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A Field Study to Investigate Repeat Homing in Pacific Lampreys

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Abstract.—In-season homing of Pacific lampreys *Lampetra tridentata* was investigated using radiotelemetry in the lower Columbia River from 1998 through 1999. A total of 50 Pacific lampreys were captured: 25 at Willamette Falls (river kilometer [rkm] 45 on the Willamette River, a tributary to the Columbia River, with its confluence at rkm 163) and 25 at Bonneville Dam (rkm 238 on the Columbia River). Each fish was fitted with a radio transmitter, transported, and released in the Columbia River approximately 26 km downstream from the confluence of the Willamette River. Movement of the radio-tagged Pacific lampreys was monitored for several months using mobile and fixed receiver stations to observe rates of homing towards the site of original capture. Results indicated that the lampreys exhibited nonsignificant in-season homing fidelity (p = 0.622) based on the null expectation that one-half of the total recoveries would home and the other half would stray. Final location classifications were 17 homed, 20 strayed, and 13 undetermined. The undetermined classification included individuals that were not detected upstream of the confluence of the Willamette River or in other Columbia River tributaries. Final location classifications were not influenced by fish length (p = 0.594). Although considered weak swimmers, Pacific lampreys were capable of traveling at velocities near 2.5 km/h and sustaining that activity for at least 24 h.

Introduction

Pacific lamprey *Lampetra tridentata* is endemic to the Columbia River basin and plays an important role in the region's river and marine ecosystems, along with having cultural, medicinal, and religious significance to Native American Indians of the Pacific Northwest. Counts of Pacific lampreys at fishway counting stations in the Columbia River basin are currently a fraction of the numbers that were reported 40–50 years ago, indicating a dramatic decline in lamprey abundance (Close et al. 2002).

Pacific lampreys have a unique anadromous life history. Mating individuals build nests and spawn in headwater streams; larvae live as filter feeders in freshwater for several years prior to their metamorphosis and then migrate to the ocean. Lampreys spend several years feeding in the ocean prior to returning to freshwater to spawn (Beamish 1980). Besides perpetuating the species, these spawning migrations provide a vehicle for deposition of marine nutrients to the streams, as well as a buffer for avian (Merrell 1959), marine mammal (Jameson and Kenyon 1977; Roffe and Mate 1984), and piscivorous (Beamish 1980; Poe et al. 1991) predation on Endangered Species Act-listed Pacific salmon *Oncorhynchus* spp. Since natal homing is common in other anadromous species, it is often assumed that Pacific lampreys also exhibit this life history characteristic.

Natal homing has been described for a

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broad range of taxa, including the highly studied salmonids. Natal homing was demonstrated in Gulf of Mexico sturgeon *Acipenser oxrhynchus desotoi* (Stabile et al. 1996), American shad *Alosa sapidissima* (Carscadden and Leggett 1975), and rainbow trout *O. mykiss* (Lindsey et al. 1959), and repeat homing occurs in American shad (Melvin et al. 1986), Windermere char *Salvelinus willughbii* Günther (Frost 1963), brook trout *S. fontinalis* (O'Connor and Power 1973), and brown trout *Salmo trutta* (Tilzey 1977). In-season homing was demonstrated in Colorado pikeminnow *Ptychocheilus lucius* (Tyus 1985), lake trout *Salvelinus namaycush* (Martin 1960), flathead catfish *Pylodictis olivaris* (Hart 1971; Hart and Summerfelt 1974), muskellunge *Esox masquinongy* (Margenau 1994), black-and-yellow rockfish *Sebastes chrysomelas* (Hallacher 1984), mosshead sculpin *Clinocottus globiceps* (Green 1973), Windermere char (Frost 1963), Florida largemouth bass *Micropterus salmoides floridanus* (Mesing and Wicker 1986), cutthroat trout *O. clarkii* (Platts 1959; McCleave 1967; McCleave and Horrall 1970), rainbow trout (Lindsey et al. 1959), brook trout (O'Connor and Power 1973), brown trout (Harcup et al. 1984; Halvorsen and Stabell 1990), largemouth bass *Micropterus salmoides* (Quinn et al. 1978), and American shad (Dodson and Leggett 1973). Prior to this work, homing has not been studied in Pacific lampreys; however, Beamish (1980) speculated that at least some Pacific lampreys homed as evidenced by differences in adult length compositions among rivers that he investigated.

