Spatial distribution, survival, and growth of sibling groups of juvenile coho salmon
(Oncorhynchus kisutch) in an experimental stream channel

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The spatial distribution, survival, and growth of two full-sibling families of coho salmon (Oncorhynchus kisutch) in an experimental outdoor stream channel were compared between the families and with the performance of one of the families in an allopatric control channel after 75 d of rearing. No difference in survival was observed between families (81.2% overall), but their spatial distributions in the channel differed markedly. One family or the other numerically dominated 5 of 7 riffle–pool habitat units within the sympatric treatment channel. The family that was larger at the beginning of the experiment (0.52 vs. 0.37 g mean mass) was also larger at the end (2.03 vs. 1.58 g). While there was little evidence of density-dependent growth overall, the growth of each family was correlated with the density of siblings in the unit. However, the larger bodied family showed negative density-dependent growth, whereas the smaller bodied family showed positive density-dependent growth. These patterns of distribution and growth may have arisen from sibling recognition or some other proximate mechanism such as assortative distribution based on size or interfamiliar variation in aggression. Regardless of the mechanism, intrapopulation variation in distribution and growth may lead to considerable variation in fitness among families because these factors affect success in subsequent freshwater and marine life history stages.


Deux familles totalement apparentées de Saumons coho (Oncorhynchus kisutch) ont été comparées l’une à l’autre quant à leur répartition spatiale, leur survie et leur croissance dans un ruisseau expérimental installé à l’extérieur et leur performance a aussi été comparée à celle de l’une des deux familles dans un ruisseau témoins, dans des conditions allopatriques, après 75 jours d’élevage. La survie s’est avérée la même chez les deux familles (survie globale de 81.2%), mais leurs répartitions spatiales respectives différaient fortement. La densité d’une famille ou l’autre était supérieure dans 5 des 7 unités rapide-bassin du ruisseau où les deux espèces étaient sympatriques. La famille la plus importante au début de l’expérience (0.52 vs. 0.37 g mass moyenne) était toujours plus importante à la fin (2.03 vs. 1.58 g). Bien qu’il y cit peu d’indices d’une croissance globale en fonction de la densité, la croissance de chaque famille s’est avérée en corrélation avec la densité des jeunes de la famille dans l’unité. Cependant, la famille à taille plus importante avait une croissance en corrélation négative avec la densité, alors que la famille à taille plus petite avait une croissance en corrélation positive avec la densité. Ces patterns de répartition et de croissance peuvent être le résultat de la reconnaissance entre frères et soeurs, ou de tout autre mécanisme, par exemple la répartition sélécive basée sur la taille ou la variation de l’agressivité entre les familles. Quel que soit le mécanisme, les variations intra-population de la répartition et de la croissance peuvent entraîner une variation considérable du fitness d’une famille à l’autre, car ce sont là des facteurs qui affectent le succès des stades subéclus marins ou dulicéoles du poisson.

[Traduit par la Rédaction]

Introduction

Stream-dwelling salmonid fishes typically occur under conditions of low productivity and high competition. Aggressive defense of feeding territories is characteristic (e.g., coho salmon, Oncorhynchus kisutch, Chapman 1962; Atlantic salmon, Salmo salar, Stradmeyer and Thorpe 1987; chinook salmon, O. tshawytscha, Taylor 1988; brook char, Salvelinus fontinalis, Grant and Noakes 1988), though nonterritorial “floaters” are also observed (Nielsen 1992). Size plays an important role in determining the outcome of aggressive encounters (Chapman 1962; Abbott et al. 1985; Maynard 1987; Huntingford et al. 1990). Size at the end of the summer affects over-winter survival (e.g., coho salmon; Hartman et al. 1987), and size in spring affects the tendency to emigrate to sea after 1 year in fresh water or, for an anadromous species, to remain for a second year (coho salmon, Holtby et al. 1989; Atlantic salmon, Metcalfe and Thorpe 1992). In addition to the effect of size, emergence date (Mason and Chapman 1965; Chandler and Bjornn 1988; Metcalfe and Thorpe 1992) and innate aggressiveness (Swain and Riédl 1990) may also influence the outcome of territorial interactions.

