Original Article

Attraction of migrating adult sockeye salmon to conspecifics in the absence of natal chemical cues

Nolan N. Bett and Scott G. Hinch
Department of Forest Sciences and Conservation, University of British Columbia, 3604-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

Received 13 January 2015; revised 15 April 2015; accepted 25 April 2015; Advance Access publication 25 May 2015.

INTRODUCTION

Natal philopatry, defined as an individual’s return to its birthplace prior to reproduction, occurs in a variety of species (Greenwood 1980). Animals that exhibit such behavior can benefit from local adaptation to their natal area or from the assurance of suitable habitat and potential mates on arrival at breeding grounds (Hendry et al. 2004). They also avoid certain costs to leaving the natal area, such as “risk costs” (e.g., movement into unsuitable habitat) and “opportunity costs” (e.g., loss of familiarity-related advantages) (Bonte et al. 2012). There are consequences to natal philopatry, however, including increased competition and the risk of inbreeding depression (defined as a reduction in fitness of offspring resulting from inbreeding) (Lambin 1994). In contrast to natal philopatry, dispersal, which involves movement away from the natal area prior to reproduction (Howard 1960). Increased rates of dispersal have been documented when population density (Matthysen 2005) and chance of inbreeding (Bollinger et al. 1993; Lambin 1994; Daniels and Walters 2000) are greater, suggesting that dispersal might help counter some of the drawbacks to natal philopatry.

Large-scale movement in animals, such as toward a natal site as in the case of philopatry, or away from it as in dispersal, is often directed by navigation using 1 or more sensory systems (Able 1991). Many species of anadromous fish, for example, are philopatric, and the use of sensory information as they navigate to spawning grounds, as well as the evolutionary implications of homing and dispersal, have been well documented (Hasler and Scholz 1983; Hendry et al. 2004). Although navigation in the ocean requires complex coordination of multiple sensory systems (Harden Jones 1968; Dittman and Quinn 1996; Putman et al. 2014), anadromous fish rely primarily on their olfactory systems to navigate after entering freshwater (Stabell 1984; Ueda 2011). The use of olfactory navigation has been most thoroughly studied in the family Salmonidae (Bett and Hinch 2015).

Research on anadromous salmonids has demonstrated “olfactory imprinting,” a process that enables adults to identify their spawning grounds based on chemical cues (Hasler and Scholz 1983). The process begins when juveniles imprint on the chemical composition of their natal rearing site. Most evidence to date indicates that imprinting occurs primarily during the parr-smolt transformation, a period when juveniles undergo substantial physiological change in preparation for the outward migration and entrance into saltwater (Groot and Margolis 1991). On return into freshwater during the
spawning migration, adult migrants recall the imprinted chemical cues and swim toward them. In this manner, anadromous salmonids, and perhaps other species of anadromous fish (e.g., Dobson and Leggett 1974; Sahafi 2013), can locate their natal sites with high precision (Quinn 2005).

Although imprinting is known to occur in various different species of salmonids, an alternative hypothesis has also garnered attention. Nordeng (1971) proposed that these fish use the smell of conspecifics as directional cues. Juveniles often rear in freshwater before migrating to the ocean, and Nordeng suggested that adults might be attracted to the juveniles as they swim upstream, similar to the manner in which northern lamprey (Petromyzonidae) use larval pheromones as directional cues during the spawning migration (Moser et al. 2015). Known as the “pheromone hypothesis,” the use of pheromones as directional cues could provide a simpler method of navigation when contrasted with olfactory imprinting (Nordeng 1977). As other researchers have noted (Selset and Døving 1980; Keefer and Caudill 2014), however, these 2 theories are not mutually exclusive: it is possible that conspecific cues comprise part of the “olfactory bouquet” that juveniles imprint on. Limiting the role of pheromones strictly to this interpretation (a single component of the imprinted odor) would suggest that pheromones are only attractive when combined with the other components of the bouquet. There is evidence, however, that adult migrants are attracted to pheromones in the absence of other natal cues (Stabell 1984; Bett and Hinch 2015). This implies that pheromones may act as a migratory directional cue even in isolation.

