



Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka*

THOMAS P. QUINN, IAN J. STEWART & CHRISTOPHER P. BOATRIGHT

Fisheries Research Institute, School of Aquatic and Fishery Sciences, University of Washington

(Received 5 October 2005; initial acceptance 21 January 2006;
final acceptance 14 March 2006; published online 6 September 2006; MS. number: A10262R)

Fish of the family Salmonidae (salmon, trout and charr) are famous for their ability to learn ('imprint') olfactory information as juveniles and to use those odour memories as adults to home to their natal site for reproduction years later. However, the spatial scale at which salmonids home has not been determined, and this is important not only for an understanding of the imprinting and homing processes but also because homing determines the spatial scale at which salmon populations are structured. To test the hypothesis that salmon home to specific habitat units within a single small creek, we induced banding patterns on the otoliths (ear bones) of pre-hatch sockeye salmon embryos by altering the temperatures at which they were incubated. Thermally marked embryos were buried in a small pond associated with Hansen Creek, in southwestern Alaska, and allowed to complete development and migrate. In the year when the salmon were expected to return to the creek, examination of otoliths from carcasses revealed that 12 of 324 salmon in the pond were marked, whereas all 138 salmon examined in the creek were unmarked. This distribution of marked fish indicates that more of the experimental salmon returned to the pond than would have occurred by chance, although we cannot be certain that all surviving salmon did so. These results contribute to the growing literature indicating the capacity for very fine-scale populations structure in salmon.

© 2006 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

The tendency of animals to migrate back to their natal site for reproduction after feeding migrations is widely distributed among diverse animal taxa (Papi 1992; Dingle 1996). In animals with lengthy migrations, such homing behaviour is a prerequisite for the structuring of the species into discrete populations. In some cases homing must be inferred from studies of population genetics because definitive marking studies are difficult to accomplish (e.g. sea turtles: Bowen et al. 1993). The teleost family Salmonidae (salmon, trout and charr) has been one of the models for research on the mechanisms of homing and the differentiation of populations, although many fish show this behaviour (Lucas & Baras 2001). Anecdotal evidence indicates that centuries ago astute observers realized that salmon returned to their natal stream to spawn (Nordeng 1989), and by the 1930s convincing scientific evidence was accumulating to support this idea (e.g. Foerster

1936). In addition to recognizing the homing ability of salmon, these early investigators (e.g. Rich 1939) understood that the homing of salmon generates populations with unique dynamics (i.e. levels of abundance and recruitment patterns) and life history traits, necessitating management and conservation as discrete units.

Evidence has accumulated that salmon populations evolve differences in a wide variety of adaptive traits (reviewed by Ricker 1972; McDonald 1981; Taylor 1991; Quinn 1999), and research has also revealed many aspects of the mechanisms of olfactory imprinting and homing (Nevitt et al. 1994; Dittman et al. 1997). However, almost all studies of homing have evaluated the behaviour of salmon released from hatcheries at the smolt (seaward migrant) stage (e.g. Quinn et al. 1991; Candy & Beacham 2000). A hatchery is an unnatural environment for incubation and rearing (hence imprinting) and it also constrains the exploratory behaviour of returning adults (Griffith et al. 1999); unfortunately, there is little information on the homing patterns of wild salmon. In particular, it is unclear how the process of homing grades into the processes of spawning site selection by females (Hoopes 1972; Kondolf & Wolman 1993) and search for mates by males (Healey & Prince 1998). Spawning grounds are heterogeneous, and it is unclear whether the perennial

Correspondence and present address: T. P. Quinn, Fisheries Research Institute, School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, U.S.A. (email: tquinn@u.washington.edu). I. J. Stewart is now at the National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, U.S.A.

use of certain regions results from homing or habitat choice (Blair & Quinn 1991; Hendry et al. 1995). In some cases mature salmon move very little within breeding sites or among nearby sites (e.g. Hendry et al. 1995; Stewart et al. 2004; Rich et al. 2006), but in other cases they move more widely (e.g. Healey & Prince 1998). The spatial scale at which salmon imprint, and at which they home, is largely unknown, but this factor will determine the finest scale at which their populations can be structured.

Salmon undoubtedly home to tributaries within large river systems (e.g. Quinn et al. 1991; Youngson et al. 1994; Candy & Beacham 2000). In addition, Wagner (1969) and Cramer (1981) reported that steelhead trout, *Oncorhynchus mykiss*, smolts released experimentally in different reaches of large rivers tended to return to those reaches as adults, although there was considerable overlap in the distributions of all groups. However, other studies showed weaker (Slaney et al. 1993) or negligible effects of release site on return location (Tipping & Hillson 2002). The release sites in all of these rivers were spread out over tens of kilometres, and we are not aware of any direct information on the homing of salmon that incubate and emerge from the gravel naturally and home to precise locations within a small creek. Such information would reveal the spatial unit at which salmon home, and also the extent to which salmon populations can differentiate with a single creek.

To address the question of fine-scale homing, we artificially spawned adult salmon, incubated and marked the otoliths (ear bones) of their progeny as pre-hatched embryos, and then buried the embryos within the substrate in a site within the creek system. The embryos completed development, emerged, migrated to the lake to feed for a year, migrated to sea to feed for two more years, and then migrated back to the creek. We then examined the otoliths of carcasses at the release site and the rest of the creek to see whether more of the marked salmon returned to their natal site than would have occurred by chance.

