer 2003—*this volume*). Indeed, simultaneously considering parity and anadromy in the context of salmonid phylogeny suggests a general association between the traits. Pacific salmon, the most strictly semelparous group, are usually anadromous. One nominative “salmon” species, *O. masou*, occasionally has iteroparous males in the wild but those individuals also tend to be non-anadromous. Other species of *Salmo* and Pacific trouts, such as brown trout and cutthroat trout, are often less extensively anadromous and highly iteroparous. Application of paired contrasts between anadromous and non-anadromous populations within species, to control for phylogeny (Harvey and Pagel 1991), suggest that anadromy is indeed correlated with a lower probability of iteroparity (Fleming 1998).

Given that the evolution of parity may be viewed as a tradeoff between initial and future reproduction, it becomes logical that additional “salmon” traits tied to reproductive investment may be correlated with the evolution of parity. An independent contrasts analysis by Crespi and Teo (2002) confirmed that among iteroparous species the degree of iteroparity is negatively correlated with investment into ovarian mass, suggesting that selection for greater reproductive investment contributes to reduced iteroparity. However, semelparity was associated with a substantial increase in body size and egg size but not in total ovarian mass or egg number (Crespi and Teo 2002). A potential explanation for this result is that the additional reproductive investment associated with the transition from iteroparity to semelparity comes in the form of increased breeding competition (Fleming 1998; Fleming and Reynolds 2003—*this volume*). In support of this view, males of supposedly semelparous species can be functionally iteroparous if freed from some of the metabolic costs associated with breeding. For example, studies on captive chinook salmon have shown that males can mature repeatedly if they are not exposed to salt water, are freed from migration and breeding competition, and are raised on high nutrition diets (Unwin et al. 1999).

Another “salmon” trait potentially tied to semelparity is increased investment into secondary sexual development, particularly hump size and snout size at maturity. Mature individuals with larger humps and snouts generally have increased mating success (Fleming and Reynolds 2003—*this volume*) but may also expend more energy constructing the traits and may suffer increased predation or decreased swimming ability (Blair et al. 1993; Quinn and Kinnison 1999; Quinn et al. 2001a,c; Kinnison et al. in review). Additional trade offs may extend past the breeding season if post-reproductive individuals cannot revert to their original morphology (or if doing so is energetically costly) and if breeding morphology reduces the performance of post-reproductive individuals. Secondary sexual development does seem roughly correlated with parity. Most iteroparous Pacific trout species exhibit minimal secondary sexual trait development, whereas predominantly semelparous Pacific salmon display significant snout and hump development, with the latter reaching a peak in *O. nerka* and *O. gorbuscha*. Interestingly, these two species often experience some of the

highest levels of breeding competition and are invariably constrained to semelparity, even when freshwater-resident.

With only two recognized species, neither fully semelparous, it is more difficult to make phylogenetic comparisons within *Salmo*. Nevertheless, in comparison to Atlantic salmon, brown trout generally show less hump and snout development, and are more often freshwater resident and iteroparous. Furthermore, iteroparity and secondary sexual development covary within Atlantic salmon. Males that mature early in fresh water (mature parr) develop little if any secondary sexual characters and have a greater probability of iteroparity (often later becoming anadromous) than do initially anadromous males (Fleming and Reynolds 2003—*this volume*). These mature parr do not attempt to compete with anadromous males for access to females but instead adopt a “sneaking” tactic (Fleming 1998; Fleming and Reynolds 2003—*this volume*).

Given the likely evolutionary parallels, it is interesting to consider some of the notable species differences. While enhanced secondary sexual trait development seems to be characteristic of both groups of “salmon,” *Salmo* develop an extended lower jaw (mandible) and *Oncorhynchus* an extended upper jaw (maxilla and premaxilla). Furthermore, breeding coloration is a conspicuous element of all salmon mating systems but species color patterns differ extensively, even among Pacific salmon species. Do these variations on a common theme reflect contingency influencing otherwise deterministic patterns of parallel evolution (i.e., the evolution of secondary sexual traits), or adaptive divergence driven by different selective pressures? The former seems more likely, although divergent coloration might also result from selection to avoid hybridization, which now appears to be relatively rare among Pacific salmon species (Taylor 2003—*this volume*). The issue of color variation becomes even more intriguing when one considers the evidence for repeated evolution of a conserved color pattern within a sockeye salmon, as discussed in the next section.

In summary, shared phylogenetic origins have probably contributed to the patterns of life history variation currently found in salmonines. However, parallel and convergent evolution have probably also contributed strongly to the suites of traits found in different species. For example, both *Oncorhynchus* and *Salmo* have species that are predominantly anadromous and semelparous and species that are predominantly non-anadromous and iteroparous. Thus, no matter what their shared ancestral life history, a diversity of convergent life histories arose within each lineage. This diversity appears driven by selection for suites of traits compatible with optimal investment into initial versus future reproduction. This tradeoff seems to have led to a continuum of life history variation bound at one end by nominally “salmon” life histories exhibiting anadromy, semelparity (or low iteroparity) and exaggerated secondary sexual development. The covariance among these traits suggests a degree of determinism in their evolution but subtle variation among species suggests that contingency may also be important.

