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LEARNING AND SIBLING ODOR PREFERENCE IN JUVENILE ARCTIC CHAR, *Salvelinus alpinus* (L.)

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Abstract—The importance of learning for sibling odor preference in juvenile Arctic char was analyzed in the present study. Fish were reared in the following eight conditions: (1) communally with siblings for 15 months; (2) communally with siblings for 17 months; (3) in isolation since fertilization; (4) in isolation since fertilization and exposed to sibling scent during the whole rearing period; (5) in isolation since fertilization and exposed to sibling scent from time of free swimming; (6) in isolation since fertilization and exposed to sibling scent during the whole rearing period, except two months without scent until testing; (7) in isolation since fertilization and exposed to sibling scent from time of free swimming, except two months without scent until testing; and (8) communally with siblings followed by a two-month isolation until testing. Char were followed individually in a Y-maze (fluviarium test) with a video-computer-based image analysis system for 12 hr. Sibling-scented water was supplied to one lateral half of the test area and water from nonsiblings on the opposite half. Isolated individuals without any preexposure to siblings showed no significant preference. Test fish reared with siblings and those that had been reared in isolation but exposed to sibling scent until testing preferred water conditioned by their own siblings. Isolated fish that had been exposed to sibling scent since fertilization, or since free swimming, followed by a two-month period with only pure water, showed no significant preference. Char isolated for two months after being communally reared preferred water scented by siblings. The results demonstrated that behavioral discrimination between siblings and nonsibling odors occurred after total isolation (isolated both from siblings and sibling odors) only in individuals that had been communally reared. This may suggest that social interactions are important for learning and long-term memory of sibling odors in Arctic char.

Key Words—Arctic char, attraction, fish, fluviarium, kinship, odor, salmonids, *Salvelinus alpinus*, siblings.

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INTRODUCTION

Behavioral discrimination of siblings or close relatives has been demonstrated in social organisms of various taxonomic groups (reviews: Holmes and Sherman, 1983; Blaustein and O'Hara, 1986; Fletcher and Michener, 1987; Waldman, 1987, 1988). Such behavior has been proposed to be part of a kin recognition or discrimination mechanism. It has been suggested that the ability to discriminate kin may increase an individual's inclusive fitness (its own and close relatives' reproductive success) and decrease the risk of inbreeding (Hamilton, 1964).

Four mechanisms have previously been proposed for kin recognition (Blaustein, 1983; Holmes and Sherman, 1983), (1) spatial distribution—relatives are distributed predictably in space; (2) familiarity or previous association, i.e., recall of features learned during previous social interactions with a special group of kin; (3) phenotypic matching—an individual learns the phenotypes of relatives or itself, and relationships with other individuals are determined by comparing the learned phenotype with that of an unfamiliar conspecific; and (4) both the phenotype and its recognition have genetic bases and no learning is involved. This division into four mechanisms has recently been revised by some authors. Waldman (1988, 1991) divided kin recognition mechanisms into two categories: indirect (item 1 above) and direct (items 2–4 above) recognition. He suggested that direct recognition is composed of a series of events. Individuals expose labels, which are perceived by a second individual, and due to the fit of these labels to a template (innate or acquired) recognition occurs, which, in an appropriate social context, may lead to behavioral discrimination. It is the behavioral response that tells the observer that recognition and discrimination has occurred.

In fish, very little is known about the ability to distinguish between individuals or groups with different degrees of relationship. Most studies have been concerned with the ability of salmonids to use olfaction for kinship discrimination (Olsén, 1992). In salmonids sibling discrimination by chemical cues has, up to now, been demonstrated in three species, i.e., coho salmon, *Oncorhynchus kisutch*, Arctic char, *Salvelinus alpinus*, and rainbow trout, *Oncorhychus mykiss* (Quinn and Busack, 1985; Quinn and Hara, 1986; Olsén, 1989; Winberg and Olsén, 1992; Brown et al., 1993). Test fishes preferred water scented by unfamiliar siblings over unfamiliar nonsiblings. These studies indicated that the olfactory cues acting as intraspecific attractants are genetically determined. The results also suggest that odor traits from siblings are learned and then used as templates against which unfamiliar traits are compared.