Bergstedt and Seelye (1995) used coded wire tag and recovery methods to reject the hypothesis that Lake Huron sea lampreys *Petromyzon marinus* home to natal streams. However, Wright et al. (1985) used allozyme data to identify statistically significant differences among five sample sites within Lake Huron, which they interpreted to indicate stock structure. For stock structure to exist, Lake Huron sea lampreys must exhibit natal homing.

Gerking (1959) used the term "homing" in a general sense to mean the return of fish after migratory, accidental, or experimental displacement "to a place formerly occupied instead of going to other equally probable places." McCleave (1967) described equally probable places as areas "occupied by other individuals of the same species." In spawning migrations of fishes, three types of homing are recognized (McCleave 1967): (1) natal homing: the return of adults to spawn in the same location in which they were hatched, termed "reproductive, parent stream, or natal homing" by Lindsey et al. (1959); (2) repeat homing: the return of adults to spawn in subsequent breeding seasons at the location of initial spawning; and (3) in-season homing: the return of adults within the same breeding season to the location of initial choice after displacement. This study uses the third definition of homing.

Pacific lamprey homing fidelity has many implications for restoration and management of the species. If lampreys demonstrate high homing fidelity, then substantial population substructuring can be inferred and restoration efforts will need to be focused on multiple distinct populations, as is the case for Pacific salmon. On the other hand, if homing fidelity is low, then a large panmictic metapopulation can be inferred and recovery efforts can be focused at a basin or multibasin scale. The objective of this study was to investigate in-season homing of Pacific lampreys using radiotelemetry.

Study Area

The study area includes the Columbia River between Columbia City, Oregon (river kilometer [rkm] 137) and Bonneville Dam (rkm 238) and the Willamette River, a tributary of the Columbia from the confluence at rkm 163 to Willamette Falls (rkm 45).

Five fixed receiver sites were located at various points between the upstream locations of capture and the downstream release site (Figure 1). Specific sites were chosen based on the following criteria: usefulness to the study, security from vandals, ambient noise levels,

