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Site fidelity of spawning sockeye salmon (*Oncorhynchus nerka* W.) in the presence and absence of olfactory cues

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Abstract – We examined the site fidelity of spawning adult sockeye salmon (*Oncorhynchus nerka*) by tagging and releasing fish in the same stream reach (controls) and displacing them among different but nearby sites (*c.* 50 m away). Three sites – two above a stream junction (‘upper’ reach and ‘pond’) and one below (‘lower’ reach) – allowed us to compare the behavior of salmon in the presence and absence of olfactory cues and habitat similarity. Most controls of both sexes (90%) remained in the immediate vicinity of the tagging and release site. When displaced downstream, where the odors of both the upper reach and the pond were detectable, most salmon returned to their former site (65%). Displaced sockeye were more likely to return to the pond from the lower reach than from the upper one ($P = 0.05$), consistent with olfactory orientation and the hypothesis that salmon prefer certain habitats. Salmon displaced from the upper to the lower reach were much more likely to return than those displaced to the pond ($P < 0.01$), consistent with the role of odors in orientation and inconsistent with the habitat choice hypothesis.

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Key words: Pacific salmon; Alaska; habitat selection; spawning behavior; tagging

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Un resumen en español se incluye detrás del texto principal de este articulo.

Introduction

Homing is the primary source of structuring among populations of salmonid fishes. The vast majority of Pacific salmon (*Oncorhynchus* spp.) that survive to maturity return to their natal river, although some straying occurs (Quinn 1993). Olfaction appears to be a primary mechanism for recognition of the home river (Scholz et al. 1976; Hasler & Scholz 1983). Juvenile salmonids learn chemical characteristics of the natal site at the smolt stage, and also at or prior to emergence from the gravel where they incubate as alevins (Nevitt et al. 1994; Dittman & Quinn 1996; Quinn et al. 1999), or possibly at multiple sensitive stages (Nevitt & Dittman 1998). Even within a river, salmonids tend to return to the region where they were released (e.g., Wagner 1969), indicating a high degree of homing fidelity.

Homing has been demonstrated by marking juveniles and determining the location where they return to spawn (e.g., Quinn et al. 1991; Candy & Beacham 2000). In addition, when adults are caught at a breeding site, displaced from the site, and are released, they tend to return (e.g., Hartman & Raleigh 1964; Helle 1966; McCart 1970; Blair & Quinn 1991). This behavior may reflect homing to a natal site, or the tendency to form a site association once the salmon have reached suitable breeding areas.

At some point, the process of homing must give way to spawning site selection and nest defense by females, and courtship by males. Despite the large body of research on the reproductive behavior of salmonids, relatively little work has focused on the movements of individuals within a single spawning area. There is a large literature on the attributes of sites that are preferred for nests, including water depth, velocity, and gravel size (sockeye salmon, *O. nerka* Walbaum: Hoopes 1972; chinook salmon, *O. tshawytscha* Walbaum: Neilson & Banford 1983; cutthroat trout, *O. clarki* Richardson: Thurow & King 1994; reviewed by Kondolf & Wolman 1993). In the semelparous species, the females defend their redd until they die or are too weak to withstand competition, but they may leave the site to attack competitors. In the iteroparous species, females generally leave shortly after completion of spawning (reviewed by Fleming 1998).

The movements of males are strongly influenced by attraction to ripe females (Keenleyside & Dupuis 1988), but are not known in much detail. Some studies indicate that males move frequently between nest groups as ripe females become available (Chebanov 1980), but Hendry et al. (1995) reported very limited male movement, and the movement patterns may depend on the social status of the male (Healey & Prince 1998). Thus, the interfaces between homing to the natal site, habitat selection upon arrival, and movements after the settlement period are poorly understood, especially in males, but are of considerable importance in understanding the behavior and population structure of salmon.

The objective of this study was to determine the site fidelity of spawning sockeye salmon at fine spatial scales, and the factors influencing the tendency to return to a site previously occupied. We specifically addressed the distinction between the motivation to return and the ability to locate the home site. We hypothesized that the tendency of salmon to return to their original location would be greater in the presence of olfactory cues from their site, and that they would be more likely to remain if displaced to a site similar to their own than to a dissimilar site.