METHODS

Field Methods

This study was conducted on Hansen Creek (Fig. 1), a small stream that flows 2 km from a beaver pond to Lake Aleknagik, in the Wood River system of southwestern Alaska. This shallow (10-cm deep) and narrow (4-m wide) creek supports a dense population of sockeye salmon (*O. nerka*) that spawns in late July and early August. The salmon not only spawn in the creek but also in a small (19-cm-deep, area $\sim 510 \text{ m}^2$) spring-fed pond that flows 27.5 m to enter the main creek about 1.5 km from the mouth (Fig. 1; Marriott 1964; Stewart et al. 2004). The pond is occupied by tens to hundreds of spawning sockeye salmon while the rest of the creek is occupied by several thousand conspecifics (Fisheries Research Institute, University of Washington, Seattle, U.S.A., unpublished records). Previous research showed that adult sockeye

salmon (no other Pacific salmon species spawn in Hansen Creek) entering the pond tended to remain there, those displaced from it tended to return to the pond, and those displaced from the creek into the pond tended to return to the sections of the creek where they had been caught (Stewart et al. 2004). To determine whether the salmon that spawned in the pond tend to return there rather than to other sites in the creek, we marked embryos that would hatch, emerge from the gravel naturally, and complete their migrations.

We captured 28 female salmon and 25 male salmon on 1 August 2000 from the lower section of the creek and spawned them artificially by mixing the eggs from two females into a bucket with the milt from two or more males. The experimental fish thus comprised an essentially random sample from the creek and probably included few fish originating in the pond because most salmon spawn in Hansen Creek proper, both below and above the pond. Based on a fecundity estimate of 3162 eggs per ripe female in Hansen Creek (Fisheries Research Institute, unpublished data), the spawning was likely to have resulted in about 88 500 fertilized eggs. The fertilized eggs were treated with Wescodyne (Steris Corp., Mentor, Ohio, U.S.A.) to control bacteria and incubated in standard vertical stack trays at our Aleknagik field camp, in a mixture of water from the lake and a well to produce a temperature of about 10–11°C. One day after fertilization 468 dead eggs were culled, indicating high ($\sim 99.5\%$) fertilization success. The sagittal otoliths (ear bones) of sockeye salmon begin to develop after the 'eyed stage', about 269 accumulated temperature units (TUs) after fertilization ($\text{TU} = \text{days} \times ^\circ\text{C}$; (Velsen 1987). Banding patterns on the otoliths reflect natural variation in temperature, and sharp changes in temperature can induce visible dark bands (e.g. Volk et al. 1990). Such 'thermal marking' is now widely used in Pacific salmon hatcheries.

Temperature in the incubator was checked daily with a mercury thermometer and also recorded by an automatic data logger (Onset Corp., Pocasset, Massachusetts, U.S.A.) throughout August. Logistic constraints prevented us from incubating the embryos any later than the beginning of September but, based on the temperatures from the mercury thermometer, we estimated that the embryos had developed otoliths by late August. We then exposed them to three pulses of well water at 4°C for 12 h, separated by 12-h periods of 10–11°C water from 30 August to 2 September. The drops ($\sim 6^\circ\text{C}$) in temperature were designed to induce three equally spaced marks on the otoliths. Ideally this would have been done even later in the season, as the otoliths would have been more fully developed and the marks easier to detect. On 5 September the embryos were transported to the pond and carefully buried. This process entailed excavation of the substrate to a depth of 10–15 cm, approximating the depth of naturally spawned embryos in the pond, distribution of the experimental embryos among the gravel, and replacement of the substrate. The coarse substrate appeared to result in sufficient interstitial space to largely prevent immediate smothering or physical damage to the embryos. A set of 10 voucher embryos were retained on the date of burial, and subsequent examination revealed detectable marks

