

Rheotactic response of fry from beach-spawning populations of sockeye salmon: evolution after selection is relaxed

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Abstract: Rheotactic response was quantified for newly emerged sockeye salmon (*Oncorhynchus nerka*) fry from a beach population (Pleasure Point) and from an adjacent inlet population (Cedar River). The Pleasure Point population was small in number and had been established by straying from the much larger Cedar River population no more than 13 generations previously. When tested in laboratory raceways, fry from the Cedar River population were displaced downstream in the dark but not in the light. Such behavior is typical of inlet populations and presumably reflects selection for rapid movement to rearing lakes with minimal losses to predation. Fry from the Pleasure Point population showed greater downstream displacement than the Cedar River fry. Behavioral divergence of the Pleasure Point population could not be explained by selection, because water movement was absent from the beach environment. Genetic drift appeared to be a more plausible divergence mechanism. We suggest that the rheotactic response of beach populations should reflect the founding genotypes, gene flow from other populations, and random genetic drift. The results of previously published studies on the rheotactic response of beach fry in two other lake systems qualitatively support our hypothesis.

Résumé : La réponse rhéotaxique a été quantifiée chez des alevins fraîchement émergés du Saumon rouge (*Oncorhynchus nerka*) d'une population de plage (Pleasure Point) et chez ceux d'une population d'un tributaire avoisinant (Cedar River). La population de Pleasure Point était une petite population et s'est probablement formée par migration à partir de la population beaucoup plus considérable de Cedar River il y a tout au plus 13 générations. Dans des canaux de laboratoire, les alevins de la population de Cedar River se sont déplacés vers l'aval dans l'obscurité plutôt qu'à la lumière. Un tel comportement est typique des populations de tributaire et reflète probablement l'action d'une sélection favorisant le déplacement rapide vers les lacs d'élevage avec un minimum de pertes par prédation. Les alevins de la population de Pleasure Point se sont déplacés plus rapidement vers l'aval que ceux de la population de Cedar River. Cette divergence ne peut s'expliquer par la sélection, puisqu'il n'y a pas de courant dans le milieu de Pleasure Point. La dérive génétique est probablement un facteur de divergence plus plausible dans ce cas. Nous croyons que la réponse rhéotaxique des populations de plage résulte des génotypes fondateurs, du flux génétique venant d'autres populations et de la dérive génétique aléatoire. Les résultats d'études antérieures sur la réponse rhéotaxique des alevins de plage dans deux autres systèmes lacustres apportent des arguments qualitatifs en faveur de notre hypothèse.

[Traduit par la Rédaction]

Introduction

This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. Variations neither useful nor injurious would not be affected by natural selection, and would be left a fluctuating element... (Darwin 1859, p. 81).

Sockeye salmon (*Oncorhynchus nerka*) are unique among Pacific salmon in that their juveniles usually live in lakes during their freshwater residence, a period of 1–2 years (Burgner 1991). Within a lake system, different populations may spawn in inlet streams (streams flowing into lakes) or outlet streams (streams flowing out of lakes), or on gravel beaches within lakes (Wood 1995). Precise homing by ma-

turing adults maintains the reproductive isolation of these populations despite the subsequent mixing of their offspring in the lake (Varnavskaya et al. 1994; Quinn et al. 1999). Numerous studies have revealed that inlet, outlet, and beach populations have adapted in various ways to their local selective regimes (Blair et al. 1993; Wood 1995; Taylor et al. 1997).

After emerging from the gravel in stream incubation areas, sockeye salmon fry must migrate either upstream (from outlet streams) or downstream (from inlet streams) to reach their rearing lake. This migration is guided, at least in part, by their directional response to water current (rheotactic response). Field observations and laboratory experiments have

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shown that fry from inlet populations typically move downstream at night and hold during the day, whereas fry from outlet populations typically hold during the night and move upstream during the day (Hartman et al. 1962; Raleigh 1967; Brannon 1972; Clarke and Smith 1972). These rheotactic responses are known to be genetically based, because they have been documented under common laboratory conditions (e.g., Raleigh 1967), and hybrids between inlet and outlet populations show an intermediate response (Brannon 1972).

The adaptive significance of particular rheotactic responses by the fry of stream-spawning sockeye salmon populations is clear. Predation on lakeward-migrating fry can be intense (Ginetz and Larkin 1976; Beauchamp 1995), and nocturnal downstream movement of fry from inlet populations should greatly reduce their susceptibility to predation (Hartman et al. 1962; Ginetz and Larkin 1976). In contrast, the fry of beach spawners need not migrate through streams because they emerge directly into their rearing lake. Because fry from beach populations do not experience conditions of strong directional water current, selection for a particular rheotactic response would be lacking in the beach environment. What is as yet unknown, however, is the manner in which ancestral rheotactic responses evolve once a new beach population becomes established by straying.