While size, date of emergence, and aggressiveness may affect the territorial behavior of juvenile salmonids, recognition or differential response to siblings or other kin also seems to mediate social interactions in salmonids. Sibling recognition (i.e., differential attraction to odors in two-choice mazes) has been shown in coho salmon (Quinn and Busack 1985; Quinn and Harra 1986), Arctic char, Salvelinus alpinus (Olsen 1989; Winberg and Olsen 1992), Atlantic salmon, and rainbow trout, O. mykiss (Brown and Brown 1992). Recently, Brown and Brown (1993a, 1993b) reported that young rainbow trout...
Atlantic salmon were less aggressive towards siblings than towards nonsiblings. Thus, there are complex interactions between emergence date, size, aggression, growth, survival, and life history events in salmonid fishes that may vary among families within populations. Such variation could result from genetic control of one or more of these factors or from maternal effects (egg size affects fry size, spawning date affects emergence, siblings tend to emerge in the same area, etc.). Regardless of the mechanism, variation in distribution, growth, or survival among families within a stream would be an important source of variation in fitness among families. Accordingly, we conducted an experiment to test the hypotheses that sibling coho salmon associate with each other in a field situation and that such association influences their growth and survival.

### Materials and methods

Four mature coho salmon, two males and two females, from the wild population in Big Beef Creek, a small tributary of Hood Canal, Washington, were spawned on 13 December 1991 to produce two full-sibling crosses. The eggs differed in mean mass prior to fertilization (family A, 0.25 g; family B, 0.18 g). The embryos were incubated in well water at this site under identical conditions except that the families were subjected to periodic brief (4 h) decreases in water temperature from 9.5 to 6.0°C. These temperature changes produced optical dense otolith increments corresponding to the day of the temperature change (Volk et al. 1990). By using four or five such thermal events on different dates, we uniquely identified each family without any external marks or dyes. A subsequent double-blind test verified the 100% accuracy of the marking technique. The embryos had all hatched by 26 January and completed yolk absorption by 11 March 1992.

The experiments were conducted in two parallel outdoor rearing channels fed by water from Big Beef Creek. Each 34 m long × 4.5 m wide channel was composed of seven riffle-pool units of similar size (2.4 m riffles and 3 m pools, 0.5 m deep) and natural gravel substrate. Fish could move among the units on each of the two channels but a wooden barrier between the channels prevented movement from one channel to the other. Screens could be inserted to isolate units for sampling. Fish moving downstream from the lowermost unit of each channel were trapped and identified. The fry were held for 12 d in 2 × 3 m net pens in the channels and were then released into the uppermost unit of each channel on 23 March.

The control channel had 778 fish from family A and the experimental channel had 778 fish in total. 389 from each of the two families. At this time the fish from family A were larger than those from family B (0.52 (SE = 0.01) vs. 0.37 (SE = 0.01) g, t = 9.08, P < 0.001). The channels were exposed to ambient light and temperature and avian predator pressure but no predacious fishes were present. Sufficient natural food is produced in the channels themselves or drops into the channel to support these densities of coho salmon, and the food resources do not differ between or within channels (Spalding et al. 1995). Hypothesizing that one family might exhibit competitive dominance over the other and that instream cover might be a desirable feature (McMahon and Hartman 1989), we installed Douglas-fir "Christmas trees" of uniform size and shape in four of the seven pools in each channel. The fish were allowed to feed, grow, and move throughout each channel without any interference for 75 d (until 6 June), then screens were installed to isolate the units from each other and all fish were removed. The salmon were sacrificed, measured, and wet-weighed, and the otoliths were removed and examined to determine each fish's family.

### Results

In the control channel with only fish from family A, the overall survival rate was 77.6% and the fish grew from an average of 0.52 to 2.02 g (Table 1). Their spatial distribution was nonrandom ($\chi^2 = 118.92, df = 6, P < 0.001$). The upstream unit had a disproportionately high density but the other units had similar densities (72.5 fish/unit with cover vs. 68.5/unit without cover, $\chi^2 = 1.54, P < 0.001$). The survival rates of families A and B were similar in the experimental channel (81.8% vs. 80.7%; $\chi^2 = 2.39, df = 1, P > 0.05$). The control and experimental channels, respectively) but more fish from family B than family A left the experimental channel (19 vs. 6; $\chi^2 = 6.76, P < 0.01$).

### Table 1. Distribution and mean mass of juvenile coho salmon after 75 d in control (family A only) and experimental (families A and B) channels