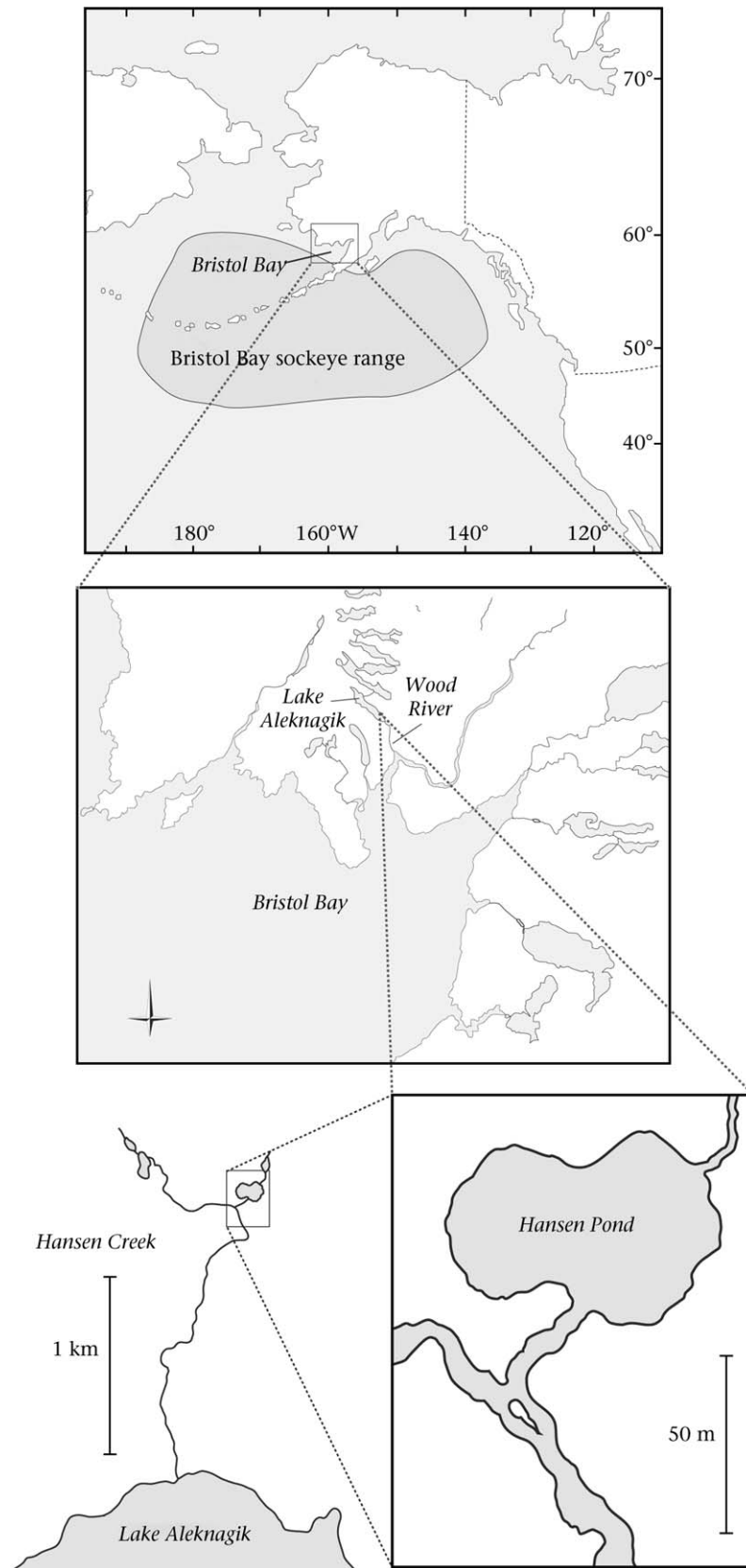


Figure 1. Maps showing the spatial scales relevant to homing by sockeye salmon from the open ocean to Bristol Bay, into the Nushagak River, then into the Wood River, to Lake Aleknagik, to Hansen Creek, and finally to the side pond where this study was conducted.

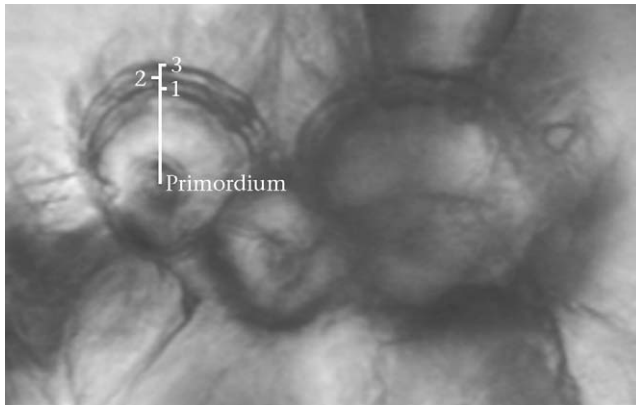


Figure 2. Thermally induced banding pattern observed on an experimentally marked otolith. The three marks are identified in order of formation.

(Fig. 2) in only four. The complete temperature records from the data logger indicated that this was a result of the embryos having just barely reached the stage at which otoliths develop at the time of marking. After accounting for mortalities during spawning, artificial incubation (only a few hundred) and reburial, approximately 87 000 embryos were successfully returned to natural rearing conditions in the pond. Some salmon spawned naturally in the pond in 2000; on the last day we surveyed the pond (14 August) there were 15 live females, and by that date three had died of senescence and 15 had been killed by bears, indicating that subsequent production from the pond would include both marked and unmarked fish. The following spring (25 June 2001), 29 fry were collected from the pond prior to their migration downstream to the lake, and we observed a mark on one of these fry, indicating that some of the marked embryos had survived the winter.

The great majority of sockeye salmon in the Hansen Creek population mature at 4 years of age (Rogers 1987), so in summer 2004 we sampled all 446 sockeye salmon returning to the pond. Examination of the otoliths indicated that 324 of them (72.6%) were age 4 and so might have been marked. The total run to Hansen Creek in 2004 was estimated at 3913 sockeye salmon based on the number of carcasses counted during daily surveys and the number of live salmon on the last day surveyed. The creek is very shallow, and many salmon (over three-fourths in 2004) become stranded or are killed by bears or gulls at the mouth, or during their migration upstream (Quinn & Buck 2001). We therefore restricted our sampling to 215 salmon that had died of senescence in the creek, avoiding those fish found dead of other causes that might still have been migrating when killed. Of the 215 salmon sampled from the creek, 138 (64.2%) were age 4 (12 recovered below and 126 upstream of the pond). The otoliths from these creek and pond fish were examined 'blind' by staff of the Alaska Department of Fish and Game. Specifically, they were presented with voucher specimens of the marked embryos and asked to indicate which adult specimens (in numbered vials with no indication of collection site) possessed the mark.

They did so conservatively, only identifying otoliths as marked if they were unequivocally so.

Data Analysis

Under ideal circumstances we would have marked 100% of the embryos in the pond, but this was not possible because we could not artificially spawn every salmon that entered the pond in 2000 and we did not prevent natural spawning by salmon in the pond. Given this limitation, it would have been desirable to know what fraction of the embryos were marked, but this was also impossible. We could estimate how many embryos were alive when we buried them but we had no way of knowing how many survived to the free-swimming fry stage, nor did we know how many fry were produced by the females spawning in the pond. Survival of sockeye salmon from fertilization to fry emergence varies around an average of about 10% (Quinn 2005). Much of the natural mortality seems to occur between fertilization and the 'eyed' stage (when we buried the embryos), but the experimental embryos may have incubated faster than naturally spawned ones in the creek or the pond because the mixture of lake and well water was warmer than the water in the pond. Thus the experimental embryos could have hatched and emerged earlier than the naturally spawned ones, and this may have compromised their survival. Finally, examination of the voucher specimens indicated that the marking was initiated prematurely, so the otoliths of only a fraction were successfully marked. Given these issues, we took three analytical approaches to test the hypotheses that the experimental salmon returned to the pond.

