

The Evolution of Philopatry and Dispersal Homing Versus Straying in Salmonids

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Brown bear feeding on a sockeye salmon

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Many animals reproduce at the same site as their parents, a phenomenon called philopatry. In some cases, philopatry can be the simple result of geographic isolation or limited movement ability. In other cases, philopatry can be strong even when migratory movements take individuals far from their natal site. Thus, we must seek explanations for philopatry through selective factors that favor return to natal sites rather than non-natal sites. The tendency for philopatry in any population or species is balanced to varying degrees by some dispersal to non-natal sites, with some animals showing high philopatry and low dispersal and others low philopatry and high dispersal. Again, some of this variation may be the result of varying isolation or movement ability, whereas some can only be explained through natural selection. Our goal in the present chapter is to use data from salmonids to evaluate theories for how selection might influence the evolution of philopatry and dispersal.

Philopatry can be evaluated at a variety of spatial scales, ranging from precise nest locations to broad geographic areas. We focus on philopatry to spatially discrete locations that are predictably occupied by breeding aggregations. These aggregations often correspond to “populations”: groups of individuals that breed together and are at least partially reproductively isolated from other such groups. By “reproductive isolation,” we here mean that the different groups are not freely interbreeding within or between generations (i.e., not panmictic). Many factors can contribute to reproductive isolation (Dobzhansky 1937; Mayr 1963; Schluter 2000). “Extrinsic” isolation is caused by geographic barriers that severely limit movement between populations. This category does not apply to populations in separate physical locations as long as movement among them remains possible. Extrinsic isolation is of limited interest here because philopatry has been imposed on the organisms rather than evolving in response to selection. “Intrinsic” isolation is caused by features of organisms that limit gene flow between aggregations, even in the absence of strict geographic barriers. Intrinsic isolation can be the result of factors that reduce mating between individuals from different aggregations (“pre-zygotic”) or reduce the success of hybrid progeny after mating (“post-zygotic”). Because philopatry reduces mixing even in the absence of strict geographic barriers, it is an intrinsic, pre-zygotic isolating mechanism.

“Dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate” (Howard 1960). Although this is only one of many possible definitions of dispersal, it effectively encapsulates the phenomena considered in this chapter and is widely accepted (Johnson and Gaines 1990). Before proceeding, a number of features of dispersal warrant mention: (a) dispersal may or may not reflect individual choice (“voluntary” versus “enforced” dispersal, Greenwood 1980), (b) dispersal may take place before first breeding or between different breeding episodes (“natal” versus “breeding” dispersal, Greenwood 1980), (c) dispersal may or may not be influenced by environmental conditions (“environmental” versus “innate”, Howard 1960), (d) dispersal may be density-dependent (Travis et al. 1999) or influenced by how close a population is to its carrying capacity (“saturation level”, Kokko

and Lundberg 2001), (e) effects of the environment and individual condition are often referred to as “condition-dependent” dispersal (Ims and Hjermmann 2001), (f) dispersal can occur between spatially discrete populations or within continuous but spatially structured populations (e.g., Hastings 1983), (g) dispersal may be sex biased (Greenwood 1980), and (h) successful reproduction by a disperser results in gene flow (Endler 1977).

Dispersal is not the same as migration (Endler 1977), with the latter being the spatially and temporally predictable movement of individuals between breeding and foraging habitats. Individuals may thus migrate but not disperse (move from natal sites to foraging areas and then back to natal sites for breeding), disperse but not migrate (move from natal sites to non-natal sites without leaving breeding areas for separate foraging areas), migrate and disperse (move from natal sites to foraging areas and then to non-natal sites for breeding), or not migrate and not disperse (stay at natal sites for their entire lives). In the present chapter, we focus on the evolution of philopatry and dispersal, leaving migration for a separate chapter (Hendry et al. 2003b—*this volume*). However, it is important to remember that dispersal and migration may often interact. For example, the long-distance movements undertaken by migratory animals may make it more difficult to find the natal site. Conversely, philopatry may be increasingly favored in migratory individuals as an effective way of ensuring their return to suitable breeding areas.

In the following, we first outline how selection might favor philopatry or dispersal. This discussion is devoid of references to salmonids because our goal is to outline general theories, particularly those with mathematical formalization. Second, we describe the basic biology of salmonids and ways of gathering data on philopatry (“homing”) and dispersal (“straying”). Third, we review basic patterns of homing, straying, and genetic diversity in salmonids. Finally, we consider each of the general theories in light of information from salmonids. Our overall goal is to provide a salmonid-based evaluation of existing general theories for the evolution of philopatry and dispersal.

1. Theory

Philopatry and dispersal are alternative behaviors for an individual but they represent opposing ends of a continuum for families, populations, or species. In fact, individuals can also be placed along this continuum by considering alternative behaviors as probabilities. Substantial variation in philopatry and dispersal among individuals, kin, and groups suggests that selection has the potential to act at each of these levels and, indeed, all have been invoked in mathematical models (Johnson and Gaines 1990; Table 2.1). Selection acting to increase the fitness of individuals (individual selection) is included in nearly all models, often appearing in the form of inbreeding depression or survival costs (“Inbreed” and “Costs” columns of Table 2.1). Selection acting to increase the fitness of closely related individuals (kin selection) also figures heavily (“Kin” column of Table 2.1). Selection acting to increase the success of unrelated groups (group selection)

also appears in several models, particularly those examining effects of local extinctions ("Extinction" column of Table 2.1). In the following, we outline theories for how selection might favor philopatry ("Why philopatry?") and dispersal ("Why dispersal?"), and list empirically testable predictions of each theory. We typically focus on putative benefits of philopatry or dispersal but the benefits of one could just as easily be considered costs of the other. The theories are presented separately but are not mutually exclusive, and considering each alone assumes that "all else is equal." Ultimately, variation in philopatry and dispersal should reflect a balance between many interacting benefits and costs.

1.1. Why Philopatry?

Theory P1

Philopatry increases the likelihood of finding a suitable breeding habitat and mate. Suitable breeding habitats are distributed heterogeneously across space, and organisms whose foraging movements take them beyond natal areas may have difficulty finding suitable sites for breeding. If so, individuals predisposed to return to natal sites may have greater success than dispersing individuals because the former are more likely to find suitable habitat. Under this hypothesis, we predict that philopatry should increase with decreasing availability or accessibility of suitable alternative breeding sites (see also Travis and Dytham 1999) and with increasing temporal stability at natal sites (because successful reproduction by one's parents becomes an increasingly reliable predictor of successful reproduction by oneself at the same site). However, even if physically suitable alternative sites are easily discovered, reproductive success will still depend on the number of conspecifics. At least some individuals of the opposite sex are obviously necessary, and average individual reproductive success will still increase with increasing density ("Allee effect," Courchamp et al. 1999), although it presumably declines again at higher densities. If dispersal is density-dependent, philopatry in such systems should be highest at intermediate densities.

Theory P2

Philopatry increases familiarity with local breeding conditions. The reproductive success of repeat breeders often increases with age (Martin 1995), implying benefits of prior experience. Some such benefits may result from first-hand knowledge of natal sites. For example, individuals that are familiar with an area may be better able to find high-quality nesting sites (Greenwood 1980; Pärt 1994). Social interactions, including mate choice, also influence reproductive success, and individuals breeding at natal sites may benefit from previously established relationships (Greenwood 1980, 1983). Competitive benefits of philopatry under this hypothesis parallel Greenwood's (1980, 1983) "resource enhancement" or "resource competition" mechanism (see also Perrin and Mazalov 1999). Under this hypothesis, we predict that philopatry will be higher

Table 2.1. Theoretical models examining the evolution of philopatry and dispersal, along with the major factors they consider.

| Model | Spatial | Temporal | Extinction | Inbreeding | Kin | Costs | CD |
|-------------------------------|----------------|----------------|------------|------------|-----|-------|----|
| Bengtsson 1978 | | | | Y | | Y | |
| Bull et al. 1987 | Y | | | | | Y | |
| Cohen and Levin 1991 | Y | Y | | | | Y | |
| Comins 1982 | | | Y | | Y | Y | |
| Comins et al. 1980 | | | Y | | Y | Y | |
| Crespi and Taylor 1990 | Y | | Y | | Y | Y | Y |
| Frank 1986 | | | | | Y | Y | |
| Gadgil 1971 | Y | Y | | | | Y | Y |
| Gandon and Michalakis 1999 | | | Y | | Y | Y | |
| Gandon and Rousset 1999 | | | | | Y | Y | |
| Gandon 1999 | | | | Y | Y | Y | |
| Hamilton and May 1977 | | | | | Y | Y | |
| Hamilton and May 1977 | Y | | | | | | Y |
| Hastings 1983 | Y | | | | | | |
| Holt 1985 | Y | | | | | | |
| Holt and McPeck 1996 | Y ^a | Y ^a | | | | Y | |
| Irwin and Taylor 2000 | | | | | Y | Y | |
| Jánsosi and Scheuring 1997 | | | | | | | Y |
| Karlson and Taylor 1992, 1995 | | | Y | | | Y | |
| Lemel et al. 1997 | Y | | | | | Y | Y |
| Levin et al. 1984 | Y | Y | Y | | | Y | Y |
| Mathias et al. 2001 | Y | Y | | | | | |
| McPeck and Holt 1992 | Y | Y | | | | | Y |
| Morris 1991 | Y | | | | | | Y |
| Motro 1982a, 1982b, 1983 | | | | Y | Y | Y | |
| Motro 1991 | | | | | Y | Y | |

for iteroparous species, which may breed multiple times at the same site, and for semelparous species that remain at natal sites for all (no migration) or a substantial fraction (delayed migration) of their lives. For such species, we might also expect higher philopatry in the sex that experiences higher competition for resources and receives greater benefits from prior experience (Greenwood 1980, 1983; Perrin and Mazalov 1999).

Theory P3

Philopatry returns locally adapted individuals to appropriate habitats. Many species are distributed across multiple breeding habitats that differ in biotic and abiotic features. Populations in different environments should thus experience divergent selection, which should lead to adaptive divergence (Endler 1986; Schluter 2000; Arnold et al. 2001; Reznick and Ghalambor 2001). As a result, individuals returning to natal sites should have higher average fitness than individuals dispersing to other sites: because dispersers are less likely to arrive at a site for which they are as well adapted. These conditions should strongly favor the evolution of philopatry (e.g., Balkau and Feldman 1973; Asmussen 1983). Accordingly, several studies have found that residents have higher fitness than immigrants (e.g., Verhulst and van Eck 1996; Orell et al. 1999), and some have implicated divergent adaptation as the reason (e.g., Hendry et al. 2000; Via et al. 2000). Under this hypothesis, we predict that philopatry will increase as the degree of divergent selection increases. However, it is important to recognize that (a) lower success of immigrants may arise for reasons other than maladaptation (e.g., site familiarity or assortative mating), and (b) immigrants may have higher success than residents when populations are inbred (Ingvarsson and Whitlock 2000; Ebert et al. 2002).

Theory P4

Philopatry is favored by spatial variation in habitat quality. Envision a group of populations linked by dispersal, where (a) the environments experienced by different populations differ in intrinsic quality (e.g., carrying capacity), (b) intrinsic site quality does not vary in time, (c) fitness within populations is density-dependent (higher when densities are lower), and (d) dispersal occurs at a fixed per-capita rate (a fixed percentage of each population disperses). Because high-quality sites have larger populations and therefore produce the most dispersers, emigration will be higher than immigration at high-quality sites but lower than immigration at low-quality sites. The resulting decrease in density at high-quality sites will increase average fitness at those sites, and the resulting increase in density at low-quality sites will decrease average fitness at those sites. These conditions favor philopatry (Gadgil 1971; Hastings 1983; Holt 1985) “because dispersal is basically moving individuals down gradients in fitness” (Holt and McPeck 1996). Under this hypothesis, we predict that philopatry will increase as spatial variation in site quality increases, relative to temporal variation at each site. If, however, philopatry is condition-dependent

(higher when site quality is higher), spatial variation in habitat quality may favor some dispersal (Gadgil 1971; Pulliam 1988; Morris 1991; McPeck and Holt 1992; but see Lemel et al. 1997).

