To Sea or Not to Sea? Anadromy Versus Non-Anadromy in Salmonids
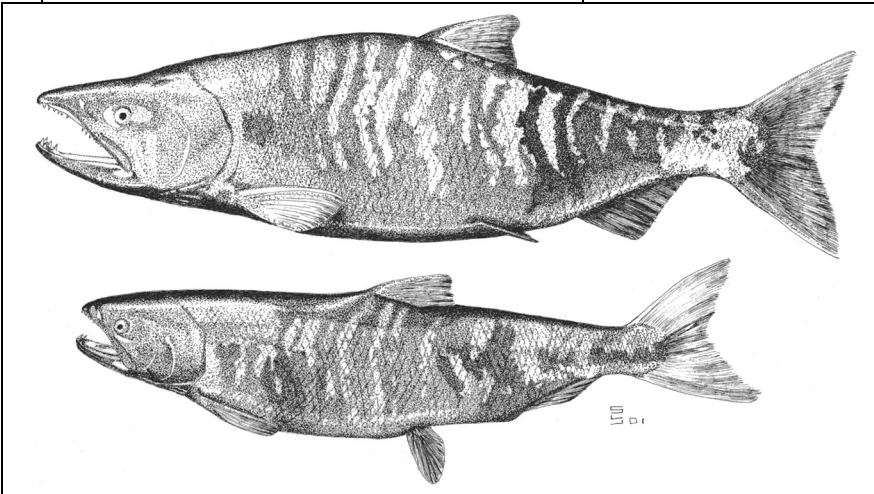
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Male and female chum salmon

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''Migration'' has been defined in many ways with a variety of connotations (Endler 1977; Dingle 1996). Here we follow Endler (1977) in considering migration to be ''relatively long-distance movements made by large numbers of individuals in approximately the same direction at approximately the same time . . . usually followed by a regular return migration.'' This definition is useful because it corresponds to salmonid migrations, and because it explicitly excludes dispersal, which is the subject of another chapter (Hendry et al. 2003a—*this volume*). Breeding often takes place at one terminus of the migration but not the other, and migrations may sometimes be undertaken multiple times over the course of an individual's life. Migratory tendency also varies at multiple levels: among species, populations, sexes, individuals, and years. In this chapter, we use salmonids (primarily salmon, trout, and charr) as a model system for examining evolutionary factors that may generate and maintain this variation.

Variation in migratory tendency is present at many levels in salmonids, making them a good system for examining how, when, and why anadromy/non-anadromy will evolve, as well as how other traits will evolve in parallel. Salmonid migrations take place between a variety of contrasting environments (small streams vs. large rivers, streams vs. lakes, fresh water vs. the ocean) but we focus our analysis on migrations between fresh water and the ocean (''anadromy''; McDowall 1988). In salmonids, anadromy takes the form of individuals that hatched in fresh water migrating to the ocean, and later returning to breed in fresh water. In some instances, individuals may move back and forth between fresh water and the ocean several times in their life, and may enter and leave fresh water without breeding. In contrast, non-anadromous individuals remain their entire life in fresh water. In the present chapter, we typically (but not always) use the terms ''anadromous'' and ''non-anadromous'' rather than ''migratory'' and ''resident'' because the latter terms could also refer to migrations between different freshwater environments.

Whether salmonids had a freshwater or marine origin has long been debated (McDowall 2002), with some evidence suggesting an origin in fresh water (e.g., only some extant populations are anadromous whereas all breed in fresh water) and other evidence suggesting the opposite (e.g., non-anadromous populations seem to be the derived state in many species). Recently, McDowall (2002) has argued that the ancestral salmonid may already have been anadromous. In this chapter, we will not attempt to resolve this debate. Instead, we are interested in how the present diversity of salmonid migratory behavior has evolved. It is thus useful to know if extant anadromous populations can give rise to non-anadromous populations, and vice versa. Shifts from anadromy to non-anadromy are quite common in many species. For example, many of the non-anadromous populations of salmonids in Europe and North America arose after the last glaciation, owing to the colonization of newly exposed areas by anadromous fish (Berg 1985; Wood 1995). Moreover, anadromous salmonids have been transplanted all over the world, frequently giving rise to non-anadromous populations, often (but not always) because access to the ocean is difficult.

Well-documented examples of the opposite shift (from non-anadromy to anadromy) are less common, particularly within the native range of a species.

However, such shifts are physiologically possible because at least some populations that have been in fresh water for thousands of generations retain the ability to osmoregulate in salt water, although usually not as well as ancestral anadromous forms (e.g., Atlantic salmon, Staurnes et al. 1992; kokanee, Foote et al. 1994). Moreover, Foerster (1947) showed that kokanee (the non-anadromous, lake-resident form of *Oncorhynchus nerka*) could successfully undertake an anadromous migration when released at a non-natal site lacking access to a lake. Smolt to adult survival for these kokanee was more than an order of magnitude lower than for sockeye salmon released from the same site but this difference was confounded by different ages (kokanee were older when they returned) and different origins (sockeye were native but kokanee were non-native). Rounsefell (1958) summarizes additional unpublished kokanee release experiments that support Foerster's (1947) results. Finally, non-anadromous forms of some species have adopted anadromy following introduction to sites without native salmonids (e.g., rainbow trout in Argentina: Pascual et al. 2001). The apparent paucity of shifts from non-anadromy to anadromy within the native range of a species may simply reflect the rapid colonization by anadromous fishes of all sites with access to the ocean (e.g., Milner and Bailey 1989; Milner et al. 2000).

Our goal is to interpret variation in anadromy/non-anadromy in the context of "ultimate" considerations (i.e., as a function of relative costs and benefits) rather than proximate considerations (i.e., individual responses to internal and external stimuli). The latter approach is certainly useful (e.g., Thorpe et al. 1998) but is often context-specific and cannot be covered within the confines of the present chapter. In the following, we first outline theoretical expectations that (1) anadromy and non-anadromy have both benefits and costs, (2) anadromy or non-anadromy will increase as its benefits increase or its costs decrease, (3) populations will adapt to anadromy/non-anadromy so as to reduce the proximate costs, (4) populations will offset any proximate costs that cannot be eliminated by compensatory adaptations in other life history traits, and (5) the tendency for anadromy/non-anadromy is likely to be condition-dependent, frequency-dependent, and density-dependent. These expectations are developed in the form of specific, testable predictions. We then outline variation in anadromy/non-anadromy in salmonids, and examine whether this variation supports the predictions. We also identify specific areas requiring further research.

1. Theory

The change in relative fitness conferred by a given behavior (e.g., migration) is determined by the influence of that behavior on survival to maturity, age at maturity, and reproductive output at maturity (extended to multiple reproductive episodes for iteroparous organisms). As we will show, migration has the potential to decrease survival to maturity, which would represent a cost, and increase reproductive output at maturity, which would represent a benefit. Migration might also influence age at maturity, with an increase possibly representing a cost and a decrease possibly representing a benefit. Variation in migra-

tory tendency should therefore reflect its differential benefits and costs under different circumstances. In the following, we outline predictions regarding the benefits and costs of migration, and consider the evolution of migratory tendency as a function of those costs and benefits. Many other predictions could certainly be developed but the ones we present can be tested using salmonids. Although the hypotheses are framed around costs and benefits of migration, specifically anadromy, they could just as easily be reformulated around costs and benefits of non-anadromy. It is not our intention to imply a universal direction of evolutionary transitions between the two life histories.

When considering the fitness consequences of alternative behaviors, it is important to remember that fitness is best interpreted relative to other individuals within a given population or environment, not relative to other populations or environments. Consider an anadromous population in the lower reaches of a river and a non-anadromous population in the upper reaches of the same river. If these two populations are both stable in size, anadromous individuals within the downstream population might be interpreted as having equal fitness to non-anadromous individuals within the upstream population (because an individual in either population produces an average of one offspring that survives to maturity). The more relevant comparison, however, is between anadromous and non-anadromous individuals within each population. If a non-anadromous individual would have lower fitness than an anadromous individual in the downstream population (and vice versa for the upstream population), then the difference in life history between the populations is adaptive.

1.1. Benefits and Costs

Prediction 1

Migration should be beneficial to breeding adults. Benefits of migration may arise when the best breeding habitat is geographically separated from the best non-breeding habitat, or when certain locations are habitable for only part of the year. For example, high latitudes often have high productivity during the summer but low productivity during the winter. Accordingly, many migratory organisms spend their summers at high latitudes and their winters at low latitudes (Dingle 1996). With respect to anadromy, migration may be a way to avoid stressful conditions in fresh water or to take advantage of higher productivity in the ocean. For example, anadromy is rare in tropical regions, where freshwater productivity exceeds ocean productivity, but is common in temperate regions, where ocean productivity exceeds freshwater productivity (Gross 1987; Gross et al. 1988). Greater productivity in the ocean clearly enables higher growth rates, larger size-at-age, and greater energy stores but what remains worthy of testing is whether or not these traits increase reproductive success. This should be the case if anadromy provides an evolutionary benefit.

Prediction 2

Migration should be costly during migration itself. Such costs might include increased mortality or decreased reproductive output and might arise owing to increased energy expenditure, increased stress, increased predation, decreased foraging, or increased risk of not finding a suitable breeding site. With respect to anadromy, each of these costs might come into play. Anadromous individuals swim long distances, which should increase energy expenditure and time investment, and undertake stressful physiological transitions between fresh water to salt water. Anadromous individuals may also experience higher predation if they are exposed to more predators or are less able to avoid them. Anadromy may increase the difficulty of finding natal breeding habitats because individuals must return from the open ocean (McDowall 2001). We will examine these costs by comparing anadromous and non-anadromous salmonids, as well as salmonids that migrate different distances.

Prediction 3

Migration should become less common as its benefits decrease or its costs increase. A major *benefit* of migration should be higher growth opportunity in the ocean than in fresh water, which should translate into greater reproductive output for anadromous individuals. Thus, the tendency for anadromy should be greater as growth rates in fresh water decrease, or as growth rates in the ocean increase. Freshwater productivity will be more informative here because it varies more than ocean productivity across the native range of salmonids. Conversely, a major *cost* of migration should be increased mortality owing to energy loss, stress, or predation. Thus, the tendency for anadromy should be less for populations that would experience more difficult migrations. These predictions can be tested by jointly examining the degree of anadromy/non-anadromy among populations that differ in freshwater productivity (e.g., latitude) and migratory difficulty (e.g., distance or elevation). Another useful approach is to examine inter-annual or interindividual variation in freshwater growth opportunity and migratory tendency. Specifically, non-anadromy should be more common in years and for individuals with higher freshwater growth.