First, we used a chi-square contingency test to estimate whether the distributions of marked and unmarked fish in the pond were similar, against the predicted alternative that marked fish would be more prevalent in the pond. Second, we reasoned that if many experimental fish returned to the pond, this would elevate the proportion of age-4 fish, relative to the creek as a whole, in 2004. A chi-square test was therefore used to determine whether the proportions of age-4 and age-5 differed between the pond and the creek in that year.

Because the proportion of experimental fish homing to the pond was a function of several quantities, each based on relatively small samples and therefore subject to sampling error, we used a Bayesian approach to estimate the proportion homing and to retain the appropriate degree of uncertainty about this estimate. Bayesian methods are ideal for this type of analysis, and the results can be easily interpreted in terms of relative probability, unlike conventional confidence intervals or *P* values (Hilborn & Mangel 1997; Wade 2000).

There were four sources of information relating to four unknown quantities in this analysis: the proportion of fish in the creek that were age-4 (*A*), the proportion of experimental fish that were marked (*E*), the proportion of age-4 fish in the creek that were marked (*M*) and the proportion of marked age-4 fish that homed to the pond (*H*). Therefore, the total likelihood was the product of the following four components:

$L(215, 138|A)$ = likelihood of observing 138 age-4 fish from the 215 fish of known age, given A .

$L(10, 4|E)$ = likelihood of observing four marked embryos from 10 retained vouchers, given E .

$L(138, 0|M)$ = likelihood of observing no marked fish from the 138 age-4 fish in the creek, given M .

$L(\hat{N}_m, n_m|\hat{R})$ = likelihood of observing n_m marked age-4 fish in the pond from \hat{N}_m total expected marked age-4 fish in the creek, given \hat{R} , the proportion of age-4 fish homing to the pond (H) or returning to the pond by chance (\hat{C}), where

$$\hat{N}_m = 12 + (3467 \times A \times M) \quad (1)$$

is a function of the 12 marked fish that we observed in the pond, the 3467 fish in the creek and the two unknown parameters A , M ;

$$\hat{R} = H + (1 - H) \times \hat{C}. \quad (2)$$

Without a direct estimate for \hat{C} , we conservatively assumed that the proportion of marked fish returning to the pond by chance would be equal to the proportion of all nonexperimental age-4 fish in the creek that returned to the pond.

$$\hat{C} = \frac{\left[324 - \left(\frac{12}{E} \right) \right]}{\left[324 - \left(\frac{12}{E} \right) + (3467 \times A) - \left(\frac{\hat{N}_m - 12}{E} \right) \right]} \quad (3)$$

is again a function of the 12 marked fish that we observed in the pond, the 3467 fish in the creek, the quantity \hat{N}_m from above and the unknown parameter E .

Each likelihood was assumed to be binomially distributed with the following general form,

$$L(n, x|p) = \frac{n!}{x!(n-x)!} p^x (1-p)^{(n-x)}$$

where n is the number of trials, x is the number of successes and p is the probability of success.

We used the sampling/importance resampling (SIR) method (Rubin 1987) to sample from the joint posterior density of the four model parameters, conditioned on uniform priors from 0.0 to 1.0 for each of the four proportions. SIR provides a simple approach to numerical integration well suited to a problem of small dimension with relatively easily calculated likelihoods (McAllister et al. 1994; Punt & Hilborn 1997). This method draws parameters randomly from the prior distributions, calculates the total likelihood of each draw and retains a sample of the total draws with a probability proportional to the likelihood of each draw. The algorithm was run until 50 000 unique samples had been obtained from the joint posterior distribution of model parameters.

RESULTS

Marks were detected in 12 of the 324 fish of age-4 in the pond and 0 of the 138 fish of that age in the creek. The chi-square test, after Yates' correction for small samples, indicated that the proportions of marked and unmarked

fish were unlikely to have differed this much by chance ($\chi_1^2 = 3.88$, $P < 0.05$). Similarly, the proportion of age-4 fish in the pond (324 of 446 = 72.6%) was significantly higher than the proportion in the creek (138 of 215 = 64.2%; $\chi_1^2 = 4.93$, $P < 0.05$), consistent with the hypothesis that the artificially spawned fish had contributed to the population in the pond. Such a difference might arise from exclusion of old (thus large) fish from the pond by physical access up the shallow creek linking the pond with Hansen Creek proper. To evaluate this possibility, we compared the lengths of males and females in the pond and the creek from all years ($N = 6$) with sufficiently large numbers of measured fish. For both males and females, there were 3 years in which the fish in the pond were smaller than those in the creek at large, and 3 years in which this was not the case. In addition, males are considerably larger than females in length and body depth, so if large fish were unable to enter the pond, we would expect higher proportions of males in the creek than in the pond in each year. However, there was only one year in which females were more numerous in the pond; in 2 years, males were more numerous in the pond, and in 3 years, the proportions were similar. One final piece of evidence that the experimental fish augmented the population was the fact that the pond generally supports only a small fraction of the spawning in the creek (range 0.0–11.71% during 1991–2004) but the value in 2004 (11.65%) was the second highest on record.

Despite the small sample size and substantial parameter uncertainty in this analysis, we found strong evidence that a large proportion of the marked fish homed back to the pond where they were incubated. The median of the posterior probability distribution for the proportion of marked fish homing to the pond was 0.580, with a 90% probability that the value was between 0.156 and 0.937. The median posterior probability estimates for the other three model parameters were very close to the partial maximum likelihood estimates from each component; the proportion of adults marked = 0.003, proportion of marked age-4 fish in the creek = 0.640, proportion of embryos carrying a readable mark = 0.413. The marginal posterior distributions are shown in Fig. 3.

