Electronic tags and genetics explore variation in migrating steelhead kelts (Oncorhynchus mykiss), Ninilchik River, Alaska

Jennifer L. Nielsen, Sara M. Turner, and Christian E. Zimmerman

Abstract: Acoustic and archival tags examined freshwater and marine migrations of postspawn steelhead kelts (Oncorhynchus mykiss) in the Ninilchik River, Alaska, USA. Postspawn steelhead were captured at a weir in 2002–2005. Scale analysis indicated multiple migratory life histories and spawning behaviors. Acoustic tags were implanted in 99 kelts (2002–2003), and an array of acoustic receivers calculated the average speed of outmigration, timing of saltwater entry, and duration of residency in the vicinity of the river mouth. Ocean migration data were recovered from two archival tags implanted in kelts in 2004 (one male and one female). Archival tags documented seasonal differences in maximum depth and behavior with both fish spending 97% of time at sea <6 m depth (day and night). All study fish were double tagged with passive integrated transponder (PIT) tags implanted in the body cavity. Less than 4% of PIT tags were retained in postspawn steelhead. Molecular genetics demonstrated no significant differences in genetic population structure across years or among spawning life history types, suggesting a genetically panmictic population with highly diverse life history characteristics in the Ninilchik River.


[Traduit par la Rédaction]

Introduction

Steelhead, the anadromous form of the Pacific salmonid species Oncorhynchus mykiss (Smith and Stearley 1989), originate from coastal streams and rivers throughout the North Pacific Ocean (Behnke 1966; Scott and Crossman 1973; Burgner et al. 1992). Their native anadromous range currently extends from southern California to the Kamchatka Peninsula (Quinn 2005). Oncorhynchus mykiss are iteroparous and can display partial anadromy with some populations maturing in fresh water (Jonsson and Jonsson 1993; Keefer et al. 2008; Narum et al. 2008).

Postspawning migrations of steelhead are typically dominated by first time kelts returning to the sea after their first spawning event, but can include older multisea winter adults who have spawned more than once. Among Pacific salmon, iteroparity is unique to steelhead and coastal cutthroat trout (Oncorhynchus clarkii clarkii), but is common in Atlantic salmon (Salmo salar). Migrations to and from salt water are energy demanding and physiologically challenging (McKeown 1984; Hendry and Berg 1999; Cooke et al. 2006). Despite the increased costs associated with secondary migrations, iteroparous fish are thought to contribute substantially to the genetic and demographic structure of some salmon populations (Ward and Slaney 1988; Fleming and Reynolds 2004; Keefer et al. 2008). Rates of iteroparity in steelhead vary widely (0%–79%) and can change considerably year to year (Withler 1966; Savvaitova et al. 1996; Narum et al. 2008). Repeat spawning is thought to be more common in females (Jones 1973; Burgner et al. 1992; Wertheimer and Evans 2005), suggesting valuable genetic trade-
offs from this life history (Keefer et al. 2008). We assume that there is an age-limited senescence to the number of times any individual can return to fresh water to spawn (Hendry et al. 2004), but data on long-lived steelhead are few. Jones (1973) documented one female steelhead in Petersburg Creek, Alaska, that had spawned five times; Leider et al. (1990) documented individuals spawning up to four times; and a male steelhead spawning for the sixth time was found on the South Fork Eel River, California (J.L. Nielsen, unpublished data). The length of time at sea between spawning events can also vary among steelhead, with adults spawning on consecutive or alternate years (Burgner et al. 1992; Lohr and Bryant 1999). These latter categories of steelhead life histories remain poorly described. Radio telemetry has been successfully used to describe migratory behavior of many salmonids in fresh water (Eiler 1995; Meka et al. 2003; Cooke et al. 2005). Ruggereone et al. (1990) used ultrasonic tags to individually track adult steelhead captured in British Columbia, as they migrated from the ocean to spawning locations in the Dean River. While we know something about the upstream spawning migrations of steelhead from radio telemetry studies, little is known about the behavior of postspawning steelhead during their downstream and saltwater migrations. Because of radio signal attenuation in salt water, this method is not generally applicable to migrations in marine habitats, although ultrasonic telemetry has been used to track salmon during their homeward migration at sea in near-surface waters (Ogura and Ishida 1992).

In recent years, acoustic technology has been developed and successfully applied for tracking the freshwater to marine transitions in anadromous fish (Voegeli et al. 1998; Welch et al. 2004; Kristianson and Welch 2007) and to monitor salmon in marine habitats (Voegeli et al. 1998; LaCroix and Voegeli 2000; Welch et al. 2004). The development of automated subsurface receivers that can be deployed at key locations or in a gate-like configuration across constrictions or shallow marine areas has enabled the tracking of larger numbers of fish carrying coded acoustic tags (Welch et al. 2002; Heupel et al. 2006). While acoustic tags have been used to describe movements of juvenile salmon (Welch et al. 2004; Melnychuk et al. 2007), no evidence is found in the literature on the freshwater–marine migration of steelhead kelts (however, see Haltunen et al. 2009 for acoustic data on Atlantic salmon kelts).

Once steelhead enter open marine habitats, tracking their movements becomes more difficult. During their first year at sea, steelhead are thought to move rapidly offshore avoiding habitats along the continental shelf (Hartrt and Dell 1986; Quinn 2005). Published high-seas research data suggest that young steelhead are widely distributed in offshore waters and that at least some adult steelhead from North America migrate across the Pacific Ocean into the western subarctic gyre off the Kamchatka Peninsula (Burgner et al. 1992; Myers et al. 1996; Myers et al. 2001). Despite over 80 years of research, we know little about the behavior of salmon during open-ocean migrations (Walker and Myers 2009).

Electronic data storage tags (DSTs, or archival tags) have been applied in many studies of fish distribution and movements in marine habitats (Metcalfe and Arnold 1997; reviewed in Sibert and Nielsen 2001). Many types of environmental sensors have been developed, but depth (pressure) and temperature are the most common sensors used in DST studies. This new technology holds great promise for understanding the oceanic distribution and behavior of different fish (Walker et al. 2000; Nielsen et al. 2009).

In this study, we used acoustic tags with moored receivers and long-term archival tags to explore the transit time of downstream migration, timing and duration of transition from fresh water to salt water, behavioral response to tides at first ocean entry, and environmental conditions during open-ocean migrations for postspawning steelhead kelts from the Ninilchik River, Alaska. We compiled life history and genetic data on downstream migrating fish at the weir and explored the variety of life histories found in steelhead kelts in this system. Population genetic analyses were used to explore genetic relationships among and between sample years and life history types of steelhead in the Ninilchik River. Our objective was to better describe the migratory and genetic characteristics of steelhead near the northern extent of their range and test the utility of electronic tags as tools to better understand the marine life stages of adult steelhead.