   A more direct but logistically difficult approach is to experimentally manipulate costs and benefits, such as the productivity of fresh water (e.g., through artificial fertilization or reductions in competition) or the difficulty of migration (e.g., by introducing a barrier or increasing mortality rates for migratory fish). In such manipulations, an immediate shift in migratory tendency would reflect an existing reaction norm linking migratory tendency to environmental conditions, where a reaction norm is defined as the phenotypic expression of a given genotype across a range of environments (Schlichting and Pigliucci 1998; Hutchings 2003—*this volume*). Such a reaction norm would likely reflect an adaptive plastic response that evolved to maximize fitness under variable costs and benefits. In contrast, demonstrating an evolutionary change in response to altered costs or benefits would require monitoring migratory tendency over multiple genera-

tions. For example, one might increase and maintain fishing pressure while quantifying how migratory tendency changes through time.

Prediction 4

When costs and benefits of migration differ between the sexes, males and females should differ in migratory tendency (e.g., Adriaensen and Dhondt 1990; Jonsson and Jonsson 1993). In organisms with indeterminate growth, such as salmonids, larger females produce more eggs. The reproductive success of a female should therefore increase with body size, especially when all else is equal (which is not necessarily so—e.g., density dependence). Because anadromy increases body size, it should have strong positive effects on the reproductive success of females. The benefits of anadromy are less concrete for males. A male's success is a function of the number of eggs he fertilizes, which may not be strongly correlated with body size (see below). Moreover, the benefits of large size are often absolute in females (larger females produce more eggs, independent of other females) but relative in males (fertilization success depends on the size, condition, and behavior of other males). As a result, anadromy should be more common for males than for females in populations where only some individuals migrate.

1.2. Evolutionary Compensation

In the strictest sense, the above predictions assume that migratory and non-migratory individuals are similar in all respects, except for those imparted in a proximate sense by migration. It seems likely, however, that when reproductively isolated populations differ in migratory tendency, they should exhibit divergent adaptations that reduce the costs of each life history. If such compensatory adaptation takes place, we might expect the following predictions to be true. Each prediction relates to differences between separate populations, where selection has the potential to drive divergent adaptation. The predictions are not always relevant to migratory versus non-migratory individuals within populations.

Prediction 5

Non-migratory populations should show adaptations that decrease the proximate costs of not migrating. For example, growth opportunities are often lower for non-migratory individuals, and so selection may favor an evolutionary increase in their growth rate under those conditions. This prediction derives from evidence that large size (and hence fast growth) is usually beneficial for survival and reproduction (Arendt 1997; Blanckenhorn 2000). Fast growth in fishes may also carry some costs, such as reduced strength of skeletal elements and scales (Arendt and Wilson 2000; Arendt et al. 2001), reduced swimming ability (Billerbeck et al. 2001), and increased vulnerability to predation (Lankford et al. 2001). However, as long as the costs and benefits do not scale equally with a change in growth rate, a shift in environmental growth potential should favor a

compensatory shift in growth rate. Such adaptation might proceed in two ways (Conover and Schultz 1995; Yamahira and Conover 2002). First, populations might shift their optimal conditions for growth: the peak of the reaction norm linking growth rate to environmental conditions should fall near the average conditions a population experiences in nature (''local adaptation''). Second, populations might change their ''intrinsic'' growth rate: i.e., the elevation of the reaction norm should be higher for populations adapted to environments with lower growth potential (''counter-gradient variation''). These two forms of compensation are not mutually exclusive: both the elevation and the peak of the reaction norm may vary among populations.

Environmental growth potential should be higher for anadromous salmonids, which have access to the productive ocean, than for non-anadromous salmonids. We might therefore predict that populations of the latter will increase their growth rate in fresh water. Ideally, empirical tests for such compensation would raise both forms under a range of environmental growth potentials (e.g., ration, day length, or water temperature), or would perform a reciprocal-transplant experiment. If non-anadromous fish show higher growth rates than anadromous fish under low-growth conditions but not under high-growth conditions, compensation has shifted in the peak but not the elevation of the reaction norm (i.e., local adaptation). If non-anadromous fish show higher growth rates than anadromous fish under all conditions, then compensation has shifted the elevation of the reaction norm but not the peak (i.e., counter-gradient variation). These predictions depend on the assumption that selection acting on size or growth is otherwise identical. One way to reduce possible variation in other factors is to compare genetically distinct anadromous and non-anadromous populations that are in sympatry for much of their life.

Prediction 6

Migratory populations should evolve traits and behaviors that decrease the proximate costs of migration. One approach is to store large amounts of fat, which can then be drawn upon to fuel migration. Another approach is to improve migratory efficiency by taking advantage of prevailing atmospheric winds (in birds and insects) or oceanic currents (in fishes and marine invertebrates; review: Dingle 1996). With respect to anadromy, adaptations that reduce migratory costs might relate to body size (if size influences migratory ability or efficiency), energy allocation (longer migrations should select for increased fat stores), or energy efficiency (longer migrations should select for greater swimming efficiency). For downstream migration, these traits can be compared between sympatric anadromous and non-anadromous populations, or among anadromous populations that vary in migratory difficulty (e.g., distance or elevation). For upstream migration, the comparison of anadromous and non-anadromous populations is not very useful because the traits in question are also influenced in a proximate sense by anadromy: anadromous fish are larger and have greater fat stores. Comparisons of populations that migrate different distances are more useful

but should be made at the start of upstream migration, before migration has had its proximate effect.

Prediction 7

Anadromous populations should have adaptations that reduce the ultimate costs of migration. If increased stress or energy costs associated with migration have the proximate effect of reducing the expression of traits that influence reproductive success (e.g., egg size, egg number, reproductive life span), migratory populations should develop compensatory adaptations in these traits, and any such compensation should be greater for populations that experience greater migratory costs. In testing this prediction, common-garden experiments might be used to compare sympatric anadromous and non-anadromous populations, or to compare anadromous populations that migrate different distances. It is difficult to develop specific expectations for the first comparison because increased relative reproductive output might be predicted for anadromous fish (because of the proximate cost of migration) or for non-anadromous fish (because they have lower absolute reproductive output). For the second comparison, the specific prediction is more clear: populations with more difficult migrations should have a genetic tendency for greater relative reproductive output.

1.3. Other Predictions

Migratory tendency often varies among individuals within populations, and the relative frequency of migration may vary among years and among populations. Several hypotheses have been developed to explain this variation (Figure 3.1). First, migration may be density-dependent. If, for example, survival or growth is negatively correlated with density, increasing migration may be favored with an increase in density or a decrease in environmental quality (Kaitala et al. 1993). Interestingly, an increase in emigration will also benefit the remaining non-migrants through reduced competition. With respect to anadromy, we might predict that (1) increasing densities of residents at a site will decrease their average fitness and increase their anadromous tendency, (2) freshwater sites with greater carrying capacities will support higher densities of residents, and (3) the degree of anadromy should be positively correlated with the degree to which densities exceed freshwater carrying capacity. Density dependence may also have self-reinforcing effects on anadromy: an increase in the frequency of anadromy at a specific site may result in greater egg density, which should increase competition among juveniles and thereby favor anadromy to an even greater degree.

Second, migration may be frequency-dependent, wherein the relative fitness of a particular life history decreases as its relative frequency increases (Lundberg 1988; Figure 2.1). This might occur, for example, if migrants and non-migrants use alternative reproductive behaviors that are most successful when rare. With respect to anadromy, we might expect to see negative frequency dependence in
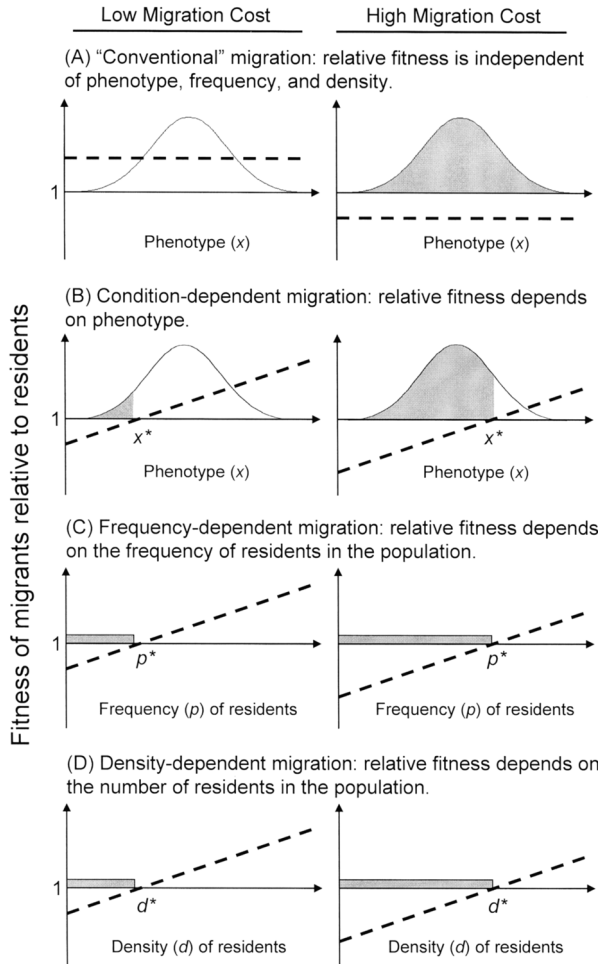
Figure 3.1. A graphical representation of how the evolution of migration may depend on migratory costs, individual phenotypes, and the density and frequency of non-migrants (residents). The cost of migration is shown in each panel by the dashed line, which represents the fitness of migrants relative to residents. Migration has a low cost (e.g., short distance) in the left column and a high cost (e.g., long distance) in the right column. Gray shading shows where residency should predominate and the absence of gray shading shows where migration should predominate. In Panel (A), the relative fitness of migrants is independent of phenotype, frequency, and density. The population is represented as a normal distribution of phenotypes taking the value x. The entire population should migrate when costs are low and not migrate when costs are high. In Panel (B), the relative fitness of migrants depends on their phenotype. Selection favors migration above some threshold phenotypic value (x^*) and residency below that value. Increasing migratory costs increase the threshold value, leading more of the population to remain resident. In Panel (C), the fitness of migrants depends on their frequency relative to residents (p). The equilibrium frequency of residents in the population (p^*) should occur where residents and migrants have equal average fitness. In Panel (D), the fitness of residents depends on their density, and migration should occur when densities exceed d^*. These are simplified representations because the different factors may act together and the two tactics need not have equal average fitness (see text).

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the mating success of anadromous males, which are large and typically fight for positions near breeding females, relative to non-anadromous males, which are small and typically act as ''sneaks'' during oviposition (Myers 1986; Hutchings and Myers 1994). If so, we might predict that (1) the average relative fitness of each life history will be highest in years when its relative frequency is lowest, and (2) an increase in the relative frequency of one life history will lead to a corresponding decrease in that life history in the next generation (assuming they are at least partially heritable). In testing this last prediction, it is important to also consider environmental factors (e.g., productivity) that have proximate effects on life history.

Third, migration may depend on an individual's phenotype, variously called its ''condition,'' ''status,'' or ''state.'' For instance, the relative costs and benefits of migrating may depend on an individual's age, sex, size, energy stores, or social status (Lundberg 1988; Adriansen and Dhondt 1990). With respect to anadromy, predictions will be context-specific. For example, larger individuals may become anadromous because they are (1) closer to the asymptotic size in fresh water (Jonsson and Jonsson 1993) or (2) more likely to successfully complete migration (Bohlin et al. 1993). Alternatively, larger individuals, or those in better condition, may become non-anadromous if larger size increases the probability of successfully maturing in fresh water (Thorpe et al. 1998). A complicating factor is that condition dependence probably acts in concert with density dependence and frequency dependence. For example, an increase in density may cause increased migration and the individuals that migrate may be larger or smaller than those that do not migrate.