2.3. Post-Glacial Evolution

The existence of heritable interpopulation variation in salmonid phenotypic traits is incontrovertible. To review all such work is beyond the scope of this chapter and interested readers should refer to work by T. Beacham, C. Foote, B. Jonsson, T. Quinn, B. Riddell, E. Taylor, and others (e.g., Riddell et al. 1981; Beacham and Murray 1989; McIsaac and Quinn 1988; Taylor 1990b; Foote et al. 1992; Jonsson et al. 2001a,b). Furthermore, most salmonid biologists would agree that such differences generally reflect adaptations to local environments (Ricker 1972; Taylor 1991b but see Adkison 1995). Here we consider a few examples of adaptive divergence that relate to one of our recurring themes: determinism versus contingency.

Most modern populations of salmon likely became established in the last 8000–15,000 years. Glaciation prior to this time restricted most salmonids to a limited number of isolated refugia (Hocutt and Wiley 1986; Wood 1995; Bernatchez and Wilson 1998). Following the recession of ice sheets, these refugial populations acted as sources for dispersal and colonization of their current ranges in North America, Asia, and Europe. Although the refugial lineages may have undergone substantial evolutionary diversification prior to and during the most recent glaciation, a significant component of extant interpopulation variation has clearly arisen post-glacially. This scenario of multiple source populations colonizing multiple locations across a diversity of environments allows us to assess whether evolutionary diversification within species is best explained by contingency (e.g., vicariance events and colonization owing to glaciation) or determinism (i.e., natural selection driving parallel, convergent, and divergent evolution). We address this question by examining life history variation in *O. nerka*, *O. tshawytscha*, and *S. salar*.

For our first example, we return to a consideration of anadromy, or more appropriately, the secondary development of non-anadromy. Although Pacific and Atlantic salmon are primarily anadromous, many natural non-anadromous populations also exist and many others have been established by introductions. Even pink salmon, which possess one of the most marine-dependent life histories, have become established in fresh water following accidental introduction to the North American Great Lakes (Kwain and Lawrie 1981). However, only a few species of salmon frequently give rise to freshwater resident populations.

Many freshwater populations of *O. nerka* and *S. salar* have become naturally established following the last glaciation (Hendry et al. 2003b—*this volume*). These freshwater forms are sufficiently divergent from their anadromous counterparts for some taxonomists to consider them separate species or subspecies. Non-anadromous *O. nerka*, called “kokanee,” live their entire lives within lakes in the northwestern United States, western Canada, and northeastern Asia. Natural populations of non-anadromous *S. salar*, often referred to as “land-locked salmon,” are found in northeastern North America (including Lake Ontario) and in northern Europe (Berg 1985). Associated with their freshwater life history, non-anadromous salmon of both species are smaller at maturity than anadromous salmon, but the two forms are outwardly similar in general appear-

ance (Hendry et al. 2003b—*this volume*). Kokanee populations may be found in systems without anadromous sockeye salmon but the two forms are also frequently found in sympatry, often breeding at the same times and places (Taylor et al. 1996; Taylor 1999). Anadromous and non-anadromous Atlantic salmon populations are occasionally found in sympatry but non-anadromous populations are more often “landlocked” above barriers to marine migration (Berg 1985; Hendry et al. 2003b—*this volume*).

Interestingly, analyses of presumed-neutral genetic markers indicate that freshwater populations are often, although not always, reproductively isolated from adjacent or even sympatric anadromous populations (Taylor et al. 1996; Primmer et al. 2000; Tessier and Bernatchez 2000; Hendry et al. 2003b—*this volume*). Furthermore, kokanee are more closely related to sympatric sockeye salmon than to allopatric kokanee (Taylor et al. 1996), a pattern suggesting multiple independent origins of the freshwater form. Multiple independent origins are also likely for different non-anadromous Atlantic salmon populations, which probably arose when migration routes to the ocean were lost through isostatic rebound (Berg 1985). With each independent origin of non-anadromous forms came the repeated evolution of a suite of traits appropriate for a wholly freshwater life history. These traits are related to gill-raker morphology (associated with diet shift), growth rates, development rates, and many others (Wood and Foote 1996; Taylor 1999; Hendry et al. 2003b—*this volume*).

An excellent example of parallel, and probably deterministic, evolution is the ability of kokanee to acquire carotenoids from their carotenoid-poor freshwater diet and to use carotenoids in their characteristic red breeding coloration. Craig and Foote (2001) reared anadromous sockeye salmon and non-anadromous kokanee on similar diets in similar freshwater tanks. At maturity, the skin of the sockeye salmon was considerably less red than that of the kokanee, indicating that kokanee have evolved an improved ability to make use of the carotenoids limited lake environment. Thus, genetic divergence in carotenoid uptake underlies phenotypic convergence of breeding coloration (both forms are red at maturity in the wild). This is thought to have occurred because red coloration is important for mate choice in the breeding system of *O. nerka* (Craig and Foote 2001). Though different freshwater populations likely possess unique adaptations to their respective lake systems, it is noteworthy that, given a similar set of selective conditions and genetic architecture, evolution appears to follow parallel lines. Taylor (1999) reviewed how such multiple independent origins of ecologically similar forms generates an awkward taxonomic and management dilemma.