Winberg and Olsén (1992) demonstrated that individual Arctic char kept in isolation since fertilization showed no preference when given a choice between two water currents scented by siblings and nonsiblings. The results indicated that juvenile Arctic char either learn the odor quality of siblings but not their

own smell, or they do not use the information (i.e., no self-matching). The study also indicated that the olfactory features are learned at an early age, because fish that were placed with siblings for 50–62 days after 15 months in isolation still showed no preference. In the present study we try to analyze the impact of isolation and communal rearing for sibling odor preference in juvenile Arctic char. Isolated fish were exposed to sibling-scented water either from the time of fertilization or from free swimming until testing. In some other isolated individuals, sibling odors was removed for two months before testing. Moreover, char were placed in isolation for two months after they had been reared communally since fertilization. The results suggest that communal rearing is important for permanent learning of sibling odors in Arctic char.

METHODS AND MATERIALS

Fish. Two full-sibling families were created by using two pairs of Arctic char at the Kälarne hatchery of the Swedish National Board of Fisheries. The parents were offspring of individuals caught in Lake Hornavan, Lapland, Sweden. Egg lots from these two pairs, family A and family B, were transported to the Department of Limnology, Uppsala University, within 12 hr of fertilization at the hatchery.

Most eggs from family A (ca. 300) were placed together and supported for communal rearing (called rearing regimes 1a and 1b in Figure 1) and hereafter referred to as test groups 1a and 1b. These eggs from family A and the fertilized eggs from family B (ca. 300) (B fish were only used as odor donors in fluviarium tests, not as test fish) were placed in two separate troughs (41 cm long, 69 cm wide, and 12.5 cm deep) supplied with 800 ml/min of aerated tap water. These two families were later transferred to a fiberglass holding tank (500 liters), supplied with 1200 ml/min of aerated tap water.

Twenty-five fertilized eggs from family A were placed individually in a trough with separate compartments (58 × 58 × 45 mm deep). Each compartment had its own water supply and outlet and was supplied with 40 ml/min of aerated Uppsala tap water (oxygen at least 80% of saturation). Eleven of the fish were reared in total isolation (i.e., only supply of tap water) up to testing (rearing regime 2). When fish became free swimming (four months after fertilization), the supply of sibling-scented water was started to the remaining 14 (rearing regimes 4a and 4b). Fish supported to rearing regime 4a were exposed to sibling odors up to testing as group 4a. At 15–16 months after fertilization, the supply of sibling odors was stopped to seven fish, giving rearing regime 4b (group 4b), and the group was tested two months later (median 56 days; range 52–60).

Another 25 eggs from family A were individually placed in a similar trough

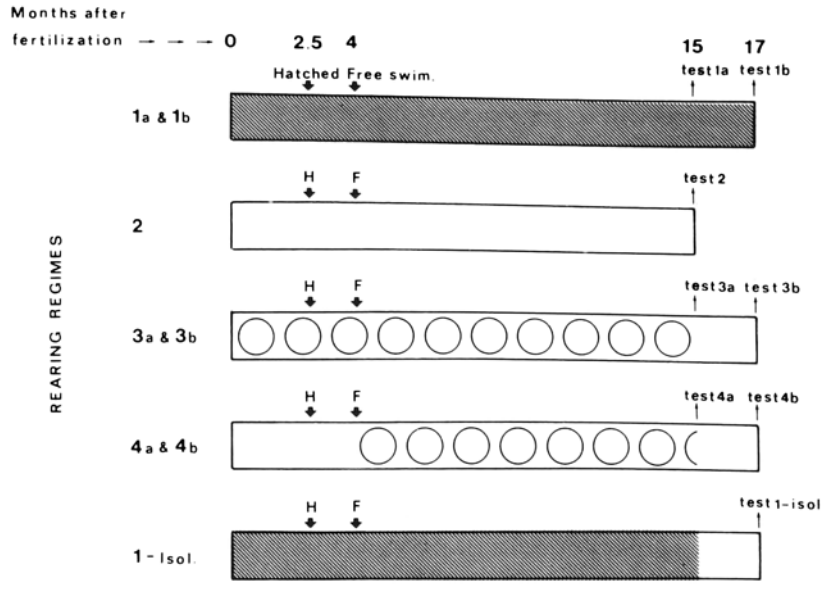

FIG. 1. Diagram of the different rearing regimes giving rise to eight different groups tested in the fluviarium. Two groups of 1b were tested, but for all other groups only one group of each rearing regime was used. Each individual was tested only once. Hatched bar or hatched part of a bar indicates fish kept together with siblings; open bar or open part of a bar indicates isolated fish without any contact with sibling odor; circles in an open bar indicate sibling-scented water was supplied to isolated fish. "Free swim." indicates time when fish had filled their swim bladder and were free swimming.