Mechanisms of population divergence

Genetic variation among conspecific populations is mediated through the interplay of gene flow, natural selection, and random genetic effects (Ehrlich and Raven 1969; Lande 1976; Endler 1986; Slatkin 1987; Lynch 1988). Gene flow provides a homogenizing influence, preventing the divergence of populations that are not sufficiently isolated (Slatkin 1987). When gene flow is limited, however, populations can diverge genetically, owing to natural selection, random genetic drift, and mutation. Natural selection can lead to genetic differences among populations in response to environmental heterogeneity, so that populations become adapted to their local environments (Ehrlich and Raven 1969; Endler 1986). Random genetic drift may contribute to genetic divergence, especially for small populations and for traits that are selectively neutral (Lande 1976; Lynch 1988). Mutation can also contribute, but usually would do so over much longer periods of time.

Pacific salmon (*Oncorhynchus* spp.) provide excellent opportunities for examining mechanisms of population divergence, because they have been successfully introduced to several new locations (Gharrett and Thomason 1987; Hendry et al. 1996; Quinn et al. 1996). In some instances, limited introductions from a single source have given rise to several new populations that inhabit different environments. Between 1937 and 1945, hatchery-produced sockeye salmon from Baker Lake were transferred to Lake Washington (reviewed in Hendry 1995). The largest population established by these introductions is currently found in the principal tributary to the lake, the Cedar River. Beginning in 1957, sockeye salmon were first observed spawning at certain beaches along the shores of Lake Washington, particularly at Pleasure Point (Woodey 1966). Allelic variation at allozyme loci has indicated that the Pleasure Point population is also of the Baker Lake lineage and was most likely colonized by straying from the Cedar River (Hendry et al. 1996). Since

the founding event, the Pleasure Point population has become at least partially reproductively isolated from the Cedar River population, as revealed by the screening of allozyme and microsatellite-DNA variation (J.K. Wenburg and A.P. Hendry, unpublished data) and the analysis of otolith microstructure (Quinn et al. 1999). In accord with this evidence for limited gene flow, the two populations have diverged in some traits considered to be adaptive (female size and male body depth, Hendry and Quinn 1997; yolk conversion efficiency, Hendry et al. 1998).

In the present study, we tested for divergence in the rheotactic responses of Cedar River and Pleasure Point sockeye salmon fry. We predicted that Cedar River fry would display behavior typical of inlet spawners (moving downstream in the dark but not in the light). We did not, however, make specific predictions about behavior of the Pleasure Point population because selection would be absent in that environment. Rather, we tested our data against the null hypothesis of no difference in rheotactic response between the fry from Pleasure Point and the Cedar River. To verify that the observed differences could be attributed to genetic variation, we tested for the effects of fry size and condition on rheotactic response. We interpret our results in the context of possible mechanisms of divergence, and evaluate the strength of our inference by reference to other studies that have reported the rheotactic response of beach fry. Our findings have implications for the study of population divergence, and are relevant to various strategies for the conservation of Pacific salmon populations.

Materials and methods

Study populations

Within the Lake Washington watershed, the Cedar River has by far the largest population of sockeye salmon, with the annual number of spawners (1967–1993) ranging between 76 000 and 350 000 (R. Egan, Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, unpublished data). Spawning takes place in the lower 34.8 km of the river and no major tributaries are present. Mean daily discharge ranges between about $5.58 \text{ m}^3 \cdot \text{s}^{-1}$ (late summer) and $30.93 \text{ m}^3 \cdot \text{s}^{-1}$ (early winter), and the mean surface water velocity was measured at $1.12 \text{ m} \cdot \text{s}^{-1}$ (in November 1993; Hendry and Quinn 1997).

The Pleasure Point Beach is situated about 7 km north of the Cedar River (Fig. 1) and includes about 700 m^2 of spawning area (A.P. Hendry, unpublished data). Annual escapements at Pleasure Point have been estimated at 100–1000 (1963–1965; Woodey 1966) and 520–8180 (1976–1991; R. Egan, unpublished data). Estimates for the more recent of these two periods include several other beach sites near Pleasure Point, but spawners at those sites are much less abundant. (The overall population size for Lake Washington beach spawners is estimated by multiplying the peak daily count at index sites by 10; R. Egan, personal communication.) Habitat surveys at the beach failed to detect any directional flow of lake water (Hendry and Quinn 1997).