Two ''tactics'' (in this case, migrate or not) may be maintained within populations through a ''conditional strategy'' (Repka and Gross 1995; Gross 1996; Gross and Repka 1998). According to this theory, the individuals in a population share a genetically based strategy linking an individual's condition (or ''state'') to its choice between alternative tactics. The combination of individual condition and tactic then determine fitness. In the conditional strategy, the two tactics have equal fitness at a specific phenotypic state, or ''evolutionary stable strategy (ESS) switchpoint,'' but they will typically not have equal average fitness (see also Hutchings and Myers 1994). Traditional game theory models would predict that the tactic with lower fitness would be lost from the population but this is not so in the conditional strategy. In the words of Gross and Repka (1998, p. 447): ''The two tactics are regulated by the same strategy genotype, and although individuals compete with each other by using their tactics, the tactics do not compete in an evolutionary sense because they belong to the same conditional strategy. The conditional strategy evolves as a means of maximizing the fitness of the individual, essentially by allowing each individual to maximize its potential among alternative tactics.'' Frequency-dependent fitness may increase stability of the ESS switchpoint but frequency dependence is not necessary for maintenance of the conditional strategy (Gross and Repka 1998). Additionally, density-dependent fitness may influence the location of the ESS switchpoint (Gross 1996).

2. The Salmonid System

Salmonids show great variation in migratory tendency, and thus provide a good system for evaluating the evolution of migration (specifically anadromy), as well as its consequences for other aspects of life history. Differences in migratory tendency among species are substantial (Rounsefell 1958; Kinnison and Hendry 2003—*this volume*). For example, chinook, coho, chum, and pink salmon rarely (if ever) have non-anadromous populations within their native range. In contrast, golden, lake, and bull trout seldom (if ever) have anadromous populations. Other species, such as Atlantic salmon, sockeye salmon, masu salmon, brown trout, rainbow trout, and cutthroat trout have both anadromous and non-anadromous populations. This variation among species is intriguing but difficult to interpret in an adaptive context because it may reflect a strong phylogenetic signature. We therefore concentrate on variation within and among conspecific populations.

2.1. Landlocked Populations (i.e., Isolated Above Barriers)

Many river systems have obvious barriers to anadromous migration (such as waterfalls), and some of these systems have conspecific populations both above and below a barrier. In some cases, substantial genetic differences at allozyme, mtDNA, or microsatellite loci are present between the upstream and downstream populations (e.g., Skaala and Nævdal 1989; Vuorinen and Berg 1989; Appendix 3). These genetic differences presumably reflect mutation and random genetic drift during a period of allopatry caused by the barrier. Such populations also differ phenotypically in ways that reflect the proximate effect of and adaptations to anadromy/non-anadromy (Appendix 3).

  Genetic differences between populations can only be maintained through reproductive isolation. Genetic integrity of landlocked populations is enforced by the physical barrier to upstream movement. Genetic integrity of the downstream populations, however, has the potential to be compromised by individuals that move over the barrier. Thus, reproductive isolation of downstream populations can only be maintained if few individuals actually move over the barrier, or if upstream individuals have reduced reproductive success when breeding in downstream populations. Some populations below barriers are a mix of anadromous and non-anadromous individuals but genetic studies have shown that the two forms are part of a common downstream gene pool, which is distinct from upstream landlocked gene pool (Hindar et al. 1991a; Cross et al. 1992; Pettersson et al. 2001). These results suggest that individuals from landlocked populations do not contribute substantially to downstream populations.

  How do landlocked populations originate? In some systems, areas above barriers may have been colonized by landlocked populations that arose in other systems. This can occur when geological processes cause dramatic shifts in drainage patterns (e.g., ''stream capture''). In other systems, landlocked populations may have arisen directly from anadromous populations within that system. Here is one possible scenario. At the end of the last glaciation, ice receded

from large areas of North America and Europe, opening up new streams to anadromous fishes. These streams were probably rapidly colonized, as has been found for Glacier Bay, Alaska (Milner and Bailey 1989). With time, areas formerly covered by large masses of ice would rise through isostatic rebound, perhaps exposing barriers that had formerly been under the ocean (Berg 1985). These new barriers would progressively isolate upstream areas, making anadromous migrations more difficult. This increasing difficulty would steadily decrease the fitness of migratory individuals and ultimately lead to an evolutionary decrease in their frequency within the population (assuming migratory tendency has a genetic basis—see below).

2.2. Sympatric Populations

Anadromous and non-anadromous populations can sometimes coexist without being separated by a strict physical barrier. A classic example occurs in O. *nerka*, where anadromous sockeye salmon and non-anadromous kokanee co-occur in numerous lake systems around the Pacific Rim (Ricker 1940; Nelson 1968; Wood 1995). In many of these systems, the two forms breed in the same streams at overlapping times, and yet maintain genetic differences at neutral loci and adaptive traits (Appendix 3). At this point, it is important to distinguish between kokanee, which are populations of O. *nerka* that have adapted to life entirely in fresh water, and residual sockeye salmon, which are non-anadromous progeny of anadromous fish (Ricker 1938). Kokanee presumably evolve through residuals but residuals are not specially adapted for freshwater life and show little if any genetic differences from sockeye salmon (Ricker 1940; Krogius 1982). Examples of sympatric anadromous and non-anadromous populations are also found in Atlantic salmon (Couturier et al. 1986; Verspoor and Cole 1989; Birt et al. 1991a, 1991b), rainbow trout (Neave 1944; Zimmerman and Reeves 2000, 2002; Docker and Heath 2003), and brook charr (Boula et al. 2002). Reproductive isolation in these later examples may involve considerable (but not necessarily absolute) spatial and temporal separation during breeding.

   Did currently sympatric anadromous and non-anadromous populations originate in sympatry, or have they come into secondary contact after originating in allopatry? A common way to address this question is to sample populations of both forms within multiple independent systems, and to test whether populations cluster genetically by system (suggesting independent sympatric origins within each system) or by form (suggesting allopatric origins followed by secondary contact). When sockeye salmon and kokanee are analyzed in this fashion, different populations from the same lake cluster together regardless of form, but different populations within lakes cluster by form and not by creek (Foote et al. 1989; Taylor et al. 1996). Most of these lakes were colonized following the recession of glaciers 10,000 years ago, and so it seems that (1) kokanee may be independently derived from anadromous sockeye salmon within each system but (2) may only have arisen once within each system. Unfortunately, a pattern of genetic clustering by system rather than by form could also arise if the two forms originated in allopatry but interbred following secondary contact.

Similarly, a pattern of clustering within lake systems by form rather than by creek could arise if kokanee originated independently in each creek and then interbred with kokanee from other creeks. The genetic data and geological evidence make it most likely that kokanee arose from sockeye salmon independently in many different lakes (Taylor et al. 1996) but it remains unknown whether kokanee had single versus multiple origins within lake systems.

How do anadromous and non-anadromous populations maintain their genetic integrity in sympatry: that is, without a geographic barrier that prevents their mixing? One possibility is that they breed at different times or places. Within the Deschutes River, Oregon, mean breeding date is 9–10 weeks earlier for anadromous steelhead than for non-anadromous rainbow trout, and steelhead tend to breed in deeper water with larger substrate (Zimmerman and Reeves 2000). These differences could cause substantial isolation because even very slight differences in breeding time (a few days) and location (15 m) can greatly reduce mixing within a season (Hendry et al. 1995; see also Quinn et al. 2000). But what about sockeye salmon and kokanee, which often breed in the same locations and at overlapping times (Foote and Larkin 1988; Wood and Foote 1996). In this case, interbreeding is reduced through size-assortative mating (kokanee are much smaller) and perhaps some additional ''form-assortative'' mating (Foote and Larkin 1988). However, kokanee males do sometimes act as ''sneaks'' on anadromous females and likely fertilize substantial numbers of eggs (see below). Thus, we must invoke selection against hybrids or backcrosses to explain the persistent genetic differences. Sockeye salmon and kokanee lack intrinsic genetic incompatibilities (e.g., Wood and Foote 1990) and so postzygotic reproductive isolation must have an ecological basis: that is, hybrids are inferior because they are poorly adapted for either parental environment (Bernatchez 2003—*this volume*). This seems eminently plausible because the two forms differ dramatically in traits that reflect adaptation to their different life histories (Appendix 3).

2.3. Variation Within Populations (Partial Migration)

Some populations with access to the ocean contain a mixture of anadromous and non-anadromous individuals that do not represent distinct gene pools but rather alternative life histories within a common population (Jonsson and Jonsson 1993). Confirmed or putative examples occur in sockeye salmon (Krogius 1982), brown trout (Hindar et al. 1991a; Cross et al. 1992; Pettersson et al. 2001), Arctic charr (Nordeng 1983; Reist 1989), white-spotted charr (Morita et al. 2000), brook charr (Wilder 1952; Jones et al. 1997), and Dolly Varden (Maekawa et al. 1993). Such populations are said to exhibit partial migration (Lundberg 1988; Adriaensen and Dhondt 1990; Jonsson and Jonsson 1993; Kaitala et al. 1993) and are often polymorphic because the two forms differ phenotypically (Jonsson and Jonsson 1997; Appendix 3).

What determines whether or not a particular individual in such populations will migrate to the ocean in a given year? In many systems, individuals that will migrate initially differ from those that will not in phenotypic traits such as size,

growth rate, or energy status (e.g., Rowe et al. 1991; Prévost et al. 1992; Berglund 1992; Bohlin et al. 1994; Rikardsen and Elliott 2000). Opinions vary as to the evolutionary reasons for these differences. Jonsson and Jonsson (1993) suggested that fish will remain in a particular niche until they approach the asymptotic body size in that niche (i.e., until they become growth limited), at which time they either mature or switch to a new niche. The new niche may be new food resources, such as fish, or a new environment, such as the ocean. Based on this logic, downstream migrants may be larger than non-maturing residents because larger fish are nearer their asymptotic size. Variation in growth rate may have related effects: faster growing fish have higher metabolic requirements and so may be selected to undertake niche shifts at smaller sizes (Økland et al. 1993).

Thorpe (1994) has argued that an individual's evolutionary priority is to reproduce in any given year (even their first year of life), and that migration will take place only when energy resources are insufficient to mature. By this logic, "[anadromy] should be viewed as evidence of failure to meet the conditions necessary for maturation as parr in fresh water" (Thorpe 1994). If this is so, why do some fish remain in fresh water and yet not mature in a given year, and why are these fish initially smaller and in poorer condition than those becoming downstream migrants? Perhaps these non-maturing resident fish have not yet become growth limited (Jonsson and Jonsson 1993), or perhaps migration selects for fish that are larger or in better condition. Indeed, size-dependent or condition-dependent survival during downstream migration may be an important reason for when (or if) a particular individual leaves fresh water for the ocean (Bohlin et al. 1993).