Materials and methods

This study was conducted during the sockeye salmon spawning seasons in 1999 through 2002 on Hansen Creek (Fig. 1). Hansen Creek flows 2 km from a beaver pond to Lake Aleknagik in the Wood River system of south-western Alaska, and is also fed by spring ponds that enter about 1.5 km from the mouth. The stream is very shallow, averaging a depth of 10 cm and a width of 4 m (Marriott 1964). Despite its small size, it supports dense populations of sockeye salmon, averaging over 9500 from 1990 to 2002 (Quinn et al. 2003). The water is very clear and flow fluctuations are negligible even after rainfall because of the moderating influences of the ponds, springs, and topography. These features greatly facilitate surveys for tagged salmon.

The controls were captured and released at one of the three sites, and the experimental groups were reciprocal displacements of settled adults among the three sites. The ‘lower reach’ was located 26.5 m below the confluence of the creek’s main channel and the tributary draining a small spring-fed pond. The ‘upper reach’ was located 38.7 m above the confluence of the tributary draining the pond along the main channel. The outlet of the pond itself was located 27.5 m above the confluence of its tributary and the main-stem creek (Fig. 1, inset). The creek averages a width of 4.1 m throughout this area, and the outlet channel of the pond averages 2.0 m. The upper and lower reaches each consisted of a pool where fish were observed resting and spawning in all years, but were still shallow (average depth = 15 and 11 cm) with flowing water and 80–90% small gravel substrate. There was some suitable spawning habitat between the reaches, but there were also riffles that were too

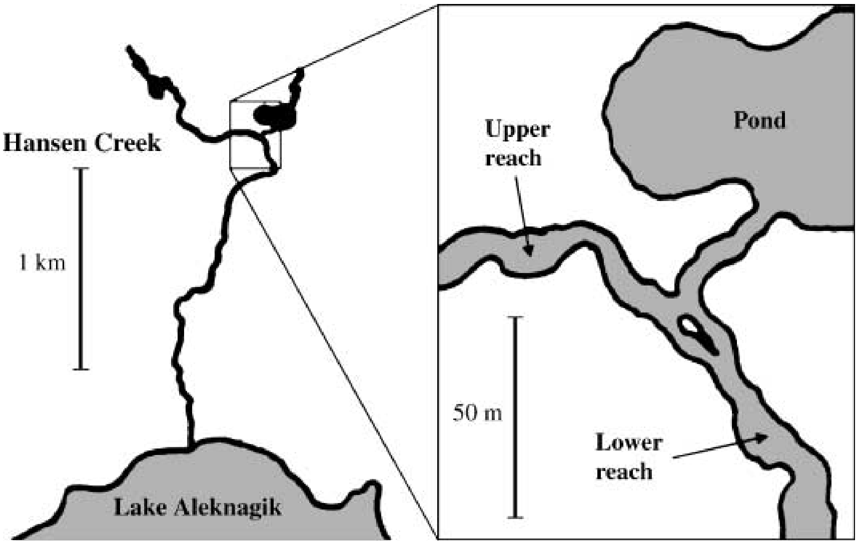

Fig. 1. Map of Hansen Creek, a tributary to Lake Aleknagik, Alaska. Inset shows the three sites where experiments were conducted.

shallow for constant occupation by spawning sockeye, and fish were neither tagged in nor transplanted to these areas. The pond is much larger than the study reach pools (area = 510 m^2), deeper (average depth = 18.7 cm), and has much lower (virtually immeasurable) velocities than the creek (Quinn & Buck 2001). Groundwater percolates up through nearly 100% fine gravel substrate, and it also receives water from a much smaller pond upstream. The pond used in this study has been occupied by spawning sockeye in all years of observation on this creek. The olfactory cues present varied in each of the three locations. In the pond, the only odor present was that of the pond. In the lower reach, the odors from the pond and the upper reach were present. In the upper reach, only the odor of the creek itself was present. In addition to this difference in odors, the pond also represented a distinctly different habitat, being deeper, wider, and having much less flow and finer substrate than the lower and upper reaches of the creek. As a consequence of the greater width and depth in the pond, the sockeye salmon are much less subjected to predation by bears than those in the creek (Quinn & Buck 2001).