Experiments

We collected gametes from randomly selected sockeye salmon spawning in the Cedar River and at the Pleasure Point Beach in 1993. For each population, three females were individually mated with three males, giving rise to three independent full-sib families from each population. We limited our collections to only three females, in order to minimize potential impacts on the small Pleasure Point population. The fertilized eggs of each family were incubated

separately in Heath vertical-stack incubation trays, using recirculating Lake Washington water chilled to 6–8°C. When 95% of the eggs within a family had hatched, 100 alevins were randomly selected from that family and transferred to an emergence chamber. Each family was held in its own chamber and incubated in a substrate of glass marbles infused with upwelling water (8–10°C). Water flowed past the developing embryos and out a small notch at the top, so that emerging fry would leave the chamber of their own volition but could not reenter (for details on the emergence chambers see Hendry 1995). Laboratory lights were maintained on a 12 h light : 12 h dark schedule. Almost all fry emerged during the dark period, with most of these emerging just after lights-off.

We randomly selected fry within 8 h of their emergence, and tested their rheotactic response in experimental raceways (Fig. 2). Testing took place either in the light (within 6 h after lights-on) or in the dark (within 6 h after lights-off). Lake Washington water (8–10°C) was used in the raceways, and water velocity was volumetrically calibrated to 4.5 cm·s⁻¹. For each trial, an individual fry was placed in a central holding trap and allowed to acclimate for 5 min. The trap was then removed using an overhead pulley, and the fry was free to move about the raceway for 30 min. At the end of each trial, the fry's location was recorded in one of five positions (Fig. 2). It was then captured, killed, using an overdose of MS 222 (3-aminobenzoic acid ethyl ester), and preserved in 10% buffered formalin. Individual fry were tested until 19 replicates were obtained for each family in the light and in the dark (time constraints imposed by the testing design and by emergence patterns determined the number of replicates). To provide a "group-effect" control, 10 fry from each family were tested together in the light and another 10 in the dark. To provide a "no-flow" control, additional fry from each population were tested individually in the absence of current (18 in the light and 19 in the dark). Each fry was tested only once, and all were naive with respect to horizontal water movement.

After about 60 d of preservation, all fry were measured (fork length to the nearest 0.1 mm) and weighed (to the nearest milligram). The remaining yolk reserves were then removed and weighed (to the nearest milligram). The proportion of the total wet mass that was composed of yolk was calculated and normalized for analysis, using the arcsine square root transformation. The condition of each fry was calculated using Bams' (1970) k_D index.

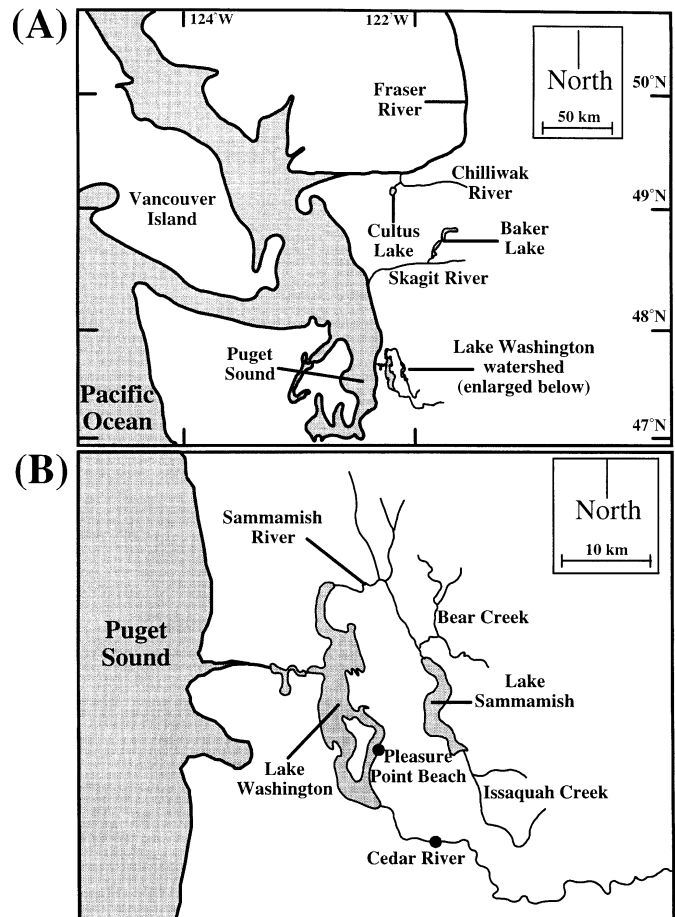
Analysis

We use "population" when referring to either the Cedar River or the Pleasure Point Beach, "light condition" when referring to tests in either the light or the dark, and "treatment" when referring to the different combinations of population and light condition (Cedar–light, Cedar–dark, Pleasure–light, Pleasure–dark). Binomial tests were used to determine if the fry had a directional preference in the experimental raceways in the absence of current. For each treatment, the numbers of fry in positions 1 and 2 were summed and compared with the number in positions 4 and 5 (the five positions are depicted in Fig. 2). In these no-flow tests, similar numbers of fry moving in each direction were interpreted as evidence of a lack of environmental cues (other than current) influencing movement in one direction versus the other.