<table>
<thead>
<tr>
<th></th>
<th>Control channel</th>
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<th>Experimental channel</th>
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<tr>
<td></td>
<td>Family A</td>
<td>Family A</td>
<td>Family B</td>
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<tr>
<td></td>
<td>No.</td>
<td>Mean, SE</td>
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<td>Unit No.</td>
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<tr>
<td>1</td>
<td>177</td>
<td>1.87, 0.07</td>
<td>1C</td>
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<tr>
<td>2C</td>
<td>90</td>
<td>2.20, 0.13</td>
<td>2C</td>
</tr>
<tr>
<td>3</td>
<td>68</td>
<td>2.19, 0.14</td>
<td>3</td>
</tr>
<tr>
<td>4C</td>
<td>62</td>
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<tr>
<td>5C</td>
<td>59</td>
<td>2.15, 0.14</td>
<td>5C</td>
</tr>
<tr>
<td>6</td>
<td>69</td>
<td>1.75, 0.07</td>
<td>6C</td>
</tr>
<tr>
<td>7C</td>
<td>79</td>
<td>2.05, 0.13</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td>604</td>
<td>2.02, 0.04</td>
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Note: Units containing instream cover are designated "C." Asterisks indicate experimental channel units in which the proportion of the two families differed from that expected by their overall abundance: *, P < 0.05; **, P < 0.01; ***, P < 0.001.
Categories (dominant, subdominant, and floater) differed in all cases. Family A also displayed greater variation in final mass (variance = 0.89 vs. 0.34 g for family B; $F = 2.58, P < 0.001$), in spite of the fact that family B masses varied more at the beginning of the study (variance = 0.010 vs. 0.006 for family A; $F = 1.71, P = 0.03$). Moreover, while the average masses for family A fish in the control and experimental channels were similar ($2.02 \pm 0.04$ vs. $2.03 \pm 0.05$ g), the variance in mass was greater in the control (i.e., single family) channel than in the mixed family channel (variance = 1.08 vs. 0.89; $F = 1.21, P = 0.03$).

There was no relationship between overall density and average fish mass among units in the experimental channel ($r^2 = 0.30, P = 0.21$, Fig. 1A), but the mean masses of both families varied among units ($F = 4.48, df = 6,310, P < 0.001$ for family A; $F = 3.00, df = 6,307, P < 0.01$ for family B). The mass of fish in experimental channel units was related to the density of siblings, but the density-dependent patterns were opposite in the two families ($t$ test for difference in slopes, $t = 4.38, P = 0.002$). For family A (the larger fish), mean mass decreased as the density of siblings increased ($r^2 = 0.78, F = 17.22, P < 0.01$; Fig. 1B), but family B fish were generally heavier at higher densities of siblings ($r^2 = 0.51, F = 5.26, P = 0.07$; Fig. 1B). These relationships were also evident when mean mass was compared with the proportion of siblings, independently of total density (arc-sine transformation, family A: $r^2 = 0.65, F = 9.33, P = 0.028$; family B: $r^2 = 0.57, F = 6.69, P = 0.049$). Mass differences within families among units were unrelated to the abundance of nonsiblings ($r^2 = 0.00$ for family A, $F = 0.97$ and $r^2 = 0.20$ for family B, $F = 1.24, P = 0.32$). Finally, males and females did not differ in abundance, size, or distribution in the experimental channel ($P > 0.05$).

We were unable to determine if there were differences related to sex in the control channel because the fish were not all sacrificed at the end of the experiment.

**Discussion**

Coho salmon fry tended to associate with members of their family, and growth (both average and variance) was affected by the relative abundance of siblings. It was unclear whether these patterns resulted from responses based on phenotypic similarities or differential responses to siblings per se. Establishment of social hierarchies, feeding territories, and spatial distribution of stream-dwelling salmonids is affected by fry size (Chapman 1962; Mason and Chapman 1965), date of emergence (Mason and Chapman 1965; Chandler and Bjornn 1988), and aggressiveness (Huntingford et al. 1990).

We released both families in the same (uppermost) unit of the channel at the same time to reduce the effect of prior residence on social hierarchies and distribution, but we cannot rule out some residence effect because we do not know what behavioral processes resulted in the final, nonrandom distribution of the two families. The families did vary in size when introduced into the channel and such variation would be a normal feature of salmon fry populations. Fleming and Gross (1990) reported variation in egg mass of up to 255% within populations and egg size is correlated with fry size (Beacham and Murray 1990). Large size is generally associated with social dominance (e.g., Abbott et al. 1985), though it has been argued that size may result from dominance rather than cause it (Huntingford et al. 1990).

Nielsen (1992) observed that coho salmon in three status categories (dominant, subdominant, and floater) differed in

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**Fig. 1.** Masses (mean ± SE) of juvenile coho salmon in experimental riffle-pool units in relation to the number of fish in the unit. (A) Mean mass versus total number of fish (all from family A in control channel units and from families A and B combined in experimental channel units). (B) Mean mass of families A and B in the experimental channel units in relation to the number of siblings in that unit.
size and growth rate. However, habitat units contained fish in all three categories and growth of fish in each category was generally similar among habitat units. Our experimental units were similar in size and food resources (Spalding et al. 1995), hence habitat units should have had fish representing mixtures of size and social status rather than having certain units occupied by all large, dominant fish and others occupied by small, low-status fish. While size was likely correlated with status of fish within each unit, the patterns of distribution could not be explained simply as a consequence of the difference in size between the families at the beginning of the experiment.