**Materials and methods**

**Demographics**

The Ninilchik River is a 350 km² watershed located on the southern Kenai Peninsula in south-central Alaska, USA (Fig. 1). The Ninilchik River flows into Cook Inlet, a large marine watershed (~100 000 km²) that is a semi-enclosed coastal body of water connected to the North Pacific Ocean. Lower Cook Inlet is extremely rugged with deep pockets and shallow shoals (Fig. 1). The depths in the central inlet near the Ninilchik River are generally less than 60 m. Cook Inlet has the fourth largest tidal bore in the world (9.2 m). At the mouth of the Ninilchik River, the spring mean tidal range is 5.8 m, resulting in strong tidal currents during kelt outmigration. All downstream migrating steelhead adults were collected at a weir located at river kilometre 6 on the Ninilchik River (2002–2005; Fig. 2). The weir was installed as early as weather would allow in May and operated 24 h a day until the end of June 2002–2005, encompassing the full distribution of downstream migrating steelhead kelts (Table 1). After completion of our kelt study, the weir was operated as a full downstream blockage in an effort to monitor upstream migrating Chinook salmon (*Oncorhynchus tshawytscha*) by the Alaska Department of Fish and Game. No adult steelhead were observed at the weir following our study in any year the weir was operated.

Randomly selected individuals in good health (*N* = 162) were selected for tagging with electronic devices (2002–2003). No secondary external markers were used because of regulations imposed by Alaska Department of Fish and Game. All electronically tagged fish were implanted with individually coded passive integrated transponder (PIT) tags. PIT identifications were scanned for all fish passing the weir using a handheld detector. A metal detector was also used to scan all steelhead passing the weir (2003–2005) to monitor previously tagged fish that may have lost their PIT tag. Scales from the preferred area (Koo 1962) were taken from 160 tagged fish and seven freshwater adult males collected at the weir (Table 2). Scale patterns were used to identify reproductive life history types when annuli and spawning
checks were clearly defined and the scales not affected by regeneration or major resorption along the lateral axis. Mean Fulton’s condition factor (K) was calculated for each life history type across all years (Guy and Brown 2007).

Fig. 1. Map of Cook Inlet, Alaska, showing bathymetry and currents. Red circle is approximate location of mouth of Ninilchik River. (Graphic adapted with permission, G.S. Drew, originator: http://alaska.usgs.gov/science/biology/seabirds_foragefish/maps/Cook_Inlet/bathy.php.)

Acoustic tags

The freshwater-to-marine migration of postspawn steelhead kelts was studied using acoustic tags with individual fish identification codes and an array of moored acoustic receivers set in and around the mouth of the Ninilchik River in Cook Inlet. Ultrasonic transmitters (Vemco, Ltd., Nova Scotia; 9 mm × 30 mm, 5 g) were surgically implanted in the peritoneal cavity of 49 (2002) and 50 (2003) steelhead kelts. The acoustic tags were powered by a lithium battery and had a life expectancy of 125 days. Tags were programmed to transmit acoustic signals with a random pulse interval between 30 and 90 s. All tags transmitted at the same frequency (69 kHz), but each tag produced a unique six-ping coded signal so individual fish could be identified.

Surgeries were performed on a raised platform in the Ninilchik River just downstream of the weir. Appropriate measures were taken to minimize infection associated with surgery (Mulcahy 2003). A topical antiseptic, chlorhexidine diacetate, was used at the incision point followed by a 2.0 cm incision made anterior to the tip of the pelvic girdle on the midventral axis. The acoustic tag was inserted, gently massaged into position in the peritoneal cavity, and the incision was closed with four simple interrupted sutures. All tagged fish were held in a live box until they were alert and swimming freely (typically 5–24 min) and then allowed to volitionally leave the live box in the downstream direction.

Fig. 2. Ninilchik River, Alaska, showing sampling weir and approximate locations for acoustic receiver moorings in Cook Inlet (circles).
Acoustic tags were detected by ultrasonic receivers (Vemco, Ltd., VR2 single channel) that were deployed in a gate-like configuration surrounding the mouth of the Ninilchik River (see Fig. 2). The VR2 data loggers were suspended 3–5 m from the bottom of Cook Inlet at distances 0.65–1.88 km from the river mouth, approximately 0.5–2.8 km from shore. Receivers were deployed on short moorings with subsurface floatation and a surface buoy. Disposable, degradable anchors were used to secure the moorings to the bottom. Receiver arrays were deployed prior to tagging and recovered during the last week in June. In 2003, an additional receiver was deployed within the mouth of the Ninilchik River to gain accuracy on river migration times.

Each receiver contained 2 MB of flash memory and can operate up to 15 months on a single D-cell battery. Detection range of 0.5–1.0 km were expected using these receivers, depending on the power output of each tag. Mean distance between neighboring receivers was 710 m (range 283–806 m). The spacing of the receivers was based on the distance between neighboring receivers was 710 m (range 283–806 m). The spacing of the receivers was based on the calculated range of 0.5–1.0 km were expected using these receivers, with subsurface floatation and a surface buoy. Disposable, degradable anchors were used to secure the moorings to the bottom. Receiver arrays were deployed prior to tagging and recovered during the last week in June. In 2003, an additional receiver was deployed within the mouth of the Ninilchik River to gain accuracy on river migration times.

Both types of tags were programmed to start recording at 15 s sampling intervals using a time extension recording program. When allocated memory was full for any sensor, every other sample in memory was overwritten with new time and date associated data. This memory extension program predicted that each tag would have approximately 32760 data point storage capacity. Pressure data was programmed to have a maximum range of 3000 m with ±3 m accuracy. Standard depth calculations were corrected for gravitational density (latitude) and liquid density (temperature) using a formula from Lotek Wireless Inc., based on Harris (2000). The largest difference in estimated and corrected depth was 39 mm (0.13%); average depth correction was 3.8 mm. Temperature sensors were set to range between –5 and 35 °C with an accuracy of ±0.3 °C. Light sensors were programmed to record ambient light levels to

