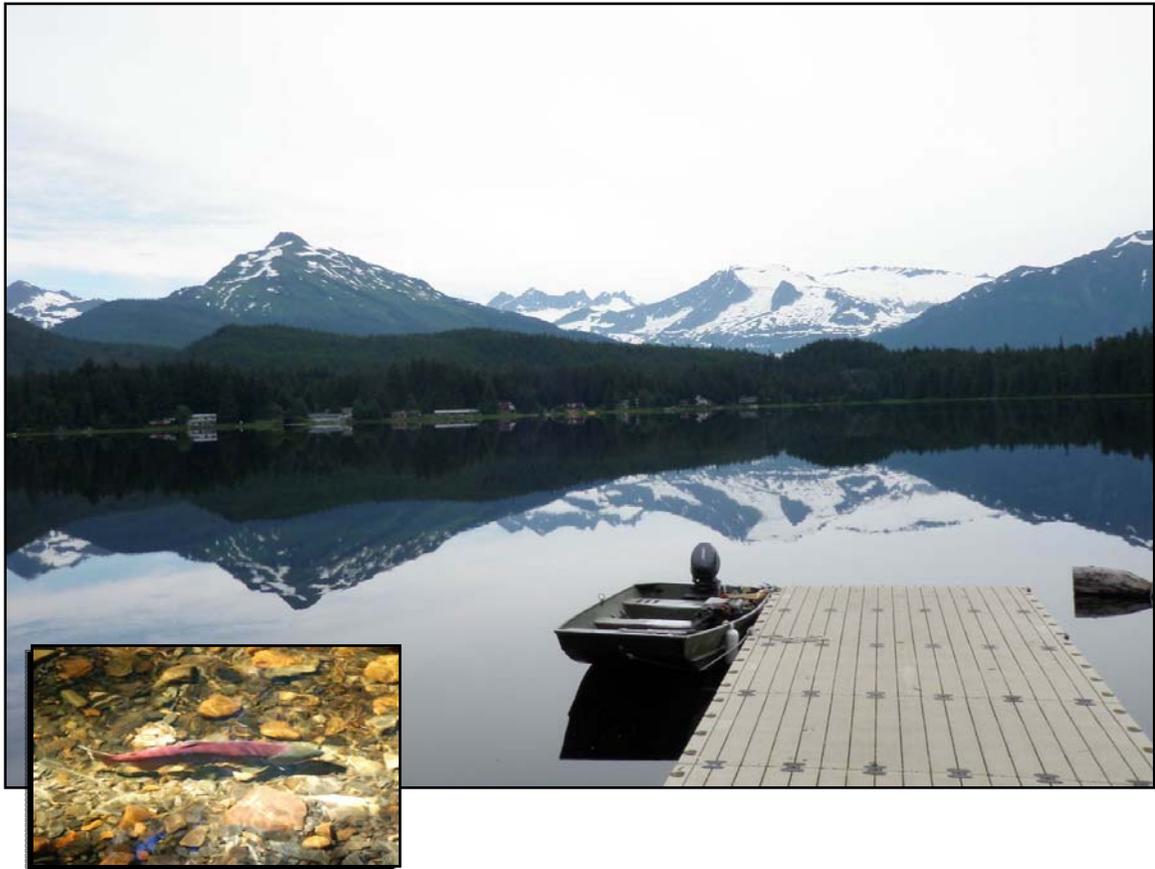


Distribution and Habitat Use of Adult Sockeye Salmon in the Auke Lake Watershed

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Abstract

The efficacy of fish habitat conservation in land planning processes in Alaska is often constrained by the extent of current knowledge of fish distributions and habitat use. Previous work suggests a substantial proportion of the Auke Lake sockeye salmon population use lakeshore habitat for spawning. In response to increased development with potential to impact lakeshore habitat functions, cooperating agencies determined that accurate identification of sockeye distribution and habitat use would contribute useful information to inform land management decisions within the Auke Lake watershed. Radiotelemetry was used to track 80 fish to determine the pre-spawning and spawning distribution of sockeye in the Auke Lake watershed and, specifically, to identify the extent and locations of lakeshore spawning habitat. The pre-spawning distribution of sockeye salmon in Auke Lake in 2012 was not random; five spatially and temporally distinct areas of high fish usage were identified. Four of these high-use sites were considered potential locations for lakeshore spawning. However, SCUBA surveys did not identify spawning activity and habitat was unsuitable or of low quality for sockeye salmon spawning. The Auke Lake sockeye population was dominated by stream spawning fish (98.5%), with some lakeshore spawning (1.5%) observed. In addition to the main tributaries, tracking showed spawning occurred in a small unnamed tributary of the lake and that the only observed lakeshore spawning occurred adjacent to this tributary. Due to the predominance of the creek-spawning life history strategy, conservation of intact riparian habitat and stream channel processes will be important for maintaining Auke Lake sockeye spawning habitat. Pre-spawning distribution patterns observed in Auke Lake in 2012 were highly similar to those observed 20 years ago. We recommend the high-use pre-spawning sites be considered important staging areas for sockeye and be protected during land planning processes. Although only a small component of the escapement was identified spawning on the lakeshore, life history diversity is important for long-term resilience of populations. Therefore, habitat supporting different life histories should also be considered a high priority for protection by land managers and regulatory agencies.

Introduction

The Auke Lake watershed supports populations of pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), coho (*O. kisutch*) and sockeye (*O. nerka*) salmon, cutthroat (*O. clarki*) and rainbow (*O. mykiss*) trout, and Dolly Varden char (*Salvelinus malma*) (Lum and Taylor 2006). Populations of sockeye salmon distributed throughout northern Southeast Alaska provide locally important

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subsistence fisheries and contribute to mixed stock commercial fisheries (Bednarski et al. 2012). Previous studies in Auke Lake by Bucaria (1968) and Nelson (1993) indicate a large proportion, between 28% and 48%, of sockeye that enter the watershed do not spawn in the lake tributaries or outlet stream, suggesting a significant component may use lakeshore habitat for spawning or otherwise die in the lake itself. Sockeye salmon can exploit a diverse range of spawning habitats including lakeshores (Margolis et al. 1995). However, the extent of lakeshore spawning, and thus the importance of lakeshore habitat, is often not well defined in systems supporting sockeye populations. This is due to the difficulties working in lakes where visibility is often poor, and sockeye may spawn at depths exceeding 12 m (e.g., Olsen 1968; Kerns and Donaldson 1968). Auke Lake is highly tannic with low visibility and shoreline spawning locations cannot be easily observed

Auke Lake substrate is dominated by extensive deposits of fine sediment and decayed vegetative matter, which results in low benthic dissolved oxygen (DO) concentrations. Such substrate conditions are generally not considered suitable spawning habitat for salmonids. However, a growing body of research (e.g., Eiler et al. 1992; Young and Woody 2007) has demonstrated that spawning sockeye salmon can successfully utilize areas, such as glacial rivers, that were traditionally perceived to be too high in fine sediment to be productive. The redds of salmon utilizing these glacial habitats are commonly associated with upwelling water, which presumably provides sufficient flow to remove metabolic waste products and supply oxygen to developing embryos. Upwelling may be present in Auke Lake, and could potentially allow for sockeye spawning in the heavily silted substrate along the lakeshore.

Residential, urban, and recreational development have impacted fish and wildlife habitat and water quality in the Auke Lake watershed (Juneau Watershed Partnership 2009a and 2009b). Approximately 50% of the lakeshore is developed (Lum and Taylor 2006), with a walking trail encompassing an additional 30% of shore line. Increasing development is considered likely to further impact salmonid habitat. The Auke Lake Watershed Assessment (2009a) identifies processes associated with development such as land clearing, wetland filling, riparian impacts, stormwater discharge, and road building as the most likely factors that may contribute to future habitat degradation.

The efficacy of fish habitat conservation in land planning processes in Alaska is often constrained by the extent of current knowledge of fish distributions and their habitats. The regulatory protections afforded anadromous fishes and other aquatic life by the Anadromous Fish Act (AS16.05.871), the Magnuson-Stevens Fisheries Conservation and Management Act, and the Clean Water Act are most effective when detailed fish distribution and habitat use information is available. In response to development projects with potential to individually and cumulatively impact lakeshore habitat functions, as well as likely future development projects, cooperating State, Federal, and local government agencies determined that accurate identification of sockeye distribution and habitat use would contribute useful information to inform land use planning processes within the Auke Lake watershed.

Radiotelemetry is a useful approach for identifying sockeye spawning habitat in areas where visual observation is not possible (e.g., Eiler et al. 1992; Burger et al. 1995). This project used radiotelemetry to identify and map sockeye pre-spawning and spawning distribution within the Auke Lake Watershed. Specific objectives of this study were:

- 1) Identify and map the pre-spawning and spawning distribution of sockeye salmon in the Auke Lake watershed.
- 2) Estimate the proportion of sockeye salmon using different spawning locations and different spawning habitat types (i.e., stream or lake environments).
- 3) Determine if habitat use and spawning behavior differs as a function of run timing.

Objectives 1 and 2 provide information necessary to understand overlap between spawning salmon activity and potential land development. Objective 3 will provide further detail as to whether different components of the Auke Lake sockeye run exhibit different habitat use behavior.

Study Area

Auke Lake is located at latitude 58.388, longitude -134.630 approximately 10 air miles NW of downtown Juneau in southeast Alaska (Figure 1). The lake surface area is approximately 175 acres, with a maximum depth of 116 feet. The watershed encompasses an area of approximately 2,500 acres. The lake has two main inlet streams, Lake Creek and Lake Two Creek, and several small unnamed tributaries. A single outlet stream, Auke Creek, flows for 0.3 miles into salt water at Auke Bay. Much of the watershed is owned by local, state, and federal government entities. Private residences and the University of Alaska Southeast line the south, west and north shores of Auke Lake. Fish populations in the lake have been monitored at a fish weir in Auke Creek since 1963 as part of a cooperative effort by the National Marine Fisheries Service, Alaska Department of Fish and Game (ADF&G), and the University of Alaska.