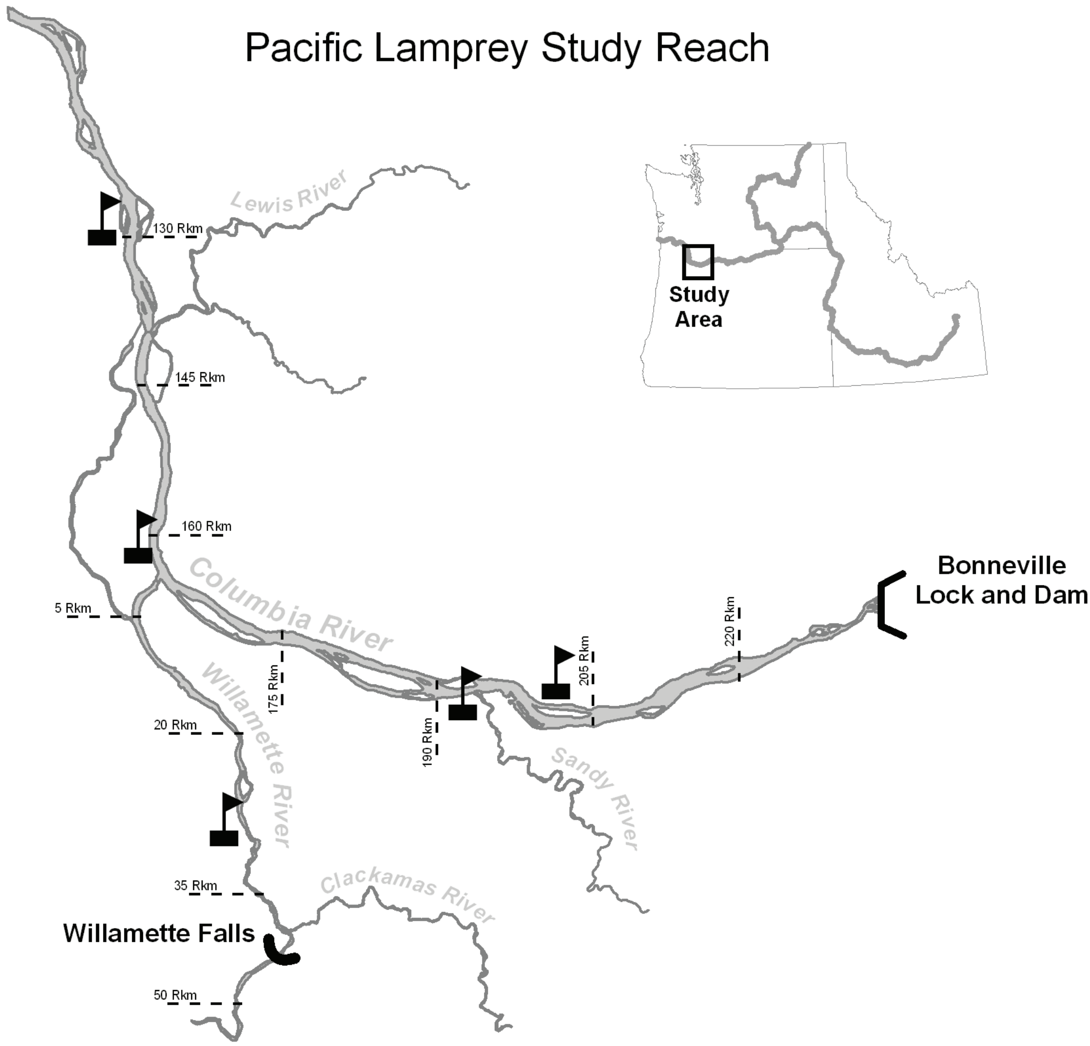

Figure 1. Study area, with locations of the five fixed receiver sites denoted by tower icons. One fixed site was located at river kilometer (rkm) 127 below the release site, one at the confluence of the Willamette and Columbia rivers, one on the Willamette at rkm 27, and two on opposing sides of the Columbia River at rkm 193 on the north shore and at rkm 190 on the south shore.

and elevation. Each fixed receiver site consisted of a Lotek SRX-400 radiotelemetry receiver, a nine-element Yagi antenna, and a deep cycle battery. The SRX-400 receivers stored data to permanent memory (Lotek Engineering 1994) and were set to continuously scan only channel 16 (149.960 MHz). We set the gain levels at each site as high as possible while trying to minimize the number of false detections received.

Capture sites

Adult Pacific lampreys were collected at Bonneville Dam and Willamette Falls at approximately 10-d intervals from June 11 through September 24, 1998. Fish at Bonneville Dam were collected with an adult lamprey trap at the Washington Shore Adult Fish Facility. We collected Willamette River fish by dip net at the Willamette Falls fish ladder while the ladder was in operation and by hand from Willamette Falls after the ladder was dewatered. We immediately transported captured fish to the Abernathy Technology Center near Longview, Washington and held them for 1–4 d until tagging.

Methods

Tagging procedure

We surgically implanted uniquely-coded Lotek MCFT-3BM radio tags with 3-s pulse rates and a guaranteed battery life of 163 d in 50 Pacific lampreys (25 from each collection site). The tags had an air weight of 7.7 g and a water weight of 3.7 g. To ensure that the water weight of the tag was less than 1% of the weight of the fish as recommended by Winter et al. (1978), a minimum lamprey length of 620 mm was used.