### Table 1. Demographic data on Ninilchik River steelhead kelts passing through the weir, 2002–2005.

<table>
<thead>
<tr>
<th>Year</th>
<th>Dates</th>
<th>Total fish</th>
<th>Tagged fish</th>
<th>Tag recoveries</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>N (M/F)</td>
<td>N (M/F)</td>
<td>Previously tagged (N)</td>
</tr>
<tr>
<td>2002</td>
<td>24 May – 26 June</td>
<td>449 (120/27)</td>
<td>729 (73/1)</td>
<td>0</td>
</tr>
<tr>
<td>2003</td>
<td>16 May – 29 June</td>
<td>412 (145/35)</td>
<td>268 (65/1)</td>
<td>0</td>
</tr>
<tr>
<td>2004</td>
<td>13 May – 30 June</td>
<td>416 (172/41)</td>
<td>244 (59/1)</td>
<td>16</td>
</tr>
<tr>
<td>2005</td>
<td>6 May – 30 June</td>
<td>681 (128/19)</td>
<td>553 (81/1)</td>
<td>14</td>
</tr>
</tbody>
</table>

### Table 2. General statistics on steelhead life history categories determined by scales.

<table>
<thead>
<tr>
<th>LH type</th>
<th>Months at sea</th>
<th>N</th>
<th>Sex (M/F)</th>
<th>Mean FL (mm)</th>
<th>SD</th>
<th>Mean mass (g)</th>
<th>SD</th>
<th>Mean Fulton’s K</th>
<th>SD</th>
<th>Gene diversity</th>
<th>Allelic richness</th>
<th>PO</th>
<th>FS</th>
<th>HS</th>
</tr>
</thead>
<tbody>
<tr>
<td>FW males</td>
<td>0–17</td>
<td>7</td>
<td>7/0</td>
<td>479.4</td>
<td>45.8</td>
<td>118.4</td>
<td>30.4</td>
<td>0.104</td>
<td>0.002</td>
<td>0.531</td>
<td>2.91</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>First spawn</td>
<td>4–6</td>
<td>126</td>
<td>50/76</td>
<td>643.8</td>
<td>65.9</td>
<td>222.8</td>
<td>64.5</td>
<td>0.089</td>
<td>0.063</td>
<td>0.533</td>
<td>3.08</td>
<td>2</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>Consecutive</td>
<td>8–12</td>
<td>20</td>
<td>7/13</td>
<td>734.0</td>
<td>55.3</td>
<td>319.0</td>
<td>86.8</td>
<td>0.079</td>
<td>0.006</td>
<td>0.522</td>
<td>2.94</td>
<td>2</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Alternate</td>
<td>16–20</td>
<td>14</td>
<td>5/9</td>
<td>714.5</td>
<td>57.8</td>
<td>289.3</td>
<td>76.2</td>
<td>0.077</td>
<td>0.006</td>
<td>0.547</td>
<td>3.13</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>

*Note: LH, life history; FW, fresh water; FL, fork length; SD, standard deviation; K, Fulton’s condition factor.

*PO, parent offspring; FS, full sibling; HS, half sibling.

Archival tags containing temperature and pressure sensors (Lotek Wireless, Inc., LTD_1110; N = 26) and tags with temperature, pressure, and light sensors (Lotek Wireless, Inc., LTD_2410; N = 37) were used in this study. Archival tags were surgically implanted 4–20 June 2002 (N = 33) and 28 May – 18 June 2003 (N = 30) under the same surgical conditions as acoustic tags. Archival tags were cylindrical (3 mm long × 11 mm diameter; 5 g). A 5 cm plastic stalk was attached to the beta-type LTD_1110 tags to mimic active light stalks developed for the LTD_2410 tags by Lotek Wireless, Inc. A second small (2 mm) incision was made anteriorly adjacent to the tag insertion point to pass this stalk through the skin. The tag and stalk were secured by a single suture to the interior wall of the peritoneal cavity before closing such that the light stalk hung laterally along one side of the lower abdomen and extended to just above the vent of the fish. LTD_2410 tags used in 2003 were virtually identical in size and mass to beta-type LTD_1110 tags, but were equipped with a 10 cm functioning light stalk and equivalent sensor. Batteries used in the LTD_2410 were smaller. Battery technology also improved in the LTD_2410, and these tags were predicted to have up to a 3-year battery life. Electronic data from all sensors was stored in 32 kB of nonvolatile EEPROM, and all data records were correlated with an onboard clock.

Both types of tags were programmed to start recording at 15 s sampling intervals using a time extension recording program. When allocated memory was full for any sensor, every other sample in memory was overwritten with new time and date associated data. This memory extension program predicted that each tag would have approximately 32760 data point storage capacity. Pressure data was programmed to have a maximum range of 3000 m with ±3 m accuracy. Standard depth calculations were corrected for gravitational density (latitude) and liquid density (temperature) using a formula from Lotek Wireless Inc., based on Harris (2000). The largest difference in estimated and corrected depth was 39 mm (0.13%); average depth correction was 3.8 mm. Temperature sensors were set to range between –5 and 35 °C with an accuracy of ±0.3 °C. Light sensors were programmed to record ambient light levels to
predict apparent sunrise and sunset and allow estimates of geolocation (approximate longitude and latitude) for fish during ocean migrations (Hill 1994; Welch and Eveson 1999). Unfortunately, the light stalk failed in the one archival tag with an active sensor recovered in this study, and no light data were analyzed.

**Genetic analyses**

Nonlethal caudal fin clips were randomly collected from outmigrating adults at the Ninilchik River weir for population genetic analysis in 2002 (N = 91), 2003 (N = 79), and 2005 (N = 126). Fin clips were stored in 100% ethanol and analyzed at the US Geological Survey Alaska Science Center’s Molecular Ecology Laboratory, Anchorage, Alaska. Genetic samples were not collected in 2004 because of funding constraints. DNA was successfully extracted from 296 samples using the Puregene DNA Isolation kit (Gentra Systems, Inc.).

Eleven microsatellite loci were used to analyze genetic structure for Ninilchik River steelhead (Table 3). Loci were selected based on documented variability in *O. mykiss*, ease of polymerase chain reaction (PCR) amplification, and a history of allele scoring rigor (Table 3). Several primers were redesigned for use in this study: Ogo4 forward (F), 5'-CAGAATCAGTAAAGGACGC-3'; Ogo4 reverse (R), 5'-GAGGATAGAAGAGGTGGGC-3'; and Ots3 (R), 5’-CACAATGGAAAGACCAT-3’. Ogo4, Ogo4, and Ots3 forward primers were modified by the addition of M13 (R) tails, and Oney8 and Oney11 forward primers were modified with M13 (F) tails. All M13 tails were added to the 5’ ends and allowed for allele fragment visualization by annealing to labeled complementary M13 tails added to the PCR mix. The remaining loci were visualized by adding directly labeled forward primers.