Theory P5

Philopatry improves access to parental resources. Philopatry may be favored if previous generations provide breeding resources that are used by subsequent generations (Waser and Jones 1983). Such resources may pass directly from specific parents to their offspring (e.g., inheritance of mates, nests, or nest locations; e.g., Brown and Brown 1984), and this should be particularly important when high-quality sites are limited (Pen and Weissing 2000). Alternatively, benefits may pass more generally from all parents to all offspring that breed in the same location (e.g., Stacey and Ligon 1987). Similarly, breeding adults may “condition” the environment, making it more suitable for subsequent reproduction. For example, penguins dig their nest burrows in the guano produced by previous generations, and this increases reproductive success (Paredes and Zavalaga 2001). The first of these mechanisms (benefits from a specific parent) directly favors philopatry because offspring must breed at the same location as their parents. The second mechanism (benefits from all previous breeders) does not directly favor philopatry because offspring simply need to breed at established sites, whether natal or non-natal. However, this mechanism may still indirectly favor philopatry as a way of increasing the likelihood that offspring return to an established site (invoking Theory P1). Under this hypothesis, we predict that philopatry should be higher when previous generations provide resources that increase the breeding success of subsequent generations.

Theory P6

Philopatry avoids costs of movement. In some species, philopatric individuals never leave the natal site, whereas dispersers may travel long distances. When this occurs, dispersers may incur costs that philopatric individuals do not. The preceding theories include some dispersal costs, such as failing to find a suitable breeding site, but not other costs, such as increased stress, predation, or energy expenditure. For example, some insects have winged morphs that disperse and wingless morphs that do not (Roff 1994), with the development of wings increasing energy costs and reducing reproductive output (Stirling et al. 1999). Béliçon et al. (1996) reviewed the literature and found that dispersal costs were often associated with the movement (“transience”) and settlement phases of dispersal. This suggests that dispersal costs may be very important for the evolution of philopatry and, indeed, such costs figure prominently in most theoretical models (Table 2.1), usually represented as a decreased probability of survival. Under this theory, we predict that philopatry should increase with increasing dispersal costs. This mechanism may be less important for migratory species, where philopatric and dispersing individuals may incur similar costs of movement (see below).

1.2. Why Dispersal?

Several general issues regarding the evolution of dispersal must be considered before outlining theories for how it might be favored by selection. First, we consider how dispersal might be heritable, which is necessary for it to evolve in response to selection. Second, we consider how dispersal might be maintained within populations even though genes for dispersal tend to leave. Third, we consider how new populations might be established by dispersers, even though they produce offspring that might likewise be inclined to disperse (if dispersal is heritable).

The heritability of dispersal, or the *probability* of dispersal, might take several forms. First, dispersal could be a specific behavior (or related to a specific trait) coded by alleles at one or a few Mendelian loci. Second, dispersal could be a threshold trait related to some underlying continuous distribution of migratory “liability” (Roff and Fairbairn 2001). Third, dispersal could be a continuous (quantitative) trait such as “the duration of directed movement” (Roff and Fairbairn 2001). Fourth, dispersal could be condition-dependent (Ims and Hjermann 2001), wherein a reaction norm links dispersal to the condition (e.g., energy) of an individual or the environment (e.g., density). Fifth, dispersal might be a “mistake” made by individuals attempting to be philopatric. In this case, when selection for philopatry is weak, mutations that impair philopatric abilities will accumulate and dispersal should increase. When selection for philopatry is strong, such mutations will be purged and dispersal should decrease.

How might a heritable dispersal potential be maintained within a population when individuals with the greatest genetic proclivity for dispersal are always leaving? One possible way is through condition-dependent dispersal. If the conditions favoring dispersal are rare and dispersal is probabilistic under those conditions, the loss of heritable dispersal potential should be slow. However, this mechanism will not allow the permanent persistence of dispersal potential beyond that maintained by mutations compromising philopatric ability. Instead, dispersal might be maintained in perpetuity through metapopulation dynamics, where multiple populations are linked by dispersal (Hanski and Simberloff 1997). Here, the loss of dispersal genes from a population is counterbalanced by the gain of dispersal genes from other populations (Bull et al. 1987; Morris 1991; Wilson 2001).

How can dispersal establish new populations when colonizing individuals had a genetic predisposition for dispersal and should therefore produce offspring that are similarly inclined? One possibility is that the *probability* of dispersal is heritable. In this case, some individuals colonizing new sites may actually have had a low genetic probability of dispersal, and will thus produce primarily philopatric offspring. Condition-dependent dispersal may also help. For example, competition may have been high in the ancestral environment, inducing dispersal, but low in the new environment, inducing philopatry. Yet another possibility is that individuals colonizing new sites may have been forced to leave their natal sites owing to inhospitable conditions or competitive interactions. In this case,

dispersing individuals may have a strong genetic tendency for philopatry and will thus produce philopatric offspring.

Theory D1

Dispersal buffers against temporal variation in habitat quality. When habitat quality varies across years within sites, so too will the fitness of philopatric individuals. If this temporal variation is asynchronous among sites, the best site for breeding will vary among years. Under these conditions, an individual that disperses may have often have higher fitness than an individual that does not. A number of theoretical models have examined this effect, with most assuming that temporal variation is caused by extrinsic conditions that influence carrying capacity (Table 2.1). However, temporal variation in site quality might also result from variation in population size relative to a fixed carrying capacity. This type of variation can result from chaotic population dynamics (Holt and McPeck 1996) or probabilistic dispersal in small populations: some sites will receive more migrants than others just by chance (Travis and Dytham 1998). General conclusions of these models, and thus predictions under this theory, are that dispersal rates should increase with increasing temporal variability and with increasing spatial asynchrony in temporal variation. We predict that these effects might also cause sex-biased dispersal if the relative amount of temporal variation in site quality differs between males (e.g., availability of mates) and females (e.g., availability of nest sites).

Theory D2

Dispersal allows colonization of new environments. Individual selection should often favor philopatry but group selection may favor dispersal as the only way of colonizing new sites. If philopatry is too strong, entire metapopulations may go extinct because local populations die out faster than vacated sites can be recolonized. Most theoretical models examining local extinctions (Table 2.1) predict that dispersal should increase with increasing extinction rates (e.g., Van Valen 1971; Comins et al. 1980; Levin et al. 1984; Olivieri et al. 1995; Gandon and Michalakis 1999, 2001). However, Ronce et al. (2000a) showed that incorporating realistic population growth into such models should lead to a peaked relationship between dispersal and extinction rates. This is the result of two opposing effects of increasing extinction: more empty sites favors increasing dispersal (as above) but lower competition within sites favors decreasing dispersal (populations may not reach carrying capacity). Karlson and Taylor (1992, 1995) also predict a peaked relationship between dispersal and extinction rates. Under this theory, we predict that dispersal should increase as local extinctions increase as long as new populations can reach their carrying capacity. Dispersal rates may also vary through time within local populations: starting high because colonists were dispersers but declining with time because philopatry is favored within populations (Roff 1994; Olivieri et al. 1995). We therefore predict that dispersal should be higher in younger than in older populations.

Theory D3

Dispersal reduces inbreeding depression. Inbreeding depression can reduce individual fitness and increase extinction risk (Charlesworth and Charlesworth 1987; Lande 1994; Lynch et al. 1995; Nieminen et al. 2001; Keller and Waller 2002). Selection might therefore favor behaviors that reduce mating between close kin, with dispersal being one such behavior. Furthermore, dispersal may be favored when populations are inbred because dispersers may have higher fitness than residents (Ingvarsson and Whitlock 2000; Ebert et al. 2002) and because gene flow can increase population fitness (Newman and Tallmon 2001). Theoretical models of dispersal under inbreeding depression (Table 2.1) often predict that one sex will be entirely philopatric, whereas the other will show some dispersal (Bengtsson 1978; Waser et al. 1986; Perrin and Mazalov 1999, 2000; Perrin and Goudet 2001). The sex that disperses is strongly influenced by initial conditions and sex-specific costs (Perrin and Mazalov 1999). Some models of inbreeding depression also include effects of competition among kin (Theory D4; Table 2.1), and these often predict that both sexes disperse at rates depending on the relative intensity of sex-specific dispersal costs, inbreeding depression, and competition (Motro 1991; Gandon 1999; Perrin and Mazalov 2000; Perrin and Goudet 2001). Under this theory, we predict that species susceptible to inbreeding depression will show higher dispersal and that dispersal will be sex biased. An important caveat, however, is that this theory is based on inbreeding depression, rather than inbreeding per se. For example, a population that survives a prolonged period of inbreeding may have purged its deleterious mutations and no longer suffer strong inbreeding depression (Barrett and Charlesworth 1991; Keller and Waller 2002). If so, dispersal will no longer be favored under this theory, even if populations remain inbred.

Theory D4

Dispersal reduces competition among kin. This theory originates from the concept of inclusive fitness, in which fitness depends not only on an individual's reproductive success but also that of its kin, weighed by their relatedness (Hamilton 1964a). Inclusive fitness recognizes that related individuals are more likely to carry copies of the same alleles, and that selection should therefore favor altruistic behavior toward relatives. One such altruistic behavior might be dispersal that reduces competition, even in the face of dispersal costs (Hamilton and May 1977). Many theoretical models have explored this idea (Table 2.1), sometimes in conjunction with local extinctions (Theory D2) or inbreeding depression (Theory D3). Under this hypothesis, we predict that dispersal should increase as the potential for kin competition increases. Also, because iteroparity increases relatedness, dispersal should be higher as repeat breeding increases (Irwin and Taylor 2000), unless offspring dispersal varies with maternal age (Ronce et al. 2000b). Finally, the sex that experiences stronger competition among kin should disperse at higher rates (Perrin and Mazalov 2000).

The preceding theories each make qualitative predictions that can be subjected to empirical tests. However, some make similar predictions and may be difficult to distinguish. In addition, multiple selective factors probably act simultaneously, and the outcome will thus depend on the relative strengths of each factor. Experimental approaches would be the most powerful way to isolate individual selective factors but such experiments are logistically cumbersome, particularly for philopatry and dispersal. An alternative is to use comparative analyses. Our goal in the rest of this chapter is to use comparative analyses of salmonids for evaluating the relative merits of each theory. We start with some general information on homing and straying in salmonids, and then move to an explicit consideration of each theory.

2. The Salmonid System

2.1. Background

Here we provide a short review of the relevant salmonid life history, with detailed reviews appearing elsewhere (e.g., Balon 1980; Groot and Margolis 1991; Elliott 1994). Salmon, trout, and charr lay their eggs in the gravel of streams or lakes, where they incubate for several months and then hatch. Hatched embryos (“alevins”) remain in the gravel for weeks to months, and then emerge as free-swimming “fry.” In some cases, offspring remain for their entire life near their parent’s original nest site (non-migratory), but in most, they move to other freshwater environments or the ocean (migratory). As they begin to mature, most salmonids return to the same general location where their parents bred (“homing”), whereas some disperse to non-natal sites (“straying”). Homing and straying will be strongly influenced by migration. For example, some wholly freshwater resident (non-anadromous) populations are isolated by physical barriers (landlocked) and so generate and receive few strays. Other non-anadromous populations are not isolated by barriers and can stray within their river system. However, straying between different river systems is greatly facilitated by movement between fresh water and the ocean (anadromy).

Much of the early evidence for salmonid homing came from observations that phenotypic traits vary greatly among conspecific breeding aggregations (e.g., Robertson 1921). Presumably such variation could only arise if different aggregations represented different gene pools. Homing was later confirmed by experiments where juveniles tagged in a particular stream typically returned to that stream as adults (Scheer 1939; Ricker 1972; Stabell 1984). The principal mechanism of homing was then revealed by experiments where juveniles exposed to a particular odor overwhelmingly returned as adults to streams where that odor was released (Cooper et al. 1976; Scholz et al. 1976). These and other experiments, such as transplanting fish or cutting the olfactory nerve, confirmed that juveniles learn (“imprint”) chemical characteristics of the water at their natal sites, and then use that information to guide their return migration

(Hasler and Scholz 1983). Accurate homing appears to be achieved by “sequential imprinting” (Harden Jones 1968), where “juvenile salmon learn a series of olfactory waypoints as they migrate through fresh water and later retrace this odor sequence as adults” (Dittman and Quinn 1996).