We tested fry individually to ensure their behavioral and statistical independence (other than familial relationships). Migration in the wild, however, would almost certainly be undertaken in the presence of conspecifics. We therefore compared the distribution of fry tested individually with that of fry tested in groups of 10. For these treatment-specific analyses, the likelihood ratio (G statistic) was used to compare the distributions of fry in the five raceway positions.

We tested for differences in fry size and condition among the two populations using a nested ANOVA (families nested within populations) for each of the size and condition measures (fry

Fig. 1. (A) Locations of Lake Washington, Baker Lake, and Cultus Lake. (B) Locations of the Cedar River and Pleasure Point Beach.



length, fry mass, k_D , and percent yolk). To then determine if fry size or condition influenced the rheotactic response, forward stepwise linear regression was conducted using position in the raceway as the dependent variable and population, family, light condition, fry length, fry mass, k_D , and percent yolk as independent variables ($P < 0.05$ to enter, $P > 0.10$ to remove).

For fry tested individually in the current, mean position in the raceway was calculated for each family in each light condition (equivalent to the "net rank number score" of Kelso and Northcote 1981). Variation among these family means was analyzed using a repeated-measures split-plot ANOVA (Littell et al. 1991, p. 272) with population, family, and light condition as factors. All analyses were conducted in SAS (release 6.12).

Results

In the absence of current (no-flow controls), the number of fish that moved upstream did not differ from the number that moved downstream (river–light, $P = 1.0$; river–dark, $P = 0.27$; beach–light, $P = 0.79$; beach–dark, $P = 0.61$; Fig. 3A). In the presence of current, the distribution of fry tested individually did not differ from that of fry tested in groups of 10 (river–light, $P = 0.15$; river–dark, $P = 0.92$; beach–light, $P = 0.17$; beach–dark, $P = 0.39$; Fig. 3). These results imply that (i) the choice of upstream versus downstream movement by the fry in our experimental raceways

Fig. 2. Apparatus used to test rheotactic response. Fry were acclimated and released from a central holding trap (HT). After 30 min, the location of each fry in the raceway was recorded: ++, strong upstream; +, upstream; 0, no response; -, downstream; --, strong downstream.