Independently of initial fry size, which has the strong maternal influence of egg size, there might be variation between families in aggressiveness, as has been shown among populations of coho (Rosenau and McPhail 1987) and chinook salmon (Taylor 1988) and within families of coho salmon (Swain and Riddell 1990). If one family was more aggressive than the other, we expect that they would have been socially dominant within units but evenly distributed among units, contrary to our results. Thus, we doubt that differential aggression is an adequate explanation for the skewed spatial distributions of the families.

Alternatively, the association of siblings may have resulted from a combination of attraction to siblings (Quinn and Busack 1985; Quinn and Hara 1986) and reduced aggression to siblings (documented in other salmonid species; Brown and Brown 1993a, 1993b). The biased distribution of fish with respect to sibship was highly significant but never approached uniformity. As discussed by O’Hara and Blaustein (1985), many factors besides sibship may influence aggregation, leading to imperfect sibling associations. In our study, such factors as body size and aggressiveness and date when individuals established territories after leaving the upstream unit probably influenced the spatial distribution of fish independently of sibling association.

Kin recognition and differential behavioral responses to kin have been reported in a wide variety of animals (Hepper 1986; Fletcher and Michener 1987). In non-salmonid fishes, kin recognition appears to influence parent—offspring interactions in Midas cichlids, Cichlasoma citrinellum (McKay and Barlow 1976), cannibalism in poeciliids (Locke et al. 1982), and schooling in threespine sticklebacks, Gasterosteus aculeatus (Van Havre and FitzGerald 1988). The adaptive value of the salmon sibling associations is not entirely clear. If siblings are less aggressive towards each other than towards nonsiblings, more time might be available for predator vigilance or foraging in sibling groups. Consistent with this hypothesis, the final mass of family B fish was positively associated with sibling density and the proportion of siblings. However, the reverse was true for family A, and neither family’s mass was correlated with the density of nonsiblings. Family A may have been more aggressive than family B, even towards siblings. Emigration from the channels was uncommon but most of the emigrants were from the smaller bodied family, consistent with Chapman’s (1962) hypothesis that downstream movement reflects competitive inferiority.

The more variable mass of family A fish in the control versus the mixed family channel is consistent with Beacham’s (1989) finding that the growth of coho salmon reared in single-family tanks was more variable than the growth of the same families in tanks containing mixed families. Fish from a fast-growing and presumably competitive family may grow faster or show less variation in growth when reared with members of other, comparatively less competitive families than when reared with their highly competitive siblings. Growth rate is a heritable trait in coho salmon (Hersherberger et al. 1990) but there are also genetic differences in aggressiveness (Rosenau and McPhail 1987; Swain and Holby 1989).

Survival did not differ between families in sympathy, even though one family was consistently larger. A longer experimental period or heavier predation pressure might have resulted in different levels of survival; coho salmon survival during the winter in fresh water is positively related to size (Hartman et al. 1987; N.P. Peterson and T.P. Quinn, in preparation). The birds (belted kingfisher, Ceryle alcyon, and green-backed heron, Butorides striatus) observed preying on juvenile coho salmon in a previous experiment in the channel (Spalding et al. 1994) may not have been size selective. However, fish predators (cottids and salmonids) present in Big Creek but excluded from the experimental channels tend to take smaller individuals (Patten 1977; Ruggerone 1992; but see Fresh and Schroeder 1987).

The results did not indicate whether the salmon were innately attracted to their siblings, because the families were incubated and reared with only siblings prior to the experiment, and the maternal influence of egg size affected initial fry size. However, full-sibling families incubated in isolation commonly occur in salmon populations, and egg size varies substantially within salmon populations; thus, the results are relevant to natural situations. The constraints on movement imposed by the size and shape of the channel may have led to stronger kin-biased distribution than might occur in a stream. Nevertheless, the results indicate that the composition of individual pool populations may be biased towards particular families, even beyond the extent expected by variation in fecundity and egg-to-fry survival. Studies of the genetics or behavior of juvenile salmonids in streams should take such patterns into consideration when sampling programs are designed. Finally, the differences in density-dependent growth patterns and variance in growth between families suggest that these factors should be carefully evaluated in future studies of sibling association.

Acknowledgments

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Chandler, G.L., and Bjorn, T.C. 1988. Abundance, growth, and