Most of the imprinted cues are probably abiotic, but Nordeng (1971, 1977) suggested that population-specific pheromones released by juveniles in fresh water might aid the return homing of adults. Although some juveniles and adults are preferentially attracted to odors from their own population (Groot et al. 1986; Brannon and Quinn 1990; Courtenay et al. 1997), the pheromone hypothesis appears to have little support as a general explanation for homing. As an obvious example, juveniles of many populations migrate to the ocean long before adults return. Some observations, however, suggest that pheromones may play a supplementary role: homing can be higher when population sizes are higher (Quinn and Fresh 1984; Hard and Heard 1999) and homing decreases when resident fish are removed (Tilzey 1977). In sum, olfactory imprinting, particularly on abiotic features, provides the best explanation for homing in fresh water. Homing from the open ocean to the mouth of a river system, however, must involve other mechanisms, such as magnetic or celestial orientation (Dittman and Quinn 1996).

The spatial scale of homing is currently unresolved. For example, do sockeye salmon home faithfully to a river system, to a lake within that system, to a tributary within that lake, to a riffle within that tributary, or to a location within that riffle? Evidence that sockeye salmon home faithfully to specific lakes is unequivocal (Quinn et al. 1987; Wood 1995) but *direct* evidence of homing to sites within lakes has been difficult to gather. Here, homing has been inferred *indirectly* from evidence that breeding aggregations show consistent differences in allelic frequencies at neutral genetic loci (Varnavskaya et al. 1994) and in population-specific adaptations (Quinn et al. 1995, 2001a). Recently, Quinn et al. (1999) used “natural tags” to provide direct evidence that sockeye salmon home faithfully to specific locations within lakes. At some scale, however, homing based on imprinting must break down because alternative sites will be too similar to distinguish. This threshold scale has yet to be determined and probably varies among populations and species. Also, heritable differences in breeding time could partially isolate adjacent aggregations even without imprinting (Hendry et al. 1995).

Homing and straying must be heritable for selection to drive their evolution, but we are unaware of any studies that have measured the heritability of homing or straying within a population (i.e., the degree to which homers beget homers and strays beget strays). However, several studies have compared homing and straying for different populations reared in a common environment. Hard and Heard (1999) found consistent differences in straying rates between two chinook salmon populations reared and released together at a non-natal site, suggesting a genetic difference in straying. In contrast, Labelle (1992) found no differences between three coho salmon populations reared and released at a non-natal site. We contend that homing *ability* (olfaction, imprinting, memory storage, memory recall) must have a genetic basis because juveniles return to non-natal release

sites, even when no experienced individuals acted as guides and when their mothers never experienced that site.

Homing to *specific* sites, as opposed to overall homing ability, may also have a genetic basis. McIsaac and Quinn (1988) compared chinook salmon reared and released at natal sites (natal groups) to those reared and released at a non-natal site (experimental group). The natal groups homed accurately to their natal/release sites but the experimental group showed an intermediate response: some returned to the non-natal release site and some (more than expected by chance) returned to the natal site, despite never having experienced that site. This suggests that salmonids have some genetic tendency to return to a specific natal site even if they did not imprint on that site. This inference is further supported by experiments that released pure natal, pure non-natal, and hybrid natal/non-natal fish into the same streams: homing was higher for hybrids than for pure non-natal fish (Bams 1976) and was higher for pure natal fish than for hybrids (Candy and Beacham 2000). All of these observations could be explained by a genetic tendency to return to a specific site or by a genetic tendency to return to a specific habitat type. In the later case, homing and straying would depend on the distribution of natal and non-natal sites with similar habitat. Regardless, homing to specific sites or habitats is clearly overpowered by imprinting because juveniles released at non-natal sites overwhelmingly return to those sites rather than to their natal site.

Even though homing is clearly heritable, it can also be influenced by individual condition and the environment. For example, straying may differ among fish of different ages (older > younger: Quinn and Fresh 1984; Quinn et al. 1991; Unwin and Quinn 1993; Labelle 1992; Pascual et al. 1995; older < younger: Hard and Heard 1999) and is higher for fish exposed to neurotoxic pesticides (Scholz et al. 2000). Also, changes in the physical characteristics of natal streams can influence homing: the eruption of Mt. St. Helens increased straying rates for steelhead (Leider 1989) and chinook salmon (Quinn et al. 1991). Of course, these patterns could still reflect underlying genetic variation, such as an adaptive reaction norm (Hutchings 2003—*this volume*) that links a threshold trait (straying) to the condition of an individual or the environment.

2.2. Estimating Homing and Straying

The two general methods for estimating homing and straying parallel the so-called “direct” and “indirect” methods for estimating gene flow (Slatkin 1987). Direct estimates can be obtained in several ways. First, juveniles can be tagged and the breeding adults surveyed for the presence of tags. Some tags are administered to batches of fish: colored dyes for the skin, chemical dyes for scales or bones, and temperature-induced banding patterns on otoliths (Nielsen 1992; Schroder et al. 1995; Volk et al. 1999). Other tags are administered to individual fish: fin clips, dye marks, external tags, coded-wire tags, visual-implant tags, and passive integrated transponder tags (Nielsen 1992; Hughes et al. 2000). Some of these individual tags can be used to identify specific fish, and others are specific only to batches of fish. Second, breeding adults can be surveyed for the presence

of “natural tags” induced by the environment: chemical signatures on scales (Kennedy et al. 2000), temperature-induced banding patterns on otoliths (Quinn et al. 1999), and parasites (Quinn et al. 1987). Third, adults can be characterized phenotypically or genetically and then assigned to putative source populations using discriminant functions, mixed-stock analyses (Pella and Masuda 2001), or “assignment tests” (Hansen et al. 2001).

Two general types of straying estimates are generated by tagging studies. First, all of the juveniles in a population can be tagged and then adults in that population can be surveyed for tags. Here, the number of untagged adults divided by the total number of adults estimates the proportion of fish at a site that are strays from elsewhere (e.g., Schroeder et al. 2001). Straying estimates using this method will be biased upward when some juveniles in the focal population are not tagged, but statistical adjustments can correct for this bias (e.g., Lindsey et al. 1959). Second, all or some of the juveniles in a population can be tagged and then that population and surrounding sites can be surveyed for tagged adults. Here, the number of tagged adults at all non-natal sites divided by the total number of tagged adults (natal and non-natal sites) estimates the proportion of fish that stray from a site. This method will underestimate straying when sampling effort is higher in the focal population than at other sites. However, this bias can be corrected by obtaining estimates of the proportion of adults sampled at each site (e.g., Mortensen et al. 2002). Even with this correction, however, straying rates may be underestimates because only a fraction of potential non-natal sites can be surveyed (Candy and Beacham 2000). However, most strays return to sites near the natal stream (see below) and complete sampling at nearby sites can therefore minimize any bias.

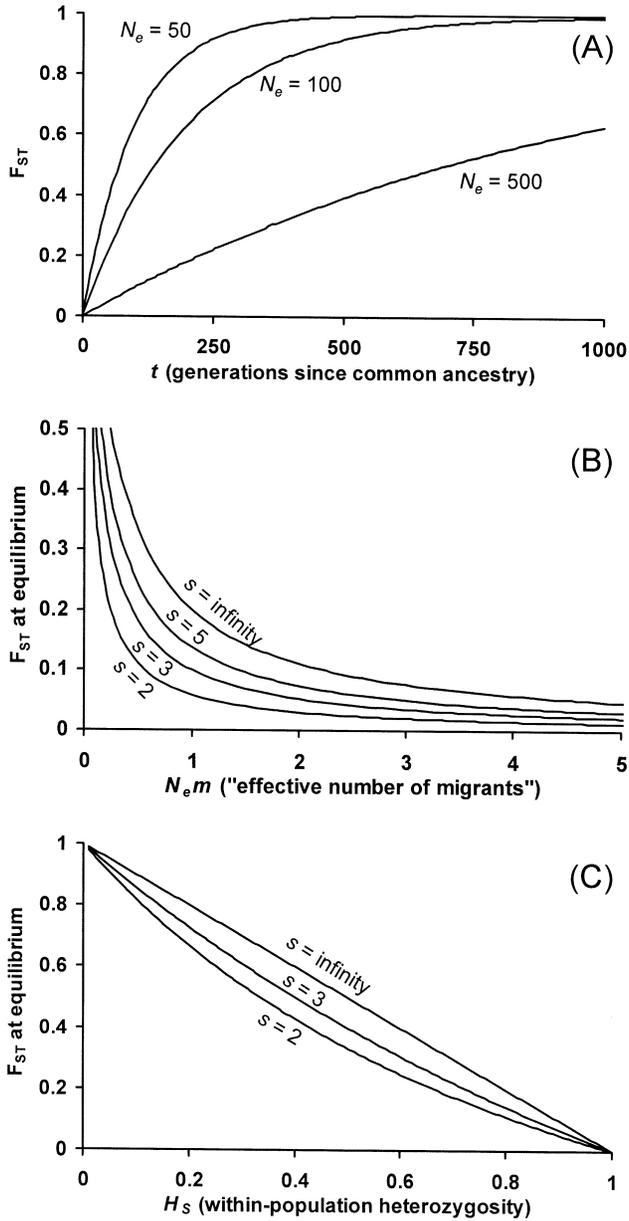
Several other direct methods have demonstrated strong site fidelity in salmonids but should not be used to estimate rates of homing and straying. First, adults can be captured at breeding sites and displaced to other sites. The extent to which these fish return to their capture site reveals site fidelity, and such return rates can be high (e.g., Hartman and Raleigh 1964). However, this approach should not be used to estimate straying because the displaced fish may already have been strays at their capture site, may not have enough time to return to their capture location (see Lindsey et al. 1959), or may not be exposed to the appropriate sequence of homing cues. Second, adults can be denied access to their natal site using a weir. Such fish will often die rather than breed at nearby sites (Hartman and Raleigh 1964) but the extent of such behavior will not reflect natural straying. Third, breeding adults of iteroparous species can be tagged and potential breeding sites can be surveyed in subsequent years (e.g., Lindsey et al. 1959). This last approach can be used to estimate *breeding* dispersal (switching sites between breeding seasons) but not *natal* dispersal (switching sites before the first breeding season).

Indirect methods rely on the expectation that the amount of among-population divergence at neutral genetic loci is negatively correlated with the amount of gene flow. The first step in this method is to obtain an accurate measure of genetic differentiation, which is facilitated by large sample sizes and many loci (Waples 1998b), as well as samples from multiple years or cohorts (E. Nielsen et

al. 1999; Tessier and Bernatchez 1999; Garant et al. 2000; Heath et al. 2002b; Kinnison et al. 2002). The second step is to convert genetic differentiation to an estimate of gene flow. A traditional method is Wright's (1931) approximation: $F_{ST} = 1/[1 + 4N_e m]$, where F_{ST} is the proportion of the total variation that is caused by differences among populations, $N_e m$ is the "effective number of migrants" per generation, m is the proportion of individuals that are "migrants," and N_e is the "effective population size." Effective population size is the size of an "ideal" population (random mating, equal sex ratio, non-overlapping generations, random variation in reproductive success) that would have the same genetic properties as the real population (Waples 2003—*this volume*). $N_e m$ thus represents gene flow in units of genetically effective individuals, which should correlate with straying rate.