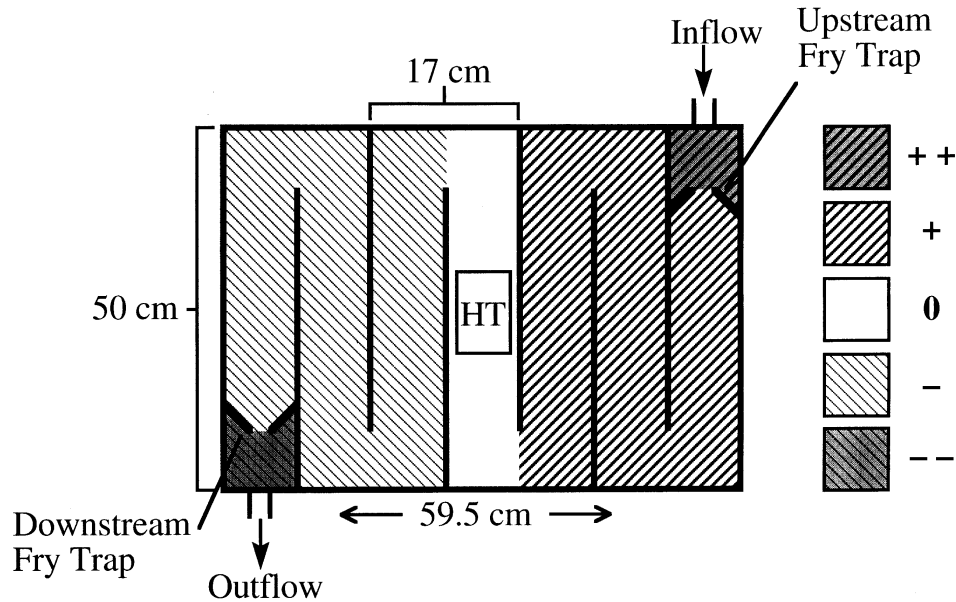
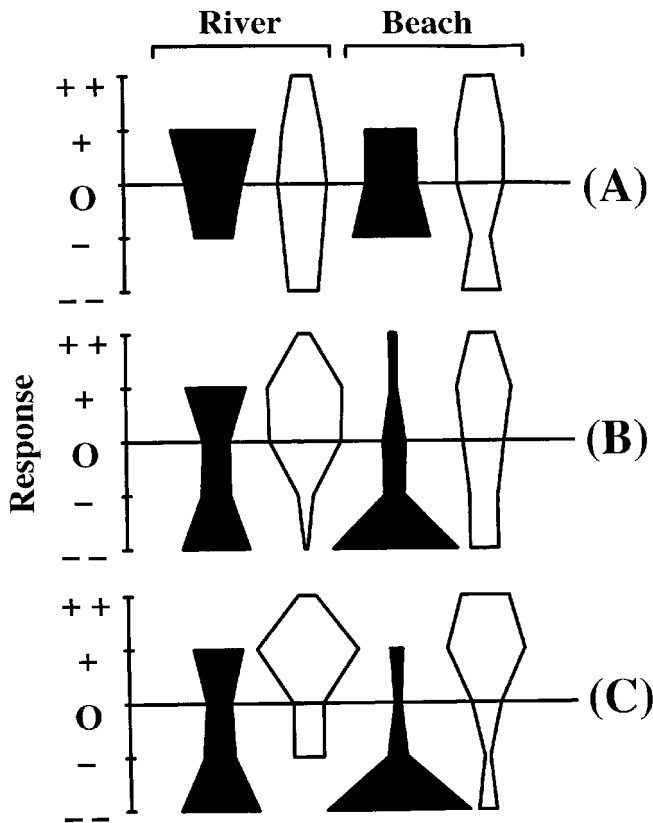


Fig. 3. Distributions of fry tested in rheotaxis experiments from the Cedar River (river) and Pleasure Point Beach (beach) populations. (A) Fry tested individually in the absence of water current. (B) Fry tested individually in the presence of current. (C) Fry tested in groups of 10 in the presence of current. Solid polygons represent results of tests performed in the dark and open polygons results of tests performed in the light. For an explanation of responses see Fig. 2.

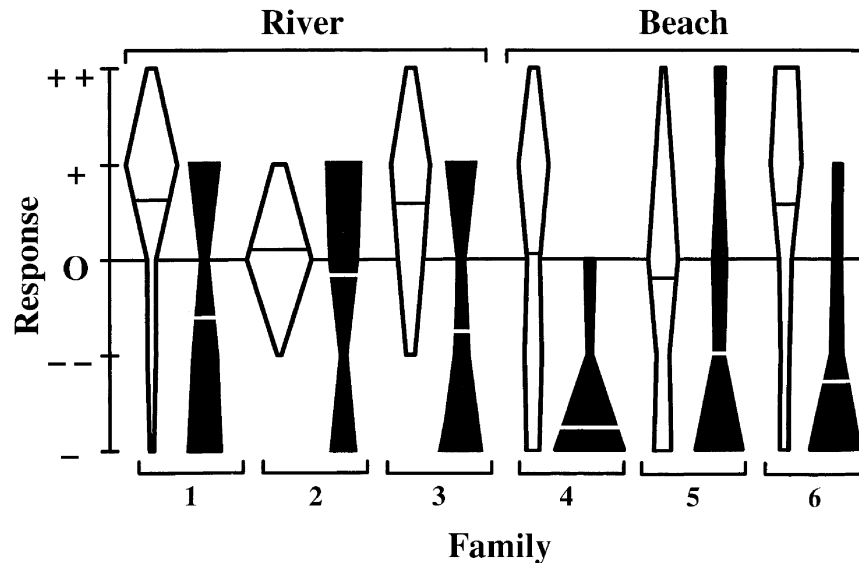


was not influenced by exogenous cues (other than water movement) and (ii) it is not necessary for fry to be tested in groups to exhibit characteristic rheotactic responses. Thus, the remainder of our analysis concentrated on the distribution of fry tested individually in the presence of current. It is important to acknowledge, however, that we cannot be absolutely certain that fry tested individually (or even in groups of 10) behave in laboratory raceways as they would in the wild. Nevertheless, the results of such field and laboratory studies generally corroborate each other, despite the different approaches.