Although few studies have attempted to address the relative importance of imprinted cues compared with conspecific cues, there is evidence that the attraction toward imprinted cues supersedes that of pheromones (Brannon et al. 1984; Black and Dempson 1986; Brannon and Quinn 1990). Pheromones, however, may act as a “secondary” cue, providing directional information in the absence of imprinted, or “primary,” cues. This method of olfactory navigation has been proposed as the hierarchical navigation hypothesis (Bett and Hinch 2015). Studies have found that adult salmonids that stray from their natal migratory route enter rivers containing conspecifics more frequently than rivers without (Jonsson et al. 2003; Dittman et al. 2010), and that coho salmon (Oncorhynchus kisutch) are attracted to juvenile conspecifics when tested in city water (Quinn et al. 1983), suggesting that pheromones may indeed attract migrants when natal imprinted cues are absent.

These findings suggest a more refined olfactory navigation process than is typically discussed in salmonid research, with an adaptation that may be influenced by its effect on dispersal success. Migrants that stray from their natal route may attempt to spawn in new areas, and an attraction to pheromones would increase the likelihood of successful dispersal by ensuring suitable habitat and the presence of potential mates. By increasing the fitness of these stray migrants, the attraction to conspecifics could promote gene flow between populations, thereby reducing inbreeding depression. To date, however, there have been few direct tests on the potential “secondary” role of pheromones as directional cues.

The objective of this study is to determine whether adult sockeye salmon (O. nerka) that have strayed from their natal water will use conspecific odors as directional cues. To test this, we conducted a pair of behavioral choice experiments in which conspecific odors were introduced in 1 of the 2 following types of water: 1) natal water, which contains imprinted chemical cues, or 2) non-natal water, lacking the imprinted chemical cues. Following the hierarchical navigation hypothesis, we predicted that adult migrating sockeye salmon would be attracted to conspecific odors when tested in non-natal water, but not when in natal water.

**METHODS**

**Study location and animals**

Experiments took place on the north bank of the Seton River, a tributary of the Fraser River, in the interior of southwestern British Columbia, Canada (Figure 1). We conducted the experiments from 14 August to 28 August 2014, during daylight hours (0700–1700). We captured all sockeye salmon (N = 85) by dipnet from the top pool of the Seton Dam fishway, located on the Seton River, and immediately transferred them to an aerated 1000-L transport tank on the back of a truck. We drove the fish approximately 100 m and unloaded them in a 10000-L holding tank adjacent to the dam.
with continuous flow of water from Seton River. We held each fish in an individual isolation chamber, constructed from PVC pipe (75-cm length × 15.3-cm diameter) with mesh ends.

We tested Gates Creek sockeye salmon, which spawn approximately 55 km upstream from the capture location in the Seton River. These fish were therefore tested during the migratory phase of their life history, 1–2 weeks prior to arrival at spawning grounds and sexual maturity. Straying, or dispersal from the natal tributary, naturally occurs during the spawning migration of Pacific salmon (Oncorhynchus spp.), and sockeye salmon from disparate populations sometimes enter the Seton River system. To identify stray salmon captured for our experiments, we first used a microwave energy meter (FM 692 Fish Fatmeter, Distell, UK) to estimate gross somatic energy. Gates Creek sockeye salmon have gross somatic levels that are significantly different from those of other populations that stray into the Seton River system (Casselman et al. 2012). DNA analysis of 64 stray sockeye salmon captured in the Seton River in 2012 (Casselman et al. 2012) and 2013 (Bett N, unpublished) determined that all originated from populations further up the Fraser River. The differences in gross somatic energy are likely attributed to the differences in distance to spawning grounds, as Fraser sockeye salmon with longer and steeper migration routes begin their migration with more somatic energy and expend less per unit of migration distance (Crossin et al. 2004). Furthermore, longer distance migrants in the Fraser system have a more fusiform body shape (Crossin et al. 2004), and are more silver on arrival at Seton River when compared with Gates Creek sockeye salmon. Following the trials, DNA samples from the adipose fins of all fish that were abnormal in any of the 3 variables (gross somatic energy, body shape, or color) were analyzed at the Fisheries and Oceans Canada Pacific Biological Station (Nanaimo, BC) to determine their population identity (Beacham et al. 2005).