Unfortunately, few natural systems meet the assumptions of Wright's approximation (Whitlock and McCauley 1999; Porter 2003). First, it assumes a genetic equilibrium, which requires thousands of generations when N_e is large, and will overestimate $N_e m$ when an equilibrium has not been reached (Nei and Chakravarti 1977; Figure 2.1A). Second, it assumes an infinite number of populations and will overestimate $N_e m$ when populations are few (Takahata 1983; Figure 2.1B). Third, it assumes that mutation rates are much lower than gene flow, which may not be the case for highly polymorphic markers such as microsatellites, and will overestimate $N_e m$ when this is not the case (Jin and Chakraborty 1995; Hedrick 1999; Figure 2.1C). Fourth, it assumes no selection on alternative alleles and will overestimate $N_e m$ when selection is purifying (removes variants) but underestimate $N_e m$ when selection is diversifying (favors different variants in different populations). Fifth, it assumes a particular population structure (island model), and may underestimate $N_e m$ for other types of population structure, such "stepping-stone" and "isolation-by-distance" (Kimura and Weiss 1964; Slatkin 1993). Despite these concerns, it is important to recognize that F_{ST} remains a good descriptor of population structure (Whitlock and McCauley 1999; Balloux and Goudet 2002; Neigel 2002).

Some of the above concerns have been mitigated by recent developments, such as new genetic markers. The majority of early studies used allozymes, some of which are under selection (e.g., Jordan et al. 1997). In contrast, DNA microsatellites do not code for a product and should not be under direct selection, although they could be linked to a coding locus. With microsatellites, however, one must be wary of higher mutation rates (Hedrick 1999). Other improvements have focused on the relationship between genetic variation and $N_e m$. First, Takahata (1983) modified Wright's approximation to allow finite numbers of populations (Figure 2.1B), and this modification provides unbiased estimates in many cases (Balloux and Goudet 2002). Second, equations relating $N_e m$ to F_{ST} can be tailored to specific scenarios. For example, Hendry et al. (2000b) used a two-population model that allowed for different population sizes, asymmetric rates of gene flow, and non-equilibrium conditions. Third, Slatkin (1985) showed how $N_e m$ can be estimated from the distribution of rare alleles. Fourth, Beerli and Felsenstein (1999, 2001) showed how maximum likelihood and coalescent theory can be used to estimate gene flow with few assumptions.



Fifth, simulation programs can accommodate diverse population structures in determining combinations of N_e , m , and divergence time that would generate observed patterns of divergence (Balloux 2001; Kinnison et al. 2002; Koskinen et al. 2002b).

Assuming an accurate $N_e m$ estimate has been obtained, several additional caveats are warranted. First, although many authors have argued that more than one migrant per generation will prevent genetic divergence (review: Mills and Allendorf 1996), divergence is still possible even if $N_e m$ is an order of magnitude larger (Allendorf and Phelps 1981). Second, $N_e m$ cannot by itself be used to argue that *adaptive* divergence is, or is not, constrained by gene flow; instead adaptive divergence is directly related to m (Hendry et al. 2001a). Third, estimates of straying produced by the direct and indirect methods may not be reliable surrogates for one another. For example, tagging work will often underestimate straying because few studies can survey all sites to which individuals might stray (Koenig et al. 1996; Candy and Beacham 2000). Also, tagging will underestimate gene flow when immigrants have higher reproductive success than residents (Ingvarsson and Whitlock 2000; Ebert et al. 2002) but overestimate gene flow when the converse is true (Hendry et al. 2000). Finally, when some individuals are migratory and some are not (“partial migration,” Hendry et al. 2003b—*this volume*), tagging and genetic studies must include both migratory and non-migratory individuals if they are to provide accurate estimates of straying and gene flow.

Figure 2.1. Factors influencing the use of F_{ST} to estimate the effective number of migrants ($N_e m$). Panel (A) shows F_{ST} as a function of time (t , in generations) since a group of populations with a common ancestry started diverging (in the absence of ongoing gene flow, an isolation model). The rate of approach to unity depends heavily on N_e , and when N_e is large it may take thousands of generations. The curves are calculated as $F_{ST} = 1 - (1 - 1/[2N_e])^t$, following Nei and Chakravarti (1977; see also Waples 1998b). If gene flow is taking place among the diverging populations, F_{ST} will asymptote below unity and will approach the asymptote more quickly than in the isolation model (Varvio et al. 1986). However, the rate of approach to the asymptote will still depend on N_e . Thus, estimating $N_e m$ from F_{ST} using equilibrium formulae will overestimate gene flow when diverging populations have not yet reached an equilibrium. Panel (B) shows equilibrium F_{ST} at different levels of gene flow ($N_e m$) and with different numbers of populations (s) exchanging migrants. Estimating $N_e m$ from F_{ST} using Wright’s infinite island model will overestimate the true $N_e m$ if the actual number of populations is small. The curves are calculated as $F_{ST} = 1/(1 + 4N_e m[s/(s - 1)]^2)$, following Takahata (1983). Once the number of populations exceeds five, the effect of further increases in the number of populations is minimal (at least in the island model). Panel (C) shows equilibrium F_{ST} at different levels of within-population heterozygosity (H_S) and different numbers of populations (s), in the absence of ongoing gene flow. Estimating $N_e m$ from F_{ST} without accounting for heterozygosity will overestimate the true $N_e m$. The curves were calculated as $F_{ST} = ([s - 1][1 - H_S])/(s - 1 - H_S)$, following Jin and Chakraborty (1995). When gene flow is ongoing among the populations, equilibrium F_{ST} will be low even at low heterozygosities (see panel B), and so the effect of heterozygosity on biasing $N_e m$ estimates should be small.

2.3. Patterns of Homing and Straying

A vast amount of data has been collected on homing and straying. Appendix 1 shows estimated straying rates from tagging studies of anadromous salmonids. The individual studies can be used to address specific questions (see below), but as a whole, the database is too small for detailed analyses of general trends. Broad generalizations, however, include (a) homing is more common than straying, (b) straying is variable within and among species, and (c) straying is more common among nearby populations than among distant populations.

Appendix 2 shows F_{ST} values from genetic studies, which should reflect the overall level of gene flow and straying. However, we did not convert F_{ST} estimates to $N_e m$ because of the aforementioned concerns. Several generalizations are possible. First, F_{ST} varies greatly among studies (0.000–0.645) and is strongly correlated with the maximum distance among populations (Figure 2.2). This matches the results of tagging studies in showing that straying and gene flow are negatively correlated with geographic distance. Second, wholly anadromous populations show less differentiation than wholly non-anadromous or mixed anadromous/non-anadromous populations (Figure 2.2; Appendix 2). Thus, species exhibiting life histories most conducive to straying do indeed stray at higher rates. Third, geographically isolated populations show greater differentiation than do populations among which straying remains possible (Appendix 2). Thus, in the absence of physical isolation, populations continue to exchange genes. Fourth, for a given geographic distance, differentiation is qualitatively greatest for coastal cutthroat trout, least for pink and chum salmon, and intermediate for the other species (Figure 2.3). This pattern likely reflects differences in their life history and migratory tendency (see below).

Before using the empirical data to examine each theory, we here address two questions common to multiple theories. One question is whether or not straying is sex biased, and we suggest that it usually is not, at least not consistently. First, tagging studies of anadromous fish usually reveal similar straying rates in males and females (e.g., Unwin and Quinn 1993; Thedinga et al. 2000). An exception is Hard and Heard (1999), where 60.6% of the strays were males. Second, genetic assignment tests of anadromous brown trout show no evidence of sex biased straying (Hansen et al. 2001; Bekkevold 2002). Third, the dispersal of foraging juveniles is not sex biased (Dittman et al. 1998), except perhaps in masu salmon, where downstream movement is higher for newly emerged females than for males (Nagata and Irvine 1997). This last difference probably reflects variation in migration rather than dispersal because females are anadromous, whereas many males are not (Nagata and Irvine 1997). Fourth, although male-biased dispersal has recently been documented among locations within a landlocked population of brook charr (Hutchings and Gerber 2003), all of the fish remain part of the same population and the dispersal thus does not constitute straying. One context in which straying may be sex biased is partial migration, where females are anadromous more often than males (Hendry et al. 2003b—*this volume*) and should therefore stray at higher rates. However, this

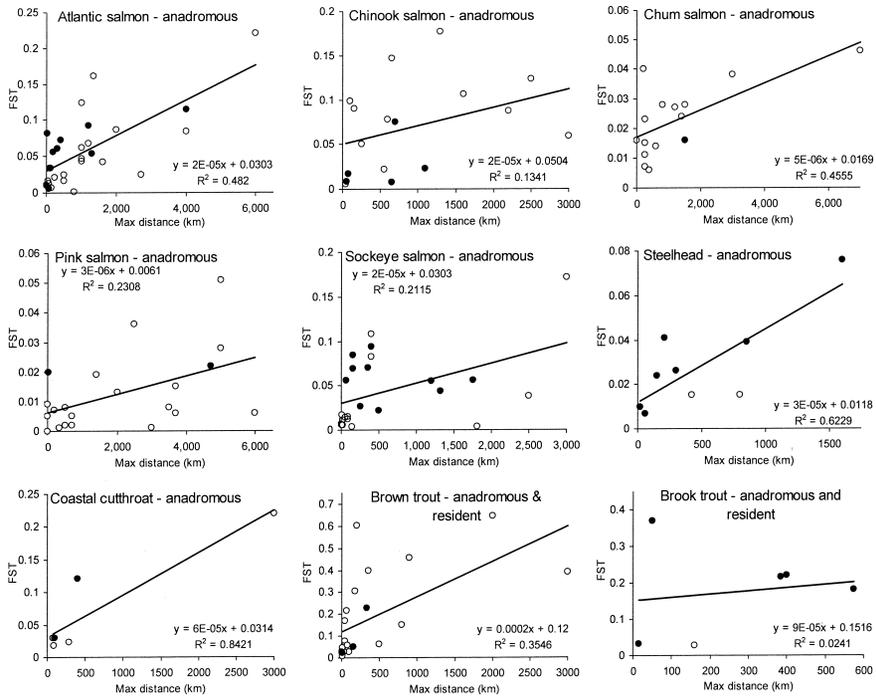


Figure 2.2. The amount of genetic variation among populations within species (F_{ST}) in relation to spatial scale, indexed as the maximum geographic distance (shortest water distance) among populations. For Pacific and Atlantic salmon, only comparisons of exclusively anadromous populations are shown. For brown trout and brook charr, the populations may be anadromous, resident, or a combination of the two, but they are not geographically isolated (i.e., they remain inaccessible to each other). Filled circles denote studies that included microsatellites or minisatellites, whereas open circles denote studies that used allozymes only. Note that the axes in the different panels have very different scales. The data are from Appendix 2.

difference probably reflects sex-specific costs and benefits of migration (Hendry et al. 2003b—*this volume*), rather than straying per se.

A second question is whether straying is density-independent or density-dependent (specifically, an increase in straying with increasing density), a distinction that is important because theoretical predictions can differ markedly between the two situations (Pulliam 1988; McPeck and Holt 1992; Travis et al. 1999). We suggest that salmonid straying typically does not increase with increasing density. First, tagging studies show that an increase in the number of adults returning to a site either decreases straying from that site (Quinn and Fresh 1984; Hard and Heard 1999) or has no effect on straying (Labelle 1992; Schroeder et al. 2001). Second, a dramatic reduction in the number of stream-resident brown trout led to reduced homing in the same year by repeat-spawning, lake-migratory brown trout (Tilzey 1977). In the absence of evidence for

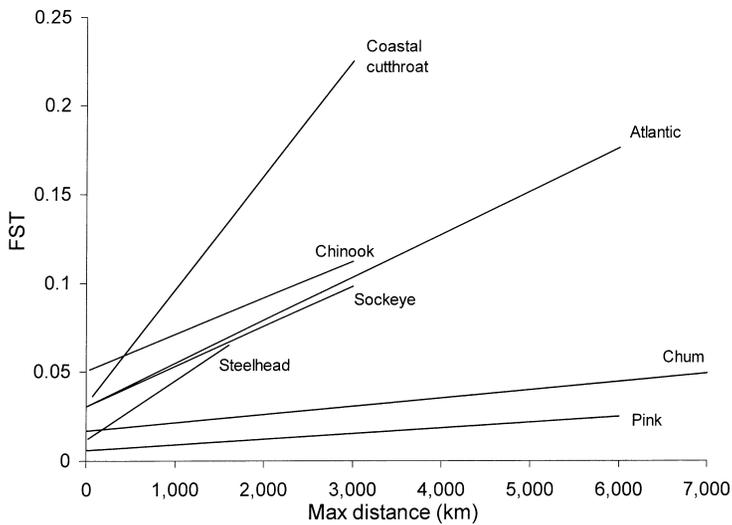


Figure 2.3. Comparison of genetic variation versus spatial scale (maximum distance between populations in a study) for the anadromous species shown in Figure 2.2. Shown are the best-fit linear relationships from Figure 2.2.

increased straying with increasing density, our analyses will concentrate on the density-independent predictions. However, the trend in salmonids for decreased straying with increasing density suggests an interesting avenue for further theoretical work.