Adult sockeye were captured with dip and seine nets operated by two or more researchers and anesthetized with MS222 (1999 and 2000) or Clove oil diluted with 100% ethanol (2001 and 2002). Fish were then tagged with 1.5-inch Peterson disk tags (Floy Tag Co., Seattle, WA, USA), each tag labeled with a unique identifier. The tags were placed through the muscle tissue just posterior of the dorsal fin. The entire capture, tagging, and release process took less than 5 min. Fish were allowed to recover from anesthesia in the creek, and were monitored (but not contained) at the release location until they regained full swimming ability. Recoveries were made by daily visual surveys conducted throughout the duration of spawning in the creek's entire length. Because of the excellent visibility in the creek, we assumed that any tagged fish not re-sighted in the creek had been killed and removed by bears. In recent years, the annual predation rate has averaged 49% in the entire creek system (Quinn et al. 2003), indicating that predation is a significant source of mortality, and extensive analysis of data on tagged and untagged fish supports the assumption that such 'missing' fish were in fact killed, rather than dying unnoticed (Quinn & Buck 2001).

High rates of predation and variation in density of salmon among reaches thwarted our effort to fully balance the sample sizes in control and treatment groups by reach and sex. Fish that were tagged and never again observed in the stream were excluded from this analysis. Additionally, fish that were observed dead at the first sighting were also excluded; an individual must have been observed alive on at least one day subsequent to the date of tagging to have had the opportunity to move (or not). Fish that moved and remained or spent the majority of their reproductive life in a single area were assigned to that area, even if they were observed downstream toward the end of their lives, as salmon approaching death may drift or be driven from their chosen areas. In addition to the fish tagged for this study, many sockeye salmon were tagged for an observational study in the upper reach in 2002, with identical procedures as the controls. These fish were combined with the other control fish for analysis purposes. Of the 186 total tagged 'controls', eight were eliminated because they were never seen again or were killed on the first day of the experiment, as were 9 of 92 treatment fish.

The number of males and females that remained in the reach of capture versus those that moved to another reach were compared using log-linear models implemented in the statistical program R (Ihaka & Gentleman 1996). This approach is an extension of the standard Chi-square analysis, with the ability to have more than two factors of interest (Zar 1999). We considered three factors: the result of the trial or 'fate' (remained or not for controls, returned to the reach of capture or not for treatments), sex, and location of release. Chi-square analysis statistics are Pearson χ^2 values, although the likelihood ratio test produced nearly identical significance levels.

Results

Few control fish moved from the reach where they were tagged, although the proportion that remained varied by sex and reach (Table 1). The proportion of fish that moved was highest in males in the lower reach (0.38) and lowest in males in the upper reach (0.06). We first tested the null hypothesis that fate, sex, and reach of release were all mutually independent for the controls. This null hypothesis was rejected ($\chi^2 = 14.43$; d.f. = 7; $P = 0.04$), indicating that at least one significant interaction existed. We could not reject the null hypothesis of partial independence of sex with fate and reach of release ($\chi^2 = 4.18$; d.f. = 5; $P = 0.52$), indicating that the patterns of distribution among reaches of release did not differ significantly between males and females. The analysis was therefore 'collapsed' to eliminate the distinction between males and females, and the behavior of the fish varied among release sites ($\chi^2 = 9.99$; d.f. = 2; $P = 0.01$). *Post hoc* comparisons revealed that the proportions moving from the upper reach and the pond were similar ($\chi^2 = 2.81$; d.f. = 1; $P = 0.09$), but that more controls moved from the lower reach than did controls from the upper reach and the pond combined ($\chi^2 = 7.70$; d.f. = 1; $P = 0.01$; Fig. 2).