Methods

Transmitter deployment

Fish were captured at the National Marine Fisheries Service fish weir located on Auke Creek 0.25 miles downstream of the lake. The fish weir has been in operation in its current form since 1980 and enumerates 100% of the adult sockeye migrating into the Auke Lake watershed. The fish weir and trap were operated on a daily basis during migration. Fish were randomly netted from the holding cage and fitted with a radio transmitter and a spaghetti tag (see below). Transmitters were inserted into the stomach cavity of adult sockeye using a plastic applicator with smooth edges as described by Eiler et al. (1992). Spaghetti tags were applied using a betadine sterilized needle-applicator. Fish were handled with wetted neoprene gloves and were supported underwater with a padded cradle throughout data collection. Radio-tagged fish were immediately returned to a calm water area of the stream and observed. Fish less than 400 mm and fish exhibiting poor condition (e.g., disease or severe wounds) were not tagged. Data recorded during each tagging event included: date, time of tagging, spaghetti tag number, code/frequency of transmitter, sex, length from mid-eye to tail fork (METF), removal of axillary processes for DNA analysis, scale sample for age analysis, overall body condition, estimated degree of maturation, and total duration of tagging event. Salmon ages were analyzed according to the standards and guidelines of Mosher (1968) and reported according to the European method described by Jearld (1983) and Mosher (1968), where the number of winters the fish spent in fresh water and in the ocean are separated by a decimal.



Figure 1. Location of the Auke Lake study site in Southeast Alaska.

The radio transmitters used for this study were F1835b digitally coded esophageal implant transmitters from Advanced Telemetry Systems (ATS). The transmitters weighed approximately 16 grams and had a 12-inch-long plastic coated antenna of 1 mm diameter. Transmitters did not exceed 2% of fish body weight. All transmitters were equipped with a mortality sensor triggered by a non-movement period of 12 hours and had an expected battery life of 96 days. Transmitters operated on eight frequencies with 10 codes on each frequency and were deployed to minimize 'collision' of signals.

To ensure good sampling coverage across early- and late-run fish, 80 transmitters were allocated for deployment in equal numbers within four strata between June 20, 2012, and August 10, 2012. To meet tag deployment objectives, transmitters were deployed at the beginning of each stratum, with excess or recovered transmitters deployed in subsequent strata.

Transmitter Tracking

Mobile Tracking – Transmitters were manually tracked throughout Auke Lake from a motorized skiff and on foot along the lakeshore and creeks. Mobile tracking commenced the day following transmitter deployment. Boat and foot tracking used R4520c data-logging receivers from ATS. Three-element Yagi antennas were used for boat tracking and H antennas were used for tracking on foot. Individual fish were tracked, but not always located, approximately every 3 days in the lake during the study period. Tracking and escapement surveys were conducted in each of the inlet streams three times during the study period. The GPS location of each tracked fish was recorded using hand held Garmin 62stc GPS units. Data collected during tracking included: date, time at which transmitters were pinpointed, GPS location of fish, accuracy of the GPS unit, and weather conditions. For fish that can be visually observed, behavior was recorded as either, actively swimming, holding, or spawning.

Fixed Receiver Arrays – Two stationary receiver arrays were positioned in Lake Creek approximately 50 m and 100 m upstream from the confluence of Auke Lake. Lake Creek is the largest of the Auke Lake inlet streams and has historically supported the greatest abundance of spawning sockeye. The stationary arrays automatically recorded movement of radio-tagged fish into and out of Lake Creek, thereby providing more detailed information than can be collected by mobile surveys alone. The stationary arrays used R4500c receivers from ATS and were equipped with 4-element Yagi antennae. Each receiver was powered by a deep cycle 12-volt battery. The antennae of the stationary arrays were positioned such that upstream/downstream movement of radio-tagged sockeye past the arrays could be determined. The fixed receiver/data logger array was set to perform a full frequency scan every four seconds. Data from the data logger was downloaded at least every two weeks.

Lake Habitat Surveys

SCUBA surveys of lakeshore habitat were conducted between August 28, 2012, and August 31, 2012. Surveys were used to characterize substrate composition and determine if spawning was occurring in areas of the lake where sockeye appeared to aggregate based on movements of radio-tagged fish. Survey transects were established on the lake bed in identified fish aggregation areas. One end of a demarcated transect line was anchored at the shore and the other end of the transect was lowered to the lake bed at a predetermined GPS coordinate. The location of the transect was marked with a dive line and buoy. Divers descended the line and surveyed

along the transect swimming towards the shore. A diver on each side of the transect visually searched for indicators of spawning activity for the full length of the transect. At 5-meter intervals divers recorded dominant substrate type and depth. Substrates were categorized, using the Wentworth (1922) grain size scale, as either: Bedrock, Boulder, Cobble, Large/Medium/Fine Gravel, Sand, Silt and Organics (leaves/twigs/sticks). Depth of organic material was measured.

Data Analysis

Assigning Fates – For the purposes of determining the spawning distribution of Auke Lake sockeye, each tagged fish was assigned one of six possible fates (Table 1). Spawning locations were identified as areas in which tagged fish were located and were observed spawning. Potential lake shore spawning areas that could not be visually confirmed were identified as areas where tagged fish remained for one week or more without activating the radio tag mortality sensor. These areas were subsequently assessed by SCUBA-based surveys (see above) for spawning activity and the presence of suitable spawning habitat. Mortalities represented located fish not exhibiting spawning activity and were identified by recovery of a tag from a carcass, or continuous transmission of the mortality signal for three or more days without moving. Regurgitation is difficult to determine and is likely under reported (Liedtke and Wargo-Rub 2012). We considered transmitter regurgitations as submerged tags recovered without a carcass; although, none such instances were observed during the study. However, regurgitation often occurs soon after tagging; therefore, fish that have been tracked for several days are less likely to regurgitate tags and may be more likely to represent mortalities.

Spawning Distribution – Using the fates of successfully tracked sockeye salmon as a sample from the general population, the proportion of sockeye utilizing different spawning locations was estimated with associated 95% simultaneous multinomial confidence limits (CLs) as described in Cherry (1996). The proportion of fish using stream versus lake spawning environments was estimated with associated 95% binomial CLs using the R statistical programming environment (RDCT 2013; Appendix 1).

Table 1. Possible fates of radio-tagged sockeye salmon, 2012.

| | | |
|---|-------------------------|---|
| 1 | Auke Lake Spawner | A fish that spawns in Auke Lake. |
| 2 | Lake Creek Spawner | A fish that spawns in Lake Creek. |
| 3 | Lake Two Creek Spawner | A fish that spawns in Lake Two Creek. |
| 4 | Other Creek Spawner | A fish that spawns in a creek other than Lake or Lake Two Creek. |
| 5 | Mortality/Regurgitation | A fish not tracked to a spawning location, but transmits a mortality signal due to death or regurgitation of the transmitter. |
| 6 | Unknown | A fish than cannot be reliably assigned another fate. |

Differences in Run Timing – Insufficient data were available to address the hypothesis that the distribution of spawners throughout the Auke Lake watershed in 2012 was identical among all time strata, or whether, for example, early-run or late-run fish spawned preferentially in different locations. For example, one fish was observed spawning in the lake, two fish spawning in ‘other

creeks' and six fish spawning in Lake Two Creek, resulting in low or zero observations in these spawning distribution categories for each of the strata. By pooling across strata, groups, or both, however, sufficient data were available to address a set of related hypotheses regarding Auke Lake salmon spawning behavior using Fisher exact tests implemented in R (RDCT 2013; Appendix 2):

1. Is there a difference in run timing between spawners in Lake Creek and Lake Two Creek (H_0 : There is no difference in run timing between Lake Creek and Lake Two Creek spawners)?
2. Is there a difference in run timing between fish that survived to spawn and pre-spawning mortalities (H_0 : There is no difference in run timing between fish that survived to spawn and pre-spawning mortalities)?
3. Is there a difference in run timing between spawners distributed in lower, middle, and upper spawning reaches of Lake Creek (H_0 : There is no difference in run timing between spawners distributed throughout the spawning reaches of Lake Creek)?

Results

In 2012, radio transmitters were implanted into 80 sockeye salmon, representing five percent of the total population. Transmitters were deployed in four tagging strata between June 20 and August 10 (Table 2). Eighty-five percent of tagged fish ($n = 68$) were successfully tracked to spawning locations, 11% ($n = 9$) were assigned a fate of 'mortality', and 4% ($n = 3$) were assigned a fate of 'unknown' (Table 3, Appendix 3).

Table 2. Realized stratum structure and transmitter deployment in 2012.

| Stratum | Date | Transmitters Deployed |
|---------|-----------------|-----------------------|
| 1 | June 20–July 1 | 20 |
| 2 | July 2–Jul 13 | 19 |
| 3 | July 14–July 25 | 19 |
| 4 | July 26–Aug 10 | 22 |

Scales were sampled from 293 sockeye salmon, including 80 radio-tagged sockeye, at the Auke Creek weir in 2012. Six age classes were observed; however, two age classes, 2.2 and 2.3, comprised 91% of the non-tagged population (Table 4). Radio-tagged sockeye were represented by four age classes, with age classes 2.2 and 2.3 comprising 95% of the tagged population (Table

4). Age classes 1.1 and 2.1 observed in the non-tagged population were comprised of precocious males (jacks) ≤ 405 mm and were not included in the tagged sample. Age could not be determined for 37 sockeye; including 9 from radio-tagged fish. Fifty-eight percent of all sockeye passing Auke Creek weir were female. Forty-six percent of sockeye implanted with radio transmitters were female (Table 5, Appendix 1).