Although few of the empirical studies were specifically designed to evaluate alternative theories, many present data that we can use to test some of the theories' predictions. In the following, we attempt this task by examining variation in homing and straying in relation to life history (e.g., semelparity versus iteroparity, age at maturity, migratory tendency, duration of freshwater residence) and the environment (e.g., temporal and spatial stability).

3. Evaluating the Theories

3.1. Why Philopatry?

Theory P1

Philopatry increases the likelihood of finding a suitable breeding habitat and mate. This theory should be most important when strays have difficulty finding suitable alternative breeding sites or mates. It should be less important when strays typically enter established populations or find relatively vacant sites with suitable habitat and some conspecifics. Tagging and genetic studies clearly show that straying occurs among established populations (Appendices 1 and 2), a tendency

that may be driven by several factors. First, most watersheds contain multiple populations, which will increase the likelihood that strays encounter established populations. Second, salmonids are attracted to water “conditioned” by conspecifics (e.g., Quinn and Busack 1985; Groot et al. 1986), which may increase the likelihood that strays will join established populations that they do encounter. Consistent with the idea that conspecifics influence adult returns, homing often increases as the number of returning adults increases (Quinn and Fresh 1984; Hard and Heard 1999). Straying among established populations is thus unequivocal but it is more difficult to determine the relative amount of straying to vacant sites because such sites are rarely surveyed.

Some straying probably does occur to sites without conspecifics because some hatcheries receive adults of species they do not propagate. Moreover, Hard and Heard (1999) found stray chinook salmon in several streams that lacked natural populations. In some cases, fish collected at non-natal sites may simply have been “proving” (Ricker 1972) or “exploring” (Griffith et al. 1999), and would have left the site had they been allowed to do so. Unambiguous evidence of straying to vacant sites comes from the colonization of areas made newly accessible by glacial recession (Milner and Bailey 1989; Milner et al. 2000), barrier removal (Bryant et al. 1999), or habitat improvement (Knutson et al. 2001). Further evidence comes from the appearance of mature individuals outside their native range (McLeod and O’Neil 1983) and the rapid spread of introduced salmonids from introduction sites (Kwain and Lawrie 1981; Quinn et al. 2001b). These examples show that straying does occur to vacant sites but they also suggest that such straying is often successful. This implies that strays are not limited in their ability to find suitable alternative sites or mates. However, this conclusion must be tempered by the realization that straying to unsuitable sites, even if common, would rarely be documented because such sites are rarely surveyed.

In sum, homing probably does not evolve owing to direct selection for access to suitable breeding sites or mates: salmonids usually stray among established populations and strays to vacant sites are often successful. This theory may, however, play an important indirect role in several contexts. First, the early stages of colonization may be tenuous if colonists are rare and poorly adapted. If so, returning adults may be few and homing may improve the chance that returning fish will find a suitable site with potential mates. Second, selection may more generally favor returning to sites with conspecifics, and homing may simply be an efficient way to achieve this goal. Accordingly, this theory is indirectly invoked in some of the following theories.

Theory P2

Philopatry increases familiarity with local breeding conditions. The potential importance of this theory varies among salmonid species and life histories. It might seem most relevant for iteroparous species, where experiences gained during one breeding season might influence success during future breeding seasons. Although this would directly select against breeding dispersal (switching sites

between breeding seasons), it would not directly select against natal dispersal (switching sites before first breeding). It might, however, indirectly select against natal dispersal if natal and breeding dispersal are correlated. Direct selection against natal dispersal requires that juveniles gain experiences at the natal site that later aid them while breeding at that site. This seems most likely for non-migratory salmonids, or for migratory salmonids with juveniles that remain at the natal site for an extended time. When juveniles leave natal sites soon after emergence (e.g., sockeye, chum, and pink salmon), it seems unlikely that they would be able to learn features of their environment that would later improve breeding success.

If this theory is important, we might therefore expect homing to be higher in iteroparous than semelparous salmonids, higher in non-migratory than migratory salmonids, and higher in migratory salmonids with juveniles that remain longer at natal sites. These predictions could be tested by comparing straying or genetic differences between these groups but this would be confounded by factors influencing the ease of homing. That is, homing should be easier for (a) iteroparous salmonids after their first return to a site (homing is higher for repeat breeders than for first-time breeders, Lindsey et al. 1959), (b) non-migratory salmonids because they do not leave the natal site, and (c) salmonids whose juveniles remain longer at natal sites because they have more time to imprint and may release pheromones that improve homing by adults (although Laikre et al. 2002 found that earlier emigration by brown trout did not decrease genetic differences among populations). Because of the directly confounding nature of this theory's predictions with the difficulty of homing, we do not further apply the comparative approach. Instead, we consider more generally whether juveniles might be able to gain experiences at the natal site that would improve their breeding success as adults.

Numerous studies have demonstrated that prior experience can improve competitive ability. For example, prior experience strongly influences the ability of size-matched juveniles to hold feeding territories (Rhodes and Quinn 1998; Cutts et al. 1999a). During breeding, prior residence increases the ability of females to defend nest sites and males to defend females (Foote 1990; Morbey 2002). To our knowledge, however, no study has tested whether experiences gained prior to breeding improve success during breeding. In sum, this theory is difficult to test but does not receive much support from salmonids. First, it does not provide a general explanation for homing because many species have life histories with which it is not compatible. Second, no evidence exists that experiences prior to breeding influence success during breeding.

Theory P3

Philopatry returns locally adapted individuals to appropriate habitats. In the following, we argue that this theory receives considerable support from salmonids. The stage is set by strong divergent selection among populations. For example, juvenile sockeye salmon usually occupy lakes for their first few years of life ("lake-type") and natal lakes differ dramatically in environmental conditions

such as temperature and productivity (Burgner 1991; Edmundson and Mazumder 2001). In other sockeye salmon populations, juveniles remain in streams or migrate immediately to the ocean (“stream/ocean-type,” Wood 1995). Sockeye salmon populations also differ dramatically in their breeding habitat: tiny streams, large rivers, spring-fed ponds, and lake beaches; with gravel size, water temperature, and water depth varying among these habitats (Quinn et al. 1995, 1999, 2001a). Many other examples of striking environmental variation among natal sites are found in all salmonid species (e.g., Groot and Margolis 1991; Taylor 1991b; Elliott et al. 1998).

Divergent environments favor divergent adaptation, and this is a prominent feature of salmonids. For example, sockeye salmon show consistent among-population environment/phenotype correlations. First, adults in small streams are younger and smaller than those in large streams, probably owing to increased bear predation and “stranding” (Quinn et al. 2001a, 2001c). Second, adults on lake beaches have deeper bodies than those in streams, probably owing to sexual selection favoring this trait but natural selection acting against it in streams (Quinn et al. 2001a; Figure 2.4). Third, egg size and gravel size are positively correlated (Quinn et al. 1995). Fourth, fry from lake inlets show a negative response to current (move downstream), whereas fry from lake outlets show a positive response to current (move upstream), behaviors well suited for reaching their natal lake (e.g., Raleigh 1971). Some of these differences are known to have a genetic basis and others are expected to. Numerous other examples of local adaptation have been described in salmonids (reviews: Ricker 1972; Taylor 1991b; Wood 1995).

The importance of divergent adaptation is best revealed by studying introduced populations (Kinnison and Hendry 2003—*this volume*). When such introductions are successful, new populations often become established in different habitats and have been found to exhibit adaptive divergence within at least 10–25 generations. Sockeye salmon introduced into Lake Washington, Washington, colonized beach and stream environments and now show apparently adaptive differences in body size, shape, and development (Hendry et al. 2000b; Hendry 2001). Chinook salmon introduced to New Zealand colonized multiple sites and diverged adaptively in many traits (Quinn et al. 2001b), particularly reproductive output in relation to migration distance (Kinnison et al. 2001). Adaptive divergence in introduced salmonids has also been documented for grayling in Norway (Haugen and Vøllestad 2001; Koskinen et al. 2002b).

If divergent adaptation has contributed to the evolution of homing, strays to a non-natal site should have lower reproductive success than homers to that site. One way to test this prediction is to compare the straying of adults (based on tagging) to the resulting gene flow (based on genetic divergence). If adult straying exceeds gene flow, strays must have reduced success relative to homers. Tallman and Healey (1994) tagged chum salmon juveniles and sampled adults from two adjacent streams. The tagging data suggested that adult straying averaged 37.9%, whereas the genetic data suggested that gene flow averaged only 5%. They concluded that “salmonids straying onto the spawning grounds of established popu-

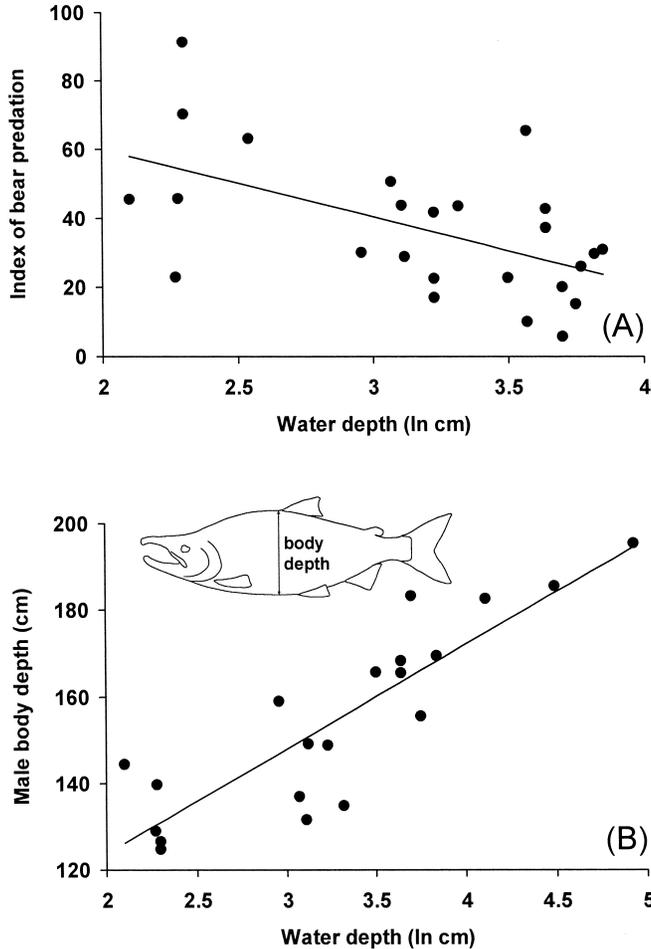


Figure 2.4. An example of probable local adaptation in sockeye salmon. Panel (A) shows that different populations in Bristol Bay (Alaska) breed in streams with very different average water depths, and that water depth is strongly correlated with the intensity of bear predation acting on the populations. Panel (B) shows that the body depth of males is highly correlated with water depth among populations, probably because large and deep-bodied males are more susceptible to stranding and predation in shallow water. Several studies have documented selection against large males owing to stranding and bear predation (e.g., Quinn et al. 2000c). Data are from Quinn et al. (2001a) and T. Quinn (unpublished).

lations of conspecifics had lower reproductive success than fish that return to their natal streams” (Tallman and Healey 1994). Unfortunately, the sample of adults they used to genetically characterize the groups was from a year when adults did not have tags. As a result, strays and homers were mixed in the genetic analysis, effectively affording them equal success and preventing an accurate estimate of gene flow.