The parallel (and convergent) evolution of freshwater life histories in salmon raises a series of interesting questions. For example, although freshwater forms are outwardly similar (i.e., phenotypically), did they achieve this similarity in the same way or different ways (i.e., genetically)? Also, it remains to be determined how much variation among independently derived freshwater populations is due to recent adaptation versus historical contingency (e.g., different ancestral lineages). A fascinating test of parallel evolution would be to evaluate the outcome of a novel contact among independently derived freshwater populations. Would kokanee from different lake systems be more likely to select one another

as mates than sockeye from their own lake systems? How would the fitness of hybrids between allopatric kokanee populations compare with the fitness of hybrids between sympatric kokanee and sockeye salmon? Questions such as these are fundamental to tests for the role of natural selection in the evolution of reproductive isolation, a process often called “ecological speciation” (Schluter 2000; Bernatchez 2003—this volume). Specifically, if adaptive divergence is driving the evolution of pre-zygotic reproductive isolation, mating should be more common between similar life history types (even from different systems) than between different life history types (even from the same system). Similarly, if adaptive divergence is driving the evolution of post-zygotic isolation, hybrids between allopatric populations of the same life history type should have higher fitness in nature than hybrids between sympatric populations of different life history types.

But what about contingency or phylogenetic constraints? As an obvious example, many freshwater populations would not have arisen without being isolated from the ocean by chance vicariance events. Another example may perhaps be found in the geographic distribution and phylogenetic relationships of alternative chinook salmon life histories. “Stream-type” populations of chinook salmon in North America migrate to the ocean after a year or more in fresh water, whereas ocean-type populations migrate in their first year of life (Healey 1983). Stream-type populations spawn in the upper reaches of the Fraser and Columbia River watersheds and in coastal rivers farther north (Taylor 1990a; Ford 2003—this volume). Ocean-type populations are found in the Sacramento River, the lower reaches of the Fraser, Snake, and Columbia River watersheds and in coastal rivers south of 56°N (Taylor 1990a; Ford 2003—this volume). Thus, large rivers like the Columbia and Fraser contain populations of both types. Common-garden experiments have revealed that juveniles from ocean-type populations have a genetic propensity to grow faster than juveniles from stream-type populations, and that the two forms have different ontogenetic patterns of aggression, rheotaxis (i.e., response to water flow), and smoltification (Taylor 1990b; Clarke et al. 1992).

We might anticipate that these alternative life histories evolved repeatedly following post-glacial colonization from a single source, in analogy to alternate forms of *O. nerka* and *S. salar*. However, analyses of allozyme variation suggest that the two forms may often represent monophyletic lineages. Stream-type chinook from the upper parts of different river systems in Washington (Myers et al. 1998; Ford 2003—this volume) and British Columbia (Teel et al. 2000; Figure 7.3), for example, are more closely related to one another than they are to ocean-type populations within their own drainages. It thus seems feasible that the two forms arose earlier, were preserved in separate glacial refugia, and by chance recolonized overlapping ranges after glacial recession (Teel et al. 2000; Ford 2003—this volume). It is hence possible that contingency and phylogenetic history have played an important role in generating at least some of the life history variation in salmonids.

Even here, however, some deterministic elements may be at work. For example, the tendency for modern stream- and ocean-type populations to use