with separate compartments. These compartments were supplied with 20 ml/min of aerated tap water and 20 ml/min of sibling-scented water taken from the trough containing the 300 family A eggs and later fry. These eggs gave test groups 3a and 3b (rearing regimes 3a and 3b in Figure 1). Fish supported to rearing regime 3a were exposed to sibling odors up to the day of testing. At 15–16 months after fertilization, the supply of sibling odors was stopped to seven fish, giving rearing regime 3b and, the group was tested two months later as group 3b (median 56 days; range 52–60).

At the same time that the supply of sibling odor was terminated to the fish of groups 3b and 4b, 14 fish from the communal holding tank were individually isolated for about two months (median 56 days; range 50–60) in compartments equivalent to the others but only supplied with tap water (40 ml/min). This rearing regime is called 1-isol (Figure 1) and the group tested is referred to as group 1-isol.

The fish hatched in early January (2.5 months after fertilization), and in March the fish isolated since fertilization were transferred to equivalent troughs with larger compartments (polyethylene beakers), but still supplied with the same water qualities at the same flow rate.

The fish were fed 1–2% of their body fresh weight per day (Astra-EWOS F139H). The automatic light/dark regimen reflected conditions at latitude 51°N, with the length of the light/dark periods being automatically adjusted to take seasonal variations into account.

Testing Apparatus. One individual at the time was tested in the standard fluviarium (Höglund, 1961) according to the procedure described by Olsén and Höglund (1985) and Olsén (1986, 1989). Each fish was tested only once. The fish was placed in the test area at least 30 min before the initial test period. Equal amounts of water (340–360 ml/min) from each aquarium (Aq 1 and Aq 2, Figure 2 in Olsén, 1989) were pumped through silicone tubes to opposite lateral halves of the fluviarium. Every 90 min for 720 min the supply was switched automatically from one side to the other. Between tests, both aquaria and the test area in the fluviarium were brushed with 95% ethanol and water. Ethanol and water were also pumped through the tubes and electromagnetic valves.

Two 20-W halogen lamps equipped with a red glass filter (RG 780, Melles Grio), with no transmission of wavelengths shorter than 750 nm (and out of range of the visual system of salmonid fish; Bone et al., 1995), were used as the light source for the video camera. This infrared light was reflected by a glass mirror and a sheet of aluminum foil through a plate of opalescent white glass situated immediately below the bottom of the test area. On the video monitor this arrangement gave a light background, without reflections, against which the fish was readily detected.

The video camera (4.8 mm lens) was placed in the plywood hood, 33 cm above the test area. The camera was connected to a monitor and a computer in an adjacent room.

The position of the fish was recorded once every 2 sec by means of a video-computer-based image analysis system. This system has previously been described for studies of fish behavior, locomotor activity measurements (Winberg et al., 1993), and preference/avoidance responses to chemical substances (Bjerselius et al., 1995). These authors have described the hardware used in the present study. The software used in this image analysis system consisted of the program EthoVision (Noldus Information Technology bv, Wageningen, The Netherlands).

In this system, the data acquisition procedure was based on the following algorithm. A picture of the empty test area was digitized. Thereafter, a picture of the test area with the fish was made. These two pictures were subtracted from each other, leaving the image of the fish and the noise. The noise was filtered

by a threshold filter, followed by transformation to a binary image. Irrelevant objects (e.g., feces) were deleted by testing objects against a criterium of size. In the present study the computer calculated the number of observations in each lateral half of the test area for each 30 min period of the trial.

Procedure. Each fish was only tested once in the fluviarium, but odor donors may have been used more than once in different situations. Each test started at 18:00 hr and ended at 06:00 hr the next morning in order to avoid ordinary working hours in the lab. All tests were run in darkness. Fish from the different rearing conditions were tested for their preference when given a simultaneous choice between water scented by siblings and nonsiblings, respectively. In a control test, unscented water from the two donor aquaria was added to opposite lateral halves of the fluviarium.

Experiment 1. All tests were performed between February 15 and March 31. Fish reared in isolation with a supply of only water (group 2 from rearing regime 2) or a supply of sibling-scented water (groups 3a and 4a), and fish reared together with siblings (group 1a) were tested. Fish of the different groups weighed the same (mean $\pm$ SD: 6.6 $\pm$ 2.4 g; $N = 33$). Twenty char were placed as odor donors in each aquaria. The weights of the odor donors were matched just before they were placed in the donor aquaria so that the difference in total weight between the donor groups was always less than 10%. The water temperature increased during the testing period from 8.3 to 12.1°C.