Fry from the Pleasure Point families were longer and heavier than those from the Cedar River families ($P = 0.028$ for length and $P = 0.029$ for mass; Table 1), but fry from the two populations did not differ in k_D ($P = 0.765$) or percent yolk ($P = 0.604$). Stepwise linear regression revealed that fry length, fry mass, k_D , and percent yolk did not influence rheotactic response (none of these variables entered the model at any step; $P > 0.05$). Furthermore, fry size and condition also did not enter any of the models when stepwise regressions were conducted within each family and light condition ($P > 0.05$). We infer that the slight difference in fry size between the two populations did not affect their rheotactic response.

Most of the fry from both populations moved downstream in the dark (Fig. 3B). In the light, fry from both populations tended to hold their position or move slightly upstream (Fig. 3B). Notwithstanding this dramatic difference in rheotactic response between light conditions ($P = 0.008$), a difference between populations was also detectable. Under both light conditions (no interaction between population and light condition: $P = 0.395$), fry from the Pleasure Point population were displaced farther downstream than fry from the Cedar River population ($P = 0.016$; Fig. 3). This difference was particularly striking, because average downstream displacement in the dark was greater for all three Pleasure Point families than for all three Cedar River families (Fig. 4).

Fig. 4. Distributions of fry from three Cedar River (river) families and three Pleasure Point Beach (beach) families tested in rheotaxis experiments. All tests were performed with individual fry in the presence of water current. Solid polygons represent results of tests performed in the dark and open polygons results of tests performed in the light. The horizontal bar within each polygon represents the mean response. For an explanation of responses see Fig. 2.



Discussion

Cedar River and Pleasure Point fry demonstrated rheotactic responses that were typical of inlet-spawning sockeye salmon populations (downstream displacement in the dark but not in the light). Despite a general behavioral similarity of the two populations, a difference between them was also evident: more Pleasure Point fry than Cedar River fry were displaced downstream in both the light and the dark (Figs. 3 and 4). These patterns of variation in rheotactic response were (i) genetically based, because the fry were all reared and tested in a common environment; (ii) a direct response to water movement, because the fry did not show a directional preference in the absence of current; (iii) not dependent on social interaction, because the fry showed similar responses when tested individually and in groups; and (iv) not due to variation in fry size or condition. We conclude that greater downstream displacement of fry from the Pleasure Point population reflects genetically based divergence from their ancestral population (Cedar River). In making this inference we assume that the rheotactic response has not changed in the Cedar River population since Pleasure Point was colonized. This assumption is defensible because the Cedar River population is large and its habitat has not changed appreciably since Pleasure Point was colonized.

Mechanisms contributing to genetic divergence can include natural selection, random genetic drift, and mutation (Wright 1931; Ehrlich and Raven 1969; Endler 1986; Lynch 1988). Natural selection is the only one of these mechanisms commonly invoked to explain genetic differences in life history, morphology, and behavior among salmon populations (Taylor 1991; Adkison 1995). In our study, however, natural selection would not have directly (or indirectly) influenced the evolution of rheotactic response in the beach environment, because such behaviors would never be expressed in the phenotype (the fry never experience directional water flow). Although mutations have the potential for large pheno-

typic effects (particularly when they influence regulatory genes controlling developmental processes; Leary et al. 1984), mutation rates are too low to generate population-level differences after only 13 generations (Hartl and Clark 1989). The implausibility of selection and mutation as divergence mechanisms led us to carefully evaluate the potential role of genetic drift.

The raw material for genetic drift is the initial allelic frequency at each locus. For the Cedar River population, the frequency of hypothetical "downstream at night" alleles has undoubtedly been high. Hence, the frequency of downstream alleles would also have been high in the strays that initially colonized Pleasure Point. Subsequent to the colonization event(s), selection would be relaxed and allelic frequencies at independent rheotactic response loci would be free to respond to genetic drift (within the constraints imposed by continuing gene flow from the Cedar River). Genetic drift changes the frequency of selectively neutral alleles at random, assuming no linkage to traits associated with fitness (Wright 1931; Hartl and Clark 1989). Thus, the frequency of downstream alleles in a newly founded beach population would be as likely to increase as to decrease over time. The potential rate of change in allelic frequencies due to genetic drift within a population is negatively correlated with N_e , the effective population size (Hartl and Clark 1989). Salmon populations exhibit many of the characteristics that reduce N_e relative to N (Waples 1990), and empirical estimates suggest that N_e is about 20% of N (Altukhov and Salmenkova 1994). Thus, N_e for the Pleasure Point population would be approximately 20–1636, which is sufficiently small for divergence due to genetic drift in the absence of selection (Adkison 1995).