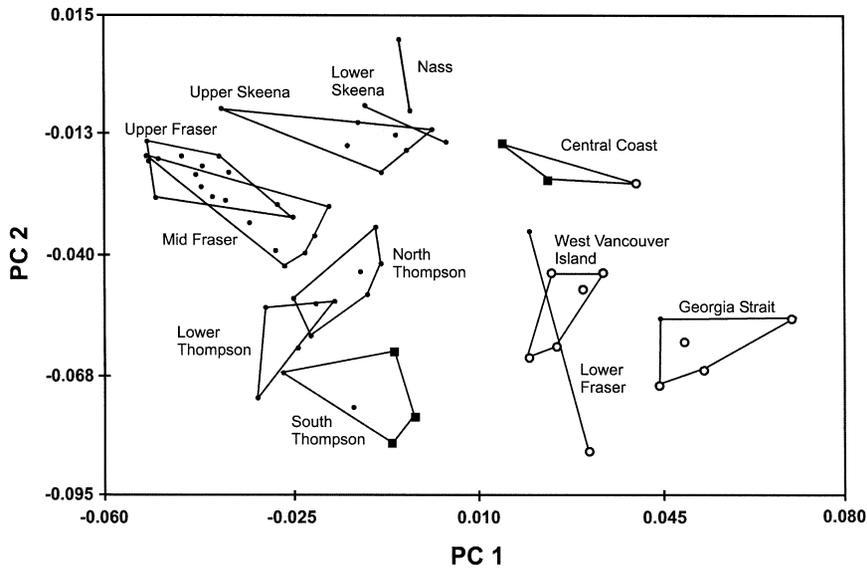


Figure 7.3. Genetic divergence of stream- and ocean-type lineages of chinook salmon as portrayed by mapping life history on to a scatter plot of the first two principal components of allozyme allele variation. Small filled circles = stream type; Large open circles = ocean type; Large filled squares = intermediate (mixed). Note that stream-type populations from the mid and upper Fraser River, and a major tributary of the Fraser (the Thompson) are genetically more similar to stream-type forms from other rivers (i.e., Skeena and Nass) than to Lower Fraser River salmon, which tend to group with nearby ocean-type coastal populations (Central Coast, Vancouver Island, Georgia Strait). A similar pattern is found for chinook salmon from U.S. rivers (see Ford 2003—*this volume*). Modified from Teel et al. (2000).

a characteristic set of habitats may bias the sites they colonize, thus favoring continued selection for the same form. It is also feasible that, had one form or the other not been preserved through the last glaciation, a similar life history would have re-arisen owing to parallel patterns of selection. Indeed, some stream-type populations in the Pacific Northwest appear to be derived from nearby ocean-type populations (Teel et al. 2000; Figure 7.3). Moreover, the presence of individuals with stream-type migratory timing within otherwise ocean-type populations suggests the potential for one form to evolve into the other. Finally, as a prelude to the next section, ocean-type chinook salmon transplanted to New Zealand have established populations with a range of juvenile life histories, including at least one with stream-type characteristics (Unwin et al. 2000).

There is tremendous diversity within all salmon species and many of their salmonine kin. One could likely make numerous further arguments for whether this variation is characterized by determinism or contingency. However, we suggest that such debates would be better supplanted by experiments aimed at using salmon and their kin to explicitly dissect the underlying genetic and selec-

tive bases of parallel evolution and their role in contributing to the cohesion or creation of species. In seeking this goal, investigators may not only find it useful to consider long extant cases of parallelism, but to also consider the early stages of population evolution and how common evolutionary patterns in salmon are initiated. In that spirit we now move on to discussion of tempo and mode of contemporary evolution in salmon and their kin.

2.4. Contemporary Evolution

Relative to rainbow trout, brown trout, and brook charr, introductions of Atlantic and Pacific salmon have been less frequent and less successful (Withler 1982; Lever 1996). The failure of many anadromous populations to become established or remain anadromous may be related to the additional complexity associated with an anadromous life history and a lower probability of obtaining a suitable initial match between genotype and environment (McDowall 1988; Utter 2000). Nonetheless, several notable cases of introduced anadromous populations can be found, and the examination of contemporary evolution in these populations allows a more precise examination of tempo and mode. In the following, we argue that it is at this evolutionary scale that determinism and continuity are most obvious, and that the trends observed in contemporary evolution contribute to long-term population divergence.

Our first example is from sockeye salmon that spawn on lake beaches versus in rivers (or streams). These two “ecotypes” are found within many natural lake systems and seemingly experience very different selective regimes (Wood 1995; Hendry 2001). For example, beach adults experience little water current and face little risk of predation or stranding (i.e., entering water too shallow to swim). Moreover, the nests of river females are much more likely to experience gravel scour that kills incubating eggs and embryos. Accordingly, beach and river populations show phenotypic differences that seem to reflect adaptation to these different environments: males on beaches are deeper bodied for their length, fish in small streams are often very small, and females in large rivers are often large (Blair et al. 1993; Quinn and Kinnison 1999; Quinn et al. 2001a,c). Hendry et al. (2000) used these extant patterns to predict evolutionary divergence between sockeye salmon that colonized a beach and a river after their introduction to Lake Washington (Washington). In accord with natural patterns and expected selective regimes, beach males were deeper bodied than river males and river females were larger than beach females (Hendry et al. 2000b; Hendry 2001). The genetic basis for these adult phenotypic differences is not known but genetic differences have been confirmed for juvenile traits and these appear to reflect adaptation to incubation temperatures (Hendry et al. 1998; Hendry 2001). These adaptive differences appear to have arisen from a common ancestral source in about 13 generations.