Experiment 2. All tests were performed between May 1 and July 1. The supply of sibling-scented water to isolated fish was removed (rearing regimes 3b and 4b). Moreover, the effect of isolation later in life was tested by transferring individual fish from communal aquaria to separate compartments, giving rearing regime 1-isol. The fish were reared under these conditions for ca. 2 months (median 56 days, range 52–60) after which they were tested as group 1-isol for their preference when given a simultaneous choice between water scented by siblings and nonsiblings, as described above. Two groups of fish reared with siblings (group 1b) were also tested. The mean weight of all test fish used was 10.7 $\pm$ 3.9 g ($N = 32$). There were 15 odor donors in each donor aquarium. An increase in size of the fish justified the use of fewer odor donors than in experiment 1. The water temperature range was 12.0–14.0°C.

Data Analysis. A fish's preference for either water quality was determined on the basis of the number of observations in each. A reaction value (Rv) for a test was calculated as stated in Olsén (1986) from the following equation:

$$Rv = [(N_1 - N_2)/(N_1 + N_2)] \times 100$$

where N_1 and N_2 represent the number of observations in each half of the test area supplied with water from donor aquaria 1 and 2, respectively. Siblings and nonsiblings were always placed in donor aquaria 1 and 2, respectively. Thus, an attraction towards sibling-scented water is indicated by a positive Rv. The

number of observations ($N_1 + N_2$) in each test was 14,400 (8 × 1800). (For further details see Olsén and Höglund, 1985; Olsén, 1986.)

The arithmetic means of reaction values from identical tests are designed *MRv*. Confidence limits (CL) of *MRv*s were calculated using *t* statistics. The reaction was said to deviate from an indifferent reaction, i.e., from $MRv = 0$, if $MRv \pm 95\%$ CL did not include $MRv = 0$. Kruskal-Wallis analysis was used as an initial test to reveal differences between groups within an experiment. When the Kruskal-Wallis analysis indicated differences between groups, the Mann-Whitney U test (two-tailed) was used to compare the reaction of two groups (Siegel, 1956).

RESULTS

Control Tests. The test fishes did not prefer either water current of unscented water from the two donor aquaria being added to opposite lateral halves of the fluviarium, i.e., the total reaction did not deviate from $MRv = 0$ ($MRv \pm 95\%$ CL: -2.9 ± 5.0) (Figure 2).

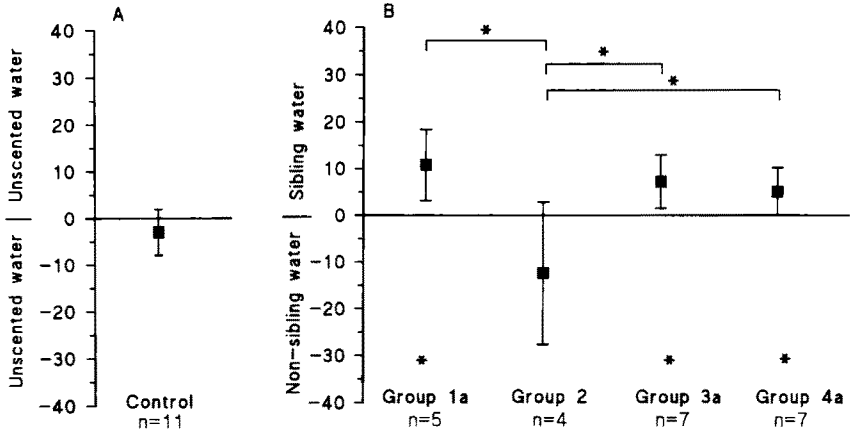

FIG. 2. Reaction of one char at a time during simultaneous choice between two types of water in the fluviarium. (A) Unscented water supplied to both sides, (B) water scented by siblings to the test fish and nonsiblings supplied to opposite sides. Reactions are given as mean reaction values, $MRv \pm 95\%$ CL, for each group (for description of groups see Figure 1 and the text). The reaction shown by a group was said to deviate from an indifferent reaction, i.e., from $MRv = 0$, if $MRv \pm 95\%$ CL did not include $MRv = 0$. Number of fish tested is indicated below each group. A significant difference between groups is denoted by asterisks and a significant difference from the control by asterisks in connection to group affiliation (Mann-Whitney U test). $^*P < 0.05$.