Experimental set-up

We stored water in 11365 L polyethylene “header” tanks (Premier Plastics Inc., Delta, BC), and the water was gravity fed through 2” diameter water suction hoses (Greenline, Delta, BC) to 2 1136 L polyethylene “mixing” tanks (Premier Plastics Inc.) (Figure 2). Water was gravity fed from each tank through 4” diameter water suction hoses into a Y-maze. We constructed the Y-maze from plywood and 2 × 4 supports, and sealed the interior with fiberglass and a fish-safe gelcoat (Rebel Fiberglass, Kamloops, BC). The Y-maze was rectangular in shape, 4.88-m long × 1.22-m wide × 1.22-m high. A 2.44-m long divider, made from fiberglassed plywood, divided the upstream end into 2 equally sized halves (or 2 “arms”). We conducted a dye test to ensure no mixing occurred between water in each of the 2 arms. Water exited the Y-maze through a standpipe, and the water level was maintained at 17 cm. Valves regulated the amount of water entering each arm of the Y-maze to 40 L/min. We also placed plywood on top of the Y-maze to block out light, and to reduce stress in the fish.

We obtained water for the “natal water” experiment from the Seton River, using a submersible pump. We obtained water for the “non-natal water” experiment from nearby Cayoosh Creek. Cayoosh Creek does not contain any spawning populations of Pacific salmon, due to an impassable barrier approximately 1 km upstream from the collection site, and we did not see any transient salmon in the creek during the time of the experiment. We transported water from Cayoosh Creek to the header tanks using a gas-powered pump with 2” water suction hose and a 1500-L transport tank on the back of a truck. Temperatures throughout the entire experimental period ranged between 16.9–20.4 °C for Seton River water and 16.1–19.4 °C for Cayoosh Creek, and the 2 arms were always within ± 0.2 °C during any given trial. The optimal migratory temperature window for adult Gates Creek sockeye salmon is 12.9–20.7 °C (Eliason Parsons 2011).

Experimental protocol

We captured sockeye salmon in the morning of each experimental day, and transported 7–10 fish to the holding tank, to be later tested in the Y-maze. Concurrently, we captured and immediately sacrificed 3 additional sockeye salmon (2 females and 1 male or 1 female and 2 males) by cerebral percussion. We then transferred these sockeye salmon to 1 of the 2 mixing tanks, where they acted as the source of conspecific odors during the trials. Previous experiments using live sockeye salmon in the mixing tanks demonstrated

![Figure 2](https://academic.oup.com/beheco/article-abstract/26/4/1180/211089/1182)

Figure 2

Experimental set-up. Gravity-fed water passed from large header tanks (A) to smaller mixing tanks (B), where sockeye salmon that provided the source of conspecific odor were held. Water then continued into each arm of the Y-maze (C) at 40 L/min.
that these fish emit a stress-related chemical signal that triggers an avoidance response from conspecifics (Casselman et al. 2013), and live Gates Creek sockeye salmon were thus unsuitable for this study. All of the sockeye salmon selected to provide the conspecific odor source were free of any visible tissue damage, to further minimize the possibility of alarm signals. Water containing the conspecifics was paired with water lacking the conspecifics, such that each water type entered a different arm of the Y-maze. The arm containing water with conspecifics was switched each day to mitigate any potential behavioral bias for one of the arms, although control tests using the same set-up demonstrated no bias (Casselman et al. 2013).