Table 1. Proportions of adult sockeye salmon recovered from control experiments by reach of release

		Result				
Sex	Capture site	Moved to lower reach	Moved to pond	Moved to upper reach	Remained	Number
Female						
	Lower reach	N/A	0.00	0.22	0.78	9
	Pond	0.00	N/A	0.14	0.86	7
	Upper reach	0.00	0.07	N/A	0.93	67
Male						
	Lower reach	N/A	0.00	0.38	0.63	8
	Pond	0.00	N/A	0.18	0.82	17
	Upper reach	0.01	0.04	N/A	0.94	70
Total				0.10	0.90	178

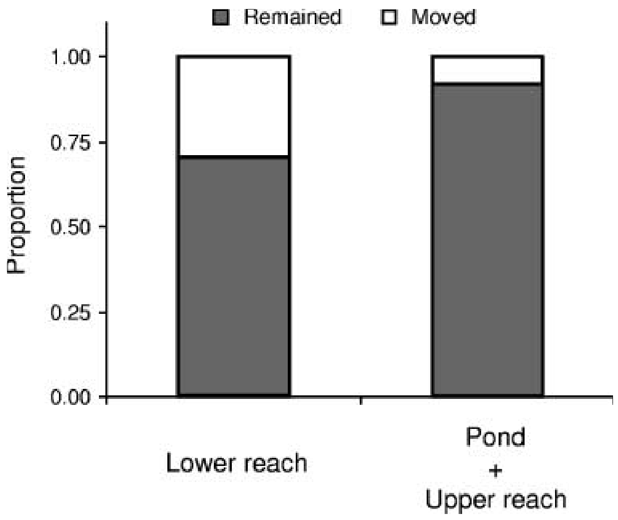

Fig. 2. Post hoc comparison of movements of control sockeye tagged and released in the same reach ($n = 17$ for lower reach, $n = 161$ for pond and upper reach combined).

Most of the fish that were tagged and displaced returned to the site where they had been captured (0.65), and most that did not return remained in the reach where they were released (0.30), rather than move elsewhere (Table 2). The proportion of fish that returned to their original reach differed with respect to the sex of the fish, the initial capture site, and the release site. We first divided the recoveries by capture site. For fish captured in the lower reach and displaced, we could not reject the null hypothesis that fate, sex, and reach of release were mutually independent ($\chi^2 = 3.48$; d.f. $= 4$; $P = 0.48$), but the sample size for this group was very small. For sockeye displaced from the pond, the test for mutual independence between fate, sex, and reach of release was marginally significant ($\chi^2 = 9.07$; d.f. $= 4$; $P = 0.06$). We tested for partial independence and could not reject the null hypothesis that sex was independent of fate and release site ($\chi^2 = 4.75$; d.f. $= 3$; $P = 0.19$). We therefore eliminated the distinction between males

Table 2. Proportions of adult sockeye salmon recovered from displacement experiments

			Result			
Sex	Capture site	Release site	Moved	Remained	Returned	Number
Female						
	Lower reach	Pond	0.33	0.00	0.67	3
		Upper reach	0.00	0.00	1.00	2
	Pond	Lower reach	0.00	0.00	1.00	7
		Upper reach	0.09	0.45	0.45	11
	Upper reach	Lower reach	0.00	0.20	0.80	5
		Pond	0.00	0.60	0.40	5
Male						
	Lower reach	Pond	0.25	0.50	0.25	4
		Upper reach	0.00	0.33	0.67	6
	Pond	Lower reach	0.14	0.00	0.86	7
		Upper reach	0.00	0.13	0.88	8
	Upper reach	Lower reach	0.00	0.15	0.85	13
		Pond	0.00	0.82	0.18	11
Total			0.05	0.30	0.65	82