An effort was made to maintain clean but not necessarily aseptic conditions. All utensils and transmitters were washed in a betadine solution and surgical gloves were worn during surgeries. To ensure the quality of sutures and speed of tagging, all surgeries were conducted by a licensed veterinarian and assisted by a fisheries technician. The adult lampreys were anesthetized in a 150-mg/L solution of MS-222 (Methane-tricaine sulfonate). Throughout the tagging process, the gills were irrigated with a continuous flow of 75-mg/L solution of MS-222; however, a 150-mg/L solution and freshwater were used to maintain a suitable level of anesthesia as needed. A 3–4-cm ventral incision was made just anterior to the second dorsal fin and slightly lateral. Approximately 3 cm posterior to the incision a 16-gauge hypodermic needle was inserted and fed through to the incised area. The whip antenna of the transmitter was inserted through the needle and the needle was removed. The transmitter was then placed into the coelom through the incision, and the incision was sutured with 3/0 nonabsorbable nylon suture. No topical antiseptic was applied because of risk of damage to epithelial cells (Klontz and Smith 1968; Herwig 1979). The Pacific lampreys were placed in freshwater for recovery immediately after suturing. We held the tagged lampreys for 3–5 d prior to release to ensure incisions healed and to allow stress levels of the fish to return to pretagging levels (Close et al. 1996).

Release and relocation

All radio-tagged Pacific lampreys from the study were released near rkm 137. Relocation was accomplished using a combination of aerial and boat tracking along with the fixed receiver sites. All methods used Lotek SRX-400 receivers. Boat tracking was accomplished in an 18’ jet sled fitted with two five-element yagi antennas mounted on 10-ft masts. The antennas were pointed forward and at a 45° angle to the side on both sides of the boat. Aerial tracking was done in a Cessna aircraft with a two-element yagi mounted on each wing pointing down and to the side of the aircraft. Boat tracking was primarily limited to the study area; aerial tracking was conducted within the study area, upstream and downstream of the study area, and in tributaries flowing into the Columbia or Willamette rivers within the study area.

When tracking by boat, we made two to four passes depending on width of the river and the number of islands and side channels present. Both antennas were active when cruising to maximize coverage. When a fish was detected, we disconnected one antenna to determine the direction of the signal and moved closer until we could record the transmitter code and determine the fish’s location. When aerial-tracking on the Willamette and Columbia rivers, upstream and downstream passes were made, and on smaller tributaries, a single pass was sufficient to cover the entire river. The transmitter code, date, latitude, and longitude were recorded along with the nearest landmark or channel marker. Fixed receiver stations were downloaded multiple times each week during the lamprey run and every 2–3 weeks in the later stages of the study.

Pacific lampreys were classified as homed, strayed, and undetermined. The last known detection had to be in the river of capture, upstream of the confluence of the Willamette River for fish to be classified as "homed." A "strayed" classification was assigned to an individual that did not return to its river of capture, and the final detection was not in the Columbia River between the confluence of the Willamette River and the release point (rkm 137). If an individual was last detected in the Columbia River between the confluence of the Willamette River and the release point, or in the lower 2 km of the Multnomah Channel, then it was classified as "undetermined."

Results

Pacific lampreys that were displaced demonstrated low fidelity to capture sites. Of the 50 tagged individuals, 34% (n = 17) homed, 40% (n = 20) strayed, and 26% (n = 13) were undetermined. Pacific lampreys captured in the Columbia had a higher recovery rate and homing rate (20 and 14, respectively) than the Willamette sample (17 and 3, respectively); however, both groups exhibited nonsignificant homing (p = 0.622) based on the null expectation that one-half of the total recoveries would home and the other half would stray. Had all of the individuals that were undetermined (five Columbia and eight Willamette origin) strayed, then the tagged Pacific lampreys would have shown a significant (p = 0.024) tendency to stray. On the other hand, if all of the individuals that were undetermined were found to ultimately home, then the tagged Pacific lampreys would have still exhibited nonsignificant homing (p = 0.157). There does appear to be some temporal variation in the degree of homing. Fewer Pacific lampreys were classified as undetermined from early releases than from later releases (Figure 2).