2.4. The Genetic Basis for Anadromy/Non-Anadromy

Anadromy/non-anadromy must have a genetic basis if it is to evolve in response to differential costs and benefits. Variation among species clearly has a genetic basis because some species are always anadromous whereas others are always non-anadromous, despite great variation in migratory difficulty and freshwater conditions. For example, chum salmon are invariably anadromous even though some migrate upstream for thousands of kilometers, whereas lake trout are invariably non-anadromous even though some occur very near the ocean. Variation between the sexes within a population presumably also has a genetic basis because they otherwise experience a common freshwater environment. Variation within and among populations within sexes, however, clearly has some environmental basis because it can be influenced by freshwater growth (Krogius 1982; Morita et al. 2000). The challenge is to detect genetic effects against this strong background of environmental influences.

Numerous studies have demonstrated genetic variation in some aspect of migratory behavior. First, adaptive variation in the directional response of juveniles to water current (rheotaxis) clearly has a genetic basis (e.g., Raleigh 1971; Kelso et al. 1981; N. Jonsson et al. 1994b). Second, populations that differ in migratory behavior show genetically based differences in swimming ability. For example, juvenile sockeye salmon are better swimmers than juvenile kokanee

(Taylor and Foote 1991) and juvenile coho from interior populations are better swimmers than those from coastal populations (Taylor and McPhail 1985b). Third, differences in the downstream migratory timing of Atlantic salmon populations has a genetic basis, at least in some cases (Riddell and Leggett 1981; C. Nielsen et al. 2001). Fourth, migrants and non-migrants may differ genetically within populations. For example, residual sockeye salmon in Lake Dal'nee have higher heterozygosities at an allozyme locus ($PGM\text{-}2^* = 62\%$) than do anadromous sockeye salmon (30%), perhaps because of positive associations between heterozygosity, growth, and maturity in fresh water (Altukhov and Salmenkova 1991; Thorpe 1993; Altukhov et al. 2000, pp. 241–242).

Despite the above, explicit tests for the inheritance of anadromy/non-anadromy have been rare and often inconclusive. Some evidence comes from Sr/Ca ratios in otoliths (Rieman et al. 1994; Doucett et al. 1999; Zimmerman and Reeves 2000, 2002). These ratios can be used to (1) identify anadromous and non-anadromous individuals (Sr is more common in salt water), and (2) determine whether or not an individual's mother was anadromous or non-anadromous (Sr/Ca ratios in an otolith's primordia reflect those in the maternal parent). Using this approach in the Deschutes River, Oregon, Zimmerman and Reeves (2000, 2002) found that anadromous steelhead had anadromous mothers and that non-anadromous rainbow trout had non-anadromous mothers. The same was generally true in the Babine River, British Columbia, although some exceptions were found (Zimmerman and Reeves 2000). This approach is informative but cannot by itself reveal the actual genetic basis for anadromy.

An alternative is to use common-garden, release, or transplant experiments. Neave (1944) raised and released the progeny of sympatric anadromous steelhead and non-anadromous rainbow trout into the Cowichan River, British Columbia. He subsequently caught more rainbow trout than steelhead progeny in fresh water, suggesting that the steelhead progeny had left for the ocean. Skrochowska (1969) raised and released the progeny of anadromous brown trout, non-anadromous brown trout, and their reciprocal hybrids. During subsequent recaptures, the progeny of non-anadromous trout were captured migrating to the ocean (likely anadromous) versus in the river (likely non-anadromous) in a ratio of 1.0:14.7. The analogous ratio for the progeny of anadromous trout ranged from 1.0:0.5 to 1.0:5.3, suggesting that the two forms usually bred true. Jonsson (1982) reciprocally transplanted juvenile brown trout between an upstream lake containing a landlocked population and a downstream lake containing an anadromous population. Subsequent recaptures revealed that downstream movement was more common in the anadromous-origin fish than the landlocked-origin fish, regardless of the lake of release. The differences in life history in these systems thus seem to have an at least partial genetic basis. In contrast, Nordeng (1983) raised the offspring of three sympatric forms of Arctic charr (anadromous, large non-anadromous, small non-anadromous) and found that each form readily gave rise to each other form in the hatchery and in the wild. He argued that this result suggested little if any genetic differences between the forms.

The above experiments demonstrate both genetic and environmental influences on migratory tendency, and suggest that these influences may vary among species and populations. One way in which these effects may be integrated is through thresholds for life history transitions. For example, individuals may migrate only when they exceed a threshold body size, energy status, or growth rate during a particular time window, with this threshold potentially varying among populations, ages, and growth rates (Myers et al. 1986; Økland et al. 1993). Alternatively, individuals that surpass a particular threshold may mature in fresh water without migration (see below). Such thresholds may be genetically determined and may vary adaptively among populations and species. For example, where the optimal size for migration is larger, populations should have a higher threshold size for migration. Thresholds may also show adaptive phenotypic plasticity (Hutchings 2003—*this volume*). For example, the optimal size for migration may be smaller (or larger) in years with lower freshwater growth opportunity, and so migration may be induced at a lower (or higher) threshold. A variety of methods have been developed for determining the genetic basis of thresholds (Roff 1997) but these have not yet been applied to anadromy/non-anadromy.

The genetic basis for anadromy is sometimes linked to the genetic basis for early maturity in fresh water (e.g., as mature parr), which is itself influenced by both environmental and genetic effects (Thorpe et al. 1983; Myers et al. 1986; Rowe et al. 1991; Berglund 1992; Prévost et al. 1992). For Atlantic salmon, Thorpe et al. (1998) has argued that the decision to initiate maturation is made in the fall (November) and is based on whether a fish exceeds a threshold condition. A fish then re-examines its condition at the end of the winter (April) and continues toward maturity if it exceeds a new threshold. If individual condition does not exceed the thresholds during both periods, maturation will not take place the following fall. A fish that will not mature in the fall then "decides" to initiate a trajectory toward smolting if it exceeds another threshold in the late summer (August). The decision to initiate the smolting trajectory can then be negated if the fish surpasses a new maturation threshold condition later that same fall (November). In this complex scenario, the genetic basis for anadromy depends on the genetic basis for several different thresholds.

3. Evaluation of the Theories

In the following, we interpret variation in anadromy/non-anadromy as an adaptive response to varying costs and benefits, but we do not intend to imply that all such variation is necessarily adaptive. First, several Pacific salmon species essentially never have non-anadromous forms, and this is probably the result of phylogenetic constraints. These species may have evolved in an environment that strongly favored anadromy, thereby eliminating alleles that would allow non-anadromy. The converse may be true for strictly freshwater populations or species, such as lake trout. Second, landlocked populations often contain some individuals that move downstream over barriers. This behavior is certainly not

adaptive *within* the population because these individuals cannot return to their natal site. Selection should eliminate migratory behavior from such populations and yet it does not always do so. One possibility is that such behavior is maintained by selection for emigration when conditions deteriorate in a local area. In this case, movement over a barrier could be maintained by selection even though crossing the barrier itself is maladaptive.

3.1. Benefits and Costs

Prediction 1

The larger size-at-age and greater energy stores conferred by anadromy should increase success during breeding. For breeding females, the expected benefits of large size are several. First, larger females produce more eggs (Hendry et al. 2001b). For example, egg number averages 3149 for sockeye salmon and 143 for kokanee breeding sympatrically in Takla Lake, British Columbia (Wood and Foote 1996). Second, larger females can acquire and defend preferred nesting sites (Foote 1990), which may increase the survival of their eggs (van den Berghe and Gross 1989). Third, larger females bury their eggs deeper in the gravel (Steen and Quinn 1999), which may protect them from disturbance by other females and by floods. Fourth, larger females produce larger eggs, which produce larger juveniles, which have higher growth and survival (Einum and Fleming 2000b; Einum et al. 2003—*this volume*). Fifth, larger females are preferred by males (Foote 1988), although this is probably a minor benefit because few if any females go without mates. In accord with these expected benefits, several studies of anadromous salmonids have found that female size is positively correlated with estimated reproductive success: coho salmon in the wild (van den Berghe and Gross 1989), coho salmon in stream channels (Fleming and Gross 1994), and Atlantic salmon in tanks (Fleming et al. 1996).

Although large size thus seems to confer an overall benefit to breeding females, some of the above claims are tempered by ambiguities. First, increasing numbers of eggs may increase density-dependent mortality. Second, large eggs and deep burial may actually increase mortality if gravel sizes are fine or dissolved oxygen is low (Hendry et al. 2001b; but see Einum et al. 2002). Third, large females may be at a disadvantage under size-selective predation, such as that imposed by bears in small streams (Quinn and Kinnison 1999; Quinn et al. 2001c). Estimates of reproductive success in the wild hint at such effects. For example, Holtby and Healey (1986, p. 1946) ''were unable to demonstrate that the reproductive success of large [coho salmon] females was consistently higher than that of small females.'' Similarly, Garant et al. (2001) found no significant correlation between female size and the number of offspring produced in Atlantic salmon. We are not aware of any studies directly comparing the reproductive success of anadromous and non-anadromous females within populations.

For breeding males, the expected benefits of large size stem from advantages during intrasexual competition for females: larger males are more likely to be dominant and to maintain positions closest to females (Fleming and Gross 1994;

Quinn and Foote 1994). Moreover, females spawn more quickly when courted by larger males (Berejikian et al. 2000; de Gaudemar et al. 2000b). These advantages should increase the reproductive success of large males but evidence from genetic parentage analyses is ambiguous. For anadromous fish, large males have more offspring than small males in some studies (Schroder 1981; Chebanov et al. 1984) but not in others (Foote et al. 1997; Garant et al. 2001). The ability of small males to fertilize a substantial number of eggs, despite their subordinate status, is due to their adoption of ''sneaking'' behavior, in which they hide near the female and dart in to release sperm at oviposition (Fleming and Reynolds 2003—*this volume*).

In polymorphic populations, dominant males tend to be large and anadromous, whereas sneaking males tend to be smaller and either anadromous or non-anadromous. In genetic parentage analyses comparing anadromous and non-anadromous males at 1:1 ratios, the former typically fertilize more eggs than the latter (Atlantic salmon: 92.5% vs. 7.5%, Hutchings and Myers 1988; 75.3% vs. 24.7%, Morán et al. 1996; 65% vs. 35%, Thomaz et al. 1997). However, a subordinate anadromous male may fertilize even fewer eggs than a non-anadromous male (Martinez et al. 2000). Only if an anadromous male is in a dominant position does his fertilization success seem guaranteed to be greater than that of a non-anadromous male. Adding to this uncertainty, the success of anadromous and non-anadromous males is expected to depend on their relative frequencies (Hutchings and Myers 1994). The mating benefits conferred by large size are thus ambiguous for males, and may be further diminished by size-selective predation, which targets males more strongly than females (Quinn and Kinnison 1999; Quinn et al. 2001c).