PCR reactions were conducted in 10–12 μl volumes using approximately 50 ng of genomic DNA, 0.06–0.1 U (1 U = 16.67 nkat) of Taq DNA polymerase (Promega), 10 mmol–L⁻¹ Tris–HCl (pH 8.3), 1.5 mmol–L⁻¹ MgCl₂, 50 mmol–L⁻¹ KCl, 0.01% gelatin, 0.01% NP-40, 0.01% Triton X-100, 200 μmol–L⁻¹ each dNTP, 0.1–0.5 pmol unlabeled primers, 0.1–0.4 pmol directly labeled primers, and 0.5–1.5 pmol labeled M13 tails. PCR reactions were carried out in MJ Research (BIORAD) or MWG thermocyclers (MWG Biotech Inc.), with an initial denaturation time of 2 min at 94 °C followed by 40 cycles of 94 °C for 15 s, 52 °C for 15 s, 72 °C for 30 s, and a final 30 min elongation step at 72 °C. The 30 min elongation step was not done for Omy325, Oney14, Ots1, and Ots4. Gel electrophoresis and visualization of alleles was performed using a LI-COR model IR2 automated fluorescent DNA sequencer, and allele sizes were assigned using GeneImagIR v. 3.00 software (LI-COR). Microsatellite allele sizes were quantified in relation to the M13 single nucleotide ladder, *O. mykiss* DNA samples of known size, and (or) the GeneScan-350 internal size standard (PE Biosystems). Approximately 10% of all samples were run on a second gel and scored independently for quality control.

Microsatellite Toolkit (Park 2001) was used to find matching samples among sampling years and create input files for subsequent analyses. GENEPOP v. 3.4 (Raymond and Rousset 1997) was used to test each locus for significant departures from Hardy–Weinberg equilibrium (HWE) and to provide a global estimate of HWE for all loci and all collection years combined. The significance level for interpreting HWE was adjusted for the number of loci using a Bonferroni correction (α = 0.0045; Rice 1989). ARLEQUIN v. 3.0 (Excoffier et al. 2005) was used to calculate observed (*Ĥo*) and expected (*Ĥe*) heterozygosity by locus and to calculate pairwise *FST* among three sampling years (θ, Weir and Cockerham 1984). Significance for pairwise *FST* was evaluated after applying a Bonferroni correction (α = 0.0017). FSTAT v. 2.9.3 (Goudet 2001) was used to test for linkage disequilibrium among loci, and a Bonferroni correction based on the total number of comparisons (55) was used to evaluate significance (α = 0.0009). LDNE was used to estimate effective population size, *Nₑ*, for steelhead kelts in the Ninilchik River using all 11 microsatellite loci (Waples and Do 2008).

Genetic diversity within and among different life history types and between genders was analyzed using SAPGeDI (Hardy and Vekemans 2002). The program ML-Relate was used to calculate relatedness and predict relationship categories between all pairs of individuals using maximum likelihood (Kalinowski et al. 2006). We assessed 39 060 relationships among all unique individuals in our genetic database. Overall relatedness among Ninilchik River steelhead was determined by averaging *r* values for all comparisons.

**Results**

**Demographic data**

The number of steelhead kelts that passed through the weir each year varied significantly (average = 490 fish; Table 1). Outmigrating female kelts outnumbered (≥59%) male kelts each year. Male–female ratios ranged from 1:1.4 (2004) to 1:4.3 (2005). Male–female ratios in tagged fish were 1:1.9 (2002) and 1:1.2 (2003). Six PIT tags (3.7%), ten acoustic tags (10.1%), and three archival tags (4.8%) were recovered from adult steelhead in subsequent years at the weir (Table 1). Thirteen downstream migrants showed various signs of previous surgeries (remaining sutures or surgical scars) with no indication of remaining tags. We assumed all tags from these fish were expelled during sea migrations or at spawning. All recovered tagged fish were found at the weir 2–3 years after the year they were tagged.

Four different migratory life histories were observed in adult steelhead scales based on growth patterns. Scales taken from two kelts (~1%) showed regeneration and were excluded from life history analyses. Migratory life histories included (i) freshwater adults with no seawater history and no evidence of prior spawning or residual gametes; (ii) kelts that were returning to sea after their first spawning event; (iii) repeat spawning steelhead that reproduced in consecutive years (after one summer and fall at sea between spawning events ~8 months at sea); and (iv) repeat spawning steelhead that reproduced in alternate years (~16 months at sea). All seven freshwater adults captured at the weir were male, and these fish appeared to be headed to sea for the first time, although actual sea entry was not confirmed because these fish were not tagged. We have no empirical data to confirm reproduction in fresh water by these males prior to migration. First time spawning steelhead dominated
the postspawn downstream steelhead migration (58%). Based on tag recoveries (all types), clearly identifiable suture or insertion scars, and (or) PIT tag retention, we were able to document that 17% of the tagged steelhead from 2002 were recovered in 2004 and 20% of the tagged steelhead in 2003 were recovered in 2005. Consecutive-year steelhead outnumbered alternate-year steelhead at the weir in both years. Females that spawned more than once were able to document that 17% of the tagged steelhead from the postspawn downstream steelhead migration (58%). Based on tag recoveries (all types), clearly identifiable suture or insertion scars, and (or) PIT tag retention, we were able to document that 17% of the tagged steelhead from 2002 were recovered in 2004 and 20% of the tagged steelhead in 2003 were recovered in 2005. Consecutive-year steelhead outnumbered alternate-year steelhead at the weir in both years. Females that spawned more than once were able to document that 17% of the tagged steelhead from the postspawn downstream steelhead migration (58%). Based on tag recoveries (all types), clearly identifiable suture or insertion scars, and (or) PIT tag retention, we were able to document that 17% of the tagged steelhead from 2002 were recovered in 2004 and 20% of the tagged steelhead in 2003 were recovered in 2005. Consecutive-year steelhead outnumbered alternate-year steelhead at the weir in both years. Females that spawned more than once were able to document that 17% of the tagged steelhead from the postspawn downstream steelhead migration (58%).

Mean condition factor ($K$) was higher in freshwater males without sea experience, but mean $K$ was not statistically different among the four life history types (analysis of molecular variance, AMOVA $F$ value $<0.0001$; $P > F = 0.938$). The four highest $K$ values were found in first spawn female kelts ($K = 0.11–0.14$). In general, females did not have significantly higher condition factors than males in years when lengths and masses of outmigrating steelhead kelts were monitored during tagging (2002–2003), but female condition did have greater variance in both years: mean $K$ ± standard deviation (SD) for females in 2002: $K = 0.079 ± 0.012$; males in 2002: $K = 0.087 ± 0.009$; $t$ test assuming unequal variance ($t = 0.01$; $P = 0.44$). Mean $K$ values for females in 2003 was 0.096 ± 0.207; mean $K$ values for males in 2003 was 0.087 ± 0.008 ($t = 0.28$; $P = 0.16$). There were no significant trends by gender for temporal downstream kelt migrations for fish measured at the weir during 2002–2003: 25 May 5 June (early) males $N = 30$, females $N = 44$; 6–30 June (late) males $= 44$, females $= 50$. No significant differences in $K$ were found for early or late migrating kelts (both genders combined; $t$ test assuming unequal variance; 2002: $t = 0.27$, $P = 0.19$; 2003: $t = 0.36$, $P = 0.32$).