At the start of each trial, we transferred a single sockeye salmon from the holding tank to the downstream end of the Y-maze. A mesh gate prevented fish from entering either of the upstream arms. After a 10-min acclimation period, we removed the gate and recorded the behavior of the fish for 20 min. We monitored behavior through a video system, using an Infrared camera (securitycamera2000.com, Hong Kong) connected to a monitor. We recorded the following behavioral variables: the amount of time spent in each arm, the number of entrances into each arm, and the number of times the sockeye salmon surfaced (breached the surface of the water with its head) at the upstream end of each arm, where water flowed in. We selected the latter behavior, which has been used in past behavioral choice experiments (e.g., Groot et al. 1986), following observations made during previous experiments. Surfacing into the water entering the Y-maze was often immediately followed by attempts to jump into the intake hose, and appears to indicate a desire to swim further in this direction. We also calculated the proportion of time spent in the arm containing the conspecific odor using the following equation:

\[
\frac{t_{\text{arm with odor}}}{t_{\text{arm with odor}} + t_{\text{arm without odor}}}
\]

At the end of the 30-min trial, we removed the fish from the Y-maze and collected blood and DNA samples, then returned the fish to the river. We flushed the Y-maze before the introduction of the next test fish.

The research conformed to protocols approved by the University of British Columbia Committee on Animal Care (A12-0250-006) and met the Canadian Council for Animal Care Guidelines.

Data analysis

We used a Shapiro–Wilk normality test for each of the variables collected. We compared the amount of time spent in each arm and the number of entrances in each arm using paired t-tests (\(\alpha = 0.05\)). We compared the proportion of time spent in the arm with the conspecific odor using a one sample \(t\)-test (\(\mu = 0.5, \alpha = 0.05\)). We compared the number of surfaces in the upstream end of each arm, which had a non-normal distribution, using a Wilcoxon signed-rank test (\(\alpha = 0.05\)). All fish that did not enter each arm at least once during the trial were removed from the analysis as these fish did not experience a full concentration of each of the waters, and therefore could not exhibit choice or preference behaviors. We ran all statistical analyses in R Studio V 0.98.501.

RESULTS

Three sockeye salmon in the natal water experiments and 2 sockeye salmon in the non-natal water experiments were identified as strays, and were removed from analyses. Eight sockeye salmon (4 from each of the natal and non-natal water test) did not enter both arms and were removed from analyses. Of these 8 fish, 2 did not enter either arm at all, and 3 entered only very briefly (<30 s). The remaining 3 entered 1 arm but then remained motionless.

When tested in non-natal water, sockeye salmon spent significantly more time (\(t_{28} = 2.45, P = 0.021\); Figure 3a) in the arm with the conspecific odor. The trend remained similar in terms of the proportion of time in the arm with the conspecific odor (\(t_{28} = 1.85, P < 0.05\)).

Figure 3

Amount of time spent by sockeye salmon in each of the 2 arms when tested in (a) non-natal water, which does not contain imprinted chemical cues from spawning grounds (\(n = 29\)), and (b) natal water, which does contain imprinted chemical cues from spawning grounds (\(n = 43\)). In each test, 1 arm contained the conspecific odor, whereas the other did not. The solid lines inside the boxes represent medians, and dashed lines represent means. Upper and lower whiskers represent sample maximums and minimums, or the upper and lower quartiles +/- 1.5 times the interquartile range. *\(P < 0.05\).
end of each arm: \( V = 28.5, n = 22, P = 0.959 \). In males, there were similarly no significant differences in any of the behavioral variables, although there was a slight trend toward an avoidance of the arm containing the conspecific odor (time in each arm: \( t_{20} = 1.51, P = 0.148 \); proportion of time in arm with conspecific odor: \( t_{20} = -1.39, P = 0.179 \); number of surfaces in the upstream end of each arm: \( V = 77, n = 21, P = 1 \)).