DISCUSSION

The homing by salmonid fish to their natal site for breeding is widely known but still incompletely understood in many respects. The 'classic' description of the phenomenon is that salmon imprint on odours that they detect during migration from freshwater to marine environments. This transition from the parr stage to the smolt stage is marked by many physiological changes, including increased levels of thyroid hormones long associated with imprinting (Hasler & Scholz 1983). Although many experimental studies have supported the concept of imprinting at this stage (e.g. Scholz et al. 1976; Morin et al. 1989), the natural history of many salmon populations dictates that olfactory imprinting must occur earlier as well, probably between the period when the embryos hatch and when they emerge from the gravel as free-swimming fry some

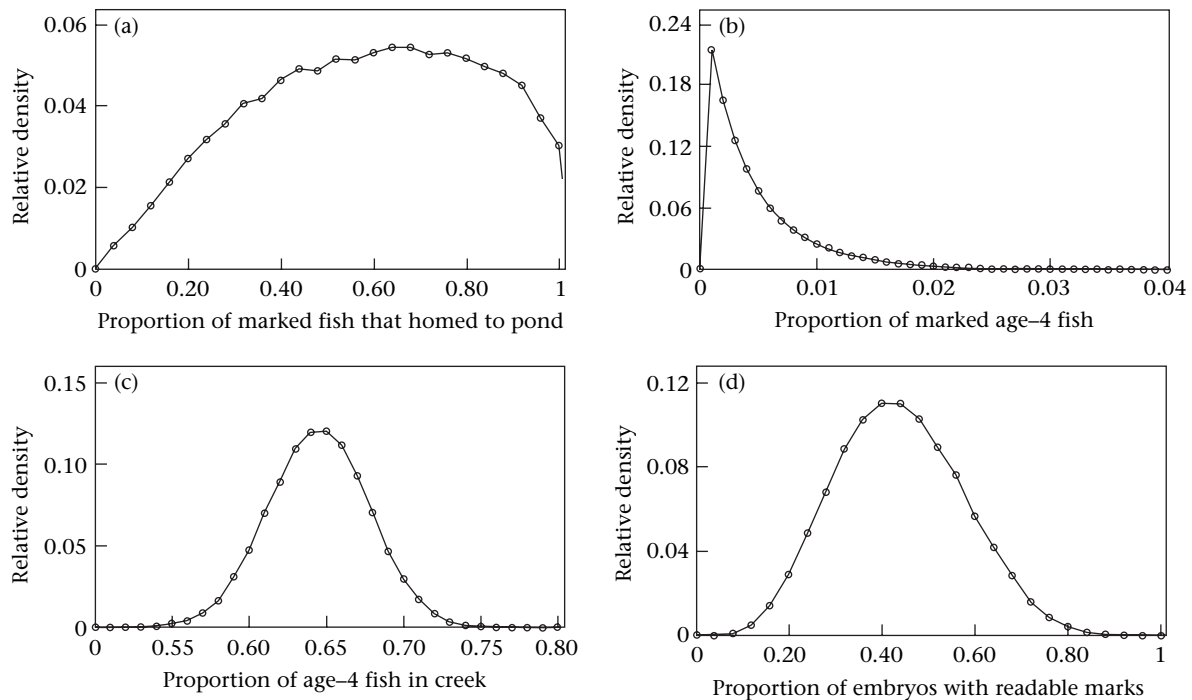


Figure 3. Posterior probability distributions for model parameters: proportion of marked fish that homed to the pond (a), proportion of age-4 adults that were marked (b), proportion of age-4 fish in the creek (c) and proportion of embryos with readable marks (d).

months later. Sockeye salmon smolts typically migrate to sea from the outlet of a lake after feeding there for 1 or 2 years after emerging from the gravel, but a single lake may have many discrete breeding populations. The persistent differences between sockeye salmon populations in life history traits (Blair et al. 1993; Quinn et al. 1995) and selectively neutral genetic markers (Burger et al. 1997; Beacham et al. 2006) present strong indirect evidence that they home to the site where they were spawned and incubated, not merely the site where they experienced the parr-smolt transformation. We previously reported evidence of natural differences in otolith microstructure among sockeye salmon populations within one lake, indicating homing to natal breeding sites (Quinn et al. 1999), but the present results take the level of homing much further, to a specific habitat unit within one small stream. This is consistent with the inference that chinook salmon, *O. tshawytscha*, homed to reaches of a river, based on the degree of genetic relatedness of individuals (Bentzen et al. 2001).

We do not conclude that all salmon return to the precise location where they were spawned, nor do we believe that all salmon in the Hansen Creek pond were necessarily spawned there. Competition for space may cause fish to compromise the homing instinct and spawn at non-natal locations. In addition, the processes of olfactory imprinting and homing are remarkable but not unerring. Numerous studies have found that at least some salmon that survive to maturity stray and spawn at non-natal locations, even if 'homing' is defined at a much coarser spatial scale than the one we studied here (Quinn 1993). The imprinting process involves odorant molecules contacting the sensory cells of the olfactory epithelium, sensitization

of those cells for those specific odorants, and retention of memories in the higher olfactory centres in the brain (Nevitt et al. 1994; Dittman et al. 1997). The olfactory systems of alevins (post-hatch embryonic salmon) are well developed and there is abundant evidence for learning during this stage (Brannon 1972). Nevertheless, most of the chemical composition of water is water, and most of the remaining 'signature' chemicals must be very similar at the fine spatial scales that we were concerned with. The vegetative canopy (alder and spruce trees) around the pond was somewhat more open than that in the creek's riparian zone but not fundamentally different from it, and many of the same grasses and other plants were present. The pond was situated in an open, boggy area, which may have leached chemicals with a sufficiently distinctive chemistry to support homing. However, the entire length of the creek was in a broad, flat valley with groundwater entering from both sides, so the chemical differences must have been subtle.