The duration of time that we were able to track radio tagged individuals averaged 108 d (standard error = 13.0, range 0–254 d, median 143 d). There was no significant difference (p = 0.620) in tracking duration between collections made in the Columbia River and those from the Willamette River. Fish length was not well correlated with tracking duration (r = 0.191), suggesting that the tags did not affect a fish's final classification location.

Using analysis of variance (ANOVA), we found that the final location determination was significantly (p < 0.001) affected by the duration of radio tag detections. This effect was entirely due to the undetermined classification having significantly (p < 0.001) lower duration than the fish that strayed or homed. In general, most fish that were undetermined were released without subsequent detection. It should be noted though that some of the tagged fish that were classified as undetermined were detected for more than 130 d, but the mean is still significantly lower than the homed or strayed (Figure 3). In addition, a few tagged fish that homed and strayed did so in a very short (2–5 d) period of time.

Pacific lampreys collected at Bonneville Dam (mean 686 mm) were significantly (p < 0.001 t = 4.428, df = 48) longer than those collected from Willamette Falls (total length mean 647 mm). However, we compared the lengths of fish that chose the Willamette River with those that chose the Columbia River following displacement and discovered no significant (p = 0.701) difference in mean total length (672 and 689 mm, respectively). This test should be viewed with some caution as a result of small sample sizes (n = 22 and n = 6, for the Columbia and Willamette rivers). Also, ANOVA results showed that final classifications (Figure 4) were not influenced by length (p = 0.594).

Several interesting migratory behaviors appeared while radio-tracking during this experiment. All of the Pacific lampreys that we continuously tracked migrated upstream approximately 100–150 m from the bank and generally were in water less than 10 m deep. A few fish would cross from one bank to the other, and due to weak or lost signals, we assume that they are in close orientation to the bottom. There was no preference for specific shorelines or any specific circadian pattern to the migrations. We observed that some radio-tagged Pacific lampreys progressed directly to an upstream location while others would move upstream and then backtrack. Some fish that backtrack would