**DISCUSSION**

In terms of the amount of time spent, proportion of time spent, and number of surfaces in each arm, sockeye salmon showed an attraction to their conspecifics when they were tested in non-natal water, but not when they were tested in natal water. The attraction may be stronger in females, although further tests with a larger sample size would be needed to conclusively determine whether there is a sex-specific response. The results suggest that sockeye salmon do not use conspecific odors as a directional cue when imprinted chemicals are present, but do use conspecific odors as a directional cue when the imprinted chemicals are absent. This finding supports the hierarchical navigation hypothesis, which proposes that philopatric, anadromous fish primarily seek imprinted cues, and secondarily seek conspecific cues during the spawning migration.

Direct comparison of the behaviors in the 2 water treatments highlights differences that may further reflect the relative importance of imprinted and conspecific cues. The sockeye salmon spent on average more time in the rear section of the Y-maze in non-natal water (mean ± standard error: 645 ± 37 s) than they did in natal water (505 ± 28 s). In addition, the sockeye salmon surfaced more frequently overall in the natal water than in the non-natal water (Figure 5). Together, these discrepancies suggest sockeye salmon tested in natal water were more strongly attracted to water entering the Y-maze than were sockeye salmon tested in the non-natal water, despite the addition of the conspecific odor. From a behavioral perspective, it seems reasonable that sockeye salmon

![Figure 4](https://academic.oup.com/beheco/article-abstract/26/4/1180/211089)

**Figure 4**
Proportion of time spent by sockeye salmon in the arm containing the conspecific odor when tested in non-natal water, which does not contain imprinted chemical cues from spawning grounds (\( n = 29 \)), and when tested in natal water, which does (\( n = 43 \)). The solid lines inside the boxes represent medians, the dashed lines inside the boxes represent means, the dashed line spanning the width of the plot designates 0.5, and “+” indicates a significant difference from 0.5 at \( P = 0.076 \).
might be more motivated to swim towards imprinted chemicals, which indicate natal spawning grounds, than towards conspecific cues in unfamiliar waters. It is possible that conspecific cues act not only as secondary directional cues for strays, but also that they do not elicit as strong an attractive response, possibly because the stray fish are less confident in their navigational movements.

The 2 stray sockeye salmon tested in non-natal water showed a particularly strong preference for the conspecific odor: one spent 349 s in the arm with the conspecific odor and 33 s in the arm without (91% in the conspecific odor), and the other spent 512 s in the arm with the conspecific odor and 191 s in the arm without (73% in the conspecific odor). The seemingly strong preference behavior in these fish may be attributed to the fact that they are “true” strays and have never experienced the “non-natal” Cayoosh Creek water, whereas Gates Creek sockeye salmon were exposed to it briefly during their outmigration. In an unrelated research project, conducted in the same system in 2012, we found further evidence that stray salmon can be attracted to conspecifics in non-natal water. We placed 20 sockeye salmon in individual isolation chambers in Cayoosh Creek, at the same location where the “non-natal water” was collected in 2014 (Figure 1). No conspecifics were seen in the creek, which is not salmon-bearing, during the 2 weeks prior to this event. The salmon were held overnight, and the following morning we counted more than 50 freely-swimming sockeye salmon adjacent to, and downstream from, the isolation chambers. We captured and biopsied 4 of these freely-swimming sockeye salmon, and DNA analyses (Beacham et al. 2003) determined all were strays (i.e., not from the Gates Creek population). Further behavioral tests, using completely unfamiliar waters, are needed to determine whether strays are as strongly attracted to conspecifics as these findings suggest.