Anadromy may increase energy stores in males and females, both absolutely (larger body size) and relatively (greater mass-specific energy). Greater energy stores may then allow the production of more eggs, the construction of better nests, more effective nest defense, and greater competitive ability. In a polymorphic population of brown trout, anadromous fish had 10% greater mass-specific energy stores (lipid content was 40% higher) and anadromous females had a 19% greater gonadosomatic index (Jonsson and Jonsson 1997). Similarly, an anadromous population of brown trout in one stream invested 30–37% of their energy into egg production, whereas those in a nearby non-anadromous population invested only 16–17% (Elliott 1988).

In summary, anadromous salmonids are larger and have more energy than non-anadromous salmonids, which should increase their production of offspring. These benefits are more concrete for females than males but some uncertainty exists even for females. Most importantly, the magnitude of any benefits will depend on specific circumstances, such as the intensity of competition, gravel scour, predation, and the relative frequency of individuals adopting each life history. It is also important to remember that the above benefits apply only during breeding, and that anadromy/non-anadromy will impose other costs and benefits. For example, non-anadromous males are often younger than anadromous males and therefore have a much higher probability of survival to maturity (Hutchings and Myers 1994).

Prediction 2

Potential costs of anadromy may include increased mortality, stress, or energy expenditure during migration. Anadromous salmonids produce many more eggs than non-anadromous salmonids (Appendix 3) and so the former must have higher mortality rates, assuming their population sizes are not increasing at a much higher rate. The critical question thus becomes: when is the higher mortality manifested for anadromous fishes? If it occurs between the time that adults reach their breeding areas and the time that juveniles leave for the ocean, increased mortality is probably just a byproduct of density dependence in fresh water. If, however, increased mortality occurs between the time that juveniles leave for the ocean and the time that adults return to breed, anadromous migrations may impose a substantial cost.

Downstream migrants may suffer increased mortality owing to predation and stress. Predation may be particularly critical because (1) predacious fishes are more abundant lower in stream networks, (2) predators often gather at difficult points along migratory pathways, and (3) migrating salmonids may be less able to escape an attack. Accordingly, the proportion of migrating smolts eaten by predators can be very high: Arctic charr consume up to 66% of the sockeye salmon smolts in the Wood River system (Burgner 1991, p. 58), three fish species consume an average of 14% of the salmonid smolts in a single Columbia River reservoir (Rieman et al. 1991), and sea birds from two colonies consume 15% of steelhead smolts in the Columbia River estuary (Collis et al. 2001). Mortality owing to stress probably occurs because of osmoregulatory challenges associated with the transition from fresh water to salt water. For example, experiments with hatchery fish have shown that such mortality can be high if the fish are not well prepared for the transition (e.g., Staurnes et al. 1993).

Increased mortality probably also occurs during upstream migrations. Some migratory routes are interrupted by waterfalls or other physical obstructions that cause considerable delays. These sites may be attended by congregations of sea lions, seals, or bears that kill substantial numbers of migrants. They may also present insurmountable barriers when environmental conditions are poor (Hinch and Bratty 2000). Increased mortality may also be caused by energy depletion during upstream migration, and this may be manifested even after fish reach their breeding sites. For example, Gilhousen (1990) reported pre-breeding mortality rates of 0–90% (mean annual rates = 3.3–23.7%) for Fraser River sockeye salmon. These are just a few of many examples of how mortality can be high during downstream and upstream migration. We would ideally compare average daily mortality rates for migratory and non-migratory individuals throughout their lives but such comparisons are not currently available. One suggestive result is that iteroparous anadromous fish have lower post-breeding survival than non-anadromous conspecifies (Fleming and Reynolds 2003—*this volume*).

Another cost of upstream migration may be sublethal energy loss that reduces the energy available for egg production, secondary sexual development, or active metabolism during breeding. These costs may be partly offset by the higher energy stores of anadromous individuals but this offset will diminish as

energy costs increase. Such costs have been assessed in several ways. First, somatic energy stores have been compared between the beginning and end of migration. Such methods suggest that sockeye, pink, and chum salmon expend 0.62–1.74 kcal per kg per km. This can represent a substantial cost: Early Stuart sockeye salmon expend 40% of their energy stores during their 1022 km upstream migration (Gilhousen 1980; Brett 1995). Second, ultrasonic telemetry can be used to measure heart rate, which correlates with swim speeds and energy expenditure. Such work has shown that energy use is higher when migratory conditions are less favorable (Rand and Hinch 1998; Hinch and Rand 1998). Third, salmon can be placed in swim chambers to measure energy depletion, oxygen consumption, and critical swimming velocities. Such work has shown that high water velocities lead to higher metabolic rates, greater energy consumption, and increased fatigue (review: Brett 1995). All of these results demonstrate that migration increases energy use per unit time. Migration may also be costly simply because it reduces the time available for other activities, such as foraging and breeding (Hedenström and Alerstam 1998).

Comparisons of energy use among natural populations may underestimate the cost of migration because populations that migrate greater distances may have adaptations that reduce migratory costs (see below). A powerful way to uncover the true cost of migration is through experimental manipulations. Kinnison et al. (2001) generated full sibling families for two populations of chinook salmon, reared them in a common environment to smolting, and then released them from two locations, one requiring a freshwater migration of 17 km (17 m elevation) and the other of 100 km (430 m elevation). When adults returned to the release sites, on which they had imprinted as smolts, those that migrated the longer distance had a 17% reduction in metabolizable energy stores and 13.7% smaller ovaries. The ovary mass was smaller because less energy had been allocated to eggs, which were smaller but not fewer (Figure 3.2). Kinnison et al. (in review) found comparable results for male chinook salmon in the same experiment: lower tissue energy reserves and smaller secondary sexual traits in fish migrating longer distances.

If migration negatively impacts fitness through increased energy costs, populations with more difficult migrations should be compromised for fitness-related traits. Kinnison et al. (2001) provides evidence for this cost because reproductive output (ovarian mass) decreased when migration was experimentally increased. Studies of unmanipulated anadromous populations similarly reveal lower reproductive output when migrations are longer (Beacham and Murray 1993; Healey 2001; Kinnison et al. 2001). A direct test for the negative fitness effects of migration is to ask whether the production of juveniles is lower in populations with more difficult migrations. Indeed, Bohlin et al. (2001) found a negative correlation between elevation and juvenile density in anadromous brown trout. This correlation was most likely the result of variation in migratory effort because juvenile density was not correlated with elevation in non-anadromous brown trout (Bohlin et al. 2001). In summary, numerous lines of evidence demonstrate that anadromous migrations are costly to the individuals that undertake them.
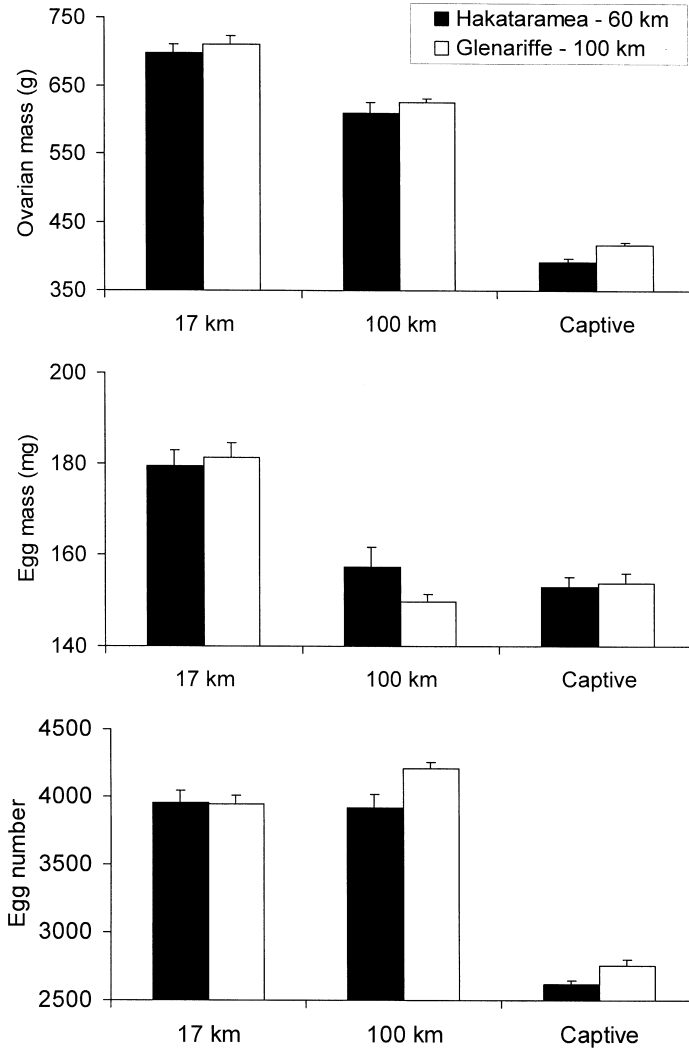
Figure 3.2. Proximate costs of migration on reproductive development, and evolutionary compensation for those costs in chinook salmon (data from Kinnison et al. 2001). Two New Zealand populations that had common ancestors 90 years previously but now migrate different distances (Hakataramea—60 km, Glenariffe—100 km) were compared under common-garden conditions (i.e., their entire lives in a common hatchery environment, ''Captive''), and after returning from the ocean to a site with a short migration (Silverstream—17 km) and a site with a long migration (Glenariffe—100 km). The top panel shows that migration exacted a proximate cost by reducing total ovarian mass (compare ovary mass between the two experimental migration distances) and that the population adapting to longer migrations (Glenariffe) showed an evolutionary compensation by investing more energy in ovaries (compare ovary mass between the two populations under captive conditions). The bottom two panels show that the proximate reduction in ovary mass with increasing migration was the result of decreased egg size but that the evolutionary compensation was an increase in egg number.

Prediction 3

The tendency for anadromy should decrease as its benefits decrease, with the converse true for non-anadromy. The relative benefits of anadromy, and therefore its prevalence, should decrease with increasing freshwater productivity (growth) or increasing migratory difficulty (distance or elevation). This hypothesis might be tested by (1) comparing populations that vary in freshwater growth or migratory difficulty, (2) comparing years that vary in freshwater growth or migratory difficulty, (3) comparing individuals that vary in freshwater growth, or (4) experimentally manipulating freshwater growth or migratory difficulty. In the following, we first present correlative evidence for effects of freshwater productivity, then correlative evidence for effects of migratory difficulty, and finally experimental evidence for the effects of both.