Hendry et al. (2000b) conducted a similar study but separated homers from strays. They examined two nearby populations that bred in different habitats (lake beach versus river) and had different population sizes (the river was two orders of magnitude larger). The physical proximity and disparate abundance of the two populations suggested that many adults breeding at the beach might be strays from the river, even if homing was strong. Breeding adults were sampled at the two sites and individual homers and strays were identified by their otolith banding patterns, which reflect site-specific incubation temperature. This analysis revealed that approximately 39% of the adults breeding at the beach were strays from the river. Microsatellites were then used to examine genetic divergence between beach residents (homed to the beach), river residents (homed to the river), and beach immigrants (strayed from the river to the beach). River residents and beach immigrants were genetically similar but river residents and beach residents were genetically distinct (Figure 2.5). This “pattern of genetic differentiation could only have arisen if beach immigrants have reduced reproductive success relative to beach residents” (Hendry et al. 2000b; see also Hendry 2001). A comparison of genetic introgression and physical straying for pink salmon in two adjacent creeks in Alaska yields the same conclusion: straying is higher than gene flow (Mortensen et al. 2002).

Voluminous circumstantial evidence further supports the contention that adapted homers have higher fitness than maladapted strays. First, introduced fish usually fail to establish new populations, particularly within their native range (Withler 1982; Wood 1995). Outside their native range, some introductions

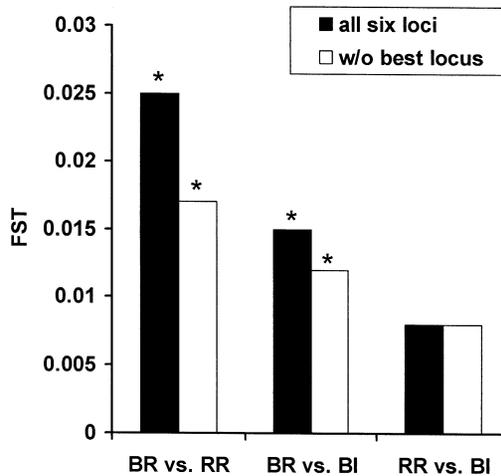


Figure 2.5. Genetic differentiation (F_{ST}) between beach residents (BR), river residents (RR), and beach immigrants (BI) for sockeye salmon introduced less than 14 generations previously into the Lake Washington system (Hendry et al. 2000b; Hendry 2001). Dark bars show F_{ST} over all six loci and white bars show F_{ST} after removing the locus that was best at discriminating between BR and RR (just in case that locus was linked to a locus under selection). Asterisks show comparisons that were statistically significant ($P < 0.05$).

have been successful (Lever 1996) but many more have failed (e.g., Harache 1992). Second, hatchery or farmed salmon released into the wild typically differ from wild fish in morphology and behavior, and have correspondingly lower reproductive success (Leider et al. 1990; Reisenbichler and Rubin 1999; Fleming et al. 2000). In fact, native gene pools often (but not always) retain their integrity despite large numbers of hatchery fish released into their midst (Hansen et al. 2000b; Utter 2000; Ruzzante et al. 2001).

Variation among species may also be explained by this theory. Relative to other anadromous species, chum and pink salmon populations typically use simple and similar freshwater habitats and have juveniles that do not remain long in fresh water (Quinn 1984). In this situation, divergent selection should be weak, divergent adaptation should be minor, strays should have similar success to homers, and straying rates should be high. As described below, tagging studies suggest that pink salmon do indeed stray at higher rates than the other species but comparable tagging data are not available for chum salmon. However, genetic variation among populations is considerably lower for both pink and chum salmon than for the other species (Figure 2.3). This difference is consistent with the present theory but it is also consistent with other explanations (Table 2.2).

We conclude that salmonid populations often show strong divergent adaptations that reduce the success of strays. At least two arguments might be raised in opposition to this as a general theory for the evolution of homing. The first is that divergent selection should be less effective at small spatial scales (review: Lenormand 2002). When populations are close together, it may be difficult for individuals to distinguish between natal and non-natal sites, which should increase straying and compromise adaptation. Indeed, most straying is to nearby sites (see above) and genetic differentiation is positively correlated with geographic distance (Figure 2.2). Divergent adaptation in salmonids will undoubtedly be minimal at very small spatial scales (Adkison 1995, Hansen et al. 2002) but these scales have not been determined and they may be very small indeed. For example, populations within a few kilometers of each other often exchange few strays (Labelle 1992; Hard and Heard 1999; Quinn et al. 1999), are distinct at neutral markers (Carlsson et al. 1999; Hendry et al. 2000; Garant et al. 2000; Gharrett et al. 2001; Ruzzante et al. 2001), and show strong evidence of divergent adaptation (Hendry et al. 2000b; Hendry 2001; Quinn et al. 2001a).

A second criticism might be that this mechanism will only work when populations are already well adapted, and it may therefore be unimportant in new systems. We disagree because new populations should begin to adapt almost immediately, even in the presence of ongoing gene flow (Endler 1973; Hendry et al. 2001a). Accordingly, studies of introduced salmonids have shown that substantial adaptive divergence is already present after 10–25 generations (Haugen and Vøllestad 2001; Koskinen et al. 2002b), in some cases arising even with ongoing gene flow (Hendry et al. 2000b; Hendry 2001; Quinn et al. 2001b). Thus, strays should be at a slight disadvantage soon after colonization, and this disadvantage should increase as adaptation proceeds. In fact, the reduced reproductive success of strays in Lake Washington was already present after about a

Table 2.2. Plausible alternative explanations for some of the observed variation in the homing and straying of salmonids.

| Observation | Key life history features | Alternative explanations |
|--|--|--|
| 1. Pink salmon stray at higher rates than other anadromous Pacific salmon. | Pink salmon are semelparous, always mature at 2 years of age, often spawn in small streams close to the ocean, and have juveniles that migrate immediately to the ocean. | <ul style="list-style-type: none"> (a) Homing is more difficult for pink salmon because juveniles spend less time in fresh water and so have less opportunity for imprinting. (b) Homing is less important for pink salmon because local adaptation is weaker: natal streams are similar and juveniles spend little time in them (Theory P3). (c) Pink salmon cannot take advantage of parental resources because juveniles do not remain in fresh water and breeding sites have high flushing rates (Theory P5). (d) Semelparity and maturity at 2 years of age increase susceptibility of pink salmon to temporal variation in habitat quality—straying compensates (Theory D1). |
| 2. Stream/ocean-type sockeye salmon show higher gene flow than lake-type sockeye salmon. | Both forms are semelparous, have multiple ages at maturity, and spawn in a diversity of environments. | <ul style="list-style-type: none"> (a) Homing is more difficult for stream/ocean type fish because streams are less distinctive than lakes. (b) Homing is less important for stream/ocean type fish because local adaptation is weaker: rivers are more similar than lakes (Theory P3). (c) Lake-type juveniles receive greater benefits from parental resources (nutrients from carcasses) because flushing rates are slower (Theory P5). (d) Interannual variation is greater for rivers than lakes, favoring increased straying in the former (Theory D1). |

dozen generations (Hendry 2001). Adaptation and homing should reinforce each other in a positive feedback loop. As adaptive divergence begins, selection against strays will increase and homing should be favored. As homing then increases, adaptive divergence should also increase because gene flow is reduced. This process should in a positive feedback loop continue until the population is maximally adapted.

Theory P4

Philopatry is favored by spatial variation in habitat quality. This theory predicts that homing is favored when fitness is negatively correlated with breeding density, straying rate is not positively correlated with breeding density, and habitat quality varies among sites but not among years. Several of these conditions are met by salmonids: (a) average reproductive success decreases with increasing density (Elliott 1994; Essington et al. 2000), (b) straying does not increase with increasing density (see above), and (c) habitat quality varies among sites as evidenced by variations in population sizes, breeding densities, and smolts-per-adult (Groot and Margolis 1991; Elliott 1994). One third condition is not met: habitat quality varies substantially among years (see below). Thus, the importance of this theory will depend on the relative magnitude of spatial and temporal variation. For example, if two metapopulations have similar levels of temporal variation but different levels of spatial variation, greater philopatry would be predicted in the case of greater spatial variation. We do not know of any data allowing a direct test of this prediction. Such data could consist of straying or genetic differences among populations in relation to spatial and temporal variation in habitat quality.

Theory P5

Philopatry improves access to parental resources. Salmonids probably do not inherit specific nest sites or mates, and so this theory would only be relevant through the general transfer of resources between generations. The nutrients released by dead and dying adults may be one such resource. Anadromous salmonids that die after breeding release large amounts of marine-derived nutrients into freshwater ecosystems (Kline et al. 1993; Schmidt et al. 1998). These nutrients increase primary productivity and invertebrate biomass (Bilby et al. 1996), and may improve the growth and survival of juvenile salmonids (Bilby et al. 1998; Schmidt et al. 1998; Wipfli et al. 2003). The chief beneficiaries of these nutrients are often heterospecifics but may sometimes include conspecifics. Among Alaskan lakes, for example, the number of sockeye salmon adults per unit of lake area (salmon-derived nutrient, SDN, loading) is positively correlated with marine-derived nitrogen in lake sediments, zooplankton, and juvenile sockeye salmon (Finney et al. 2000). Among years within lakes, SDN loading is positively correlated with the abundance of zooplankton, the primary food for sockeye salmon juveniles (Finney et al. 2000). This suggests “a positive feedback system, in which higher adult salmon abundance leads to increases in nutrient (P and N)

loadings. This enrichment, in turn, increases lake primary and secondary productivity. Completing the cycle, the increase in lake carrying capacity for juvenile salmon may ultimately result in higher numbers of adult salmon” (Finney et al. 2000).

Whether or not these parental nutrients influence homing is unclear. One constraint is that parental nutrients will favor homing only when they improve the *breeding* success of offspring. It is not enough that parental nutrients improve the foraging success of their offspring because this would favor delayed migration rather than homing. Instead, nutrients must improve the foraging success of their grand offspring, and this will depend on the flushing rate of nutrients. Another constraint is that parental nutrients will not directly favor homing if straying is between established populations, where homers and strays would benefit equally from nutrients released by previous generations. However, parental nutrients may indirectly favor homing in at least two ways. The first occurs if homing provides an efficient way for individuals to return to sites with abundant conspecifics (invoking Theory P1). The second is when potential breeding sites differ in population size and hence the availability of parental nutrients (invoking Theory P4). One prediction might be that homing should be highest for sockeye salmon because they are semelparous, abundant, and have juveniles that live in slowly flushing environments (lakes). Sockeye salmon do indeed have low straying rates but so too do chinook salmon (Figure 2.3), which are much less abundant and have juveniles that live in quickly flushing habitats (streams). Moreover, strong homing in sockeye salmon is also consistent with other theories.

Another possible parental resource is improvements that breeding adults make to the incubation environment. Fine sediments drastically reduce the survival of eggs and embryos (Chapman 1988), and nesting females purge the incubation environment of these suffocating materials (Kondolf et al. 1993). Much of this effect disappears before the next breeding season (Kondolf et al. 1993; Peterson and Quinn 1996) but frequently used and densely populated sites might nevertheless retain fewer fine sediments. (Of course, negative correlations between site use and fine sediments could also arise if salmonids prefer such sites or have greater success in them.) Nest building also coarsens the stream bed, which may reduce gravel scour (Montgomery et al. 1996). Homing may thus be favored if adults improve the long-term quality of incubation sites. As above, this mechanism favors the return of adults to established sites rather than specific natal sites but might indirectly favor homing through Theory P1 or Theory P4.

Theory 6

Philopatry avoids costs of movement. This theory considers costs associated with movement itself, such as increased stress, energy use, or predation. Because migration also requires increased movement, this theory should be evaluated in three contexts: complete migration, complete non-migration, and partial migration. For complete migration, the theory may not be relevant because

movement costs will be similar for homers and strays: most straying is to near the natal site (Appendix 1; Figures 2 and 3). For complete non-migration, the theory may be very relevant because strays should incur movement costs that homers do not. In this case, homing should be stronger when costs of movement are higher but no studies have yet related movement costs to homing. For partial migration, the theory may be relevant in indirect ways. For example, straying should be higher in anadromous than non-anadromous salmonids because anadromy increases the potential for movement between river systems. However, different populations experience different cost of migration and hence selection for or against anadromy (Hendry et al. 2003b—*this volume*). Direct selection for or against anadromy should therefore have strong indirect effects on homing and straying, and vice versa. Again, homing should be stronger when costs of movement are higher but, again, no empirical tests are available.