In order to best interpret these results, as well as results from past studies, it is important to distinguish between an attraction to pheromones, and an attraction to a combination of imprinted cues that includes pheromones. It is believed that adult salmonids migrate toward an imprinted mixture of chemicals present in their natal water (Ueda 2011), and that this mixture could include pheromones (Keefer and Caudill 2014). In a laboratory setting, juvenile salmon can be imprinted on an individual chemical, such as an amino acid (Yamamoto et al. 2010) or morpholine (Hasler and Scholz 1983), and are attracted to this chemical as adults. There is currently no evidence, however, that salmon can imprint to a mixture of chemicals and subsequently be attracted to only one, except for pheromones, which can elicit an attractive response even when isolated from the rest of the imprinted mixture (summarized in Stabell 1984). In our natal water experiment, we tested the response of sockeye salmon to natal water, presumably containing its regular background concentration of conspecific cues, paired with natal water containing a higher level of conspecific cues. It is not feasible to remove background cues from large volumes of natal water, nor would the effects of this removal accurately represent the choice a fish might make in a natural system. We therefore assumed that an attraction to pheromones in natal water, beyond which comprises 1 component of the imprinted mixture, would be evidenced by an attraction to the arm containing the increased conspecific odor.

Past studies indicate stray migrants are attracted to conspecifics, in support of our findings. Quinn et al. (1983) and Quinn and Tokson (1986) found that adult and juvenile coho are attracted to juvenile conspecifics in non-natal water, and Groot et al. (1986) found similar results with sockeye salmon. Dittman et al. (2010) conducted a broad scale analysis of spawning distribution of Chinook salmon (Oncorhynchus tshawytscha) in the Yakima River, a tributary of the Columbia River, and found that strays tend to enter rivers occupied by conspecifics. Jonsson et al. (2003) recorded a similar result—a tendency of strays to enter rivers containing conspecifics—with Atlantic salmon (Salmo salar) in Norway. White (1934) documented adult Atlantic salmon migrating toward conspecifics of a different

---

**Figure 5**

Number of surfaces made by sockeye salmon at the upstream end of each arm when tested in (a) non-natal water, which does not contain imprinted chemical cues from spawning grounds (n = 29), and (b) natal water, which does (n = 43). In each test, 1 arm contained the conspecific odor, whereas the other did not. The solid lines inside the boxes represent medians, and dashed lines represent means. Upper and lower whiskers represent sample maximums and minimums, or the upper and lower quartiles +/- 1.5 times the interquartile range. *P < 0.05.
population, and suggested this attraction occurred after confusing flow patterns disoriented the fish and prevented them from detecting their natal water. In the study that introduced the pheromone hypothesis (Nordeng 1971; see Introduction), Arctic char migrated toward conspecifics from their own population after being raised in a distant hatchery, with no “natal water” to imprint on. The char in that study may, in a sense, be considered strays, as they were deprived the opportunity to imprint on their ancestral homestream. Together, these studies support our finding in suggesting salmonids may use pheromones as a secondary directional cue during the spawning migration.

Straying occurs regularly in all species of Pacific salmon (Keefer and Caudill 2014)—as well as in other anadromous salmonids (Jahn 1969; Hendricks et al. 2002; Jonsson et al. 2003)—and a secondary attraction to pheromones may occur in many of these fish, particularly if they are attracted to conmigrating adults, as demonstrated in our experiment. One source of confusion regarding Nordeng’s (1971) pheromone hypothesis is that juvenile chum salmon (Oncorhynchus keta) and pink salmon (O. gorbuscha) (as well as some populations of other species) swim to the ocean before the spawning migration occurs. These fish presumably do not encounter juvenile pheromones during the spawning migration, yet most behavioral choice studies have focused on the attraction of salmon to juvenile conspecifics (e.g., Quinn et al. 1983; Brannon et al. 1984, Groot et al. 1986, Quinn and Tolson 1986). By demonstrating an attraction toward conspecific adults, our findings suggest that a secondary attraction to conspecific cues may occur in any species of Pacific salmon, including pink and chum salmon.