Table 3. Fate of sockeye salmon implanted with radio transmitters at the Auke Creek weir, 2012.

| Fate | <i>n</i> | % |
|-----------------------------------|----------|-----|
| Successfully Tracked ^a | 68 | 85 |
| Mortality ^b | 9 | 11 |
| Unknown ^c | 3 | 4 |
| Total | 80 | 100 |

^a successfully tracked indicates fish were tracked to a spawning location as outlined in Table 1.

^b mortalities were not tracked to spawning locations and tags were recovered from carcasses or mortality signals were transmitted for at least 3 days without moving.

^c unknown fish could not reliably be assigned another fate.

METF lengths were measured from 319 sockeye salmon, including 79 radio-tagged fish. For the non-tagged population, lengths ranged from 435 mm to 600 mm for females and 320 mm to 640 mm for males. Lengths of radio-tagged fish ranged from 470 mm to 580 mm for females and 475 mm to 620 mm for males (Table 6).

Table 4. Age composition of non-tagged and tagged sockeye salmon sampled at Auke Creek weir, 2012.

| Age | Non-tagged sockeye | | | Tagged sockeye | | |
|---------|--------------------|-----|---------------------|----------------|----|---------------------|
| | <i>n</i> | % | CL (%) ^a | <i>n</i> | % | CL (%) ^a |
| 1.1 | 1 | 0.4 | 0, 4 | 0 | 0 | 0 |
| 1.2 | 6 | 2 | 0.7, 7 | 2 | 3 | 0.4, 14 |
| 1.3 | 8 | 3 | 1, 8 | 2 | 3 | 0.4, 14 |
| 2.1 | 8 | 3 | 1, 8 | 0 | 0 | 0 |
| 2.2 | 120 | 47 | 39, 55 | 31 | 44 | 29, 59 |
| 2.3 | 113 | 44 | 36, 53 | 36 | 51 | 36, 65 |
| Total | 256 | | | 71 | | |
| Unknown | 34 | | | 9 | | |

^a confidence limits (CLs) are 95% simultaneous multinomial CLs

Table 5. Sex composition of non-tagged and tagged sockeye sampled at Auke Creek weir, 2012.

| Sex | Non-tagged sockeye ^a | | Tagged sockeye ^a | |
|----------|---------------------------------|----|-----------------------------|----|
| | <i>n</i> | % | <i>n</i> | % |
| M | 618 | 42 | 43 | 54 |
| F | 867 | 58 | 37 | 46 |

^aAll fish passing the weir were assessed for sex and these data represent a census of the Auke Lake (escapement) sockeye population.

Sockeye Pre-spawning Distribution – The pre-spawning distribution of sockeye salmon in Auke Lake was not random; spatially and temporally distinct areas of higher fish usage were identified. Radio-tagged sockeye were tracked in Auke Lake for approximately 9 weeks from June 23, 2012, to August 26, 2012, by which time all tagged fish had been assigned a fate. In general, as the season progressed, salmon holding areas shifted from the east to the south shore, followed by concentrations of fish staging on the north and west shores (Figure 3). Within the observed fish distribution on the north and west shores, four discrete high-use sites were identified; two were located at the mouths of Lake Creek and Lake Two Creek, whereas two were not associated with creeks (Figure 4).

Lake Habitat Surveys – The four discrete sockeye aggregation sites on the north and west shores of the lake coincided temporally with spawning activity in Lake Creek and Lake Two Creek and were therefore considered potential locations for lakeshore spawning. Up to six transects per site were established to provide good survey coverage of the lake bed. SCUBA surveys did not identify spawning activity at any of these high usage sites. Furthermore, surveys indicated that habitat conditions at Sites 2, 3, and 4 (Figure 4) were not suitable to support spawning sockeye salmon in 2012 (see below). At Site 1, surveys identified a limited area of poor quality spawning habitat.

Site 1 – Six transects were established at this site (Figure 5). No indicators of sockeye spawning activity were observed. Surveys identified three patches of gravel on a bedrock shelf. Patches comprised medium and coarse gravel covered in approximately 1 cm of silt. The patches were located at four meters depth, were approximately 1x1.5 m in area, and 5 to 10 cm deep.

Site 2 – Site 2 was located at the mouth of Lake Creek; six transects were established at this site (Figure 5). No indicators of sockeye spawning activity were observed. This site was dominated by gravel deposited by Lake Creek. Although substrate composition along major portions of the transects was observed to be suitable for spawning sockeye (fine/medium/large gravels), the slope of the gravel delta face was high gradient (average gradient based on six transects was 45%). Divers confirmed that the gravel face of the delta was highly unstable and could not support redd construction. At the base of the delta face, where gradient was lower, the substrate was dominated by deep silt and organic material, not suitable as spawning substrate. Independent of the transect surveys, minor spawning by sockeye salmon was observed on the surface of the gravel delta where Lake Creek transitions to Auke Lake (Figure 5). Six redds were constructed and five non-tagged sockeye salmon were observed spawning.

Table 6. Length-frequency distribution of non-tagged and tagged sockeye sampled at Auke Creek weir, 2012.

| METF Length (mm) | Non-tagged sockeye | | | Tagged sockeye | | |
|------------------|--------------------|----|---------------------|----------------|----|---------------------|
| | <i>n</i> | % | CL (%) ^a | <i>n</i> | % | CL (%) ^a |
| 430 | 2 | 1 | 0, 6 | 0 | 0 | 0, 12 |
| 440 | 0 | 0 | 0, 4 | 0 | 0 | 0, 12 |
| 450 | 2 | 1 | 0, 6 | 0 | 0 | 0, 12 |
| 460 | 4 | 2 | 0, 7 | 0 | 0 | 0, 12 |
| 470 | 9 | 4 | 1, 10 | 3 | 4 | 1, 17 |
| 480 | 13 | 6 | 2, 13 | 1 | 1 | 0, 14 |
| 490 | 20 | 9 | 4, 16 | 4 | 5 | 1, 19 |
| 500 | 20 | 9 | 4, 16 | 6 | 8 | 2, 23 |
| 510 | 20 | 9 | 4, 16 | 10 | 13 | 5, 29 |
| 520 | 14 | 6 | 3, 13 | 9 | 11 | 4, 27 |
| 530 | 25 | 11 | 6, 19 | 6 | 8 | 2, 23 |
| 540 | 25 | 11 | 6, 19 | 10 | 13 | 5, 29 |
| 550 | 19 | 8 | 4, 16 | 5 | 6 | 2, 21 |
| 560 | 15 | 7 | 3, 14 | 6 | 8 | 2, 23 |
| 570 | 15 | 7 | 3, 14 | 5 | 6 | 2, 21 |
| 580 | 15 | 7 | 3, 14 | 9 | 11 | 4, 27 |
| 590 | 5 | 2 | 1, 8 | 2 | 3 | 0, 16 |
| 600 | 2 | 1 | 0, 6 | 1 | 1 | 0, 14 |
| 610 | 3 | 1 | 0, 7 | 1 | 1 | 0, 14 |
| 620 | 0 | 0 | 0, 4 | 1 | 1 | 0, 14 |
| 630 | 0 | 0 | 0, 4 | 0 | 0 | 0, 12 |
| 640 | 1 | 0 | 0, 5 | 0 | 0 | 0, 12 |

^a confidence limits (CLs) are 95% simultaneous multinomial CLs

Site 3 – Five transects were established at this site (Figure 5). No indicators of sockeye spawning activity were observed. Average gradient of the lake bed based on five transects was approximately 4%. The substrate was dominated by silt >1 m in depth throughout the entire surveyed area, and was therefore not suitable for spawning sockeye salmon.

Site 4 – Site 4 was located at the mouth of Lake Two Creek; one transect was established at this site (Figure 5). No indicators of sockeye spawning activity were observed. Although Lake Two Creek and its associated gravel delta is significantly smaller than Lake Creek, the survey transect showed similar substrate composition and gradient as observed at Site 2, with neither the slope or base of the gravel delta at Lake Two Creek providing suitable spawning substrate.

Sockeye Spawning Distribution – Using the fate of successfully tracked sockeye salmon as a sample from the general population, 98.5% (67 of 68; 95% CL: (94% and 100%)) of sockeye entering Auke Lake watershed in 2012 spawned in stream environments, whereas only 1.5% (1 of 68; 95% CL: (0.1% and 6.0%)) spawned in the lake environment (Table 7). Stream

environment spawning comprised 86.8% (59 of 68; 95% CL: (77% and 93%)) of spawning in Lake Creek, 8.8% (6 of 68; 95% CL: (4% and 17%)) in Lake Two Creek, and 2.9% (2 of 68; 95% CL: (0.5% and 9%)) in other creeks.

Of the radio-tagged sockeye spawning in other creeks, one spawned in an unnamed tributary in the southeast quadrant of the lake and one spawned in Auke Creek (Figure 6). Four non-tagged sockeye were also observed spawning in the unnamed tributary, whereas no other sockeye spawned in Auke Creek. The one Auke Creek spawner descended from Auke Lake after being tracked for 20 days. Unable to re-ascend the creek, it constructed a redd in the pool above the fish weir. Although the lake habitat surveys did not identify lake spawning areas at the main fish aggregation sites, lakeshore spawning by sockeye was confirmed adjacent to the unnamed tributary in the southeast quadrant of the lake (Figure 6). In addition to one radio-tagged fish, four non-tagged sockeye were observed using this area of lakeshore for spawning.