Allelic frequencies in a new population are contingent on those in the colonizing individuals. If only a few fish initially colonized Pleasure Point, and if they happened to show a greater tendency toward negative rheotaxis than the average for the Cedar River population, the Pleasure Point

Table 1. Size and condition for fry from Cedar River and Pleasure Point and for fry from each full-sib family.

Population	Fork length (mm)	Mass (g)	k_D^a	Proportion of yolk mass
Cedar River	24.1 (0.8)	0.124 (0.006)	2.07 (0.06)	0.202 (0.048)
Family 1	23.8 (0.5)	0.112 (0.004)	2.02 (0.04)	0.183 (0.035)
Family 2	23.5 (0.5)	0.126 (0.006)	2.13 (0.04)	0.248 (0.036)
Family 3	25.0 (0.6)	0.135 (0.005)	2.06 (0.04)	0.174 (0.035)
Pleasure Point	25.7 (0.5)	0.148 (0.006)	2.07 (0.04)	0.186 (0.035)
Family 4	25.9 (0.5)	0.147 (0.006)	2.04 (0.04)	0.185 (0.028)
Family 5	25.5 (0.5)	0.146 (0.004)	2.06 (0.03)	0.159 (0.026)
Family 6	25.6 (0.6)	0.153 (0.004)	2.09 (0.04)	0.214 (0.028)

Note: The sample size within each family was 38. Values are given as the mean with the standard deviation in parentheses.

^aBams' (1970) condition factor for fry.

population would show more negative rheotaxis even if subsequent genetic drift was nonexistent. Such "founder effects" are another way in which genetic drift can rapidly initiate population divergence (Nei et al. 1975; Adkison 1995). For the present study, we could not conclusively determine the relative importance of genetic drift due to the founding event itself versus that occurring subsequent to the founding event. However, the Pleasure Point population showed no reduction in genetic variation at allozyme loci relative to the Cedar River population (see frequency data in Hendry et al. 1996). As reduced genetic variation is a reliable signature of founder effects and genetic bottlenecks (Nei et al. 1975; Luikart et al. 1998), we suggest that postcolonization genetic drift may be the more important contributor to population divergence.

The precise genetic basis for rheotactic responses has not been determined (i.e., monogenic vs. polygenic, disomic vs. tetrasomic, additive vs. nonadditive). The lack of such information does not hamper our ability to qualitatively consider the effects of genetic drift (as above), but the different inheritance systems would quantitatively influence rates of population divergence (Lynch and Hill 1986). For instance, if the rheotactic response was tetrasomically inherited (salmonids had a tetraploid origin, and approximately 70% of their loci may still show tetrasomic inheritance), the rate at which genetic drift and selection could change allelic frequencies would be slower than for a trait with disomic inheritance (Allendorf and Thorgaard 1984).

Genetic drift is commonly assumed to be an important mechanism for differentiating salmon populations at presumed-neutral genetic loci (allozymes, mtDNA, microsatellites). This drift has probably caused the divergence in allozyme allelic frequencies observed among introduced salmon populations (Gharrett and Thomason 1987; Quinn et al. 1996), including those in Lake Washington (Hendry et al. 1996). Genetic drift has not, however, been explicitly invoked as a mechanism contributing to divergence in salmonid life history, morphology, or behavior. We suggest here that increased downstream displacement in Pleasure Point fry can be explained most parsimoniously by genetic drift.

Rheotactic response of fry from beach populations

Opportunities to study the evolution of formerly adaptive traits in natural populations after selection is relaxed are quite rare (for another example see Coss et al. 1993). The rheotactic response of fry from beach-spawning sockeye

salmon populations may provide one of the best such opportunities, because fitness should not differ among the various rheotactic-response genotypes. The final range of genotypes in a beach population should therefore reflect a combination of (i) the genotype frequencies in the founding population, (ii) the extent of historical gene flow from adjacent populations, (iii) the effective population size, and (iv) the evolutionary age of the population (i.e., the time for divergence). The only two previous studies reporting rheotactic response of beach fry (Raleigh 1967; Brannon 1972) are qualitatively consistent with this conceptual model.

Fry from Thumb Beach in Karluk Lake (Alaska) showed a rheotactic response similar to that of fry from an inlet stream in the same lake (Raleigh 1967). Raleigh (1967) asserted that this similarity was due to the fact that the Thumb Beach population probably received many strays from the adjacent Lower Thumb River inlet population. Consistent with this hypothesis of high gene flow, females from Thumb Beach and the Lower Thumb River were similar in length at a common age (Gard et al. 1987), a result that contrasts sharply with differences observed between females from beaches and streams in other lake systems (Blair et al. 1993; Taylor et al. 1997) including Lake Washington (Hendry and Quinn 1997). Additionally, allelic frequencies at allozyme loci could not distinguish among the various late-spawning Karluk Lake populations, which include those at Thumb Beach and the Lower Thumb River (Wilmot and Burger 1985; Varnavskaya et al. 1994). Thus, the rheotactic response of Thumb Beach fry can best be interpreted as reflecting a lack of divergence from nearby inlet populations, owing to recurrent gene flow.