There is a major evolutionary benefit to using conspecific cues as a secondary directional cue that might explain how this adaptation arose: it would increase the probability that stray migrants find suitable spawning habitat and successfully spawn. Animals that are philopatric may adapt to the environmental conditions of their natal habitat, and dispersal from this area reduces fitness (Weatherhead and Forbes 1994; Hendry et al. 2004). Salmon require highly specific environmental conditions to spawn successfully, such as adequate flow, temperature, and substrate, and these requirements vary across species (Groot and Margolis 1991). Entering tributaries that are occupied by conspecifics not only ensures the presence of potential mates but also that species-specific habitat requirements are met. Additionally, the use of conspecific cues could decrease the amount of time spent searching for suitable spawning habitat, and therefore reduce search-related movement costs (Stamps, Krishman, et al. 2005). Adult salmon migrate upstream on a fixed energy budget because they are no longer eating, and longer migratory times result in high energetic costs (Hinch and Rand 1999). Stray fish would therefore benefit from an attraction to conspecifics because it would increase their probability of reproductive success by leading them to suitable spawning habitat and reducing search-related movement costs.

The adaptation of such migratory behavior, which improves the reproductive success of stray migrants, could also promote an increase in genetic diversity. Philopatric animals may be susceptible to inbreeding depression due to the lack of genetic mixing between populations (Lambin 1994; Gandon 1999; Hendry et al. 2004), but inbreeding depression can be partially avoided through dispersal (Greenwood 1980; Bollinger et al. 1993; Pusey and Wolf 1996; Szulkin and Sheldon 2000). The increased genetic diversity afforded by higher reproductive success of stray migrants could help reduce the threat of inbreeding depression.

Although rarely discussed in salmonid research, many studies have explored the use of conspecific information in the selection of breeding habitat, usually under the title of “social attraction” or “conspecific attraction” (see reviews by Stamps 1988; Reed and Dobson 1993). For example, there is evidence that many species of birds are attracted to potential breeding sites that contain conspecifics (e.g., Muller et al. 1997; Serrano et al. 2004; Ward and Schlossberg 2004). Conspecific attraction has been studied in other animals as well, such as mammals (Garrett and Franklin 1988; Smith and Peacock 1990; Weddell 1991), reptiles (Kiester 1979; Stamps 1991) and invertebrates (Stamps, McElrath, et al., 2005). In fish, there is evidence that larval coral reef fish are attracted to reefs containing conspecifics during the settlement stage (Öhman et al. 1998; Lecchini et al. 2007).

Unlike most of these animals that demonstrate conspecific attraction, salmon typically return to their natal habitat and therefore have little need to assess habitat quality when searching for spawning grounds. As a consequence, research on salmon pheromones as navigational cues has focused solely on their role as indicators of natal water. Our findings, however, suggest stray salmon may use conspecific information to select suitable non-natal reproductive sites, similar to what has been documented in other animals. Future studies that assess the response of strays to conspecific cues will further our understanding of the navigational abilities of migrating salmon outside their natal migratory routes.

**FUNDING**

This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) (RGPIN 170064-10); St’at’imc Eco-Resources (BRGMON-14); and NSERC Ocean Tracking Network Canada (NETGP 375118-08) grants to S.G.H. This work was also supported by a NSERC Post-Graduate Scholarship-D to N.N.B.

We thank J. Hopkins, W. Payne, A. Lotto, A. James, R. Ledoux, A. Adolph, M. Casselman, N. Burnett, C. Middleton, V. Minke-Martin, and C. White for field assistance. We are grateful to J. Candy, A. Araujo, and the Pacific Biological Station of Fisheries and Oceans Canada for the analysis of DNA samples. We also thank 2 anonymous reviewers for their helpful comments on the manuscript.

**Handling editor:** Bob Wong

**REFERENCES**


Casselman MT, Burnett NJ, Bett NN, McCubbing D, Hinch SG. 2012. BRGMON-14 Effectiveness of Cayoosh flow dilution, dam operation, and fishway passage on delay and survival of upstream migration of