Table 7. Proportion of sockeye salmon spawning at different locations in the Auke Lake watershed, 2012.

| Spawning Location | Proportion (%) | <i>n</i> | CL (%) |
|---------------------------------|----------------|-----------|---------------------------|
| Lake Creek | 86.8 | 59 | 73–94 ^a |
| Lake Two Creek | 8.8 | 6 | 3–22 ^a |
| Other Creeks | 2.9 | 2 | 0.4–14 ^a |
| Total Stream Environment | 98.5 | 67 | 94–100^b |
| Auke Lake | 1.5 | 1 | 0.1–12 ^a |
| Total Lake Environment | 1.5 | 1 | 0.1–6^b |

^a confidence limits (CLs) are 95% simultaneous multinomial CLs

^b confidence limits (CLs) are 95% binomial CLs

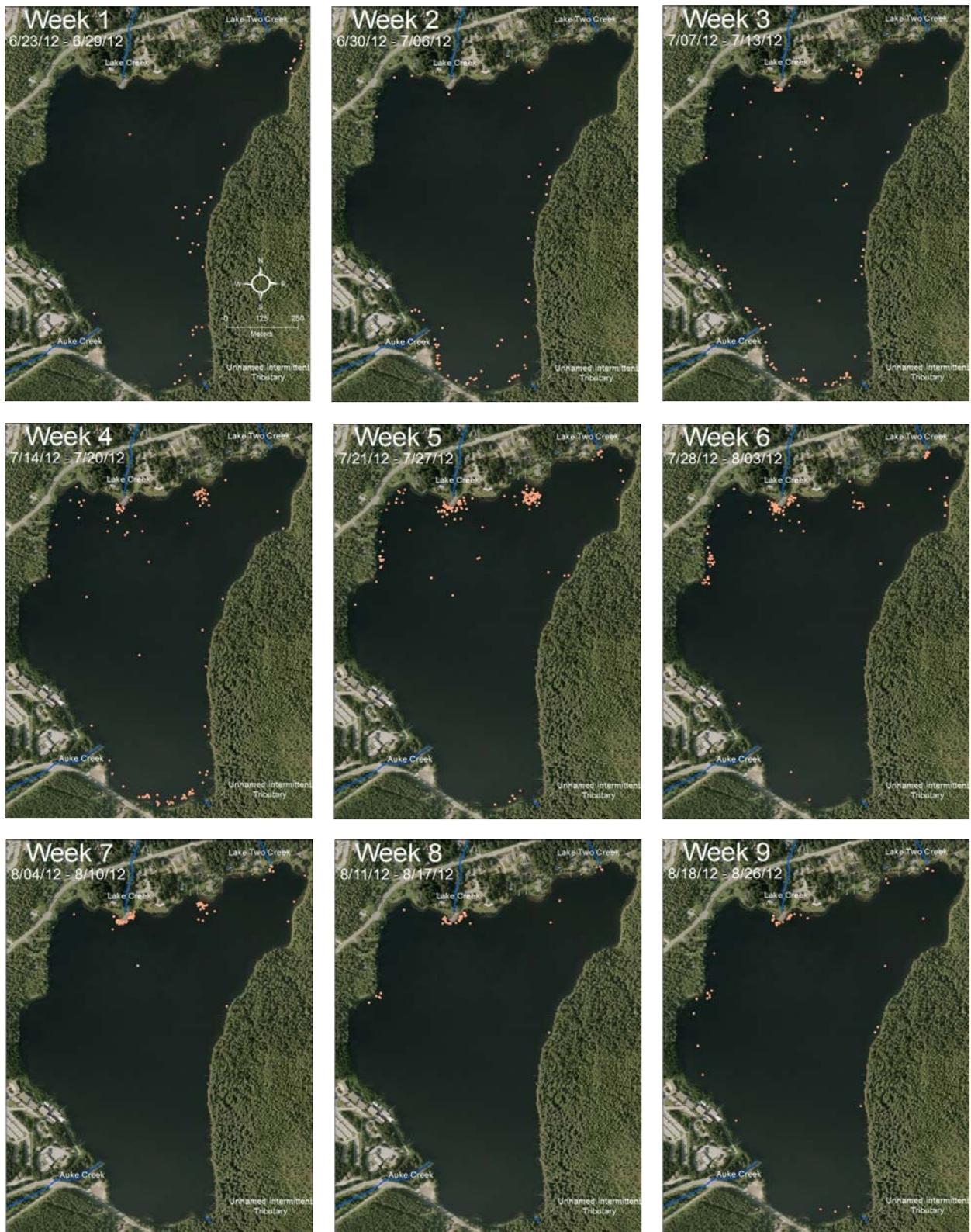


Figure 3. Locations of radio-tagged sockeye by week long strata in 2012.

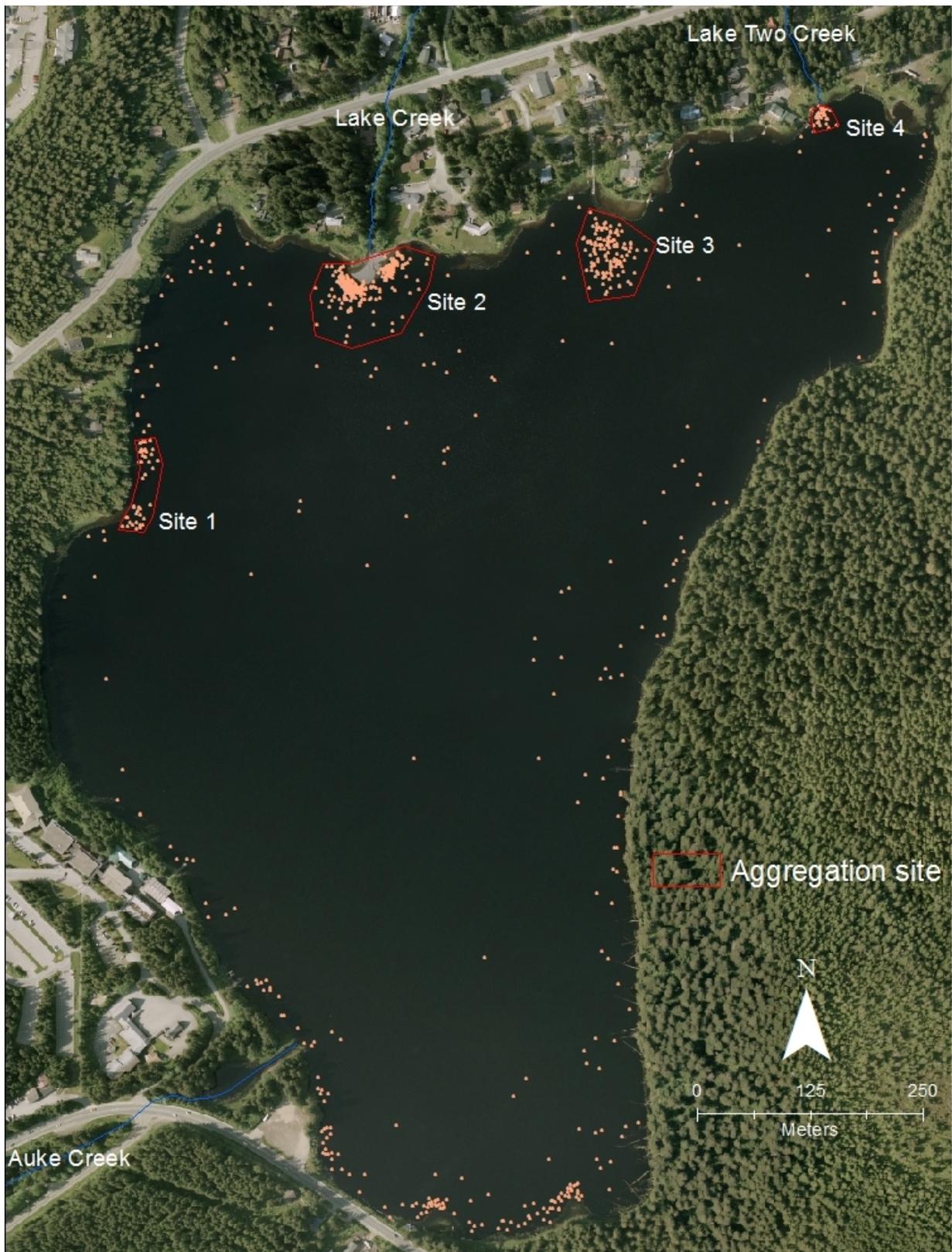


Figure 4. Sockeye salmon high-use aggregation sites that coincided temporally with creek spawning activity in 2012. Dots represent sockeye locations for the total study period.

Stationary receivers located at the mouth of Lake Creek showed sockeye access to Lake Creek was synchronized with stream flow and fish entered the creek to spawn in two flow mediated pulses in 2012 (referred to as Pulse One and Two). Fish began ascending Lake Creek during a high flow event on the night of July 31, 2012. For 11 days prior to this no surface water connectivity existed between Lake Creek and Auke Lake. Surface water connectivity persisted for 17 days from July 31, 2012, to August 15, 2012; 80% ($n = 47$) of radio-tagged sockeye that spawned in Lake Creek entered the creek in Pulse One. Ninety-six percent ($n = 45$) of radio-tagged sockeye entering the creek in Pulse One did so over the first 11 days. Seven days with no surface water connectivity between the lake and creek occurred after August 15, 2012. On August 22, 2012, a rain event re-established surface water connectivity between the lake and creek and the remaining 20% ($n = 12$) of radio-tagged sockeye that spawned in Lake Creek began entering the creek. Although surface connectivity persisted for the remainder of the study period, 92% ($n = 11$) of the tagged fish that entered the creek in Pulse Two did so within one day and 8% ($n = 1$) entered on the second day. All sockeye that entered Lake Creek in Pulse One finished spawning and most were dead prior to fish entering the creek in the second pulse.