Many studies have examined the relationship between freshwater growth and anadromy/non-anadromy. McGurk (2000) showed that body size and egg number decrease dramatically with increasing latitude in kokanee but not sockeye salmon (Figure 3.3). This shows that the relative benefits of anadromy increase with latitude and lead to the prediction that kokanee should be less common, relative to sockeye salmon, at higher latitudes. No quantitative tests of this prediction have been made but the qualitative evidence strongly suggests just such a trend (Nelson 1968; Wood 1995; McGurk 2000). Trends toward increasing anadromy with increasing latitude have also been noted for other salmonid species (Rounsefell 1958). L'Abée-Lund et al. (1990) studied the incidence of parr maturation in Atlantic salmon populations along the coast of Norway. The proportion of mature parr (relative to all mature males) varied from 0.6–60%, and was positively correlated with the mean length of parr but negatively correlated with mean smolt age. These patterns suggest that higher freshwater growth induces more males to forgo anadromy. Similarly, Myers et al. (1986) found a positive correlation between parr size and parr maturity among populations and among years within populations. Krogius (1982) showed that for cyclically abundant sockeye salmon in Lake Dal'nee, the frequency of residuals was highest in years when juvenile density was lowest and therefore freshwater growth highest. Supporting these among-population and among-year comparisons, many studies have shown that larger individuals or those with higher growth rates, greater energy stores, or better condition are more likely to mature in fresh water (e.g., Rowe et al. 1991; Berglund 1992; Økland et al. 1993; Bohlin et al. 1994).

An apparent contradiction to the above patterns is found in polymorphic Arctic charr, where increased growth in lakes *increases* the tendency for anadromy. In particular, the largest parr within populations tend to become anadromous and the smallest parr tend to remain as residents (Rikardsen and Elliott 2000). Moreover, populations in lakes with higher productivity have a greater propensity for anadromy (Kristoffersen et al. 1994; Rikardsen and Elliott 2000). What might explain this apparent exception to the general rule that high growth in fresh water leads to increased residency? One possibility is that selection strongly favors anadromy (the lakes are at very high latitudes) but also favors
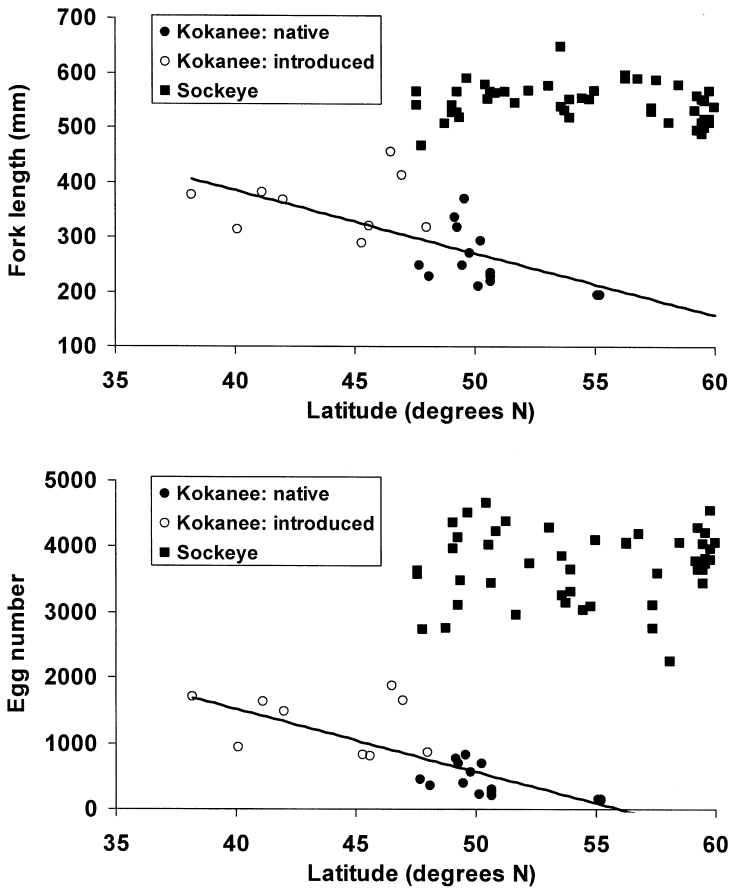
Figure 3.3. Variation in the size (fork length) and egg number (fecundity) of anadromous sockeye salmon and non-anadromous kokanee with latitude in North America (data from McGurk 2000). The top panel shows that fork length decreases with increasing latitude in kokanee ($r^2 = 0.55$, $P < 0.001$) but not sockeye salmon ($r^2 = 0.01$, $P = 0.53$). The bottom panel shows that egg number decreases with increasing latitude in kokanee ($r^2 = 0.63$, $P < 0.001$) but not sockeye salmon ($r^2 = 0.01$, $P = 0.87$). These egg numbers are not corrected for variation in body length among populations but when such a correction is performed, the negative correlation between egg number and latitude actually strengthens ($r^2 = 0.74$, $P < 0.001$). Note that the range of latitudes has been increased by the inclusion of kokanee populations introduced south of their native range.

large migrants. Indeed, the proportion of Arctic charr out-migrants that later return to fresh water is strongly correlated with their size (Finstad and Heggberget 1995; Gulseth and Nilssen 2000). Perhaps the only individuals that remain non-anadromous are those that don't grow large enough to successfully migrate to the ocean.

Several studies have examined among-population correlations between anadromy and migratory difficulty. For northern Arctic charr, Kristoffersen (1994)

showed that anadromy was less common in populations that had more difficult migrations. Similarly, kokanee are more common in interior lakes than coastal lakes (Wood 1995). Bohlin et al. (2001) recently provided a direct test of the hypothesis that variation in anadromy/non-anadromy is influenced by the costs of migration (Figure 3.4). They studied brown trout populations along the southern coast of Sweden that varied in elevation (a surrogate for migratory difficulty) and were either anadromous (migratory) or non-anadromous (resident). Some of the resident populations were isolated above barriers but near the ocean, where migration would have been easy had it not been for the barrier. At low elevations, juvenile density (a surrogate for population productivity) was higher for migratory than non-migratory populations, showing that migration provided positive fitness benefits when its costs were low (Figure 3.5). (Remember that fitness is relative to other individuals in the same population.) Juvenile density then decreased with increasing elevation in migratory but not resident trout, showing that increased migratory costs reduced the fitness benefits of anadromy. At an elevation of about 150 m, juvenile density was similar for migratory and resident populations, suggesting that the benefits and costs of anadromy were approximately equal at this elevation (Figure 3.5). As theory would predict, migration was rare above this elevation (Bohlin et al. 2001; Figure 3.5).

Experimental approaches would seem the most powerful way to test the prediction that variation in anadromy/non-anadromy is a function of relative costs and benefits. Dam construction represents one type of experiment. Morita et al. (2000) studied white-spotted charr populations above and below dams constructed 20–30 years previously. Juveniles below dams were more likely to smolt and migrate downstream than were juveniles above dams. This difference parallels the expectation that an increase in migratory costs causes an evolutionary reduction in anadromy: that is, migrants are lost from above-dam populations. However, Morita et al. (2000) then transplanted fry captured from above and below a dam in one stream to a fishless above-dam site in another stream. The transplanted fish showed very low rates of smolting and emigration regardless of whether they came from the below-dam or above-dam site. This suggested that reduced anadromy in above-dam sites is a phenotypically plastic response to above-dam environments. The factor influencing this response appears to be growth rate: natural juvenile densities were much lower and juvenile growth rates much higher at above-dam sites than below-dam sites. Thus, increasing growth rates in fresh water cause a reduction in anadromy through a reaction norm linking migratory tendency to growth rate.

A second type of experiment is to increase fishing pressure on migrating individuals, which should select for reduced anadromy. This experiment is being conducted in many places around the world (Gross 1991), albeit inadvertently, and the effects have been evaluated in several Russian lakes (English reviews: Altukhov and Salmenkova 1991; Thorpe 1993; Altukhov et al. 2000, pp. 239–240). Fishing pressure dramatically reduced the abundance of adult sockeye salmon over a 40-year period (100,000 to 300 in Uyeginsk; 62,000 to 1600 in Dal'nee). This change was matched within lakes by a decrease in juvenile den-
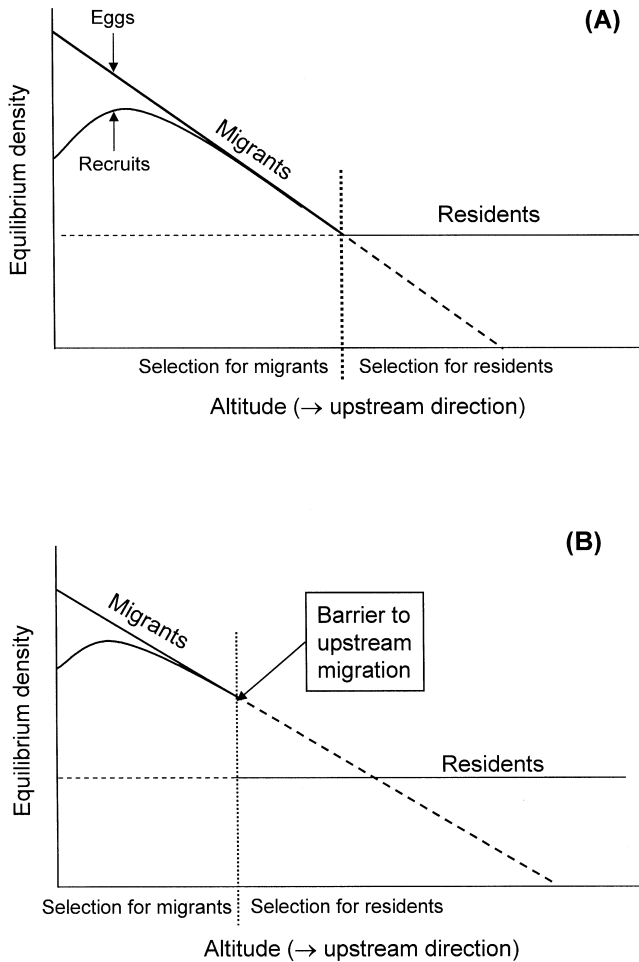
Figure 3.4. Theoretical predictions for the occurrence of anadromy (migrants) and non-anadromy (residents) in relation to migration difficulty (altitude). The equilibrium density of eggs (or recruits) remains constant with altitude for resident fishes because they do not incur any costs from migration (this assumes other factors influencing the equilibrium density do not vary with altitude). In contrast, the equilibrium density of recruits decreases with altitude for migrants because those migrating further distances incur higher costs. Panel (A) shows that migration is expected until the equilibrium density attained by residents exceeds that attained by migrants, after which residents are expected to predominate. Panel (B) shows that a barrier to migration may cause a higher equilibrium density of recruits below a barrier than above it. This figure is modified from Bohlin et al. (2001).

sities, an increase in juvenile growth, and a dramatic increase in the proportion of residuals among adult males (13% to 82% in Uyeginsk; 26% to 92% in Dal'nee). Thus, increases in the costs of anadromy (fishing pressure) and the benefits of non-anadromy (freshwater growth) led to the expected decrease in anadromy
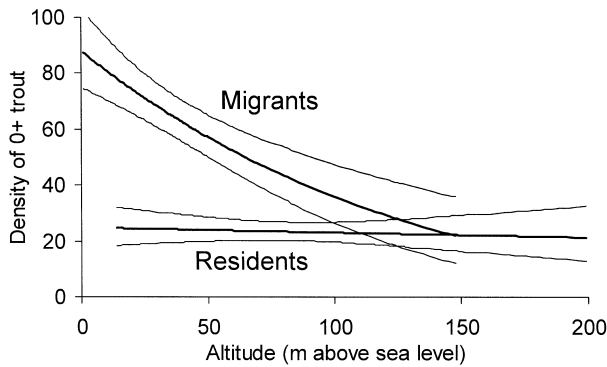
Figure 3.5. Relationship between the density of young-of-the-year (0+) brown trout (per m^2 × 100) in migratory populations and resident populations of brown trout (lines represent regressions with 95% confidence intervals, estimated from raw data). These data are consistent with the predictions outlined in Figure 3.4 that (1) the equilibrium density of recruits should decrease with increasing altitude for migratory populations but not for resident populations, (2) migratory populations should be absent above the elevation where the number of recruits produced by residents is equal to that produced by migrants, and (3) when barriers to migration isolate resident populations at low elevations they will have lower recruitment than migrant populations at similar elevations.