### Acoustic tags

Kelts tagged in 2002 ranged in length from 450 to 782 mm, and kelts tagged in 2003 ranged in length from 498 to 870 mm. The first fish was tagged on 30 May (2002) and on 25 May (2003). Detections of individual fish by the buoy array occurred until 21 June (2002) and 23 June (2003). Not all fish tagged with acoustic transmitters were detected by the automated receivers. A total of 38 (76%; 2002) and 46 (92%; 2003) tagged fish were detected leaving the Ninilchik River. In 2003, 48 (96%) fish were detected by the receiver located in the lower river before saltwater entry. Two acoustic-tagged fish were recorded in the lower river, but not in the coastal marine array. Eighty-six percent of acoustic tags were recorded by receivers for 2002 and 2003 combined. Ten acoustic tags were recovered from kelts returning to the weir in 2004 and 2005 (five tags each year).

Daily mean flow during the period that acoustic-tagged steelhead kelts migrated out of the Ninilchik River ranged from 1.78 to 3.43 $m^3/s$ in 2002 and from 2.35 to 6.97 $m^3/s$ in 2003 (Fig. 3). Transit time between the weir and saltwater (i.e., time that elapsed between after-tagging release and first detection in salt water) ranged from 8.6 to 254.9 h. There was no relationship between flow on the day of tagging and transit time (2002: $r^2 = 0.03$, $n = 38$, $P = 0.29$; 2003: $r^2 = 0.12$, $n = 46$, $P = 0.02$). Mean rate of travel ($±SD$) between the tagging site and the receiver array was 5.10 ± 4.40 km day$^{-1}$ and 8.55 ± 9.94 km day$^{-1}$ in 2002 and 2003, respectively. There was no relationship between the length of fish and transit time (years and sexes combined; $r^2 = 0.10$, $n = 84$, $P = 0.01$). The mean rate of downstream travel ($±SD$) of female fish in 2002 was 3.98 ± 1.69 km day$^{-1}$, and the mean rate of downstream travel of male fish in 2002 was 7.24 ± 6.83 km day$^{-1}$. In 2002, male kelts migrated significantly faster than females ($t = –2.28$, df = 36, $P = 0.01$). In 2003, mean rate of travel was 9.33 ± 9.66 km day$^{-1}$ for female kelts and 7.44 ± 10.48 km day$^{-1}$ for male kelts. In 2003, there was no significant difference in transit time between male and female kelts ($t = 0.6228$, df = 44, $P = 0.54$).

Steelhead kelts remained within the vicinity of the receiver array from 0 to 35.5 h. Time spent near the shore as determined by acoustic tags ($±SD$) averaged 1.47 ± 1.1 h in 2002 and 1.95 ± 0.9 h in 2003. There were no significant differences in duration that fish remained near the mouth of the river when comparing between years or between sexes. Similarly, there was no relationship between fish length and...
the length of time fish were held near the mouth of the river. In both years, fish movement from fresh water to salt water occurred primarily between the hours of midnight and 18:00, with only one acoustic-tagged fish in 2002 and two acoustic-tagged fish in 2003 making the transition between 18:00 and midnight (Fig. 4). Mean time of saltwater entry was 07:29 in 2002 and 06:01 in 2003. Timing of saltwater entry was not uniformly distributed throughout the day (Rao’s spacing test 2002: $U = 148.8, n = 38, P < 0.05$; 2003: $U = 163.3, n = 38, P < 0.01$).

Migration of kelts from fresh water to salt water was related to tidal stage with 68% of fish making the transition from fresh water to salt water at high tide and on the ebbing flow (Fig. 5). When the tide cycle was divided into three 4 h periods (i.e., the flood, high, and ebb tides), significantly fewer entries into saltwater occurred during the hours of in-coming flood tide in both years ($\chi^2$ test 2002: $n = 36, P > 0.0001$; 2003: $n = 46, P = 0.02$).

Archival tags

Tag mass to fish mass ratios fell below 1% in all surgeries. Two archival tags (LTD_1110) implanted in 2002 and recovered in 2004 from alternate-year kelts provided data on temperature and depth at 30 min intervals for steelhead at sea for 16 months and during their upstream marine–freshwater migrations. One LTD_2410 collected from a kelt in 2004 was corrupted and no data were downloaded from the sensors. We were unable to determine what caused this malfunction, but the tag was probably corrupted by seawater through the light stalk attachment point to the tag body where the light stalk was bent at the time of recovery. One steelhead captured at the weir in 2005 had a recognized PIT tag, indicating that this fish had been tagged with a LTD-2410 archival tag in 2002, but no archival tag was found in the peritoneal cavity. We assume this archival tag was expelled. Estimated minimum expulsion rate in repeat spawning kelts based on sutures, scars, and remaining PIT tags observed in archival-tagged kelts was 22% (11 females and 3 males). But this is clearly an underestimation, since several previously tagged fish lacked associated PIT tags or suture pattern to clearly indentify the type of original tag placed in the peritoneal cavity, and others may have healed without identifiable scars.

The two archival tags recovered from steelhead kelts recorded sensor data for 711 (male) to 716 (female) days at sea (Table 4). Condition factor ($K$) between the time of tagging and at recovery 2 years later (postrepeat spawning) increased in the female kelt ($K = 0.077$ to 0.102) and decreased in the male kelt ($K = 0.084$ to 0.077). Archival tags demonstrated that these kelts spent approximately 97% of their time at sea in marine waters less than 6 m deep (day and night), with the greatest proportion of time spent between 3 and 4 m depth (Table 5).

While at sea, 94% of time spent at moderate depths (6–20 m) took place during summer daylight hours (10:00–20:00) in both fish. The male kelt’s archival tag (No. 1563) recorded 134 short-duration dives over 20 m, while the female kelt’s tag (No. 1560) only recorded 27 dives below 20 m depth. The male kelt also spent significantly more time at depths $\geq 20$ m (total = 94 h; average cumulative time at each 2 m depth interval = 11.75 h) than the female kelt (total = 17.5 h; average cumulative time at each 2 m depth interval = 2.19 h; Table 5). The male kelt’s tag recorded the three deepest dives (88.7 m (02:41 on 27 November 2002), 73.9 m (10:11 on 5 February 2003), and 50.5 m (21:41 on 25 September 2003). The deepest depth recorded for the female fish (32.08 m) occurred on 25 September 2002 at 03:43.