Peak spawning activity in Lake Creek and Lake Two Creek occurred in Julian week 33 (August 13–19, 2012), whereas peak spawning activity in the unnamed tributary and adjacent lakeshore spawning area occurred in Julian week 36 (September 3–9, 2012). Peak spawning counts (live plus dead fish) were 659 for Lake Creek and 51 for Lake Two Creek. Fifty percent of the total sockeye population was observed spawning in 2012. Using predation rates of radio-tagged salmon spawning in Lake Creek and Lake Two Creek as a sample from the general population, 14% (9 of 65; 95% CL: (7% and 24%)) of sockeye spawning in the two main tributaries were depredated by black bears in 2012.

Stationary receivers showed that sockeye occupancy in Auke Lake prior to ascending Lake Creek ranged from 5 to 45 days, and averaged 29 days. Pre-spawning residence time in the lake appeared to be a function of run timing, with early returning fish residing in the lake longer than later returning fish (Table 8). However, periodic lack of access into Lake Creek because of low flow conditions may have influenced the number of days some fish spent in the lake prior to entering Lake Creek.

Table 8. Number of days spent in Auke Lake, by tagging strata, from day of release at Auke Creek weir to entering Lake Creek, 2012.

| Strata | Number of Days in Auke Lake | |
|--------|-----------------------------|------|
| | Range | Mean |
| 1 | 34–45 | 37 |
| 2 | 24–43 | 32 |
| 3 | 18–39 | 29 |
| 4 | 5–21 | 12 |

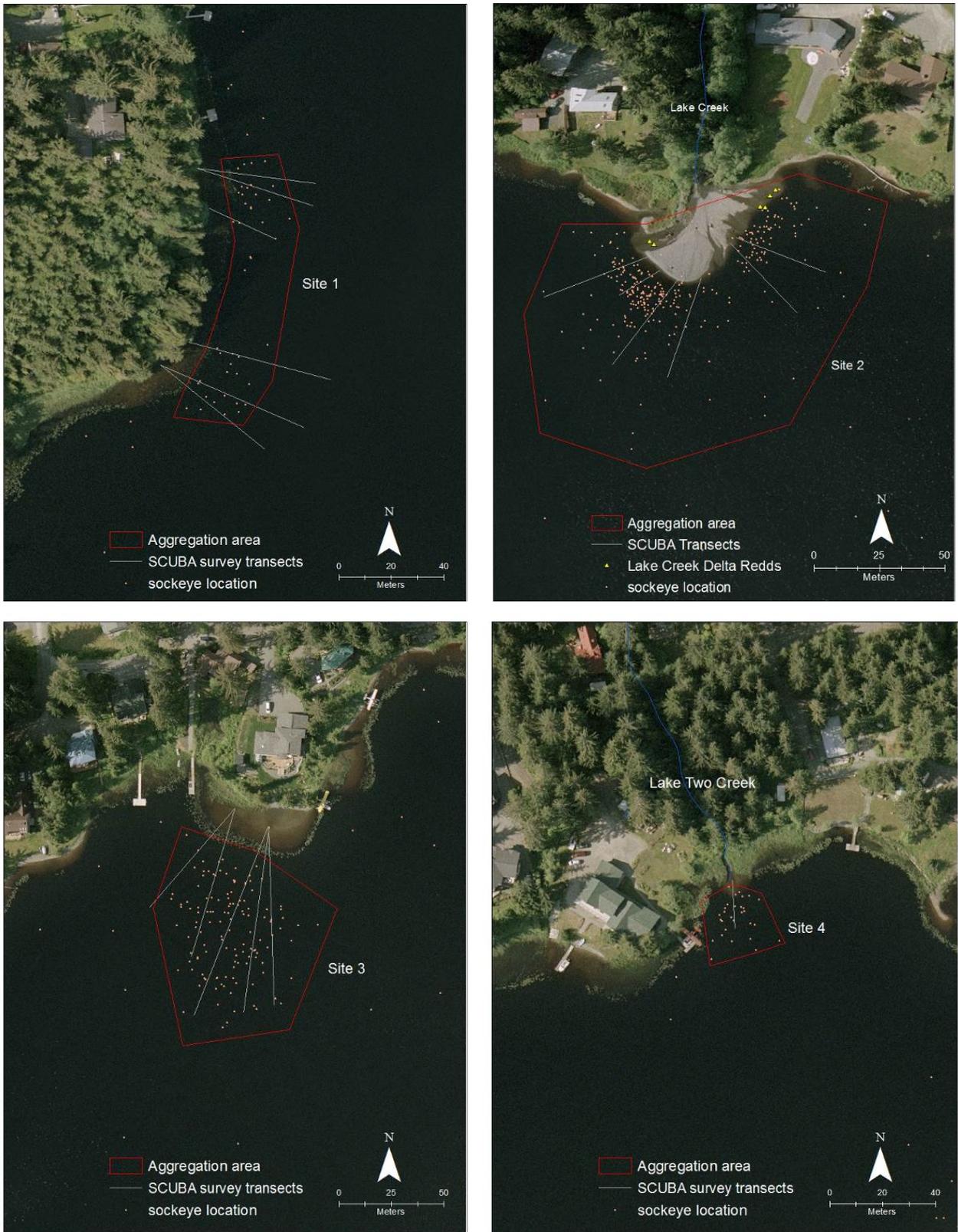


Figure 5. Sockeye aggregation sites and SCUBA transect locations, 2012. Dots represent sockeye locations for the total study period.

In 2012, nine radio-tagged sockeye were not observed spawning in any location and died in Auke Lake. Of these, four carcasses were recovered and confirmed not to have spawned, one male carcass recovered could not be determined due to condition of the carcass, and four carcasses were not recovered. The number of days spent in Auke Lake prior to mortality ranged from 8 to 42 and averaged 24. Using the mortality fates of radio-tagged sockeye as a sample from the general population, 12% (9 of 77; 95% CI: (6%, 20%)) of sockeye died in Auke Lake in 2012.

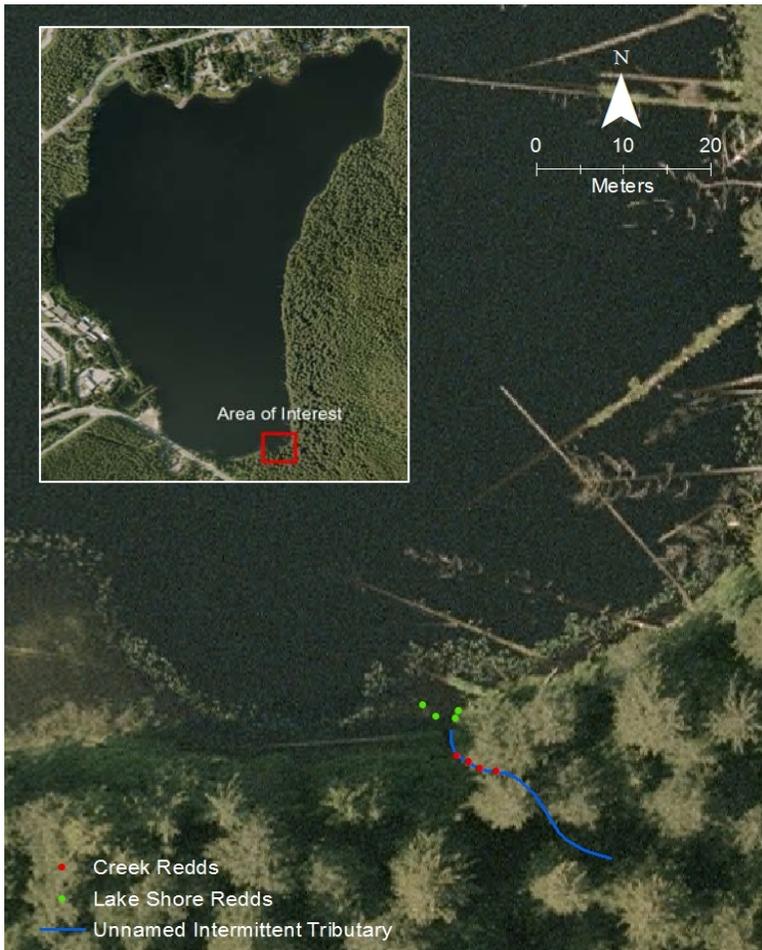


Figure 6. Location of sockeye spawning activity on lake shore and in unnamed tributary in 2012

Run Timing – At the 5% Type I error level ($\alpha = 0.05$) Fisher’s exact test of independence indicated no difference in run timing between spawners in Lake Creek and Lake Two Creek ($P = 0.64$). There was also no significant difference in run timing between fish that survived to spawn and pre-spawning mortalities in 2012 ($P = 0.08$). However, given the low or zero observations in cells of the contingency table, tests of independence may have low power to detect differences.

Dividing up Lake Creek into three equal length reaches (378 m/reach) representing upper, middle, and lower spawning areas, Fisher’s exact test showed a significant difference in run timing ($P = 0.025$) for fish utilizing different parts of the creek (Figure 7). Fish from tagging strata one and two appeared to use the middle and upper reaches to a greater extent than fish

from strata three and four, which mainly used the lower reach. *Post-hoc* pairwise comparisons of spawning reach distribution for fish across different tagging strata using Fisher’s exact test with the Benferoni Correction ($\alpha = 0.008$) showed a significant difference ($P = 0.005$) in spawning distribution only between strata one and three (Table 9).