(see also Caswell et al. 1984). Unfortunately, it isn't known whether the changes are phenomenological, phenotypically plastic, or evolutionary. The change could be phenomenological simply because the proportion of residuals among breeding males would decrease as fewer anadromous males returned from the ocean, even if the proportion of residuals among juveniles remained constant. The change could be phenotypically plastic because higher growth rates could mean that more individuals surpass a threshold for maturity in fresh water (see also Myers et al. 1986).

   In summary, a number of studies have shown that anadromy decreases when its costs increase or its benefits decrease. Much of this variation can be explained by a reaction norm linking the tendency to migrate (or not) to some threshold condition influenced by the environment (e.g., growth rate). What remains to be determined is how much of the variation in anadromy/non-anadromy is the result of varying environment conditions along a fixed reaction norm or to genetic variation in the reaction norm itself.

Prediction 4

Anadromy should be more common in females than males. A consequence of anadromy is increased adult size and energy stores, which may provide benefits during breeding. These benefits can be dramatic and absolute for females but subtle and relative for males (see above). Because the benefits of anadromy thus seem greater for females than males, the latter should be more likely to forgo

anadromy at a given level of costs and benefits. In accord with this expectation, males are more likely than females to be non-anadromous in populations with partial migration (Jonsson and Jonsson 1993). For brown trout in 17 coastal streams of Norway, 48.9% of adult males but only 3.7% of adult females were non-anadromous (B. Jonsson et al. 2001a). The difference is even more striking in some Atlantic salmon populations, where all females are anadromous but most breeding males are non-anadromous ''mature parr.'' In the 24 Atlantic salmon populations reviewed by Hutchings and Jones (1998), 0–95% of the adult males were mature parr. In ten populations, more that 50% of the adult males were mature parr (Hutchings and Jones 1998). Residual sockeye salmon are also overwhelmingly males (Ricker 1938, 1940; Krogius 1982). Partial migration is less common in other Pacific salmon species, but when it occurs, it is the males that may forgo anadromy (masu salmon, Tsiger et al. 1994; chinook salmon, Unwin et al. 1999).

3.2. Evolutionary Compensation

Prediction 5

Non-anadromous populations should compensate for the lower productivity of fresh water by evolving faster growth rates. To best test this hypothesis and determine the nature of any observed compensation (local adaptation, counter-gradient variation, or both), we would need multiple common-garden environments or reciprocal transplant experiments that compare fish from sympatric (but genetically distinct) anadromous and non-anadromous populations. No study has yet performed either of these tasks. However, one relevant study has used a uni-directional transplant experiment (Morita et al. 2000) and one has used a single common-garden environment (Wood and Foote 1996). These experiments can be used to test if non-anadromous forms show higher growth rates under the specific experimental conditions but they cannot determine the nature of such compensation.

Morita et al. (2000) studied white-spotted charr populations above and below recently constructed dams (see above). As a part of this work, they collected fry from above and below a dam in one stream and transplanted them to an above-dam site in another stream. Recaptures over the next few years revealed that the below-dam fish grew faster than the above-dam fish. This pattern seems to counter the above prediction that non-anadromous fish should grow faster than anadromous fish. In this particular system, however, it is the above-dam fish that have the higher environmental growth potential in fresh water. This is because above-dam sites have lower charr densities and correspondingly higher growth rates. Thus, populations exposed to different growth conditions have evolved compensatory adaptations in a mere 20–30 years. Interestingly, most of the evolution must have taken place in the above-dam populations (because it was their environment that changed), and it thus represents a reduction in genetically based growth rate. The direction of evolution thus suggests selection against faster growth when environmental conditions

already allow fast growth, supporting the evidence for costs of high growth (see above).

Wood and Foote (1996) sampled adult sockeye salmon and kokanee breeding sympatrically in Narrows Creek, Takla Lake, and generated pure kokanee, pure sockeye, and hybrid crosses. When these crosses were raised under common conditions, pure sockeye were larger than pure kokanee at each of five sampling times (0, 76, 173, 377, and 640 days post-ponding), and hybrids were intermediate for the first four of these times. Similar results were obtained for a different brood year of Narrows Creek fish (Craig and Foote 2001) and for sympatric populations in Shuswap Lake (Wood and Foote 1990). Apparently, non-anadromous kokanee have not evolved higher growth rates than anadromous sockeye salmon, despite the reduced productivity of their environment. Why might this be so? The two sympatric forms share the same lake for the first year or two of life, and feed on the same food items (Wood et al. 1999). However, only juvenile sockeye salmon must subsequently smolt and migrate to the ocean. Perhaps sockeye salmon are under selection for faster growth because large size will increase survival during downstream migration (Wood and Foote 1996). Support for this hypothesis comes from Takla Lake where juvenile sockeye salmon are about 35% longer than juvenile kokanee by the end of their first summer (Wood et al. 1999).

In summary, very few studies have compared the growth rate of reproductively isolated, sympatric anadromous and non-anadromous forms, and those that have find the former have higher growth rates. These results seem to counter the above prediction, but perhaps only because they violate the implicit ''all else being equal'' assumption. Moreover, none of the studies conducted thus far has used an experimental design sufficient to distinguish between local adaptation and counter-gradient variation. This is not surprising because the adaptation of growth rate to environmental conditions has generally proven difficult to demonstrate in salmonids (B. Jonsson et al. 2001b).

Prediction 6

Anadromous populations should have adaptations that reduce the proximate costs of migration. In the following, we first consider adaptations to downstream migration and then upstream migration. Evidence of adaptations to downstream migration come from comparisons of sympatric sockeye salmon and kokanee: the former show greater saltwater adaptability (Foote et al. 1992), are larger at a common age (common-garden: Wood and Foote 1996; wild: Wood et al. 1999), and are better swimmers (Taylor and Foote 1991). Similar differences in saltwater adaptability and juvenile size have been documented between sympatric anadromous and non-anadromous Atlantic salmon populations (Birt et al. 1991b). High saltwater tolerance, large size, and strong swimming are obviously beneficial for fish that must migrate to the ocean. But why have these traits shown an evolutionary reduction in non-anadromous populations? One possibility is that selection in fresh water acts against some of the traits, most obviously physiological changes that prepare smolts for salt water (although some aspects

of smolting may assist life in lakes, Foote et al. 1994). However, it seems less likely that selection in fresh water acts directly against large size and increased swimming ability. Here, the changes in non-anadromous populations may arise because selection favoring these traits is weaker in fresh water. When selection weakens, evolutionary changes can arise if the traits carry some indirect costs, such as those associated with high growth (see above). Alternatively, mutation and genetic drift could cause evolutionary change if population sizes are small and selection is weak (Adkison 1995).

Several adaptive differences have also been documented between anadromous juveniles that must migrate different distances. For example, Taylor and McPhail (1985a,b) used wild individuals, coupled with common-garden experiments, to compare juvenile body shape and swimming performance between coho salmon from coastal streams (short migrations) and interior streams (long migrations). They found that interior juveniles were more streamlined (Taylor and McPhail 1985a) and had greater swimming stamina (Taylor and McPhail 1985b), differences that would assist their long downstream migrations. In short, anadromous populations show a suite of adaptations that seem to reduce the proximate costs of downstream migration. For the rest of this section, we will examine complementary evidence for adaptations that reduce the proximate costs of upstream migration. Here, such adaptations are best revealed by comparing anadromous populations that migrate different distances.

Bernatchez and Dodson (1987) analyzed 15 populations of anadromous fishes (eight were salmonids), and found that populations migrating longer distances were more efficient in their energy use (kJ per kg per km). They also found that the populations most efficient in their energy use swam at the theoretically most efficient speeds. Hinch and Rand (2000) took a closer look at three of the Fraser River sockeye salmon populations, and found that they all swam at the theoretical optimum speed. Hinch and Rand (2000) did find one population (Chilko) that seemed to be ''superoptimal migrators,'' showing the greatest ground speed at a given tail-beat frequency and using the least energy per unit of elevation. This observation supports the prediction that populations with more difficult migrations are more efficient because Chilko is one of the highest sockeye salmon lakes (1158 m) and is reached by a grade (1.9 m per km) more than twice as steep as any other Fraser River population (Gilhousen 1980). Recently, Crossin et al. (in review) found that sockeye salmon populations undertaking more difficult migrations in the Fraser River were considerably more efficient in their energy use. However, more populations must be studied before broad generalizations can be made about correlations between migratory difficulty and efficiency.

What traits might increase migratory ability and efficiency? Increased body size and increased fat stores have been suggested as possibilities. Potential advantages of large size include higher maximum and critical swimming speeds (to overcome obstacles), greater swimming efficiency (to conserve energy), and greater energy stores (to allow longer migrations). However, although fish with longer migrations are larger in some systems (Atlantic salmon: Schaffer and Elson 1975; N. Jonsson et al. 1991a; brown trout: L'Abée-Lund 1991),

they are smaller in others (chum salmon: Beacham et al. 1988a; coho salmon: Fleming and Gross 1989; sockeye salmon: Moore 1996; Crossin et al. in review; Figure 3.6). At present, possible adaptive responses of body size to migration distance are unclear, and may depend on factors that have yet to be considered.

The potential advantage of increased fat stores is increased energy available for migration and breeding. Hendry and Berg (1999) found that a Bristol Bay population migrating only 98 km had considerably less mass-specific fat at the start of migration than did three Fraser River populations that migrate 483–977 km. A similar trend is evident within the Fraser River: fat stores at river entry are higher for longer migrating populations (Gilhousen 1980; Crossin et al. in review). Fat stores at river entry are thus one of the strongest correlates of migration distance, and seemingly reflect adaptation to migration. Another potentially important trait is body shape, with longer migrating populations being more streamlined and having shorter snouts (Fleming and Gross 1989; Blair et al. 1993; Moore 1996; Crossin et al. in review; Figure 3.6).