Both tags revealed seasonal activity at depth with frequent dives from July to early September during both summers at sea and little activity at depth during spring and winter (Table 6; Fig. 6). Our records of kelts at depths $\geq 20$ m were most common during the month of August for both fish in both summers at sea when temperatures were higher, especially during dusk and night. However, the timing and regularity of deep dives varied, suggesting a lack of consistent crepuscular diving behavior. Variation in the average temperatures recorded during surface swimming (0.3–4.0 °C) during their first 2 months at sea for the female (8.8 °C) and male (10.4 °C) steelhead suggest that they may have spent that time in different parts of the ocean or at different depths during this time. Temperature–depth profiles also varied during the steelhead’s time at sea, suggesting unique patterns of activity, but no general seasonal or temporal pattern was observed in these profiles (Fig. 7). Minimum winter temperatures at sea recorded in December 2002 (6.23–6.94 °C) suggest a possible maximum southern distribution between latitudes 44°N and 45°N in the North Pacific Ocean based on sea surface temperature (SST) reference data reported for that year (Fig. 8), assuming these fish stayed in the northeastern Pacific Ocean. Fall 2002 SST reference values reported for marine waters geographically proximate to the Ninilchik River and in lower Cook Inlet (Okkonen and Howell 2003) also parallel temperatures recorded by archival tags during that time, suggesting these fish may not have migrated out of Cook Inlet during this marine stage. Hedger et al. (2009) also reported long-term residence of many Atlantic salmon kelts in nearshore delta waters, suggesting the need to improve somatic reserves prior to seaward migrations. Steep diurnal temperature fluctuations recorded by the archival tags temperature sensors in fresh water and reduced variation in diel temperatures experienced...
at sea clearly delineated the fish’s migration to and from salt water (Fig. 9).

Genetics

Genetic tissues were taken from 18%–20% of all steelhead kelts passing through the Ninilchik River weir in each of 3 years (Table 7). Thirteen genetic samples collected in 2005 shared identical multilocus genotypes to other samples previously collected in our database. Identical samples were removed from statistical analyses of data pooled across sampling years, resulting in a total of 280 unique individuals in our genetic analyses. Ninilchik River steelhead kelts conformed to HWE for all loci and all samples combined ($P = 0.33$; $\chi^2 = 24.3$). Average $H_O$ across all loci was 0.53. The average number of alleles per locus was 4.9. No linkage disequilibrium was detected between loci ($P > 0.0009$ for all pairwise comparisons). Estimates of effective population size ($N_e$) were similar to actual weir counts in 2002 and 2005, but differed significantly in 2003 (Table 7). Pairwise $F_{ST}$ comparisons ranged from $-0.001$ to $0.002$, and no significant genetic differentiation was detected among sampled years.

Overall average relatedness among Ninilchik River kelts was $r = 0.1$. All possible paired relationships were assessed among the 280 kelts with unique genotypes. Of these, 5.8% (2265) were predicted to be parent–offspring pairs, 3.1% (1194) full-siblings, and 16.4% (6409) half-sibling pairs. The majority (74.7%) of all paired relationships were considered unrelated (29192). We tested for significant differences in genotypes among life history types despite the fact that allelic diversity at these 11 loci was relatively low (average number of alleles = 4.9) and associated sample sizes were small, reducing the power of these analyses. Alternate-year repeat spawning adults ($N = 14$) were shown to be genotypically different from first time spawning adults ($N = 126$) across all years using AMOVA ($F_{ST} = 0.015$; $P = 0.032$), but this differentiation was not statistically significant when corrected for multiple tests using Bonferroni (significant $\alpha = 0.0125$). No other patterns of genetic differentiation among life history types were found.
was diurnal, with few fish moving between the hours of 17:00 and 20:00. Steelhead have been shown to behaviorally adjust activity rates and metabolic demand in response to high water temperatures (Coutant 1985; Nielsen et al. 1994). Decreased detections, therefore, may reflect decreased activity in response to periods of higher water temperatures. Comparisons of our observations to the limited literature available on kelt migrations seem to indicate that trends and condition for kelts during their downstream migration may not be uniform across species and locations or even across years at the same location.

Kelt seaward movement was positively associated with tidal phase as previously reported in other studies (Bendall et al. 2005; Hedger et al. 2009). Two fish recorded in the lower river in 2003, but not in the coastal marine array, may indicate that some fish escaped detection by our array. This could also have resulted from illegal harvest of kelts at the river mouth. Acoustic tag reporting rates during the 2 years of deployment (86%) were lower than rates for Atlantic salmon kelts (95%; Halttunen et al. 2009). Survival rates are difficult to estimate because of possible detection errors. Several unpredictable factors may have confounded our 2002 acoustic tag data. Of the 12 tags that were not detected in 2002, nine were tagged 1 or 2 days prior to weekends during a sport fishery for Chinook salmon on the lower Ninilchik River, late May to mid-June. Steelhead were authorized as catch-and-release only on this river, but species identification by some anglers was questionable, and it is possible that steelhead were harvested (N. Szarzi, Alaska Department of Fish and Game, 3298 Douglas Place, Homer, AK 99603, USA, personal communication, 2005). We suspected that some of the tagged fish were captured in this illegal fishery. Therefore, in 2003, we avoided tagging fish prior to weekends during the Chinook fishery. This may explain differences in detection rates between the 2 years (2002 = 76%; 2003 = 96%).

The lack of recovered archival tags in repeat spawning kelts greatly compromised this portion of our study. High rates of expulsion of surgically implanted acoustic and telemetry tags have been documented in other studies (Jepsen et al. 2002; Lacroix et al. 2004). Tags have been shown to become encapsulated in a thick membrane and then expelled through the body at the surgical incision, at the abdominal wall adjacent to the healed incision or where the pressure of the tag was greatest (Lucas 1989). Tags can also be expelled through transintestinal expulsion and during spawning by passage out the oviduct (Moore et al. 1990; Jepsen et al. 2008). Suture scars and healed incision scars were obvious in some previously tagged kelts passing through the weir with no evidence of difficulty in adaptation to marine conditions despite the energy demands of repeat spawning and their prolonged period in fresh water (up to 10 months). No relationship was found between the length of fish and transit time for Ninilchik River kelts, unlike findings for brown trout (Salmo trutta) kelts by Bendall et al. (2005). In 2002, male kelts migrated substantially earlier than females, similar to results reported for Atlantic salmon kelts in Norway by Halttunen et al. (2009). This was not the case for male kelts in 2003. Females did not appear to migrate earlier and condition was not associated with migration.