Our second example is from chinook salmon introduced to New Zealand (NZ) in the early 1900s (McDowall 1994). From introductions to a single location, populations quickly became established in a number of locations that differ in migratory distance and stream temperature. These environmental factors

should be potent evolutionary forces, suggesting that adaptive divergence should be detectable among the present-day NZ populations. Within the finite energy budget available to maturing salmon, migratory costs may significantly decrease energy stores available for other aspects of reproductive allocation, including gametes, secondary sexual traits, and reproductive behavior (Fleming and Gross 1989; Hendry and Berg 1999). Kinnison et al. (2001; in review) showed experimentally that longer migrations result in a proximate reduction in ovarian investment, secondary sexual trait size, and remaining somatic energy stores. They therefore predicted that longer migrating populations should evolve compensatory patterns of energy allocation favoring investment into features most closely tied to fitness, such as ova production in females and energy for mate competition in males. Common-garden comparisons of short- and long-migrating NZ populations showed that long-migrating females evolved greater investment into ovarian production (Kinnison et al. 2001) and long-migrating males evolved smaller hump sizes that are more efficient for migration (Kinnison et al. in review). Reviews of reproductive investment among North American populations of salmon suggest that analogous migratory costs have been important in shaping natural patterns of reproductive allocation (Kinnison et al. 2001; Crossin et al. in review).

New Zealand chinook salmon also appear to have evolved in response to different temperature regimes and productivity in fresh water. In North America, populations that spawn in warm water tend to mature and spawn later than those that spawn in cold water, a difference thought to synchronize larval development with the seasonal availability of food resources (Brannon 1987). Accordingly, stream-type chinook salmon juveniles from cooler inland streams stay longer in fresh water than ocean-type juveniles from coastal streams, whereas the former have a genetic tendency to grow more slowly (see above). Within NZ, Quinn et al. (2000) found that a population spawning in warmer water had a genetic tendency to return and mature later than a population spawning in colder water. Similarly, juveniles from most NZ populations migrate to the ocean in their first year (ocean-type), whereas those from a particularly cool and low-productivity site stay an additional year in fresh water (stream-type). Longer freshwater rearing in the latter was associated with a heritable tendency for significantly slower growth (Unwin et al. 2000), a result consistent with genetically based growth rates in North American “stream-type” populations.

How do introduced salmon populations, which form under high straying and gene flow, diverge with such apparent speed? The answer is thought to lie in the interplay between adaptation and ecologically mediated reproductive isolation. We suggest the following scenario (see also Hendry et al. 2003a—*this volume*). (1) Natal imprinting rapidly causes some reproductive isolation between newly founded populations. (2) This restriction in gene flow allows some adaptive divergence in response to local environments. (3) This initial adaptive divergence reduces the fitness of individuals that stray between populations. (4) This reduction in the fitness of strays reduces gene flow and allows further adaptive divergence. Steps 3 and 4 then repeat until an equilibrium is reached. Some evidence for this process can be found in studies of introduced

salmon. For Lake Washington sockeye salmon, Hendry et al. (2000) showed that the rate of gene flow between the river and beach populations was much lower than the rate of physical straying by adults, implying the evolution of reproductive isolation as a result of adaptive divergence (see also Hendry 2001). Likewise, juvenile chinook released in their natal stream returned as adults at higher rates than juveniles from another NZ population released from the same site, implying that strays between sites would have lower fitness than locally adapted fish (Quinn et al. 2001b; Unwin et al. 2003). Moreover, Quinn et al. (2000) argued that genetic divergence in spawning time may provide an additional factor contributing to reproductive isolation.

The above studies of introduced salmon suggest that evolution on contemporary time scales may be repeatable and may reflect long-term patterns of population divergence. Such deterministic contemporary evolution may be expected in a variety of other contexts (Reznick and Ghalambor 2001). For example, historical catch records have documented long-term changes in the size and age structure of many salmon populations (Figure 7.4). Some of these changes may be the result of phenotypic plasticity, as implied by their correlations with environmental factors such as sea surface temperature (e.g., Ricker 1981; Cox and Hinch 1997). However, environment/phenotype correlations do not negate the possibility of genetic changes. The most obvious way to determine whether genetic change has occurred would be to rear fish from different years under common conditions, an obviously daunting task. In lieu of this, a variety of evidence suggests that the opportunity for some genetic change exists. First, changes in size and age at maturity have been documented for a great diversity of exploited fish species (e.g., cod and other benthic fishes—Trippel 1995), and some of these changes remain even after correcting for correlated environmental factors (Rijnsdorp 1993). Second, changes in size and age often match those expected from the evolutionary effects of size-selective fisheries. For example, the size and age of European grayling in fresh water has changed in concert with documented patterns of selective fishing (Haugen and Vøllestad 2001). Third, experimental exploitation of Atlantic silversides (*Menidia menidia*) designed to mimic selective fishing resulted in heritable changes in growth-related traits consistent with fisheries trends (Conover and Munch 2002).