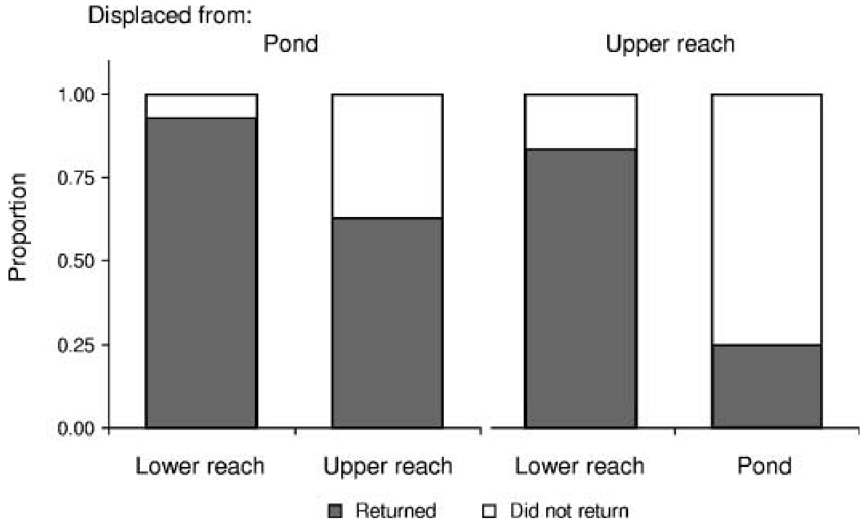

Fig. 3. Movement of treatment sockeye displaced from the upper reach and pond to the pond ($n = 16$), lower reach ($n = 18$, $n = 14$), or upper reach ($n = 19$).

and females, and the resulting comparison indicated that sockeye were more likely to return to the pond from the lower reach than from the upper one ($\chi^2 = 3.87$; d.f. = 1; $P = 0.05$; Fig. 3). For the sockeye that were displaced from the upper reach, we rejected the null hypothesis that fate, sex, and release site were mutually independent ($\chi^2 = 12.34$; d.f. = 4; $P = 0.02$). We again could not reject the hypothesis that sex was independent of fate and release site ($\chi^2 = 1.01$; d.f. = 3; $P = 0.80$) and subsequently removed this distinction. Fate depended on release site ($\chi^2 = 11.69$; d.f. = 1; $P < 0.01$); fish displaced from the upper reach to the lower were much more likely to return than those displaced to the pond (Fig. 3).

Discussion

Our first salient result was that most controls of both sexes remained in the immediate vicinity of the tagging and release site. The proportion was somewhat lower in the lower reach, but some of these fish may have still been moving upstream when they were captured, and not been fully ‘settled’. Some of the fish in the upper site may have also been migrating, but this is less likely in the pond as few fish spawn upstream of that site. In this shallow stream, the migration is not continuous, but the fish seem to hold for short periods of time (i.e. hours to a day) between periods of active upstream swimming. Notwithstanding this possible bias, fully 90% of the fish (sites and sexes combined) remained near the tagging site, indicating limited movement even on the small spatial scale of our study.

We did not find a strong difference in site fidelity between sexes. Females typically guard their redd site until they die or are too weak to resist attacks or the flow of the stream, so it was not surprising that they seldom moved. The few fish that moved probably reflect handling stress or tagging when fish were still moving upstream. However, the movements of male salmon are less well known. There is a general sense that males move widely, seeking breeding opportunities as individual females complete spawning and are no longer receptive to courtship. This may be the case in salmonids spawning at very low densities, but our observations of sockeye salmon at high densities indicated limited male movement. Most sockeye salmon at dense spawning aggregations on beaches restrict their movements (Quinn & Foote 1994; Hendry et al. 1995). For example, the average difference in locations of tagged males on consecutive observations (made two times each day) was only 2–5 m (Quinn et al. 1996). This suggests that once the dominance relationships have been developed at a given area, males tend to await the arrival of new females rather than move throughout the spawning grounds (where they would need to re-establish dominance) in search of ripe females. The densities in Hansen Creek are the highest of the creeks surveyed in the Wood River system (more than 7500 fish per hectare in recent years; Quinn et al. 2003), and comparative studies at creeks under a range of densities would help determine the generality of our findings.