Table 9. *P*-values for *post-hoc* pairwise comparisons of Lake Creek spawning distribution across different tagging strata using Fisher’s exact test with Benferoni Correction ($\alpha = 0.008$). *P* values <0.008 are indicated with bold text.

| Strata | S1 | S2 | S3 | S4 |
|--------|--------------|------|------|----|
| S1 | - | - | - | - |
| S2 | 0.33 | - | - | - |
| S3 | 0.005 | 0.15 | - | - |
| S4 | 0.1 | 0.42 | 0.78 | - |

Discussion

Sockeye salmon fitted with radio transmitters were representative of the non-tagged population and did not deviate appreciably with regard to sex, age, and length in 2012. There were no observed mortalities directly attributable to the tagging procedure and tagged fish appeared to behave normally, interacting with non-tagged fish in the lake and on the spawning grounds. Weather conditions were cooler and substantially wetter than average, prior to and during the early part of the study period (May 1–July 29); however, stream flow patterns observed in the two main inlet streams throughout the study period closely resembled those described by Bucaria (1968) and Nelson (1993). In 2012, 1,565 sockeye passed the Auke Creek weir with tagged fish representing 5% of the population. Sockeye abundance has ranged from 1,280 to 4,048 and has averaged 2,655 over the last 10 years. Although sampling only took place in 2012, we are confident the results are representative of Auke Lake sockeye behavior. This is because of the consistency in staging behavior and spawning distribution observed with similar studies by Nelson (1993) sampling in 1991–1992, and Bucaria (1968) sampling in 1963–1964.

Pre-spawning Distribution

Tagged sockeye typically ascended Auke Creek with non-tagged fish and entered Auke Lake within 2 to 8 hours depending on flow conditions in 2012. The pre-spawning distribution of sockeye salmon in Auke Lake was not random; spatially and temporally distinct areas of higher fish usage were identified. Sockeye distribution in Auke Lake remained localized, but shifted throughout the study period, reflecting changing behavior from early staging to the onset of spawning. Returning adults traversed the east shore and staged in the south shore cove during the first weeks of the study, shifting quickly to nearly exclusive use of staging areas on the north and west shores of the lake after week four for the duration of the study. Use of the east and south shores was primarily by early returning fish, with approximately 80% of observations in these areas from fish tagged in strata one and two. Later returning fish, tagged in strata three and four, generally moved directly to the north and west shores to stage, possibly reflecting more advanced sexual maturation upon entering the lake. Nelson (1993) reported that tagged fish observed at high-use sites exhibited strong site fidelity and appeared not to move around. Conversely, fish located at high-use sites in 2012 were observed moving relatively frequently.

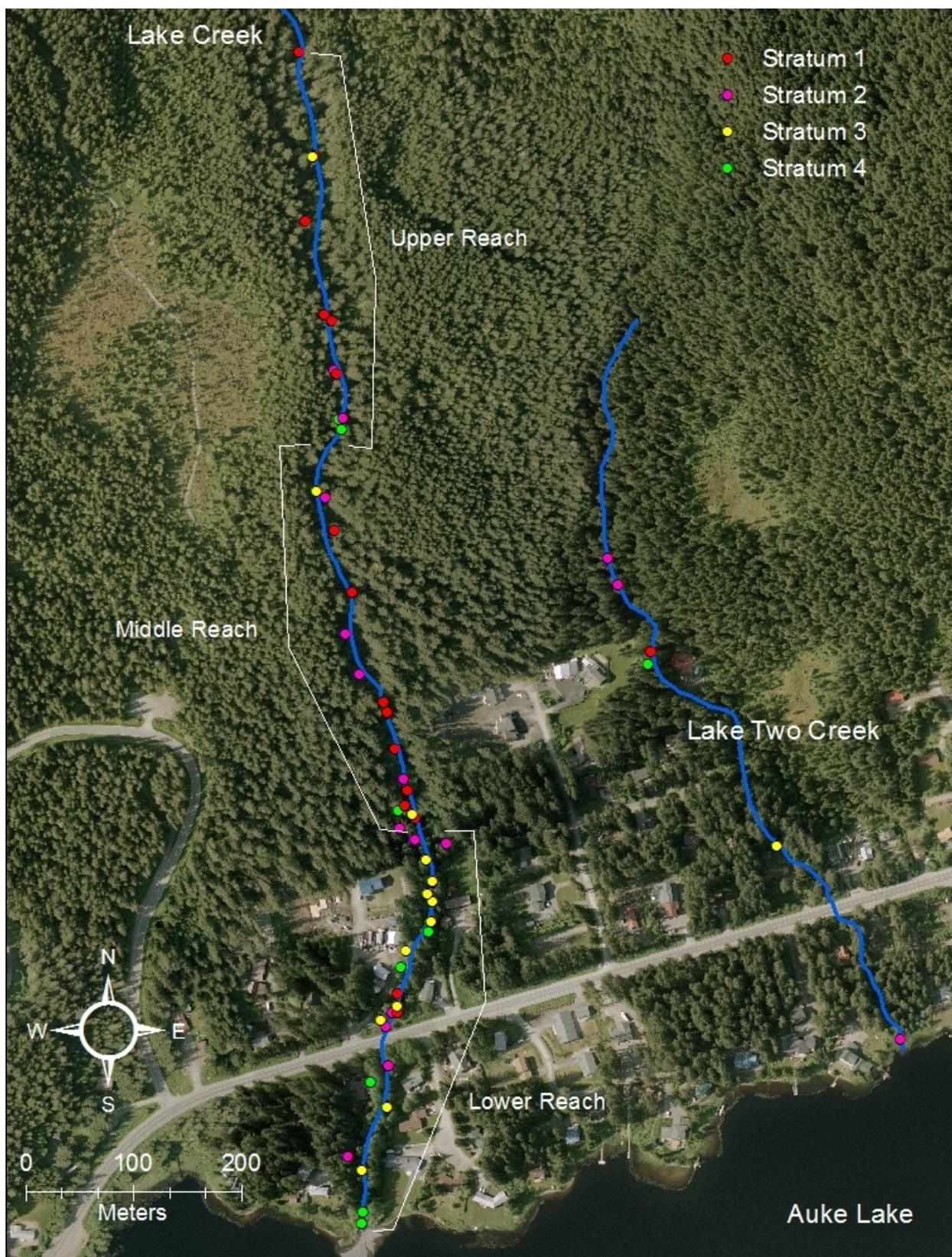


Figure 7. Spawning distribution of radio-tagged sockeye salmon in Lake Creek by tagging strata, 2012.

However, movements were not random and fish primarily moved between the high-use areas, emphasizing their importance prior to spawning.

The distribution of sockeye salmon observed in Auke Lake was remarkably consistent with observations by Nelson (1993) sampling in 1991 and 1992. Extensive use of the south shore during the first half of the study period, especially the cove in the southeast quadrant of the lake, was documented in both studies, emphasizing the importance of this area. Nelson (1993) also documented three of the four discrete high-use sites we identified on the north and west shores in 2012.

Benthic SCUBA surveys in 2012 did not identify spawning activity in Auke Lake at any of the four fish aggregation sites and confirmed that substrate conditions at three sites would not support spawning activity, with the remaining site containing marginal sockeye spawning habitat (Appendix 2). This provides strong evidence that habitat criteria important for staging behavior is influencing selection of these sites and sockeye are not selecting these areas based on their suitability for spawning. Fish frequently stage at creek mouths prior to entering them to spawn, and creek proximity is likely the strongest factor influencing the selection of staging sites at the mouths of Lake Creek and Lake Two Creek. However, factors influencing selection of the two high-use sites not associated with creeks is unclear. In addition to the benthic SCUBA surveys in high fish-use areas, 150 benthic samples were taken from 26 transects (systematically spaced at approximately 30 m intervals) in areas that received low use by tagged fish (Appendix 3). These samples confirmed substrate throughout the lake is dominated by deep silt deposits and unlikely to support spawning without substantial contributions of upwelling water.

Areas of particular importance for staging Auke Lake sockeye salmon appear to be the south bay and the four sites identified on the north and west shores. Although specific reasons for staging area selection in the lake is unclear, continued use of sites over time suggests fish are preferentially selecting these areas and the lake is not a homogenous habitat. Lake managers and regulatory agencies should carefully consider actions, such as recreational activity or shoreline development, which may impact use of these areas by sockeye, forcing fish into sub-optimal staging sites.

Spawning Distribution

Based upon the tagged sample, the Auke Lake sockeye spawning population was dominated by fish spawning in stream environments (98.5%) in 2012, whereas only a minor component (1.5%) of spawners used lakeshore habitat. This is consistent with work by Bucaria (1968), which showed 99% of spawning sockeye used stream habitat and 1% used lakeshore habitat. However, because of large discrepancies between the number of sockeye entering the watershed and the observed spawning escapement (i.e., 55% of the total population was counted on the spawning grounds in 1963 and 52% in 1964), Bucaria (1968) suggested a large component of the population may use undetected lakeshore habitat for spawning in Auke Lake. Discrepancies were also observed between total fish entering the watershed and creek-spawner escapement in 2012, with 50% of the total population observed spawning. However, we consider the estimated proportions of fish spawning in creek and lake environments derived from radiotelemetry data in this study to be an accurate reflection of spawner composition and believe the discrepancies observed between total fish entering the watershed and creek-spawning escapement are likely not indicative of undetected substantial lakeshore spawning areas, but can be explained by: 1)

efficiency of the spawning survey observer, 2) predation/scavenging, and 3) pre-spawning mortality in the lake.