Genetic domestication (or “hatchery effects”) represents another example of deterministic contemporary evolution. Artificial propagation in most salmonids uses broadly similar methodology and should therefore impose broadly similar selection, particularly on a genetically similar group of species, such as salmonines. Accordingly, general hatchery effects include changes in age at maturity, size at age, ovarian investment, morphology, behavior (agonistic, territorial, mating), predator avoidance, and fitness (Reisenbichler and Rubin 1999; Heath et al. 2003). Many of these changes in fully captive populations have long been known to have a genetic basis (Green 1952; Flick and Webster 1964). Genetic changes in supplementation programs, where adults are mated in captivity and juveniles released into the wild, are also now firmly established (Reisenbichler and Rubin 1999; Heath et al. 2003; Young 2003—*this volume*). Evidence of fishery and domestication effects is a potent reminder of our own

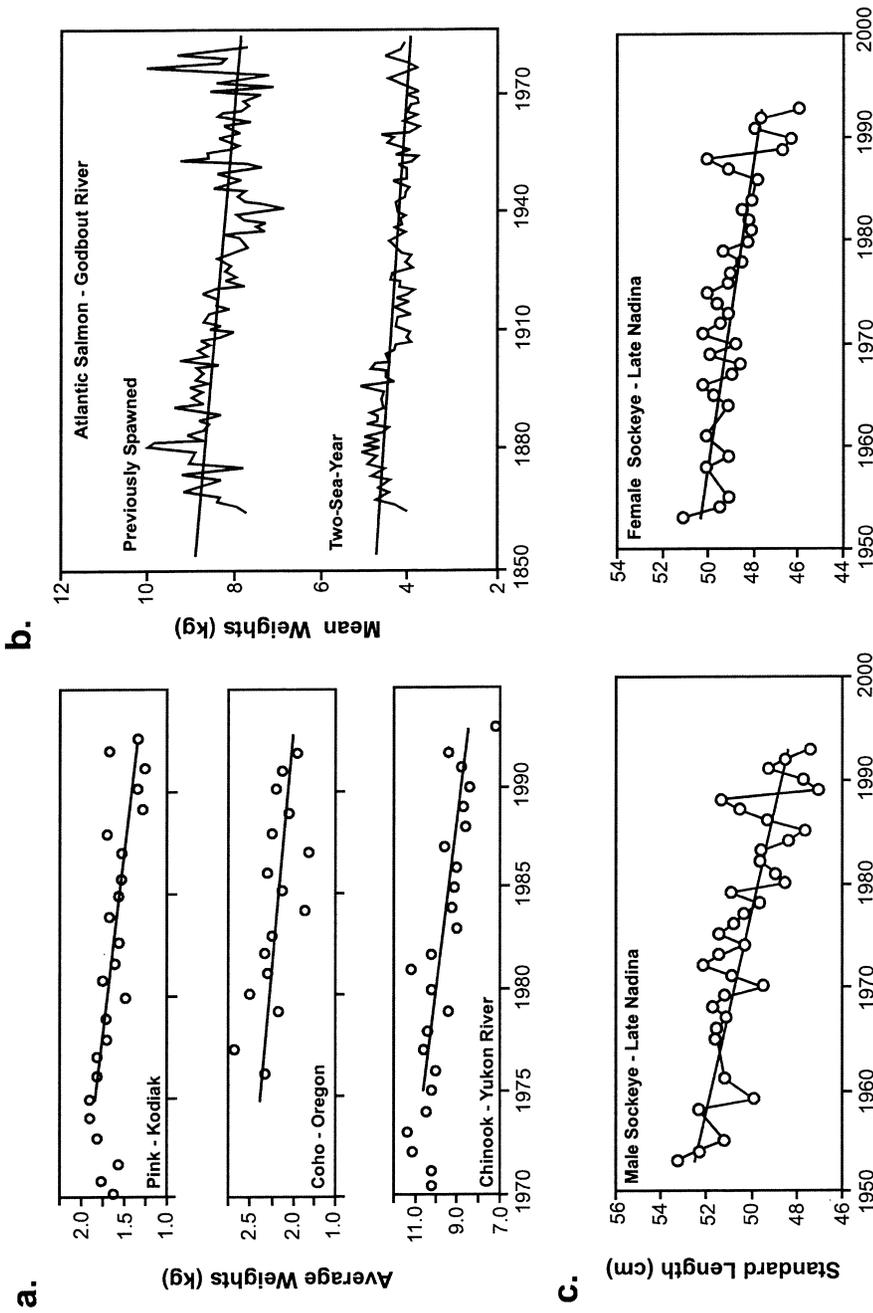


Figure 7.4. Examples of long-term changes in the body size of salmon potentially associated with environmental trends and size-selective fishing. Pink, coho, and chinook salmon data are for both sexes and all ages from commercial fishery catches (Bigler et al. 1996). Male and female sockeye salmon data are for adults measured on spawning grounds (Cox and Hinch 1997). Atlantic salmon data from records of rod catches for fish that spent 2 years at sea before first spawning, and older individuals that had already spawned in previous years (Bielak and Power 1986).

roles in the evolution of life, and indicates the importance of accounting for contemporary evolution in management strategies (Conover 2000; Conover and Munch 2002; Young 2003—*this volume*; Stockwell et al. 2003).