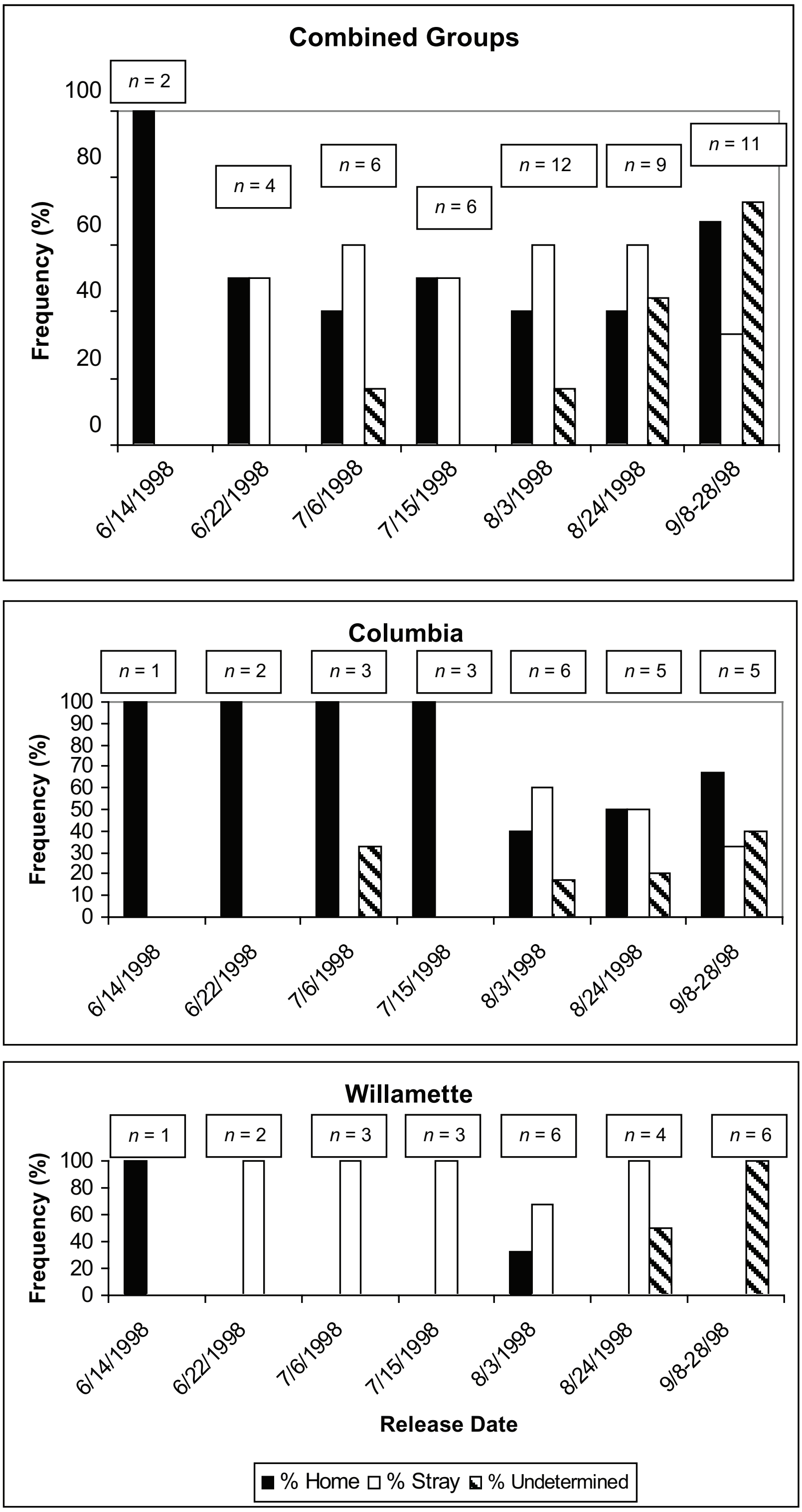

Figure 2. Frequency of final lamprey classifications by release date.

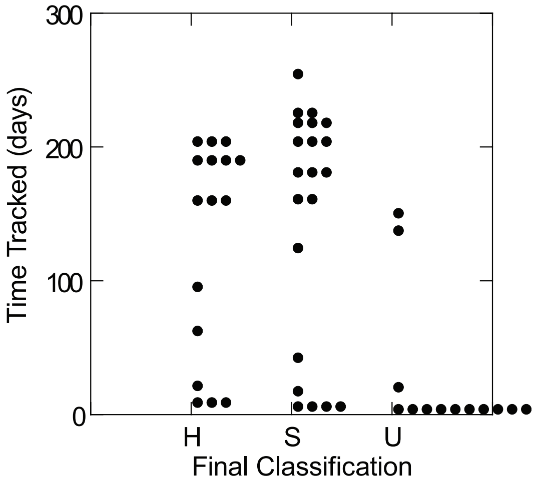

Figure 3. The duration (days) that radio-tagged Pacific lampreys were detected as a function of final location. H = Homed, S = Strayed, and U = Undetermined.

once again continue upstream and others held their position or continued downstream. None of the individuals migrated below the release location. Directionality of movements was not associated with capture location or final classification (Figure 5). The fastest migration speed