Observer efficiency – Observer efficiency of live fish and carcasses in spawning escapement surveys is highly variable with weather and river conditions, habitat type, species, survey method, and experience of the observer. Researchers report efficiencies of 28% (Shardlow et al. 1987) and 76% (Solazzi 1984) for foot-based surveys of live adult salmonids. Lake Creek and Lake Two Creek have tannic water with large woody debris accumulations and undercut banks, providing substantial hiding cover for adult salmonids. During 2012, we experienced instances where extensive searches to locate live radio-tagged fish during creek foot surveys led to observation of additional untagged fish and carcasses which would have been missed through standard spawning escapement survey methods if not co-located with radio tagged fish. Although the efficiency of sockeye spawning surveys in Lake Creek and Lake Two Creek is unknown, it is highly likely that surveys underrepresent fish actually present.

Bear predation – Bear predation on spawning Pacific salmon is well-documented (e.g., Reimchen 2000; Gende et al. 2001; Quinn et al. 2003), with bears frequently transporting salmon from capture sites into riparian forests for consumption or caching (e.g., Gende et al. 2007). Based on the tagged sample, 14% of spawning sockeye in the two main tributaries were depredated by black bears in 2012. The maximum distance a radio-tagged sockeye was transported from the stream by a bear was 100 meters. Sixty-six percent ($n = 6$) of radio-tagged salmon captured by bears were transported and would not have been detected by standard spawning escapement survey methods, which focus effort in the active channel and near-bank areas. In addition, an escapement survey in Lake Creek indicated 31 sockeye had been preyed upon by bears; however, 65% ($n = 20$) would not have been detected by standard survey methods and were observed incidentally while searching for radio-tagged fish that had been transported into the riparian forest. Systematic searching for carcasses in riparian areas would likely result in substantially higher observations of bear predation on sockeye. Given the 2012 estimated predation rate of 14%, and the indication that approximately 66% of bear predation could not be detected by standard spawning surveys, rates of predation and carcass transfer by bears appear to contribute substantially to underestimating Auke Lake sockeye spawning escapement.

Pre-spawning mortality – Nelson (1993) showed 28% of radio-tagged sockeye in 1991 and 31% in 1992 did not enter tributaries to spawn, but died in Auke Lake at a time that coincided with spawning in the inlet streams. Similarly, in 2012, nine radio-tagged sockeye died in Auke Lake without entering tributary streams when spawning in creeks was occurring. Although we did not recover all of the tagged lake mortalities, none of the recovered mortalities had spawned (one male could not be determined) and we consider lake mortalities to be pre-spawning mortalities. Furthermore, numerous non-tagged female sockeye carcasses, which had not spawned, were recovered in Auke Lake during this study. Unspawned dead sockeye were also noted in Auke Lake by Nelson (1993), showing consistent occurrence of sockeye pre-spawning mortality of sockeye in Auke Lake. Based on the tagged sample, the estimated pre-spawning mortality rate of sockeye in Auke Lake in 2012 was 12%.

Natural pre-spawning mortality in salmonids is not well documented, but is known to increase with environmental stressors, such as high water temperature and high spawning density (Quinn et al. 2007). Although, Fisher's exact test found no significant difference in run timing between fish that survived to spawn and pre-spawning lake mortalities in 2012, six of the nine fish that died in the lake were late-run fish tagged in stratum four. Mean daily water temperature in Auke

Creek in 2012 was 14.3°C for strata one, 13.3°C for strata two, 15.7°C for strata three, and 15.7°C for strata four. Mean daily water temperatures of Auke Creek during the sockeye migration were relatively high in all strata, but particularly high in strata three and four. Although strata three and four fish apparently experienced similar temperature regimes in Auke Creek and Auke Lake, elevated water temperatures, perhaps acting differentially on fish of potentially different maturity levels and energy reserves, may have disproportionately impacted strata four tagged fish, or impacted strata four fish in general. It is also possible these fish missed their opportunity to ascend Lake Creek and spawn during sufficient flows and succumbed to infection by pathogens before spawning.

Stream spawning – The two main inlet streams, particularly Lake Creek, are important to the Auke Lake sockeye population. Based on tagging in 2012, 98.5% of fish spawned in stream environments, with 87% of sockeye spawning in the first 1.1 km of Lake Creek immediately upstream of the confluence of Auke Lake. Sustainability of the population is therefore dependent on spatially limited spawning habitat, which not only exposes the population to risk from natural events such as flooding and drought, but also anthropogenic impacts. In 2012, 67% of all tagged fish and 81% of late-run (strata three and four) tagged fish spawned in the first 0.5 km of Lake Creek, which is encompassed by a housing development and intersected by a road crossing. Development activities that reduce flow or degrade stream and riparian functions in this reach could significantly impact the population and would likely disproportionately impact late-run fish. This highlights the importance of adequately protecting hydrological, stream channel, and riparian functions of the inlet streams from individual and cumulative anthropogenic impacts, as well as restoring impacted habitat where feasible.

Lakeshore spawning – Spawning was observed in two locations in Auke Lake: 1) in gravel on the Lake Creek delta and, 2) adjacent to an unnamed tributary in the southeast quadrant of the lake. Characteristics of the delta such as, substrate size, flow, and redd depth were consistent with the stream environment. Thus, we do not consider spawning in Lake Creek delta to be functionally different from stream spawning. Stationary receivers indicated that entrance into Lake Creek was synchronized with high flow events with most tagged fish entering within a few days of peak flow. Delta spawning was initiated at low flows after most fish had already entered Lake Creek, indicating that fish homing to Lake Creek likely used this area by default when creek access was restricted. Also, the delta, which is seasonally dynamic, probably results in low survival of embryos. Of the six redds constructed on the delta in 2012, five were suspected of being destroyed by a September flood event. Conversely, lakeshore habitat characteristics adjacent to the unnamed intermittent tributary in the southeast quadrant of the lake were different from the stream environment of the two main tributaries. There was no perceptible flow, substrate was fine gravel and sand, and redds were observed at greater depths than in the main tributaries. Lakeshore redds at this location are likely influenced by groundwater or hyporheic flow at the lake-tributary interface. Although numerically only a minor component of the population used lakeshore habitat to spawn, this group of fish may make important contributions to the population. Bucaria (1968) observed 20 sockeye in 1963 and 10 in 1964 spawning on the lakeshore at the mouth of an intermittent tributary, which is likely the same location where lake spawning was observed in 2012. All other ephemeral tributaries and water courses entering Auke Lake, of which the unnamed intermittent tributary was the largest, were surveyed for spawning activity in 2012, but none was observed. It is unclear if fish are opportunistically using suitable habitat at this site or whether a small component is actively homing there. However, use of this site for spawning appears to have persisted for at least 49 years. Spawning at the unnamed tributary-lakeshore site occurred 3 weeks later than peak spawning in the main lake

tributaries in 2012, suggesting that, if fish are actively homing to this natal site, they may be a partially isolated spawning group.

Population sub-structure created by at least partial reproductive isolation between spawning groups can promote genetic differentiation and contribute diversity important to population sustainability (McElhany et al. 2000). Sockeye salmon exploit a diverse range of spawning habitats and population sub-structure, with associated genetic differentiation, is common in sockeye populations (e.g., Varnavskaya et al. 1994). Sockeye spawning in the unnamed tributary and adjacent lakeshore habitat may be a partially isolated spawning group and represents important life history diversity within the Auke Lake population. Diversity is important for population sustainability because it promotes resiliency to environmental variation over a continuum of spatial and temporal scales. In the interest of conserving life history diversity, land managers and regulatory agencies should ensure that such spawning groups are a high priority for protection during land planning processes. Floating docks, which are part of the east Auke Lake trail, currently intersect the lakeshore spawning area. We observed disturbance of lake spawning sockeye by trail users. When walked on, movement and noise from the floating trail resulted in avoidance behavior by sockeye, with fish burst swimming away from redds into cover. However, the extent of this disturbance and whether it results in reduced spawning success is unclear.

Summary and Conclusions

In Auke Lake: 1) sockeye staging distribution in 2012 was not random and is consistent with the distribution observed more than 20 years by Nelson (1993); 2) the population is dominated by stream spawning fish (98.5%) and; 3) the small lakeshore spawning component of the population (1.5%) may have persisted for at least 49 years and potentially constitutes a different life history variant. Although the proportion of sockeye salmon using lakeshore habitat to spawn may vary annually, the variation is unlikely to be significant. Lakeshore spawning is common throughout southeast Alaska, with some watersheds exhibiting large proportions of lakeshore spawning fish (Conitz and Cartwright 2005; Conitz et al. 2007). However, the proportion of lake spawning fish is dependent on availability of suitable lakeshore habitat. Given the low quality of spawning substrate observed throughout most of Auke Lake, it is unlikely the lake can support a significant increase in the proportion of spawning sockeye using the lakeshore. As a result, pre-spawning mortality may be higher in years with high sockeye abundance or low accessibility to the inlet streams.

The information in this study has several implications for land use planning processes in the Auke Lake watershed. Despite the relatively short adult freshwater phase of their life cycle, sockeye salmon in Auke Lake express different behaviors with different habitat requirements. Habitat criteria for selection of staging areas by sockeye was not evaluated in this study, but future investigation of habitat variables, such as water temperature, DO, and lake flow patterns, that are important in structuring the staging distribution of sockeye will be useful in assessing impacts of development on the population. Such information could be used to predict habitat suitability in other areas of Auke Lake and determine if the staging areas observed in 2012 and by Nelson (1993) are the only optimal habitat areas available to sockeye in the lake. Long-term sustainability of the population relies on land managers and regulatory agencies giving consideration to all aspects of the sockeye life cycle and associated habitats in the Auke Lake watershed. An important aspect of salmon ecology and outstanding knowledge gap is

understanding juvenile sockeye distribution, habitat use, and outmigrant phenology in the watershed.