In addition to the mechanistic reasons for homing to be imperfect (i.e. the sensory systems involved in imprinting juveniles and in guiding adults, and the memories to assist them, are subject to some error), the postglacial colonization of newly accessible streams by salmon provides abundant ecological evidence that salmon stray (Milner et al. 2000). The structuring of salmon populations, therefore, exists in a dynamic balance. Homing to natal sites isolates breeding populations and leads to differentiation as the processes of natural selection and genetic drift operate. Straying, at broad and fine spatial scales, allows gene flow among populations, and the colonization of new habitat. Salmon populations are thus structured at a series of increasingly fine levels, characterized by more exchange

and less isolation. Our experimental salmon homed to the right continent (e.g. North America rather than Asia) and region (Bristol Bay rather than elsewhere in North America). They ascended the Nushagak River system rather than any of the other large rivers elsewhere in Bristol Bay that support sockeye salmon, then ascended its tributary, the Wood River, rather than swimming further up the Nushagak River as do other sockeye salmon migrating at the same time. Once in the Wood River they migrated no further than Lake Aleknagik, even though there are several lakes above it with dozens of sockeye salmon populations. They distinguished Hansen Creek from Happy and Eagle creeks, each less than 1 km away along the shoreline of the lake. They then ascended 1.5 km past suitable spawning habitat (used by other salmon at the same time or later in the season) to enter the pond.

We have described the homing process as being guided by odours resulting from the local geology and flora, but Nordeng (1977) proposed that population-specific odours from the juveniles residing in the natal stream or migrating from it could provide the distinctive chemicals to guide adults. Laboratory experiments have revealed that salmonid fish can indeed discriminate the chemical traces of members of their population from those of other populations (Courtenay et al. 1997, and references therein). However, a field experiment showed that adult salmon returned to their natal site, even though it was devoid of juvenile conspecifics, bypassing a non-natal site further downstream that held juveniles of their population (Brannon & Quinn 1990). In our experiment, the parents of the experimental fish were drawn from the population at large and so would have had no special attraction for odours of pond fish. More broadly, the life history of sockeye salmon (as well as chum, *O. keta*, and pink, *O. gorbuscha*, salmon) involves migration from the stream by newly emerged fry, unlike Atlantic salmon that spend several years rearing in streams prior to seaward migration. Thus population-specific odours are unlikely to guide homing adults as a rule, although they may play a role in some cases.

Our results indicate that salmon that were marked and released into the pond as pre-hatch embryos returned to the pond rather than to the rest of the creek more often than would have occurred by chance. Indeed, no marked salmon were detected among our samples from the creek proper. However, we cannot determine precisely what proportion of the experimental salmon homed. Some salmon spawned naturally in the pond in 2000, but based on the number observed, the artificially spawned offspring would have been a large fraction of the pond's production. However, our success in properly depositing the embryos in the gravel was uncertain. In addition, incubation in lake water advanced the development of the experimental embryos so they would have hatched and emerged earlier than the naturally spawned fish, and this might have compromised their survival in some way. Finally, it appeared that the marking process took place earlier in development than we had anticipated, so only about 40% of the experimental embryos were actually marked. Had we excluded all natural spawning from the

pond in 2000 (so only experimental fish could have migrated from it as fry), we would have had a direct estimate of the proportion of the naturally produced fish returning to the pond by chance because any unmarked fish would have been strays from the creek. Such a draconian approach, employed with pink salmon in Sashin Creek, Alaska (Harry & Olson 1963; Ellis 1969), revealed some straying into a creek that had been deliberately blocked to salmon in the previous generation. However, we balanced the goals of the study with potential impacts to the natural population and did not to pursue this option.

Notwithstanding the uncertainties regarding the precise proportion of experimental salmon that homed, our results show that sockeye salmon are capable of exceptionally fine-scale homing. It is unclear whether other kinds of animals show similarly precise homing. Salmon hatchlings are exceptionally large compared to other teleost fish, and they remain in the gravel environment with a prolonged opportunity for imprinting. In most fish, the larval stages disperse (although spatial scales vary) when they are much smaller and less well developed. For example, Werner & Lannoo (1994) concluded that larval white suckers, *Catostomus commersoni*, have the structures needed for olfactory imprinting at the time they leave streams, but that these structures are not nearly as developed as those of salmon. Hatchling sea turtles, *Lepidochelys kempi*, have the capacity for olfactory imprinting (Grassman et al. 1984) but the scale of natal homing is unclear. However, evidence has been presented that some coral reef fish, previously believed to disperse widely from the natal area at larval stages, may home back, so they may 'self-recruit' (Jones et al. 1999), and some species use odours for orientation during the settlement period (Atema et al. 2002). Thus, much still needs to be learned about the timing of imprinting, the spatial scale of homing and the associated structure of animal populations.

Acknowledgments

We thank the many Fisheries Research Institute field staff and students who assisted with the field work, especially Greg Buck, Kai Chamberlain, Brandon Chasco, Sara Feser, Lucy Flynn, Nick Hurtado, Erin Meehan, Richie Rich, Eric Steimle, Mark Tetrack and Jon Wittouck. Alaska Department of Fish and Game scientists who assisted with the otolith reading included Peter Hagen, Ron Josephson, Kray Van Kirk, Dion Oxman and Ryan Scott. Andrew Dittman and Mark Scheuerell provided helpful comments on preliminary drafts of the manuscript. This research was funded by the Pacific Seafood Processors Association, and the National Science Foundation's Long Term Research in Environmental Biology and Biocomplexity programmes.