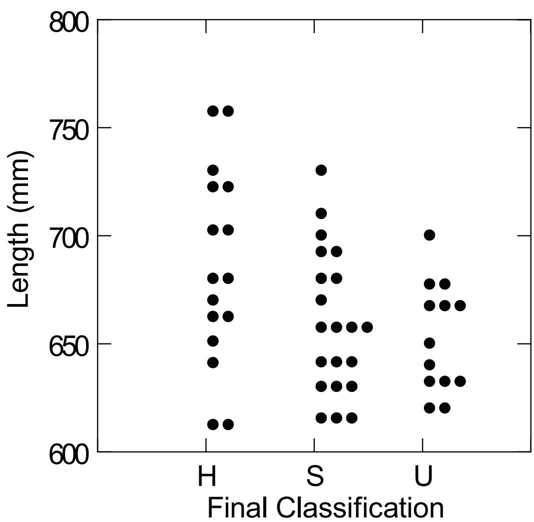

Figure 4. Total length of radio-tagged Pacific lampreys as a function of final classification. H = Homed, S = Strayed, and U = Undetermined.

for Columbia River fish was 2.4 km/h, and it was 2.5 km/h for Willamette River fish. Both groups could maintain these speeds for many hours or days.

Discussion

Pacific lampreys did not exhibit in-season homing. Many factors may have contributed to these findings: trapping and handling effects, in-river environmental factors, or some unknown physiological factor. Nonetheless, the complete lack of homing that Pacific lampreys exhibited has many management implications.

It is possible that the handling stress, the post-surgery holding time, or radio-tag size affected these results. At the time of this study, Pacific lampreys had never been radio-tagged before. Extra care was taken during the surgeries and recovery to ensure that incisions healed and that individuals recovered fully prior to release. Compared to modern radio tags, the tags used in this study were large. This was necessary to achieve a significant battery life. It's possible that the size of the tag impeded swimming performance and ultimately homing, but our data does not support this idea because larger lampreys did not home at a greater rate than smaller lampreys.

We suspected that environmental factors such as river discharge or water temperatures may be important factors influencing whether an individual ultimately homed or strayed. The Columbia River has much higher discharge than the Willamette River, and a higher frequency of Columbia-origin Pacific lampreys did return to the Columbia River than those captured in the Willamette River. However, neither population exhibited a significant homing effect. We did see an increase in the number of individuals that homed earlier in the year (Figure 2), which could be the result of increasing water temperatures (Keefer et al., in press), but we were unable to discern if temperature was the causal effect.

A photophobic response has been observed in upstream migrants of several lamprey species (Hardisty and Potter 1971). Kan (1975) specu-