Prediction 7

Anadromous populations should have adaptations that reduce the ultimate costs of migration (i.e., compensatory increases in reproductive output). The data available to test this prediction are sparse. Only one study has used a common-garden experiment to compare the reproductive output of sympatric anadromous and non-anadromous populations (Wood and Foote 1996). Unfortunately, maturation schedules and sampling dates in that study precluded a direct comparison of reproductive output. Only one study has used a common-garden experiment to compare the reproductive output of anadromous populations that migrate different distances (Kinnison et al. 2001). That study compared ovarian mass, egg number, and egg size (all standardized to a common body size) between two populations of New Zealand chinook salmon that migrate different distances (60 km vs. 100 km) and to different elevations (200 m vs. 430 m). Full sibling families from each population were (1) raised under common conditions in a hatchery, and (2) released as smolts from a location with a long freshwater migration and a location with a short freshwater migration. The authors found evidence of adaptive compensation for the proximate cost of migration: the population from the site with a more difficult migration had larger ovaries under all three treatments (Kinnison et al. 2001; Figure 3.2). This evolutionary compensation was remarkable because the two populations shared common ancestors less than 100 generations previously.

3.3. Other Predictions

Anadromy/non-anadromy may be density-dependent, frequency-dependent, or condition-dependent. The predictions here are more intricate, less well developed, and more difficult to test than those considered thus far, and the relevant data are correspondingly sparse. Here we briefly mention some relevant research and suggest potentially useful comparisons and experiments.
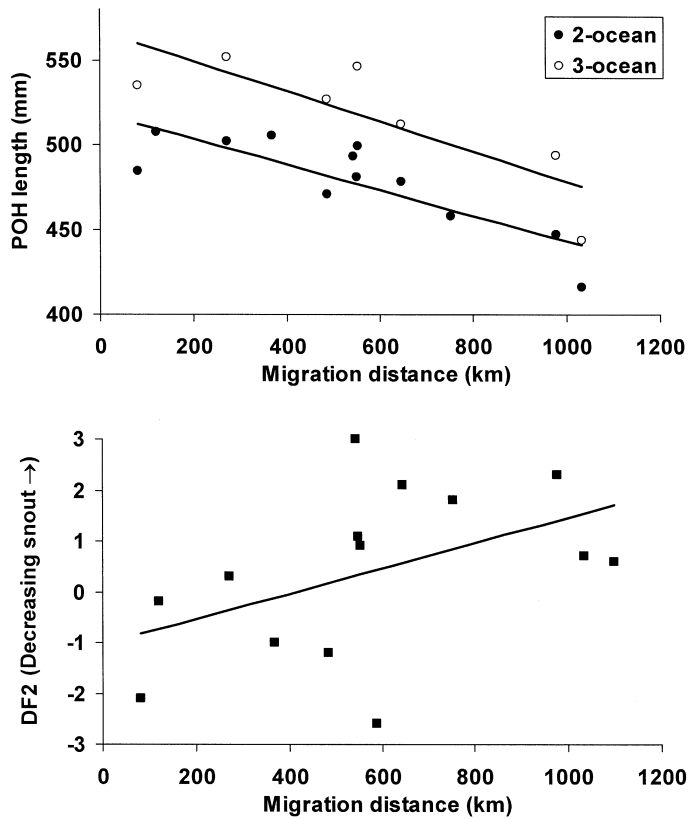
Figure 3.6. Variation in body size and shape among wild Fraser River sockeye salmon populations in relation to their migration distance (data from Moore 1996). The top panel shows variation in post-orbit to hypural (POH) length for adults that spent 2 years in the ocean (2-ocean, $r^2 = 0.68$, $P < 0.005$) or 3 years in the ocean (3-ocean, $r^2 = 0.67$, $P < 0.05$). The bottom panel shows variation in the second discriminant function (DF2) from truss measurements, on which measures of snout length load most heavily ($r^2 = 0.33$, $P < 0.05$).

First, a variety of studies have shown that survival and growth in fresh water are often density-dependent (e.g., Le Cren 1973; Burgner 1987; Jenkins et al. 1999). This suggests that the average fitness of non-anadromous individuals will decrease as they become more abundant, which should increasingly favor anadromy. Moreover, several studies have shown that increasing juvenile densities lead to increasing emigration from stream sections (e.g., Keeley 2001). With respect to anadromy, Morita et al. (2000) showed experimentally that a decrease in juvenile density for white-spotted charr led to an increase in freshwater growth rate and a decrease in anadromy. Similarly, a decrease in the density of juvenile sockeye salmon in lakes caused an increase in growth rate and an increase in the frequency of non-anadromous residuals (effects of cyclical abundance: Krogius 1982; effects of fishing: Thorpe 1993; Altukhov et al. 2000).

These studies demonstrate the existence of a reaction norm linking anadromy to freshwater density, but no studies have demonstrated an evolutionary response to variation in density.

Second, some evidence suggests that frequency-dependent mating success may play a role in the evolution of anadromy/non-anadromy (Myers 1986; Hutchings and Myers 1994). For example, genetic parentage analyses of salmon in experimental arenas have shown that non-anadromous males can fertilize many eggs, even in competition with anadromous males (see above, Fleming and Reynolds—*this volume*). Moreover, the *average* fertilization success of non-anadromous males may decrease as their abundance increases (Hutchings and Myers 1988; Thomaz et al. 1997). Unfortunately, these studies have yet to isolate frequency dependence from density dependence: that is, varying frequencies while holding densities constant. We also need more studies of fish in the wild because experimental arenas may not capture all of the factors influencing reproductive success. The few studies conducted in the wild have found that non-anadromous males can fertilize a substantial fraction of a female's eggs (Jordan and Youngson 1992; Taggart et al. 2001) but have yet to examine effects of frequency on fertilization success.

Third, many studies have shown that anadromy/non-anadromy is condition-dependent. In some systems, the body size of individuals is positively correlated with their likelihood of anadromy (e.g., Bohlin et al. 1994; Rikardsen and Elliott 2000), perhaps because smaller fish are less likely to survive migration (Finstad and Heggberget 1995; Gulseth and Nilssen 2000). In other systems, males that are larger (or faster growing, or higher in fat stores) are more likely to mature in fresh water as parr (Rowe et al. 1991; Berglund 1992; Prévost et al. 1992). Relative to anadromous individuals, these mature parr (1) have phenotypic characteristics suggesting they are of higher quality, (2) have higher survival to maturity (Hutchings and Myers 1994), and (3) are successful in fertilizing at least some eggs when competing with anadromous males (Fleming and Reynolds 2003—*this volume*). These observations suggest that non-anadromy actually has higher average fitness than anadromy (Gross 1996), and that the two life histories may be maintained through a single conditional strategy (Gross and Repka 1998). If this proves true, it calls for a re-examination of earlier analyses that assumed each life history had equal average fitness through frequency dependence (Myers 1986; Hutchings and Myers 1994). However, no studies have yet directly tested for a conditional strategy in salmonids.

To fully evaluate the theories outlined in this section, we really need empirical assessments of lifetime reproductive success (number of grandchildren produced) in nature. Such analyses would ideally examine the success of individuals of different condition (size, growth rate, age, energy stores) that adopt different life histories (anadromy vs. non-anadromy), across a range of densities and frequencies. Although difficult, such studies are feasible because hypervariable microsatellite markers for salmonids should be adequate for parentage (and even grandparentage) assignment in natural populations. Moreover, densities and frequencies of anadromy/non-anadromy vary widely among years within

populations (e.g., sockeye salmon: Krogius 1982; Atlantic salmon: Myers et al. 1986; brown trout: Dellefors and Faremo 1988).

4. Conclusions

We examined evidence that variation in anadromy/non-anadromy is the result of variation in the benefits and costs of these alternative life histories. We find strong evidence that anadromy has both benefits and costs. Benefits come in the form of increased body size and energy stores, which may then increase reproductive success. These benefits tend to be concrete and absolute for females but variable and relative for males. Costs come in the form of increased mortality and increased energy expenditure during migration. These costs and benefits apply in an opposite manner to non-anadromy. Although these general conclusions seem robust, additional work is needed. For example, comparisons of stage-specific rates of mortality between the two life histories would provide a clearer picture of the actual fitness costs associated with migration per se.

Variation in anadromy/non-anadromy should evolve as a function of variation in costs and benefits. For example, the benefits of anadromy are greater for females than for males and, accordingly, males are more likely to forgo anadromy. Among populations, anadromy should decrease with increasing migratory difficulty and with increasing freshwater productivity. These predictions enjoy support from distribution patterns (Rounsefell 1958), direct correlative tests (Kristoffersen 1994; Bohlin et al. 2001), and experimental manipulations (Morita et al. 2000; Altukhov et al. 2000). What remains entirely unknown, is the extent to which variation in anadromy/non-anadromy is the result of phenotypic plasticity or genetic variation. We encourage further quantitative analyses of variation in anadromy with respect to costs and benefits, experimental manipulations of costs or benefits, and comparisons of migratory tendency in common-garden environments.

Evolution should favor adaptations that reduce the proximate costs of anadromy or non-anadromy. One prediction is that non-anadromous populations should have higher genetic growth rates to compensate for the lower productivity of their environment. Evidence for such compensation is currently lacking. In fact, anadromous fish grew faster than non-anadromous fish in a transplant experiment (Morita et al. 2000) and a common-garden experiment (Wood and Foote 1996). Post hoc explanations for these results are that environmental growth potential was actually lower for the anadromous population in Morita et al. (2000) and migration may be size-selective in Wood and Foote (1996). Other predictions are that longer anadromous migrations should lead to the evolution of (1) increased swimming ability (true for juveniles), (2) increased migratory efficiency (perhaps true for adults), (3) larger body sizes (true for juveniles, true for adults in some systems but not in others), (4) greater energy stores (true for adults), and (5) more efficient morphology (true for juveniles, perhaps true for adults).

Evolution should also favor adaptations that reduce the ultimate costs of anadromy or non-anadromy: that is, reproductive output should increase for populations with longer migrations. In the only relevant study thus far, two populations of chinook salmon that differed in migration difficulty showed clear evidence of such compensation: the longer migrating population had greater reproductive output when reared in a common garden (Kinnison et al. 2001). This latter result was remarkable because the two populations had a common origin about 100 years earlier, and because the evolutionary compensation for increased migratory difficulty was through a trait (egg number) that was different from that directly influenced by the proximate cost of migration (egg size).

Anadromy/non-anadromy should be influenced by density, frequency, and condition dependence. Research on these topics is as yet fragmentary but some preliminary generalizations are possible. First, density-dependent survival and growth is common, and can influence emigration from a local area. Moreover, several studies have shown that anadromy may indeed be density-dependent (Krogius 1982; Morita et al. 2000; Altukhov et al. 2000). Second, studies in experimental arenas have suggested that the mating success of anadromous and non-anadromous males may be frequency-dependent, but these have yet to remove potentially confounding effects of density dependence. Third, individual condition may influence migratory tendency in different ways. In some systems, the largest juveniles become anadromous, whereas in other systems, the largest juveniles remain non-anadromous. In any given system, the average fitness of the two life histories may not be equal and instead may be maintained within populations through a conditional strategy (Gross and Repka 1998). Fully testing these hypotheses will require studies of lifetime reproductive success in natural systems.