Experiment 1. The reactions of char from groups 1a, 3a, and 4a were significantly different from the results of the control test (Figure 2). Kruskal-Wallis analysis revealed that there were differences in reactions between groups 1a, 2, 3a, and 4a ($H = 8.62$, $df = 3$, $0.02 < P < 0.05$).

Char raised communally with siblings (group 1a) preferred water scented by siblings to water scented by nonsiblings (*MRv* ± 95% CL: +10.8 ± 7.6) (Figure 2). Individuals reared in isolation without any supply of sibling-scented water (group 2) showed no preference for sibling- or nonsibling-scented water (*MRv* ± 95% CL: −12.4 ± 15.2) (Figure 2). However, fish that were raised in isolation in compartments provided with sibling-scented water (group 3a) preferred water scented by siblings to water scented by nonsiblings (*MRv* ± 95% CL: +7.2 ± 5.7) (Figure 2). Char that were reared in such compartments but with a supply of siblings odor from free swimming fish (group 4a) exhibited an attraction that approached significance (*MRv* ± 95% CL: +5.1 ± 5.1) (Figure 2).

Individuals raised in isolation in compartments supplied with sibling-scented water since fertilization (group 3a) did not differ from fish that were exposed to sibling odors since they were free swimming (group 4a, Figure 2). However, fish raised with siblings (group 1a) as well as fish raised in separate compartments supplied with sibling odor, either during the whole rearing period (group 3a) or since start of free swimming (group 4a), differed significantly ($P = 0.016$, $P = 0.042$ and $P = 0.024$, respectively) from the char that had been raised in isolation without any supply of sibling-scented water (group 2).

Experiment 2. The reaction of group 1 char (two different groups of 1b in Figures 3 and 4) and group 1-isol (Figure 4) were significantly different from the controls. Kruskal-Wallis analysis revealed differences in reaction between groups 1b, 3b, and 4b ($H = 8.51$, $df = 2$, $0.01 < P < 0.02$) (Figure 3). There was a significant difference in reaction between groups 1b and 4b (Figure 3).

Fish that had been reared in separate compartments supplied with sibling-scented water during the entire rearing period and those that had been reared in such compartments with a supply of sibling odors since they were free swimming showed no significant preference for water scented by siblings after being deprived of the experience of sibling-scented water for two months (*MRv* ± 95% CL for group 3b: +2.2 ± 7.9; and for group 4b: −2.0 ± 4.8) (Figure 3).

No difference in reaction was observed between the fish that remained in the trough with siblings (group 1b) and the fish that previously had been reared in this group but were removed to separate compartments two months prior to testing (group 1-isol) (Figure 4). Both groups showed attraction to sibling-scented water (*MRv* ± 95% CL for group 1b: +10.0 ± 7.6; and for group 1-isol: +12.0 ± 6.7).