3.2. Why Dispersal?

Theory D1

Dispersal buffers against temporal variation in habitat quality. If straying evolves via this mechanism, site quality must vary among years and this variation must be asynchronous among sites. When these two conditions are met, at least two testable predictions follow: straying should increase as temporal variation increases and as variation in age at maturity decreases. This last prediction arises because variation in age at maturity also buffers against temporal variation in habitat quality. Selection should thus act more strongly to increase straying when age at maturity is less variable (Quinn 1984; Kaitala 1990). We will first consider the two conditions and then the two predictions.

The quality of natal sites clearly varies among years. One major source of variation is flooding, which mobilizes incubation gravel, destroys nests, and causes high mortality of eggs and alevins (Montgomery et al. 1996; Peterson and Quinn 1996; Lapointe et al. 2000). For example, the number of juveniles produced per breeder in the Cedar River, Washington, varied among years from 5.6 to 24.9, largely as a result of river discharge ($r^2 = 0.94$, Thorne and Ames 1987). Episodic floods can also have dramatic effects on stream-dwelling juveniles (e.g., Good et al. 2001). Predation is another factor that varies dramatically among years. For example, the number of adult sockeye salmon killed by bears is very low in some years but very high in others (7–100%, Quinn and Kinnison 1999; 16.4–92.3%, Ruggerone et al. 2000). Many other examples of temporal variation in habitat quality have been described (e.g., Giberson and Caissie 1998).

Some temporal variation probably has a spatially synchronous component: climate is usually regional and will vary across nearby sites in a similar manner. However, nearby sites often differ in physical features and will therefore respond differently to climate variation. For example, sockeye salmon breed at inlet streams, outlet streams, and lake beaches (Wood 1995), which differ in their susceptibility to temperature, gravel scour, and predation. Even within a specific

habitat type, variation is high in physical features such as basin area, stream gradient, water depth, ground-water influence, woody debris, and gravel size (Beechie and Sibley 1997; Quinn et al. 1995; 2001a). Each of these features will influence a site's response to climate variation. Some environmental catastrophes also have localized effects, such as the damage to several streams caused by the eruption of Mount St. Helens. Although we do not know of any studies quantifying spatial asynchrony in temporal variation, we expect that it is probably high.

Do populations that experience greater temporal variation show higher rates of straying? Direct tests of this prediction are difficult because studies usually do not report both straying and temporal variation in habitat quality. However, some qualitative comparisons are possible, such as between lake-type and stream/ocean-type sockeye salmon. Temporal variation is presumably lower in lakes than in rivers, and straying should thus be lower for the former. Tagging studies have shown that sockeye salmon do home very precisely to natal lakes (Quinn et al. 1987) but no tagging studies have been performed for stream/ocean-type populations. However, Gustafson and Winans (1999) found that genetic differentiation was higher among lake-type populations than among stream/ocean-type populations, consistent with higher straying among the latter. Although this difference supports the theory's prediction, several alternative explanations are possible (Table 2.2).

Another possible comparison is between spring breeders and fall breeders. L'Abée-Lund and Vøllestad (1985) argued that stream conditions are more variable in the spring than in the fall, and that spring species should therefore stray at higher rates. Quinn and Tallman (1987) countered that spring conditions are not necessarily more variable than fall conditions, and that spring species do not necessarily stray more than fall species. For example, spring-breeding steelhead strayed much less (2.5%) than fall-breeding coho salmon (21%) between the same two creeks (Shapovalov and Taft 1954). Our review of genetic variation suggests that spring-breeding steelhead show roughly similar levels of gene flow to fall-breeding species that have stream-dwelling juveniles (coho, chinook, Atlantic salmon; Figure 2.3; Appendix 2). The prediction for spring breeders versus fall breeders thus lacks empirical support, and may not have been an appropriate prediction.

Do species with less variation in age at maturity show higher rates of straying? Pink salmon have a strict 2-year life cycle, making them the least variable Pacific salmon. Chinook salmon hold up the other end of the spectrum, with age at maturity ranging from 1 to 8 years (Healey 1991). Pink salmon should therefore stray the most, chinook salmon the least, and other Pacific salmon species at intermediate levels. Pink salmon have long been thought to stray more than other species (Heard 1991), but Quinn (1993) was "unable to locate a comprehensive study of straying by wild pink salmon populations" and felt "the conclusion that they stray more commonly than other salmon species seems premature." Recent evidence suggests that this conclusion is no longer premature. First, two recent tagging studies quantified straying rates in pink and chinook salmon in the same region (southeast Alaska) and in many of the

same streams. Sampling effort was similar for the two studies and yet straying was more than four times higher for pink salmon (5.1%, Thedinga et al. 2000) than chinook salmon (1.2%, Hard and Heard 1999). A caveat is that the release sites were surrounded by other pink salmon populations, which might attract strays, but not by other chinook salmon populations. Second, our review shows that pink salmon have the lowest levels of genetic variation in anadromous Pacific salmon (Figures 2.2 and 2.3; Appendix 2).

A counterpoint was argued by Gharrett et al. (2001), who genetically marked a subpopulation of pink salmon in Auke Lake, Alaska, and estimated gene flow into other Auke Lake subpopulations. Gene flow from the marked population was essentially 0% into two subpopulations that bred at different times and 8–9% into two subpopulations that bred at similar times. The marked subpopulation received 8% gene flow from the other subpopulations. Gharrett et al. (2001) concluded that “in some instances, the fidelity of homing in pink salmon is high.” Although this is certainly true (e.g., Little Susitna River, see below), Gharrett et al.’s (2001) results should not be used to argue that pink salmon do not stray at higher rates than other species. First, gene flow was lowest among subpopulations with different breeding times, which is to be expected even if homing is weak (Tallman and Healey 1994; Varnavskaya et al. 1994; Hendry et al. 1995; Quinn et al. 2000; Woody et al. 2000). Second, a tagging study at Auke Creek revealed that physical straying of adults was actually fairly high (5.7%, Mortensen et al. 2002). For example, Gharrett et al. (2001) estimated that gene flow from Auke Creek into nearby Waydelich Creek was essentially zero, whereas Mortensen et al. (2002) found “that 3% of Waydelich Creek spawners had originated in Auke Creek.” This difference between adult straying and gene flow implies selection against strays (Theory P3). Finally, gene flow among Auke Lake subpopulations with similar timing was actually fairly high (8–9%).

Pink salmon thus stray more than other salmonids, providing support for the theory that straying evolves to buffer temporal variation in habitat quality. A possible alternative is that homing is more difficult for pink salmon because they breed closer to the ocean and have juveniles that spend little time in fresh water (Table 2.2). Consistent with this idea, intertidal pink salmon stray more (Thedinga et al. 2000) and show lower levels of genetic differentiation (Seeb et al. 1999) than upstream populations. Another possibility that local adaptation is less important for pink salmon because they spend less time in fresh water (Table 2.2). These alternatives are plausible but not general because some pink salmon migrate long distances, and juveniles of other species sometimes leave natal sites immediately after emergence.

A related comparison is that between semelparous and iteroparous species, where straying should be lower in the latter because reproduction in multiple years buffers against temporal variation. The only study comparing adult straying rates between iteroparous (steelhead) and semelparous (coho) species in the same streams (Shapovalov and Taft 1954) found much higher straying in the later. Genetic differentiation is also greater in coastal cutthroat trout than in semelparous species but the same is not true of other iteroparous species

(Atlantic salmon and steelhead trout, Figures 2.2 and 2.3). Moreover, coastal cutthroat trout populations may contain some non-anadromous individuals that cause a reduction in total gene flow. In sum, salmonids provide some support for the theory that straying evolves to buffer temporal variation in habitat quality. The evidence is equivocal but is also wide-ranging and convincing.

Theory D2

Dispersal allows colonization of new environments. If extinction/recolonization dynamics are important in the evolution of straying, two conditions should be met: local populations should frequently go extinct and strays should rapidly recolonize vacant areas. Extinction/recolonization events have clearly influenced salmonid lineages because much of their native range has been covered periodically by glaciers. Each time the ice recedes, newly exposed sites are colonized by fish whose ancestors had persisted in refugia (Wood 1995; McCusker et al. 2000; Bernatchez 2001). But how quickly does colonization take place? In Tustumena Lake, Alaska, sockeye salmon now breed in several inlet streams that were covered by a glacier as recently as 2000 years ago. These populations are distinct at neutral genetic loci (Burger et al. 1997) and at morphological traits that reflect local adaptation (Woody et al. 2000).

Milner and Bailey (1989) studied streams exposed by receding ice in Glacier Bay National Park, Alaska. They recorded 828 adult pink salmon in a stream accessible for 15 years and thousands in two streams accessible for 150 years. Other salmonid species in these new streams included sockeye salmon, chum salmon, coho salmon, and Dolly Varden (see also Milner et al. 2000). Similarly, Bryant et al. (1999) showed that the installation of a fish ladder allowing access to Margaret Lake, Alaska, resulted in natural colonization by pink salmon, cutthroat trout, steelhead trout, and Dolly Varden charr. Knutsen et al. (2001) studied Norwegian lakes where anadromous brown trout had gone extinct because of acidification, and found that the lakes were naturally recolonized soon after the addition of lime. The rapidity of colonization is also demonstrated by artificial introductions. In New Zealand, chinook salmon introduced to one stream quickly established self-sustaining populations in several other streams, and these populations are now genetically and phenotypically distinct (Kinnison et al. 2001, 2002; Quinn et al. 2001b). In the North American Great Lakes, pink salmon released into one stream in Lake Superior colonized at least four nearby streams within 4 years, and dozens in all the Great Lakes within 23 years (Kwain and Lawrie 1981).

These examples illustrate that salmonids rapidly colonize suitable habitats and establish distinct, self-sustaining populations. If, however, the present theory is to explain straying in extant populations, local extinctions and recolonizations must be quite frequent. Local extinctions are certainly common enough in modern times: “at least 106 major populations of salmon and steelhead on the West Coast have been extirpated” (Nehlsen et al. 1991; see also CPMPNAS 1996; Parrish et al. 1998). In most of these cases, human disturbances such as dams, habitat destruction, or fishing contributed to the extinctions, and so recoloniza-

tion would not be expected until those impacts have been ameliorated. However, Hansen and Mensberg (1996) describe the natural recolonization of two streams in Jutland, Denmark, following the extinction of their original populations. Yet unless we invoke human-mediated disturbances as the primary cause of current straying rates, we must also seek evidence of frequent natural extinctions. Unfortunately, human impacts are so pervasive that it is difficult to know whether a given extinction was or was not influenced by humans. However, a variety of natural disturbances, such as volcanic eruptions (e.g., Mount St. Helens), landslides, sustained droughts, or debris flows, at least have the potential to cause frequent local extinctions.

An interesting prediction of this theory is that straying should be highest in the youngest populations and should decrease with population age (Olivieri et al. 1995). It might therefore be informative to compare straying among populations that differ in evolutionary age. For example, some populations persisted in refuges during the last glaciation, whereas others were established by post-glacial straying. Data are not yet available for a rigorous comparison of this nature but one study is suggestive. Pink salmon tend to stray at high rates (see above) but Churikov and Gharrett (2002) found one population (Little Susitna River, Cook Inlet, Alaska) that strayed at very low rates. "Not a single 'foreign' haplotype was found in the sample of 40 fish from Little Susitna and not a single haplotype from the Little Susitna lineage was detected among the samples from 6 other even-year Alaskan populations" (Churikov and Gharrett 2002). Based on a variety of evidence, the authors argued that the Little Susitna is a relict population that evolved in a glacial refuge, whereas the others were founded post-glacially. The difference in straying might thus be consistent with the above prediction. A broader speculation might be that the increase in anadromy with latitude (Hendry et al. 2003b—*this volume*) is caused by increased selection for straying because of the greater role of glaciers. In sum, straying does play an important role in recolonization and local extinctions may contribute to the evolution of straying rates in extant populations.