In contrast to Karluk Lake fry, beach fry from Cultus Lake (British Columbia) showed intermediate rheotactic responses (58.4% downstream in 1964, 39.0% downstream in 1966; Brannon 1972, p. 32). All sockeye salmon in Cultus Lake spawn on beaches (Brannon 1972), so gene flow from stream-spawning groups would be very rare. Furthermore, Cultus Lake was probably colonized by a "stream-river type" sockeye salmon lineage (C.C. Wood, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., personal communication), whose fry would tend to hold their position in the current. Thus, the rheotactic response of Cultus Lake beach fry, which was atypical of either inlet or outlet populations, was consistent with the characteristics of their likely founding group, their reproductive isolation from other reproductive ecotypes over many

generations (>10 000 years), and the lack of selection for a specific rheotactic response.

The conceptual model outlined above requires further testing. We suggest several complementary lines of investigation, the weight of evidence from which would support or refute our suggestions. A logical first step would be a broader survey of rheotactic behavior in fry from beach-spawning populations and from nearby stream-spawning populations. The presence of these ecotypes in numerous lakes (Burgner 1991; Wood 1995) provides ample opportunities for such work. Another important step would be to employ a breeding study to determine the precise genetic basis for rheotaxis. Although this is not a trivial task with salmon, its completion would allow the development of quantitative evolutionary models of rheotactic response under different selection and migration scenarios at various plausible population sizes. This modeling exercise could be used to place bounds on possible rates of divergence attainable by genetic drift, and thereby provide predictions that could be tested against data obtained from natural populations (e.g., Lande 1976; Lynch 1990).

Maintenance of variation in inlet populations

Having provided an explanation for the negative rheotactic responses shown by beach fry (see above), we must also consider why some individuals in most inlet populations show a positive rheotactic response (Raleigh 1967; Brannon 1972; Figs. 3 and 4). Strong directional selection favoring nocturnal negative rheotaxis (see the Introduction) would be expected to rapidly drive alleles that favor such behavior to fixation. Two hypotheses may be advanced to explain this apparent paradox (mutation rates are much too low to generate the observed frequencies). First, gene flow from nearby outlet populations may maintain an influx of alleles for positive rheotaxis into inlet populations. This explanation is not entirely sufficient, however, because some inlet populations are found in lake systems that lack outlet populations (e.g., Lake Washington). A second hypothesis is that alternative juvenile life history types may be viable within inlet populations. Although lake rearing is typical, fry exhibiting a "river-type" life history may spend a year or two feeding in the side channels of main rivers (Wood et al. 1987; Wood 1995). In the Cedar River, a small proportion of fry apparently feed for a time in the river, because some of those caught in a downstream trap near the lake are substantially larger than the rest (D. Seiler, Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, unpublished data). We suspect that some fry exhibiting positive or neutral nocturnal rheotaxis contribute to the Cedar River population. Successful stream-type sockeye salmon might likewise maintain a low frequency of positive rheotaxis in other inlet populations.

Implications

The rheotactic responses of sockeye salmon fry from beaches in Lake Washington, Karluk Lake, and Cultus Lake can be readily interpreted as reflecting gene flow and random genetic drift in the absence of selection. The empirical demonstration that certain life-history patterns cannot be interpreted as adaptive has important implications for the understanding of evolution, as well as for the conservation of biological diversity. We wish to mention two of these impli-

cations (a more extensive review, focusing specifically on salmon, is provided by Adkison 1995). First, identifying "evolutionarily significant units" for the purposes of conservation (Waples 1991) may be complicated by nonadaptive phenotypic divergence attributable to genetic drift. Second, captive rearing of endangered species relaxes many of the selective pressures previously acting on individuals, and small population sizes make genetic drift increasingly relevant. Thus, captive rearing has the potential to change populations in maladaptive ways, owing not only to artificial selection but also to genetic drift acting on traits for which selection has been relaxed. Although natural selection will typically be the most important force in the evolution of life history, morphology, and behavior (Endler 1986), some instances of population divergence may be interpreted most parsimoniously by invoking genetic drift. We have provided an example of one such instance and believe that it may be a fruitful endeavor to search for others.

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