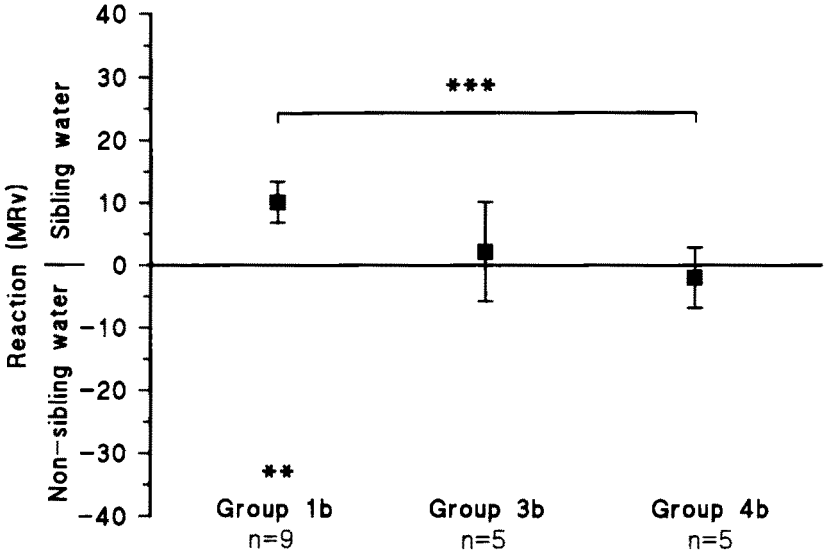

FIG. 3. Reaction of one char at a time during simultaneous choice between water scented by siblings to the test fish and nonsiblings in the fluviarium. Isolated fish preexposed to sibling-scented water were reared for two months without a supply of odors (groups 3b and 4b). For a description of groups see Figure 1 and the text. Reactions are given as described in Figure 2. The number of fish tested is indicated below each group. A significant difference between groups is denoted by asterisks and a significant difference from the control by asterisks in connection to group affiliation (Mann-Whitney U test). $^{**}P < 0.01$; $^{***}P < 0.001$.

DISCUSSION

The present study suggests that communal rearing and social interactions were important for young Arctic char to remember sibling specific odors, at least in the sibling group studied. Individuals only preexposed to water scented by siblings since fertilization or since they were free swimming, but without social contact, lost their ability or motivation to discriminate between sibling and nonsibling odors after termination of the exposure. The results support our previous study in which we suggested that social interactions during the first period after hatching are important for development of sibling recognition in Arctic char (Winberg and Olsén, 1992). We do not know how long the char retain their memory of the odors of their siblings, but salmonids do have the capacity of long-term olfactory memory as, for example, the spawning migration to the home river after one to three years in the sea (Brannon, 1972; Hasler and

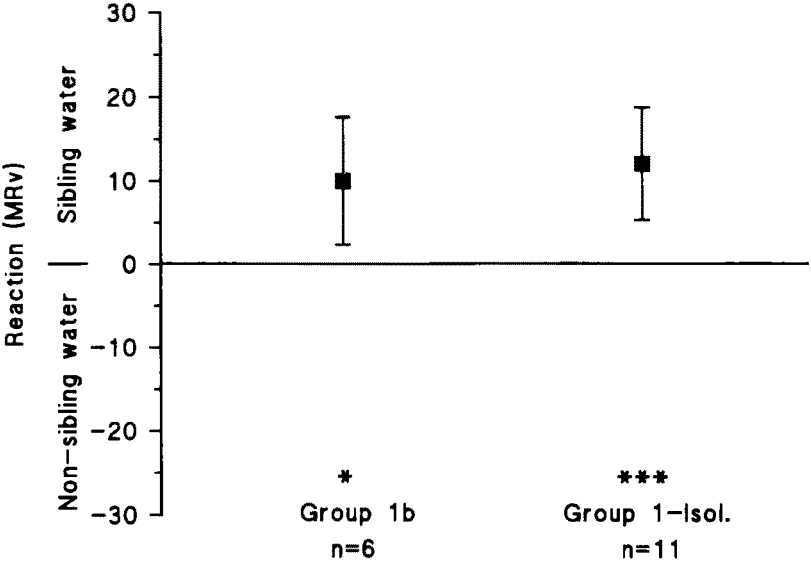

FIG. 4. Reaction of one char at a time during simultaneous choice between water scented by siblings to the test fish and nonsiblings in the fluviarium. Individuals were taken from sibling group A and reared in isolation for two months without a supply of sibling odors (group 1-isol). Test group 1b was not composed of the same fish as in group 1b of Figure 3. For description of groups see Figure 1 and the text. Reactions are given as described in Figure 2. The number of fish tested is indicated below each group. A significant difference between groups is denoted by asterisks and a significant difference from the control by asterisks in connection to group affiliation (Mann-Whitney U test). $*P < 0.05$; $***P < 0.001$.

Scholz 1983; Dodson, 1988). Odors from kin may be an important part of the home river bouquet (Nordeng, 1971; Stabell, 1984; Olsén, 1986).

In tadpoles of some species, learning of sibling odors may take place before hatching (Waldman, 1981; Blaustein and Waldman, 1992; Hepper and Waldman, 1992). In these species individuals isolated as eggs were also able to discriminate between odors of siblings and nonsiblings, an ability that seams to have an important maternal component (Blaustein and O'Hara, 1982). In contrast to our observations with juvenile Arctic char, Van Havre and Fitzgerald (1988) observed that juvenile sticklebacks could discriminate between sibling- and nonsibling-scented water even though the test fish had been isolated since the egg stage. Differences in the mechanisms behind sibling discrimination may reflect differences in natural history traits (O'Hara and Blaustein, 1988).