Bendall et al. (2005) found that migration of brown trout kelts through an estuary was predominantly nocturnal, with most fish migrating through the estuary after midnight. Migrations of brown trout in darkness were assumed to greatly reduce the risk of visual predators. Movement of steelhead kelts from fresh water to salt water on the Ninilchik River was diurnal, with few fish moving between the hours of 20:00 and midnight. This pattern in steelhead kelts may be related to water temperature. Maximum daily water temperatures, as measured by an automated data logger in the river just upstream of the mouth, ranged from 9.2 to 16.2 °C during the study period, and daily high temperature typically occurred between the hours of 17:00 and 20:00. Steelhead have been shown to behaviorally adjust activity rates and metabolic demand in response to high water temperatures (Coutant 1985; Nielsen et al. 1994). Decreased detections, therefore, may reflect decreased activity in response to periods of higher water temperatures. Comparisons of our observations to the limited literature available on kelt migrations seem to indicate that trends and condition for kelts during their downstream migration may not be uniform across species and locations or even across years at the same location.

Table 5. Time at depth (cumulative hours) for steelhead carrying archival tags Nos. 1560 (female, F) and 1563 (male, M).

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<th>Tag No. 1563 (M)</th>
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Note: Data is for marine migrations only.

Discussion

Information about downstream migration and survival of steelhead kelts is very limited (see however Narum et al. 2008). In recent years, more effort has been extended to increase survival of steelhead kelts passing through managed rivers systems such as the Columbia River with a desire to increase overall population size, presumably with increased reproductive success through repeat spawning especially in poor recruitment years or in recently bottlenecked populations (Ward and Slaney 1990; Evans et al. 2004; Keefer et al. 2008). These studies suggest that further work is needed to address the physiology and behavior of steelhead kelts as they migrate between fresh water and salt water. Acoustic tags and automated receivers were successful in this study in describing several factors that provide important information on natural kelt migration to the sea from the Ninilchik River where there are no dams or physical passage problems. Most kelts moved rapidly to salt water after passing the weir with no evidence of difficulty in adaptation to marine conditions despite the energy demands of repeat spawning and their prolonged period in fresh water (up to 10 months). No relationship was found between the length of fish and transit time for Ninilchik River kelts, unlike findings for brown trout (Salmo trutta) kelts by Bendall et al. (2005). In 2002, male kelts migrated substantially earlier than females, similar to results reported for Atlantic salmon kelts (95%; Halttunen et al. 2009).

Survival rates are difficult to estimate because of possible detection errors. Several unpredictable factors may have confounded our 2002 acoustic tag data. Of the 12 tags that were not detected in 2002, nine were tagged 1 or 2 days prior to weekends during a sport fishery for Chinook salmon on the lower Ninilchik River, late May to mid-June. Steelhead were authorized as catch-and-release only on this river, but species identification by some anglers was questionable, and it is possible that steelhead were harvested (N. Szarzi, Alaska Department of Fish and Game, 3298 Douglas Place, Homer, AK 99603, USA, personal communication, 2005). We suspected that some of the tagged fish were captured in this illegal fishery. Therefore, in 2003, we avoided tagging fish prior to weekends during the Chinook fishery. This may explain differences in detection rates between the 2 years (2002 = 76%; 2003 = 96%).

The lack of recovered archival tags in repeat spawning kelts greatly compromised this portion of our study. High rates of expulsion of surgically implanted acoustic and telemetry tags have been documented in other studies (Jepsen et al. 2002; Lacroix et al. 2004). Tags have been shown to become encapsulated in a thick membrane and then expelled through the body at the surgical incision, at the abdominal wall adjacent to the healed incision or where the pressure of the tag was greatest (Lucas 1989). Tags can also be expelled through transintestinal expulsion and during spawning by passage out the oviduct (Moore et al. 1990; Jepsen et al. 2008). Suture scars and healed incision scars were obvious in some previously tagged kelts passing through the weir after their second spawning cycle. No other obvious body scars related to expulsion were evident. We suspect that most tags in steelhead kelts were expelled during spawning, but we did not find any expelled tags during several surveys of upstream spawning habitat using metal detectors. We could easily have missed tags expelled during spawning, or they could have washed downstream into areas not surveyed.
Table 6. Monthly mean, standard deviation (SD), maximum and minimum temperatures (°C), and depths (m) of steelhead archival tags Nos. 1560 (female, F) and 1563 (male, M), June 2002 through September 2003.

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**Note:** Statistics exclude data from fresh water, October 2003 through June 2004.
In several laboratory studies, only limited near-term mortalities or obvious infection occurred as a result of tag expulsion (Moore et al. 1990; Lacroix et al. 2004; Welch et al. 2007), but it is difficult to judge tag expulsion rates and effects in the wild. Tag mass relative to fish mass has been shown to be an important factor determining tag retention in many studies (Jepsen et al. 2005). We tagged large adult steelhead and our tag-to-fish mass ratio (<1%) was within even the strictest recommendations found in the literature (Summerfelt and Mosier 1984; Perry et al. 2001). We cannot estimate actual mortality for tagged kelts at sea. Therefore, it is not possible to differentiate tag loss due to natural ocean mortality as opposed to expulsion mortality, but based on observations of repeat spawning kelts with scars it seems clear that adult steelhead can physiologically process alien material implanted into the peritoneal cavity to pass tags. Additional research on how iteroparity can affect tag loss is needed.

Even with limited sample sizes, data obtained from two steelhead kelts carrying archival tags were very informative. Decreased movement of adult steelhead at night as they migrated from the ocean into fresh waters was reported by Ruggerone et al. (1990). Archival tags recovered from kelts showed that both fish migrated into fresh water in late September (2003) between 14:00 and 17:30. While ocean migration data are beginning to accumulate for some Pacific salmon (Friedland et al. 2001; Tanaka et al. 2005; Walker et al. 2007), there is very limited data on the movements and behavior of steelhead at sea (Walker et al. 2000; Davis et al. 2008).