References

- Atema, J., Kingsford, M. J. & Gerlach, G. 2002. Larval reef fish could use odour for detection, retention and orientation to reefs. *Marine Ecology Progress Series*, **241**, 151–160.
- Beacham, T. D., McIntosh, B., MacConnachie, C., Miller, K. M., Withler, R. E. & Varnavskaya, N. 2006. Pacific rim population

- structure of sockeye salmon as determined from microsatellite analysis. *Transactions of the American Fisheries Society*, **135**, 174–187.
- Bentzen, P., Olsen, J. B., McLean, J., Seamons, T. R. & Quinn, T. P.** 2001. Kinship analysis of Pacific salmon: insights into mating, homing and timing of reproduction. *Journal of Heredity*, **92**, 127–136.
- Blair, G. R. & Quinn, T. P.** 1991. Homing and spawning site selection by sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Canadian Journal of Zoology*, **69**, 176–181.
- Blair, G. R., Rogers, D. E. & Quinn, T. P.** 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. *Transactions of the American Fisheries Society*, **122**, 550–559.
- Bowen, B. W., Avise, J. C., Richardson, R. I., Meylan, A. B., Margaritoulis, D. & Hopkins-Murphy, S. R.** 1993. Population structure of loggerhead turtles (*Caretta caretta*) in the northwestern Atlantic Ocean and Mediterranean Sea. *Conservation Biology*, **7**, 834–844.
- Brannon, E. L.** 1972. Mechanisms controlling migration of sockeye salmon fry. *International Pacific Salmon Fisheries Commission Bulletin*, **21**, 1–86.
- Brannon, E. L. & Quinn, T. P.** 1990. A field test of the pheromone hypothesis for homing by Pacific salmon. *Journal of Chemical Ecology*, **16**, 603–609.
- Burger, C. V., Spearman, W. J. & Cronin, M. A.** 1997. Genetic differentiation of sockeye salmon subpopulations from a geologically young Alaskan lake system. *Transactions of the American Fisheries Society*, **126**, 926–938.
- Candy, J. R. & Beacham, T. D.** 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged chinook salmon (*Oncorhynchus tshawytscha*) populations. *Fisheries Research*, **47**, 41–56.
- Courtenay, S. C., Quinn, T. P., Dupuis, H. M. C., Groot, C. & Larkin, P. A.** 1997. Factors affecting the recognition of population-specific odours by juvenile coho salmon (*Oncorhynchus kisutch*). *Journal of Fish Biology*, **50**, 1042–1060.
- Cramer, D. P.** 1981. Effect of smolt release location and displacement of adults on distribution of summer steelhead trout. *Progressive Fish-Culturist*, **43**, 8–11.
- Dingle, H.** 1996. *Migration: the Biology of Life on the Move*. New York: Oxford University Press.
- Dittman, A. H., Quinn, T. P., Nevitt, G. A., Hacker, B. & Storm, D. R.** 1997. Sensitization of olfactory guanylyl cyclase to a specific imprinted odorant in coho salmon. *Neuron*, **19**, 381–389.
- Ellis, R. J.** 1969. *Return and Behavior of Adults of the First Filial Generation of Transplanted Pink Salmon, and Survival of their Progeny, Sashin Creek, Baranof Island, Alaska*. Washington, D.C.: U.S. Fish and Wildlife Service.
- Foerster, R. E.** 1936. The return from the sea of sockeye salmon (*Oncorhynchus nerka*) with special reference to percentage survival, sex proportions and progress of migration. *Journal of the Biological Board of Canada*, **3**, 26–42.
- Grassman, M. A., Owens, D. E., McVey, J. P. & Marquez, M. R.** 1984. Olfactory-based orientation in artificially imprinted sea turtles. *Science*, **224**, 83–84.
- Griffith, J. N., Hendry, A. P. & Quinn, T. P.** 1999. Exploratory behavior or straying: adult sockeye salmon (*Oncorhynchus nerka*) entering a non-natal hatchery. *Fishery Bulletin*, **97**, 713–716.
- Harry, G. Y. J., Jr & Olson, J. M.** 1963. Straying of pink salmon to Sashin Creek, Little Port Walter Bay. *Manuscript Report Auke Bay Fisheries Laboratory*. No. MR 63-3. Auke Bay, Alaska: U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Biological Laboratory 1–9.
- Hasler, A. D. & Scholz, A. T.** 1983. *Olfactory Imprinting and Homing in Salmon*. Berlin: Springer-Verlag.
- Healey, M. C. & Prince, A.** 1998. Alternative tactics in the breeding behaviour of male coho salmon. *Behaviour*, **135**, 1099–1124.
- Hendry, A. P., Leonetti, F. E. & Quinn, T. P.** 1995. Spatial and temporal isolating mechanisms: the formation of discrete breeding aggregations of sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology*, **73**, 339–352.
- Hilborn, R. & Mangel, M.** 1997. *The Ecological Detective: Confronting Models with Data*. Princeton, New Jersey: Princeton University Press.
- Hoopes, D. T.** 1972. Selection of spawning sites by sockeye salmon in small streams. *Fishery Bulletin*, **70**, 447–458.
- Jones, G. P., Millicich, M. J., Emslie, M. J. & Lunow, C.** 1999. Self-recruitment in a coral reef fish population. *Nature*, **402**, 802–804.
- Kondolf, G. M. & Wolman, M. G.** 1993. The sizes of salmonid spawning gravels. *Water Resources Research*, **29**, 2275–2285.
- Lucas, M. C. & Baras, E.** 2001. *Migration of Freshwater Fishes*. Oxford: Blackwell Science.
- McAllister, M. K., Pikitch, E. K., Punt, A. E. & Hilborn, R.** 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2673–2687.
- McDonald, J.** 1981. The stock concept and its application to British Columbia salmon fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1657–1664.
- Marriott, R. A.** 1964. *Stream Catalog of the Wood River Lake System, Bristol Bay, Alaska*. Washington, D.C.: U.S. Fish and Wildlife Service.
- Milner, A. M., Knudsen, E. E., Soiseth, C., Robertson, A. L., Schell, D., Phillips, I. T. & Magnusson, K.** 2000. Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2319–2335.
- Morin, P.-P., Dodson, J. J. & Dore, F. Y.** 1989. Cardiac responses to a natural odor odorant as evidence of a sensitive period for olfactory imprinting in young Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 122–130.
- Nevitt, G. A., Dittman, A. H., Quinn, T. P. & Moody, W. J. J.** 1994. Evidence for a peripheral olfactory memory in imprinted salmon. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 4288–4292.
- Nordeng, H.** 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. *Oikos*, **28**, 155–159.
- Nordeng, H.** 1989. Salmonid migration: hypotheses and principles. In: *Proceedings of the Salmonid Migration and Distribution Symposium* (Ed. by E. Brannon & B. Jonsson), pp. 19–29. Seattle: University of Washington.
- Papi, F. (Ed.)** 1992. *Animal Homing*. London: Chapman & Hall.
- Punt, A. E. & Hilborn, R.** 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries*, **7**, 35–63.
- Quinn, T. P.** 1993. A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research*, **18**, 29–44.
- Quinn, T. P.** 1999. Revisiting the stock concept in Pacific salmon: insights from Alaska and New Zealand. *Northwest Science*, **73**, 312–324.
- Quinn, T. P.** 2005. *The Behavior and Ecology of Pacific Salmon and Trout*. Seattle: University of Washington Press.
- Quinn, T. P. & Buck, G. B.** 2001. Size and sex selective mortality on adult Pacific salmon: bears, gulls and fish out of water. *Transactions of the American Fisheries Society*, **130**, 995–1005.
- Quinn, T. P., Nemeth, R. S. & McIsaac, D. O.** 1991. Homing and straying patterns of fall chinook salmon in the lower Columbia River. *Transactions of the American Fisheries Society*, **120**, 150–156.
- Quinn, T. P., Hendry, A. P. & Wetzel, L. A.** 1995. The influence of life history trade-offs and the size of incubation gravels on egg size

- variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos*, **74**, 425–438.
- Quinn, T. P., Volk, E. C. & Hendry, A. P. 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology*, **77**, 766–775.
- Rich, H. B., Jr, Carlson, S. M., Chasco, B. E., Briggs, K. C. & Quinn, T. P. 2006. Movements of male sockeye salmon, *Oncorhynchus nerka*, on spawning grounds: effects of in-stream residency, density and body size. *Animal Behaviour*, **71**, 971–978.
- Rich, W. H. 1939. Local populations and migration in relation to the conservation of Pacific salmon in the western states and Alaska. In: *The Migration and Conservation of Salmon* (Ed. by F. Moulton), pp. 45–50. Lancaster, Pennsylvania: American Association for the Advancement of Science.
- Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. In: *The Stock Concept in Pacific Salmon* (Ed. by R. C. Simon & P. A. Larkin), pp. 19–160. Vancouver: University of British Columbia Press.
- Rogers, D. E. 1987. The regulation of age at maturity in Wood River sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences, Special Publication*, **96**, 78–89.
- Rubin, D. R. 1987. Comment. A noniterative sampling/importance resampling alternative to the data augmentation algorithm for creating a few imputations when fractions of missing information are modest: the SIR algorithm. *Journal of the American Statistical Association*, **82**, 543–546.
- Scholz, A. T., Horrall, R. M., Cooper, J. C. & Hasler, A. D. 1976. Imprinting to chemical cues: the basis for home stream selection in salmon. *Science*, **192**, 1247–1249.
- Slaney, P. A., Berg, L. & Tautz, A. F. 1993. Returns of hatchery steelhead relative to site of release below an upper-river hatchery. *North American Journal of Fisheries Management*, **13**, 558–566.
- Stewart, I. J., Carlson, S. M., Boatright, C. P., Buck, G. B. & Quinn, T. P. 2004. Site fidelity of spawning sockeye salmon (*Oncorhynchus nerka* W.) in the presence and absence of olfactory cues. *Ecology of Freshwater Fish*, **13**, 104–110.
- Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, **98**, 185–207.
- Tipping, J. M. & Hillson, T. D. 2002. Adult recoveries of winter and summer steelhead by release location on the Lewis River, Washington. *California Fish and Game*, **88**, 49–56.
- Velsen, F. P. J. 1987. Temperature and incubation in Pacific salmon and rainbow trout: compilation of data on median hatching time, mortality and embryonic staging. *Canadian Journal of Fisheries and Aquatic Sciences*, **626**, 156–178.
- Volk, E. C., Schroder, S. L. & Fresh, K. L. 1990. Inducement of unique otolith banding patterns as a practical means to mass-mark juvenile Pacific salmon. *American Fisheries Society Symposium*, **7**, 203–215.
- Wade, P. R. 2000. Bayesian methods in conservation biology. *Conservation Biology*, **14**, 1308–1316.
- Wagner, H. H. 1969. Effect of stocking location of juvenile steelhead trout, *Salmo gairdnerii*, on adult catch. *Transactions of the American Fisheries Society*, **98**, 27–34.
- Werner, R. G. & Lannoo, M. J. 1994. Development of the olfactory system of the white sucker, *Catostomus commersoni*, in relation to imprinting and homing: a comparison to the salmonid model. *Environmental Biology of Fishes*, **40**, 125–140.
- Youngson, A. F., Jordan, W. C. & Hay, D. W. 1994. Homing of Atlantic salmon (*Salmo salar* L.) to a tributary spawning stream in a major river catchment. *Aquaculture*, **121**, 259–267.