Grafen (1990) and Barnard (1990) proposed that most studies indicating the existence of kin discrimination fail to demonstrate true kin discrimination, but possibly only species recognition. Previous experiments have demonstrated that juvenile Arctic char are attracted to odors from conspecifics, but not to three other salmonid species (Höglund and Åstrand, 1973; Höglund et al., 1975). They are, in addition, able to discriminate between their own population and another sympatric population (Olsén, 1986) and also between odors from their own unfamiliar siblings and another sibling group from the same population (Olsén, 1989; Winberg and Olsén, 1992). These results give support to the view that juvenile Arctic char are not only able to recognize their own species odor ("pheromone," Karlsson and Luscher, 1959), but also intraspecific variation in odors, which may be a basis for kin recognition.

There are some experiments suggesting that intraspecific odors of salmonids are involved in nepotism (Brown and Brown, 1993a,b). Whether this is due to "true kin recognition" (Grafen, 1990), familiarity, or imprinting to genetically determined intraspecific odors (Winberg and Olsén, 1992), the result may be the same. Recent results with Atlantic salmon, rainbow trout (Brown and Brown, 1993a,b), and brown trout (Olsén, Järvi and Löv, accepted manuscript) have revealed that the aggressiveness in groups of siblings is significantly less than in mixed groups with both siblings and nonsiblings. The authors suggested that kin-biased behavior increased an individual's inclusive fitness, which, according to Hamilton (1964), includes the survival and reproductive success of an individual and its close relatives. Results from Brown and Brown (1993a,b) supported this hypothesis. The authors also observed that the territories were smaller and the growth rate better in pure sibling groups. Brown and Brown (1993a,b) suggested that these benefits of kin-biased behavior may increase the probability of survival.

The sibling group of Arctic char followed in the present study belongs to a lacustrine population with the entire life cycle in Lake Hornavan, Swedish Lapland. Individuals of Arctic char are, at least in lakes, thought to remain together in schools (Aass, 1970; Klemetsen and Grotnes, 1980). Thus kin-biased behavior should not be connected to territorial behavior, as suggested in young specimens of the above-mentioned three salmonid species. If, however, schools of Arctic char are composed of siblings, altruistic behavior towards kin and cooperation within the group may increase an individual's inclusive fitness (cf., Hamilton, 1964). Young individuals of lacustrine Arctic char, including the present population studied, may, however, show high degrees of aggressiveness in small experimental groups (Winberg et al., 1991, 1992), indicating that there is a high degree of plasticity in their occurrence and behavior. Changes in behavior within a group from schooling to agonistic or the reverse may reflect the local distribution of food and predator risk, as has been suggested for juvenile

chum salmon (*Oncorhynchus keta*) (Ryer and Olla, 1991). Fish presented with a defensible source of food abandon schooling and instead fight for access to the source. Kin-biased behavior with positive effects on the individual's inclusive fitness may still work, although schooling is abandoned in favor to territorial defense. The aggressiveness in pure sibling groups of juvenile Lake Hornavan char was significantly lower than in groups of mixed relationship (Olsén and Järvi, unpublished data).

The selfish herd theory proposed by Hamilton (1971) suggests that individuals in a school act in a selfish way to decrease the risk of predation. It may, however, be possible that individuals in schools of kin act in a cooperative way, not observed in groups of unrelated individuals, that increases the members' chances to avoid being eaten by predators (Waldman, 1991). We still do not know, however, if char and other fish species prefer to school with related individuals, as has been demonstrated for tadpoles of some species (Waldman, 1991). The possible preference of juvenile Arctic char to school with kin has to be examined before an analysis of the significance of kinship among school members in relation to predation and survival in general can be tested.

Present knowledge of the behavioral ecology of different local populations or stocks of Arctic char, especially during the first year of life, is scarce and further investigation is needed (Johnson, 1980; Noakes, 1980). We do not know if the present results with the sibling group tested are representative of the population. The high plasticity in behavior within the species is further stressed by the observation that significant population differences in aggressiveness (Olsén and Karlsson, 1990) and foraging behavior (Skúlason et al., 1993) are present during the same experimental conditions.

In summary, communal rearing, which included social interactions, was probably obligatory for long-term memory of sibling-specific odors in the group used in the present study. Social interactions may be obligatory for sibling discrimination in juvenile Arctic char in general. The functions of and mechanisms behind sibling recognition ability and behavioral discrimination in Arctic char have to be investigated further in the context of a plastic species with diverse behavior at individual and local population levels.

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