The above evidence clearly shows that contemporary evolution is prevalent in salmon and that it often has a deterministic element. Furthermore, contemporary evolution in wild populations is at least superficially similar to patterns found among indigenous populations. This suggests that contemporary evolution may reveal the seeds of long-term population divergence. In the following, we ask how rates of contemporary evolution in salmon compare with such rates in other “classic” examples of contemporary evolution, and whether such rates are consistent with increasing amounts of divergence over longer evolutionary scales.

Kinnison and Hendry (2001) computed evolutionary rates for salmon populations described in the above studies. Overall, rates of divergence and evolution for introduced and harvested salmon populations fall within the range of rates documented for many other taxa. However, evolutionary rates tend to scale negatively with time interval, largely because of a negative autocorrelation produced by plotting rates, which have time in the denominator, versus time itself. Still, we can draw some meaningful conclusions by examining residuals from a regression through the data. This approach reveals that rates of contemporary evolution in salmon are neither much greater nor much less than the range of rates for other organisms over similar time intervals (Figure 7.5). Salmon evolve just as rapidly as fruitflies (Gilchrist et al. 2001), Galapagos finches (Grant and Grant 1995) or Trinidadian guppies (Reznick et al. 1990), among others.

Although this conformity may imply that salmon have few additional insights to contribute to the field, this is far from the case. Most of the other organisms in which contemporary evolution has been measured have very short generation lengths, live their entire lives in confined habitats, and are often isolated from other conspecific populations. These features should favor particularly rapid adaptive divergence. In contrast, the complex life cycles of anadromous salmon, which span many different habitats, their long generation lengths, and the presence of ongoing gene flow (in Lake Washington and New Zealand) should limit the potential for adaptive divergence. The fact that substantial evolution has occurred, despite these potential impediments, suggests that salmon are actually exceptional in their conformity.

The evidence presented thus far suggests that contemporary evolution is consistent with patterns of diversification among indigenous conspecific populations. But does contemporary evolution actually contribute to macro-evolution (e.g., the origin of new species) and long-term evolutionary diversification? And is evolution punctuated or gradual? Kinnison and Hendry (2001) showed that evidence from salmon (particularly harvested populations) and other organisms suggest that longer time intervals are associated with increasing amounts of divergence. Moreover, the evidence reviewed above suggests that adaptive divergence in salmon contributes to the evolution of reproductive isolation. These results imply that contemporary evolution may contribute to larger changes—perhaps even macro-evolution.

At the same time, contemporary rates of evolution do not appear to persist unabated. Rather, Kinnison and Hendry (2001) found a tendency for the incre-

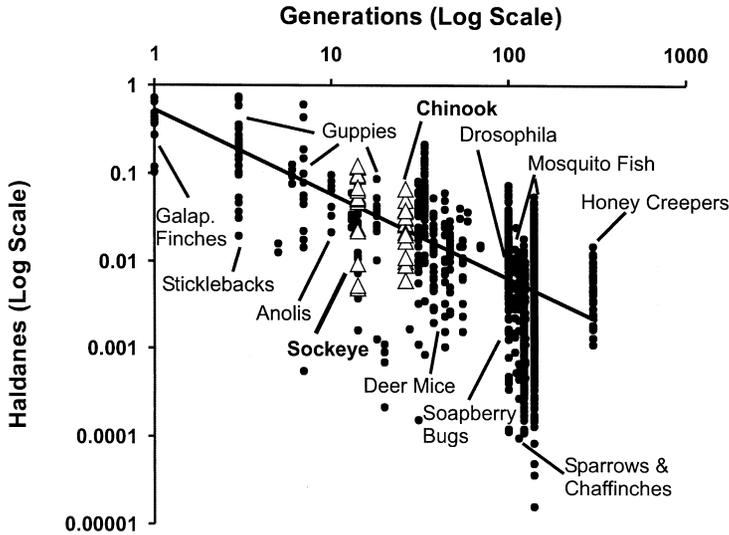


Figure 7.5. Evolutionary rates (haldanes) relative to time interval (generations) for studies of contemporary evolution. A 50% quantile regression line is provided as a standard for judging rates slower or faster than expected on a given time scale. Rates for Lake Washington sockeye salmon and New Zealand chinook salmon are labeled (large open triangles) along with rates for other organisms. Rate estimates include studies based on the measurement of wild individuals (i.e., including genetic and environmental effects on traits) and studies employing a controlled rearing design (i.e., genetic effects). Details of estimation methods and studies included can be found in Kinnison and Hendry (2001).

ment of maximum evolutionary change to decrease with increasing time interval. They suggested that large-scale divergence likely accrues from contemporary evolutionary change in a micro-punctuational pattern of evolution “writ in fits and starts” (Kinnison and Hendry 2001). Unfortunately, few time series of contemporary evolution can be used to evaluate these questions, particularly because it is so hard to confirm that observed changes have a genetic basis. Time series of size and age in exploited salmon populations show little evidence that change is tapering off but the resolution of such time series is limited. Furthermore, harvest could be an unusual selective factor in that anthropogenic selection can remain strongly directional as the population evolves. For example, selective exploitation of the largest fish in a population may continue to target ever smaller fish as the mean size of fish in the population decreases. Harvest, therefore, may not be an apt representation of natural evolutionary processes.