The behavior of displaced salmon showed two patterns. First, the great majority returned to their original site, even though conspecifics were present at all sites. No difference in this pattern was detected between males and females; the levels observed were consistent with the limited movements of controls. In the course of aggressive encounters or when fleeing from predators, a female salmon may move beyond her redd site and a male may move beyond the areas where his dominance status is determined. It is thus not surprising that they would have the ability and tendency to return to their sites. Second, our results indicated that site fidelity and movements over an area that would generally be considered a single spawning ground may be guided by olfactory cues as much or more than habitat features. When displaced downstream, where the odors of both the upper site and the pond were detectable, most salmon returned to their prior site of settlement. When moved to a reach where they could not detect odors from the 'home' site (i.e., upstream of their original site), they returned at a significantly lower rate. This seems to indicate that sockeye salmon have the ability to detect relatively small changes in olfactory cues at a very fine scale.

In addition to olfactory cues, the pond was physically different from the lotic reaches of the creek. Displacement of fish from the lower to the upper reach and to the pond was designed to test the propensity of fish to swim downstream, in the absence of a unique odor, to return to their 'home' site. However, the density of fish in the lower reach was low and they suffered significant predation, resulting in a small sample size, so we were unable to conclusively test this hypothesis despite considerable effort. Finally, the pond also provided some refuge from predation, and this may have increased the incidence of sockeye that remained there when displaced. In 1997–1999, intensive surveys indicated that only 9% of the salmon in the pond were killed by bears compared to 42% in the creek itself (Quinn & Buck 2001). The pond is both wider and deeper than the creek, making the fish less vulnerable to bears. Thus, salmon that homed to the upper and lower reaches after displacement into the pond were leaving a refuge to return to a very dangerous area, yet most did so. In this case, the difference between the pond and their site of prior residence in odors and habitat features was sufficient to offset the greater safety of the pond.

In conclusion, our results documented low levels of movement by sockeye salmon of both sexes on the spawning grounds, and a strong tendency to return to familiar sites, probably using odors. However, we have no evidence that the salmon were staying at or returning to the site where they had been spawned. There is experimental evidence that salmon return to the general region of a river where they were released as smolts (e.g., Wagner 1969), but we know of no evidence to document homing on spatial scales relevant to our study. In this regard, we have initiated a study using otolith-marked embryos to determine if salmon incubated in the pond return to that site, and expect results in 2004. Until such evidence is available, it is parsimonious to conclude that behavioral processes, such as nest site selection and responses to competition by females, and responses to female distribution by males, determine the initial distribution of adults within a reach of stream set by olfactory imprinting and homing. However, once this site is determined, there is a strong tendency to remain there and return there after displacement.

Resumen

1. Realizamos experimentos para analizar la fidelidad al sitio en reproductores adultos del Salmón del Pacífico *Oncorhyncus nerka*, y detectar los factores que determinan la tendencia a volver a los lugares previamente ocupados. Marcamos y soltamos peces en el mismo sitio (i.e. control) y los movimos entre localidades diferentes pero cercanas (i.e. 50 metros), para analizar las hipótesis: (1) el movimiento está mas influenciado por la preferencia a un sitio similar al propio y (2) los movimientos deben reflejar la disponibilidad de olores que emanan de un sitio previamente ocupado. Con este fin, tres sitios, dos de ellos justo por encima de la unión de un río (localidad superior y localidad pozo) y uno por debajo de la confluencia de la localidad superior y el pozo (localidad inferior), permitieron comparaciones del comportamiento en presencia y ausencia de señales olfativas (Fig. 1).

2. La mayor parte de los individuos-control de ambos sexos (90%) permanecieron en las cercanías inmediatas a los sitios de marcado y suelta (Tabla 1). Al ser desplazados aguas abajo donde los olores de localidad superior y de la localidad pozo eran detectables, la mayor parte de los salmones volvieron a la localidad original (Tabla 2). Encontramos más probable que los individuos desplazados volvieran a la localidad pozo desde lugares aguas abajo que desde lugares aguas arriba ($P = 0.05$), consistente con la hipótesis de que estos salmones prefieren ciertos hábitats (Fig. 3). Alternativamente, la localidad pozo podría proveer un olor más discreto o ser incluso la localidad natal. Además, los salmones desplazados de la localidad superior hacia la inferior fueron más probables de volver que los desplazados a la localidad pozo ($P < 0.01$), consistente con el papel que juegan los olores en la orientación e inconsistente con la hipótesis de selección de hábitat (Fig. 3).

Acknowledgements

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