Theory D3

Dispersal reduces inbreeding depression. If inbreeding depression influences the evolution of straying, inbreeding should reduce fitness, wild populations should have the potential for inbreeding, other inbreeding avoidance mechanisms should be less effective, and males should disperse more than females. In the following, we consider each expectation in turn. Numerous studies of captive salmonids have examined the fitness effects of inbreeding (Su et al. 1996; Pante et al. 2001; Wang et al. 2001). For example, Myers et al. (2001) found no significant effects in coho salmon when each of five generations was founded by six males and six females from ten full-sib families. However, the progeny of highly inbred full-sib matings had 25% lower body mass than their outbred half-sibs. Heath et al. (2002a) found positive, but weak ($r^2 = 0.06-0.08$), correlations between genetic variation at microsatellite loci and reproductive traits in chinook salmon. Arkush et al. (2002) found that the offspring of full-sib inbred

matings had lower survival than the offspring of outbred matings when challenged with one pathogen but not two others. In summary, inbreeding depression seems variable and often weak, except under intense inbreeding (Wang et al. 2001). Myers et al. (2001) suggested that the lack of strong inbreeding depression in salmonids was because they “have evolved through at least one tetraploid event, and the duplication of genes provides a buffer against inbreeding effects.” As a caveat, studies of inbreeding depression in salmonids have thus far been for captive fish, whereas negative effects of inbreeding may be stronger in the wild (Wang et al. 2001). In the only study in the wild, Ryman (1970) released Atlantic salmon into Swedish rivers and recaptured more outbred than inbred individuals.

What is the potential for inbreeding in the wild? Unfortunately, inbreeding is usually quantified only for manipulated populations (Wang et al. 2001), wherein supportive breeding can reduce effective population sizes and increase inbreeding (Tessier et al. 1997; Hansen et al. 2000a). As a result, some breeding programs actively minimize inbreeding by equalizing individual contributions to the next generation (Hedrick et al. 2000b) or avoiding matings between genetically similar individuals (Letcher and King 2001). In unmanipulated populations, the potential for inbreeding will vary among species. In healthy populations of Pacific salmon, inbreeding is probably unlikely because population sizes are often large (thousands to hundreds of thousands), and long migrations would make it difficult for siblings to remain in close contact. In contrast, some trout and charr populations can be very small and have siblings that remain in close contact. For example, Laikre et al. (2002) estimated that effective population sizes were very low in some natural brown trout populations (e.g., $N_{e(\text{females})} = 7.2, 15.7, 16.5, 17.6, 20.3, 24.0, 26.3, 27.8$). Some populations appear to have experienced severe inbreeding, perhaps because of founder effects or genetic bottlenecks. For example, two populations of brown trout in northwestern Scotland were genetically monomorphic at 46 allozyme loci, six mtDNA restriction sites, and eight minisatellite loci, in sharp contrast to substantial genetic variation in other populations (Prodöhl et al. 1997). Despite the lack of genetic variation, growth rates were as high as in less inbred populations nearby (Prodöhl et al. 1997). Either inbreeding does not have strong fitness effects in these populations or deleterious mutations were purged during the bottleneck.

Do other inbreeding avoidance mechanisms operate in salmonids? One possibility is that individuals may be able to recognize close kin and avoid mating with them. For example, juvenile Arctic charr can distinguish between water scented by individuals with similar versus different major histocompatibility complex (MHC) genotypes (Olsén et al. 1998). Because MHC genotypes are highly polymorphic, mate choice favoring dissimilar genotypes would reduce mating between siblings, as appears to be the case in mice (Potts et al. 1991). Landry et al. (2001) studied mate choice in a population of 41 male and 35 female Atlantic salmon. They captured all adults at a weir, genotyped them at five microsatellite loci, and determined their genetic relatedness and MHC genotypes. They then sampled offspring from the stream and used multilocus genotypes to determine the matings that produced them. The results were

suggestive of disassortative mating by MHC genotype ($P = 0.049$) and relatedness ($P = 0.094$; Landry et al. 2001). In contrast, Ruzzante et al. (2001) examined relatedness in anadromous brown trout and found that “in no case was the median individual inbreeding coefficient lower than the population inbreeding value, F , thus lending no support to the presence of inbreeding avoidance mechanisms.” The evidence for inbreeding avoidance mechanisms in salmonids is thus equivocal.

Straying should be sex biased if it has evolved to reduce inbreeding, and the breeding system of salmonids would predict that males should be the sex with higher dispersal (see Section 1.2). Empirical evidence contradicts this prediction because dispersal is usually similar between the sexes, at least after controlling for migratory tendency (see above). When not controlling for migratory tendency, straying may be higher for females because they are anadromous more often than males (Bekkevold 2002; Hendry et al. 2003b—*this volume*). In summary, inbreeding is probably rare for healthy populations of many species, especially Pacific salmon, which have large populations and extensive migrations. Inbreeding is more likely in small, freshwater populations but here mate choice may reduce inbreeding (although empirical evidence is ambiguous). Even if inbreeding occurs, it may have only mildly deleterious effects (although studies in the wild have not been undertaken). Additional work is certainly warranted, especially studies of inbreeding depression in the wild, but the current evidence argues against a major role for inbreeding avoidance in the evolution of straying.

Theory D4

Dispersal reduces competition among kin. Kin selection might influence straying in two ways. First, kin might compete directly for mates, which should favor increased straying. This seems unlikely for many salmonids because large populations and extensive migrations make it unlikely that siblings will remain in close contact. In small, non-migratory populations, kin might compete for mates but no study has directly tested for this possibility. If such competition does occur, straying should be higher for iteroparous than semelparous species and should be sex biased (see Section 1.2), probably higher in males because they may experience higher breeding competition. Neither of these predictions is supported by salmonids: iteroparous species do not stray more than semelparous species (Figure 2.3, Appendices 1 and 2) and males usually do not stray more than females (see above). We conclude that competition among kin for mates is probably not an important factor driving the evolution of straying in most systems.

Second, kin might compete for resources as juveniles. This is certainly possible because stream-dwelling juveniles often experience intense competition for territories and food, and may have reduced growth at high densities (Chapman 1966; Grant and Kramer 1990; Jenkins et al. 1999; Bohlin et al. 2002; Vøllestad et al. 2002). However, the type of dispersal considered in this chapter is movement from natal to non-natal sites, whereas juveniles may disperse while foraging and yet return to natal sites for breeding. This “foraging dispersal” might reduce

competition among kin without increasing straying. To assess the relevance of foraging dispersal to straying, we ask if juvenile salmonid kin might obtain benefits from dispersing, if foraging kin actively disperse to avoid competition, and if foraging dispersal might increase straying.

Do kin benefit from dispersal as juveniles? In laboratory studies, kin groups have some advantages over non-kin groups, including reduced aggression, increased growth, and reduced variance in growth (Brown and Brown 1993; Olsén and Järvi 1997; Brown et al. 1996). Some of these benefits, however, may be exaggerated because laboratory experiments often use recirculating water, which concentrates odors above natural levels (Griffiths and Armstrong 2000). The costs or benefits of kin association have rarely been examined in the wild but Griffiths and Armstrong (2001) found that groups of full-sib Atlantic salmon juveniles had lower densities and lower condition factors than mixed-family groups. They suggested that mixed family groups have greater genetic variation and therefore use the environment more efficiently (“heterogeneous advantage” theory).

Do kin actively disperse to avoid competition? In laboratory studies, juveniles spend more time in water conditioned by kin than by non-kin (Quinn and Busack 1985; Brown et al. 1993; Courtenay et al. 2001), suggesting that kin prefer to remain together. Studies in stream channels have shown that kin may remain in some degree of association with each other (e.g., Quinn et al. 1994) but evidence from the wild is mixed. A few studies of brown trout have found that juveniles from a specific stream location are more likely to be related than those from different locations (Hansen et al. 1997; Ruzzante et al. 2001). Other studies have found that within-river associations between genetic relatedness and geographic distance are either very weak (Mjølnerød et al. 1999) or entirely absent (Fontaine and Dodson 1999). Although these latter results might suggest active dispersal by kin, they might also reflect an inability of kin to remain together because of adverse conditions. Griffiths and Armstrong (2001) controlled for environmental conditions by releasing similar numbers of fish from full-sib and mixed-family groups into different sections of the same stream. Five months later, densities were lower in the full-sib sections than the mixed-family sections, which could reflect selection favoring dispersal of kin or simply lower performance when surrounded by kin. The latter seems more likely because condition factors were higher in the mixed groups despite their higher density.

Griffiths and Armstrong (2002) attempted to reconcile the results of laboratory studies, which find that kin remain together and benefit from doing so, with the results of field studies, which sometimes suggest that kin may avoid each other and benefit from doing so. They suggested that the heterogeneous advantage hypothesis leads kin to disperse in the wild but that kin selection leads dominant fish to be more tolerant of subordinate kin when they do come into contact. This idea is supported by recent work showing that juvenile Atlantic salmon have fluid spatial distributions with considerable home range overlap (Armstrong et al. 1999). For this hypothesis to work, however, kin cannot disperse very far because otherwise they would rarely come into contact with each other and kin selection would not be important. Considering all the above, it

seems unlikely that salmonids actively disperse to avoid kin competition, except perhaps for short distances (see also Hutchings and Gerber 2003). It therefore seems unlikely that such dispersal would have a large effect on straying rates. In sum, the theory that straying evolves to avoid competition among kin does not currently receive much support from salmonids.

4. Conclusions

Some general theories for the evolution of philopatry and dispersal receive strong support from salmonids. The most important factor favoring philopatry may be that it returns locally adapted individuals to appropriate environments (Theory P3). Salmonid populations in different locations show remarkably strong and rapid adaptive divergence, and strays should therefore have lower reproductive success than homers. A variety of evidence supports this assertion, most importantly the higher rates of adult dispersal than gene flow between populations in different habitats. The most important factor favoring dispersal may be that it buffers against temporal variation in habitat quality (Theory D1). Natal site quality varies dramatically among years, and populations in more variable environments appear to stray at higher rates, as do species with less variation in age at maturity.

Other theories receive moderate support from salmonids but their relative importance is not yet clear. For example, philopatry may sometimes be favored because it increases the likelihood of finding suitable breeding sites and mates (Theory P1). Although this is not a general explanation for philopatry (because dispersers often enter established populations), it may be a complementary mechanism to other theories because it is an efficient way for dispersers to find established populations. For dispersal, extinction/recolonization dynamics may be important, especially on longer time scales, because local salmonid populations often go extinct and strays rapidly establish new populations at suitable vacant sites (Theory D2). However, it is uncertain how often extinction/recolonization events take place in contemporary populations.

Other theories are clearly not general explanations for philopatry and dispersal in salmonids. Specifically, philopatry probably rarely evolves because (a) it increases familiarity with local environments and individuals (Theory P2—because most salmonids spend little time at natal sites before they start breeding), (b) it provides access to parental resources (Theory P5—because population sizes must be large, juveniles must spend extended periods in fresh water, and strays entering established populations would not be at a disadvantage over homers), (c) it compensates for spatial variation in habitat quality when temporal variation is absent (Theory P4—because temporal variation is prevalent), and (d) it avoids “costs” associated with leaving natal sites (Theory P6—because most costs are associated with migration rather than dispersal). Dispersal probably rarely evolves because (a) it reduces inbreeding (Theory D3—because strong inbreeding will not be common and will have limited effects when it occurs), and (b) it reduces competition among kin (Theory D4—because per-

formance often seems higher in the presence of kin). However, each of these theories may still be relevant in specific contexts, suggesting the intriguing possibility that homing and straying evolve for different reasons in different situations.

Salmonids show great variation in philopatry (homing) and dispersal (straying), making them a good system for examining alternative theories for these phenomena. Our investigation is far from complete and we hope that future work will focus specifically on tests of alternative theories.

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