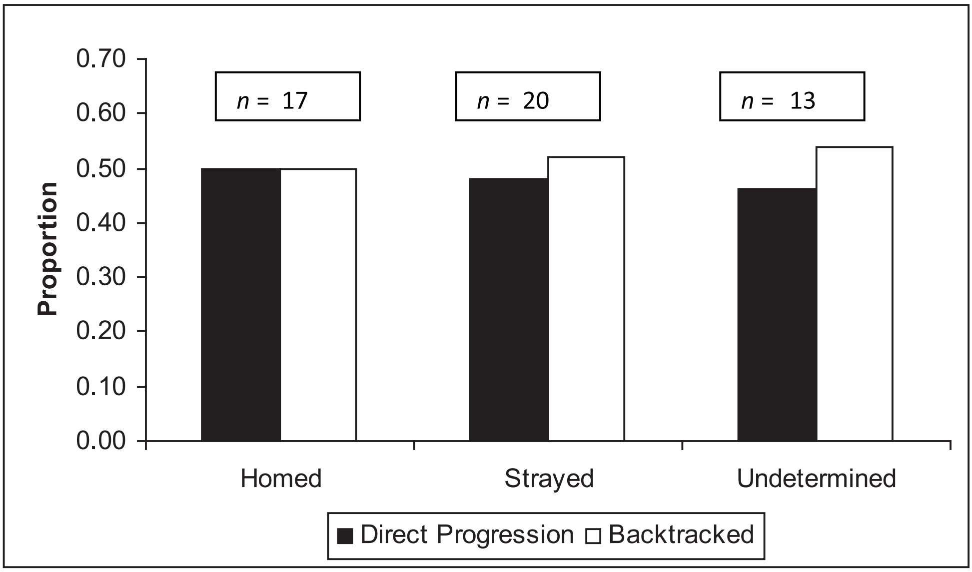

Figure 5. The proportion of radio-tagged Pacific lampreys that were observed to progress directly upstream and those that backtracked by final classification. Samples sizes were 17, 20, and 13 for homed, strayed, and undetermined classifications, respectively.

lated that this response might be true for Pacific lampreys based on observations in fishways where prespawning fish were seen attaching to the shaded side of fishway walls. Based on our telemetry observations, we would conclude that during upstream migrations in the lower Columbia River, adults readily moved during daytime and nighttime periods and did not seem to exhibit any photophobic response. However, this may be more related to water clarity than to phototaxis. Kan (1975) estimated migration time as 4.5 km/d for Pacific lampreys in Clear Creek, a tributary to the John Day River. Our telemetry observations illustrate that although considered weak swimmers (Beamish 1974), Pacific lampreys were capable of traveling at velocities near 2.5 km/h and sustaining that activity for at least 24 h.

Experiments conducted by Bjerselius et al. (2000) showed that adult sea lampreys use larval bile acids as a migratory pheromone to help locate spawning areas during their spawning migrations, and the effect of the pheromone was dependant on river flow, adult sexual maturity, and time of day. In a similar experiment conducted on Pacific lampreys, only one of six individuals exhibited similar responses to juvenile bile acids (Sorensen and Close 1998). Lack of homing in our experiment could be an indication that Pacific lampreys do not follow stream specific migratory pheromones as do sea lampreys. Unlike sea lampreys, Pacific lampreys typically spend at least a year in freshwater prior to spawning (Beamish 1980). It has been shown that olfactory sensitivities in sea lampreys diminish shortly after entering spawning streams and continue to lessen as individuals mature (Sorensen et al. 1995). Therefore, migratory pheromones for Pacific lampreys may only operate at the level sufficient to guide individuals into rivers where lampreys have produced juveniles in the past but may not be as important for in-river homing and detection of specific spawning locations.

Length differences at various collection sites have been taken as evidence supporting a homing hypothesis and hence an inferred stock structure (Beamish 1980; Keefer et al., in press). A similar difference in length was found between our two lamprey populations, but in this case it may be the result of sampling bias since the length composition of fish returning after displacement showed no differences between the Columbia and Willamette rivers. The location of the trap at Bonneville Dam required individuals to traverse the lower (one-fourth) of the fish ladder prior to entering the trap. Moser et al. (2002) demonstrated that Pacific lampreys have difficulty negotiating the Bonneville Dam fish ladders. This phenomenon may be related to size, thus skewing the length composition of Pacific lampreys collected in the trap. Alternatively, the Pacific lampreys collected at Willamette Falls may be biased toward smaller fish as a result of collecting fish by hand.

If Pacific lampreys exhibited a high degree of homing fidelity, one would also expect a high degree of genetic stock structure as seen in Lake Huron sea lampreys (Wright et al. 1985). The lack of in-season homing found in this study combined with no statistical support for genetic population structure or subdivision found in Goodman et al. (2006) supports the hypothesis that Pacific lampreys do not home to natal streams. In our review of the literature, the vast majority of fish species exhibit some level of homing fidelity and it is difficult to consider the idea that an anadromous species with such a large range would not exhibit a similar behavior. Pacific lampreys do have a novel life history that is not fully understood and is considerably different than other fishes. It is possible that lampreys do home at some level and do have some form of population structure that are currently undetectable, but conservation and management of the species must consider the potential implications of managing for a single population.

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