3. Conclusions

We have considered the tempo and mode of salmonid evolution from the level of contemporary evolution within and among populations to the level of diver-

sification among genera. From the standpoint of mode, we find ample evidence of parallel, convergent, and divergent patterns primarily by deterministic natural selection acting on similar genetic backgrounds. Picking apart the relative roles of selection versus genetic background would prove challenging and may be of questionable practical relevance. Most of evolution's experiments in parallel evolution, with salmon or other organisms, involve similar genotypes that often become established in similar habitats, which in turn may be subject to the same sorts of contingent events. By considering tempo and mode in a related group of fishes, we have constrained ourselves to witness a set of evolutionary replicates of only modest genetic or selective independence.

From the standpoint of mode, we find strong evidence for continuity of evolutionary processes from the level of contemporary evolution through to post-glacial diversification. Specifically, patterns of population divergence on contemporary scales fit well with patterns among indigenous populations facing similar environmental conditions. It therefore seems likely that contemporary trends persist and develop to the scale of indigenous population diversity. The detailed pattern of that transition requires more research, but we argue that the pattern is unlikely to be one of complete linear gradualism. Indeed, if contemporary rates were to persist unabated (i.e., perfect gradualism) over even a thousand generations, the resulting phenotypic range would likely be outside the realm of current intraspecific variation. On the other hand, widespread presence of contemporary evolution argues against true "stasis" between large punctuated events. The most logical tempo is hence likely to be one integrating gradual and punctuated patterns. For example, at large time scales, evolution may seem driven by punctuated events that occur owing to dramatic shifts in selective regimes, such as climate change (e.g., glaciation). During the period of environmental change, however, net evolution might appear generally gradual. If one looks with even finer resolution, micro-punctuated events may again be evident within periods of apparently gradual change or stasis, reflecting variable and reversing selective conditions on generational scales.

A critical and yet tractable question of the tempo of population evolution remains to be addressed. How does the magnitude of contemporary divergence compare with the scale of indigenous population divergence measured over similar ranges of environmental conditions? Does divergence over a few decades approach 80% of the mean difference found among post-glacial populations or does it account for less than 20%? The implication of such work could be an appreciation of not only the nonlinear pattern of evolutionary rates, but also a more meaningful understanding of the relative significance of contemporary evolution in shaping modern population diversity.

Translating population-level variation to species-level variation is much more challenging. Although both intra- and interspecific variation in salmonids is extreme, some of the variation among species (e.g., breeding coloration) has seemingly little parallel to variation within those species. This is perhaps not surprising under an assumption that repeatability and determinism are less likely over larger phylogenetic scales. Nonetheless, some traits do seem to show parallel variation within and between species, such as along the iteroparity/semel-

parity continuum and the anadromy/non-anadromy continuum. Furthermore, we have presented evidence that the seeds of processes that contribute to speciation, such as the evolution of reproductive isolation, can be seen acting in the divergence of populations within species.

In closing, we want to emphasize that appreciation of parallelism and continuity of scale in salmon and their kin by no means argues for the redundancy of populations or undermines the value of preserving as much existing diversity as possible. The isolated traits we have emphasized vary overtly among populations in association with easily recognized environmental gradients. This vantage point skims over less overt variation of potentially significant adaptive value, such as resistance to parasites, and over the potential integrated significance of adaptive trait complexes. Likewise, parallel phenotypic evolution does not necessarily dictate parallel genetic change, hence the potential for striking evolutionary convergence suggests that similarities among populations could at times belie critical genetic differences. Modern conservation of salmonids focuses on “evolutionarily significant” groups of populations that are likely to share common ancestry, adaptive features, and migrants (Waples 1991a; Ruckelshaus et al. 2002; Ford 2003—*this volume*; Young 2003—*this volume*). This focus fits well with maintaining the evolutionary processes that likely underlie evolutionary parallelism and continuity in salmonids.

Contemporary evolution in salmon, in particular, has at times been misrepresented as evidence against the need for preservation of indigenous populations. It is thus crucial to note that most attempts to introduce anadromous salmon have failed utterly, suggesting that contemporary evolution may often not even have an opportunity to recapture lost diversity. Furthermore, the evolution observed in introduced populations, although short in evolutionary time, is still very long from the perspective of human interests and we have little insight as to how its magnitude compares with post-glacial divergence. It would almost certainly be much more efficient to preserve existing variation than to attempt to create adapted populations *de novo*. A “fix it later” philosophy may further contribute to complicating factors associated with loss or degradation of habitat. The real implication of contemporary evolution in salmon is that we are indeed preserving an evolutionary “legacy” and not just a collection of interesting but stagnant populations. That legacy not only includes the evolutionary history of populations, but extends from today until extinction. Perhaps the most critical question surrounding tempo and mode is how our contemporary impacts will determine the future legacy of salmonid evolution.

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