Activity at depth was most common in the late summer at sea, with little movement to depth during the winter months. Seasonal ocean surface temperatures vary only slightly between Cook Inlet and the North Pacific Ocean. Minimum winter temperatures recorded by the archival tags gave us only inexact indications of possible broad geographic locations during winter. These fish spent a large proportion of their time at sea at the surface, and even the deepest records reported by the tags could be found in Cook Inlet, so depths may not be directly correlated to bathymetry in the North Pacific Ocean. Depth and temperature profiles demonstrated unexpected relationships that may be linked to variation in seasonal forage strategies. Numerous movements at depth recorded just after seawater entry and just before freshwater reentry seem to indicate levels of activity that could be associated with feeding behavior due to high bioenergetic demands before and after spawning or to orientation behavior upon entry and exit from different water bodies. Swimming behavior at depths >20 m occurred throughout the kelts’ time at sea. Unlike diving patterns shown in many deep-sea pelagic fishes (Block et al. 2001), steelhead kelts demonstrated no consistent crepuscular pattern of deep dives during dawn and dusk periods. Hedger et al. (2009) reported diving behavior in Atlantic salmon was more frequent during daytime. Most steelhead kelt swimming behavior >20 m took place during daylight hours in August for each year at sea, although many of the deepest locations for steelhead (>32 m) were recorded at night, August – September 2003.

The most intriguing data drawn from these two tags was our finding that ocean-migrating steelhead kelts spent 97% of their time at sea in the top 6 m of the ocean, with the greatest time at depth between 3 and 4 m. Ruggerone et al. (1990) demonstrated that adult steelhead swam primarily at the surface (72% of time in the top 1 m) in a coastal fjord in British Columbia, regardless of salinity and temperature. Walker and Myers (2009) reported on a Yukon River Chinook salmon that spent its first summer at sea in the top 50 m. In other studies, Hubley et al. (2008) and Halttunen et al. (2009) demonstrated near-surface migrations of Atlantic salmon kelts in fjord and coastal habitats immediately following seawater entry, but no data were available for...
open ocean migrations in these studies. These studies together with our data on near-surface swimming behavior for steelhead kelts during 16-month ocean migrations suggest unique marine migratory behavior in iteroparous kelts that differs from that reported for other salmonids (Walker et al. 2007).

Theoretically, there is a direct relationship between the degree or scale of repeat breeding in iteroparous species and reproductive investment at each breeding event (Crespi and Teo 2002). The female kelt in this study was more conservative in her behavior at depth and spent less time below 20 m depth when compared with the male. This depth is well above the typical thermocline for the Gulf of Alaska during the winter when the surface mixed layer is typically greater than 35 m (Stabeno et al. 2004). The relationship between iteroparity and reproductive investment at sea may be gender-specific in Alaskan steelhead. Actual biological and physical factors leading to differences in behavior at depth between these two fish would have to be confirmed with a larger sample size of tagged kelts from both sexes and associated geolocation data to test the alternative hypothesis that these fish were simply swimming in very different marine environments. Geolocation appears to be a critical missing element in the study of salmonid ocean behavior using archival tags.

The diversity of iteroparity shown by steelhead in this study was complex and highly variable. Other forms of iteroparity have been reported in the literature for salmonids (Crespi and Teo 2002; Hendry et al. 2002; Keefer et al. 2008). Genetic analyses, however, showed no significant differences in population structure or allelic richness among...
any of the life history types found in repeat spawning kelts. Most kelts were not highly related based on familial relatedness likelihoods. Parent-offspring, full-sibling, and half-sibling relationships were few and evenly spread across the different life histories. All the genetic evidence suggested a heterogeneous population lacking unique structure based on spawning history or type of iteroparity. This result supports previous evidence that population genetic structure in *O. mykiss* is based on homing and evolutionary history rather than relative scales of anadromy, iteroparity, or life history type (Heath et al. 2001; Narum et al. 2004; Thrower et al. 2004).

Typical in-river spawning mortality rates are unknown in Alaskan steelhead, and the numbers of repeat spawning adults vary year to year on any given stream (Johnson and Jones 2001). The number of iteroparous steelhead found in this study was not substantially different from those reported in several other Alaskan streams making up 20%–70% of the upstream migration (Lohr and Bryant 1999). Declines in an individual fish’s ability to spawn at age are expected because of the cumulative energetic demands of migration and total energy costs of iteroparity (Berg et al. 1998). Differences in compensatory growth, reproductive development at sea, and body condition after spawning may explain why some iteroparous kelts returned to spawn again in consecutive or alternate years (Rideout et al. 2005; Hubley et al. 2008). Other physiological or epigenetic mechanisms may also contribute to this variation. Jonsson et al. (1991, 1997) indicated an association between body size (or energy content) and the tendency of Atlantic salmon to spawn annually or biennially; however, we found no differences in mean body mass for consecutive and alternate steelhead life history types.

Other studies have suggested that there is significant gender variation in the degree of iteroparity in steelhead, with more females spawning multiple times than males (Burgner et al. 1992; Jonsson and Jonsson 1993; Wertheimer and Evans 2005). We found no evidence that females participated in multiple-year spawning at a higher rate than males. Highly dynamic and productive ecosystems found in southeast Alaskan marine waters may provide sufficient resources to allow multiyear spawning for both genders in Alaskan steelhead. We cannot estimate individual survival or the relationship between size and spawning success without data on sex ratios, length, and mass of upstream migrants, which were not available in this study. Genetic estimates of effective population size (*N_e*) were similar to the counts of downstream migrating steelhead adults at the weir in 2 of the 3 years when genetic samples were taken. *N_e* results in 2003 were significantly lower than the weir count, suggesting a smaller number of adults may have contributed to that year’s run. This decline did not contribute to a poor adult return in 2005 when both *N_e* and census counts were the highest recorded in this study. More rigorous genetic analyses dedicated to looking at overlapping lineage relationships in these fish would help determine the rates of contribution from iteroparous individuals over time.

The research objectives of this study were to use new electronic tagging technologies to better describe the migratory characteristics of steelhead near the northern extent of their range and analyze the genetic population structure associated with various life histories of adult steelhead. In this study, acoustic and archival tags gave important information on steelhead kelts from the Ninilchik River migrating to and from the sea and while at sea between spawning migrations. Unique patterns of iteroparity and migratory behavior were observed. The scale and rate of iteroparity demonstrated by this study was similar to that found in other Alaskan streams, but did not support unique genetic population structure based on life history. These analyses suggest a panmictic population of steelhead on the Ninilchik River with a diversity of life history expressions that can vary over time. While this study revealed many heretofore undocumented aspects of anadromous steelhead kelts, many questions remain concerning the physical and biological factors contributing to life history structure and iteroparity in Alaskan steelhead. Fine-scale tag data on kelt movements, life history analyses, and genetics from this study suggest that steelhead have multiple migratory and reproductive phenotypes that contribute to reproductive success and population structure over time. Conservation and management of one or two reproductive phenotypes may not be sufficient in this complex species.

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