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Appendix 1: R code used to estimate proportion of sockeye using the stream environment and lake environment in the Auke Lake Watershed in 2012 with associated 95% binomial confidence intervals. This requires user to have binom package installed in their library. Profile method was used.

Proportion of stream environment spawners and associated 95% binomial confidence intervals in 2012.

```
> library(binom)
Loading required package: lattice
> binom.confint(x=67, n=68)
  method x n mean lower upper
1 agresti-coull 67 68 0.9852941 0.9136774 1.0050122
2 asymptotic 67 68 0.9852941 0.9566838 1.0139044
3 bayes 67 68 0.9782609 0.9333321 0.9984087
4 cloglog 67 68 0.9852941 0.9001668 0.9979153
5 exact 67 68 0.9852941 0.9207660 0.9996277
6 logit 67 68 0.9852941 0.9029251 0.9979323
7 probit 67 68 0.9852941 0.9206519 0.9983924
8 profile 67 68 0.9852941 0.9368507 0.9987390
9 lrt 67 68 0.9852941 0.9368507 0.9991437
10 prop.test 67 68 0.9852941 0.9098808 0.9992319
11 wilson 67 68 0.9852941 0.9212903 0.9992457
```

Proportion of lake environment spawners and associated 95% binomial confidence intervals in 2012.

```
> binom.confint(x=1, n=68)
  method x n mean lower upper
1 agresti-coull 1 68 0.01470588 -0.0050121595 0.08632257
2 asymptotic 1 68 0.01470588 -0.0139043986 0.04331616
3 bayes 1 68 0.02173913 0.0015913365 0.06666786
4 cloglog 1 68 0.01470588 0.0012418103 0.06988873
5 exact 1 68 0.01470588 0.0003722514 0.07923399
6 logit 1 68 0.01470588 0.0020677403 0.09707495
7 probit 1 68 0.01470588 0.0016076073 0.07934808
8 profile 1 68 0.01470588 0.0012609890 0.06314930
9 lrt 1 68 0.01470588 0.0008563388 0.06314935
10 prop.test 1 68 0.01470588 0.0007681277 0.09011925
11 wilson 1 68 0.01470588 0.0007543132 0.07870973
>
```

R code used to estimate the sex proportion of sockeye using the in the Auke Lake Watershed in 2012 with associated 95% binomial confidence intervals. This requires user to have binom package installed in their library. Profile method was used.

Proportion of tagged male sockeye and associated 95% binomial confidence intervals in 2012.

```
> library(binom)
Loading required package: lattice
```

```
> binom.confint(x=43,n=80)
  method x n mean lower upper
1 agresti-coull 43 80 0.537500 0.4290304 0.6425333
2 asymptotic 43 80 0.537500 0.4282433 0.6467567
3 bayes 43 80 0.537037 0.4285374 0.6438034
4 cloglog 43 80 0.537500 0.4226034 0.6392358
5 exact 43 80 0.537500 0.4224175 0.6497236
6 logit 43 80 0.537500 0.4281956 0.6433150
7 probit 43 80 0.537500 0.4282055 0.6440180
8 profile 43 80 0.537500 0.4283558 0.6442757
9 lrt 43 80 0.537500 0.4283553 0.6442781
10 prop.test 43 80 0.537500 0.4229920 0.6483797
11 wilson 43 80 0.537500 0.4290436 0.6425201
```

#Proportion of tagged female sockeye and associated 95% binomial confidence intervals in 2012.

```
> binom.confint(x=37,n=80)
  method x n mean lower upper
1 agresti-coull 37 80 0.462500 0.3574667 0.5709696
2 asymptotic 37 80 0.462500 0.3532433 0.5717567
3 bayes 37 80 0.462963 0.3561966 0.5714626
4 cloglog 37 80 0.462500 0.3508064 0.5668649
5 exact 37 80 0.462500 0.3502764 0.5775825
6 logit 37 80 0.462500 0.3566850 0.5718044
7 probit 37 80 0.462500 0.3559820 0.5717945
8 profile 37 80 0.462500 0.3557243 0.5716442
9 lrt 37 80 0.462500 0.3557219 0.5716447
10 prop.test 37 80 0.462500 0.3516203 0.5770080
11 wilson 37 80 0.462500 0.3574799 0.5709564
```

Appendix 2: Coordinates and substrate classification for SCUBA habitat transects in high-use fish areas (Sites 1-4) considered potential locations for lake spawning, 2012.

Table A1: Coordinates for SCUBA substrate transects.

| Transect | Start coordinate | | End coordinate | |
|----------|------------------|-------------|----------------|-------------|
| | Latitude | Longitude | Latitude | Longitude |
| 1 | 58.390597 | -134.632416 | 58.390879 | -134.632946 |
| 2 | 58.390739 | -134.632236 | 58.390879 | -134.632946 |
| 3 | 58.39037 | -134.633257 | 58.390879 | -134.632946 |
| 4 | 58.39041 | -134.633618 | 58.390879 | -134.632946 |
| 5 | 58.390639 | -134.634071 | 58.390879 | -134.632946 |
| 6 | 58.391136 | -134.629185 | 58.391564 | -134.628502 |
| 7 | 58.390931 | -134.628835 | 58.391564 | -134.628502 |
| 8 | 58.390679 | -134.628812 | 58.391564 | -134.628502 |
| 9 | 58.390698 | -134.628409 | 58.391491 | -134.628224 |
| 10 | 58.390729 | -134.628159 | 58.391491 | -134.628224 |
| 11 | 58.39243 | -134.624277 | 58.392481 | -134.624474 |
| 12 | 58.388108 | -134.637165 | 58.388393 | -134.637848 |
| 13 | 58.388185 | -134.636912 | 58.388393 | -134.637848 |
| 14 | 58.388474 | -134.637666 | 58.38835 | -134.636742 |
| 15 | 58.389029 | -134.636857 | 58.389076 | -134.637631 |
| 16 | 58.389038 | -134.636893 | 58.389076 | -134.637631 |
| 17 | 58.388836 | -134.637122 | 58.388938 | -134.637552 |

Table A2: Site 1 SCUBA transect substrate classification

| Site 1 | | | | | |
|--------------------------|-----------|-----------------------|--------------------------|-----------|-----------------|
| Distance on Transect (m) | Depth (m) | Substrate Type | Distance on Transect (m) | Depth (m) | Substrate Type |
| Transect 12 | | | Transect 13 | | |
| 0 | 18.3 | Silt | 0 | 19.2 | Silt |
| 5 | 15.5 | Silt | 5 | 18.3 | Silt |
| 10 | 13.7 | Silt | 10 | 16.8 | Silt |
| 15 | 11.6 | Silt | 15 | 14.3 | Silt |
| 20 | 7.3 | Bedrock | 20 | 12.5 | Silt |
| 25 | 5.8 | Bedrock | 25 | 9.4 | Bedrock |
| 30 | 4.3 | Bedrock | 30 | 6.1 | Bedrock |
| 35 | 3.0 | Boulder/Coarse Gravel | 35 | 5.2 | Bedrock |
| | | | 40 | 4.0 | Bedrock/Boulder |
| | | | 45 | 3.0 | Bedrock/Boulder |

Table A2 continued: Site 1 SCUBA transect substrate classification.

| Site 1 | | | | | |
|--------------------------|-----------|--------------------|--------------------------|-----------|------------------|
| Distance on Transect (m) | Depth (m) | Substrate Type | Distance on Transect (m) | Depth (m) | Substrate Type |
| Transect 14 | | | Transect 15 | | |
| 0 | 18.0 | Silt | 0 | 10.7 | Silt |
| 5 | 17.1 | Silt | 5 | 8.5 | Silt |
| 10 | 16.5 | Silt | 10 | 6.4 | Silt |
| 15 | 14.6 | Silt | 15 | 4.9 | Silt |
| 20 | 12.8 | Silt | 20 | 4.0 | Fine Gravel/Silt |
| 25 | 10.7 | Silt | 25 | 3.7 | Silt |
| 30 | 8.5 | Silt | 30 | 3.0 | Silt |
| 35 | 6.4 | Silt | | | |
| 40 | 4.9 | Silt | | | |
| 45 | 4.3 | Silt | | | |
| 50 | 3.0 | Boulder/Logs | | | |
| Transect 16 | | | Transect 17 | | |
| 0 | 10.4 | Silt | 0 | 4.9 | Silt |
| 5 | 7.9 | Silt | 5 | 4.6 | Silt |
| 10 | 6.1 | Silt | 10 | 3.7 | Silt |
| 15 | 4.6 | Silt | 15 | 3.0 | Silt |
| 20 | 4.0 | Silt/Medium Gravel | | | |
| 25 | 3.0 | Silt | | | |
| 30 | 2.1 | Silt | | | |

Table A3: Site 2 SCUBA transect substrate classification.

| Site 2 | | | | | |
|--------------------------|-----------|---------------------|--------------------------|-----------|---------------------|
| Distance on Transect (m) | Depth (m) | Substrate Type | Distance on Transect (m) | Depth (m) | Substrate Type |
| Transect 1 | | | Transect 2 | | |
| 0 | 21.6 | Organic debris/Silt | 0 | 19.2 | Silt/Organic debris |
| 5 | 18.9 | Silt | 5 | 18.0 | Fine Gravel |
| 10 | 15.8 | Coarse Gravel | 10 | 16.5 | Fine/Medium Gravel |
| 15 | 12.8 | Fine Gravel | 15 | 13.7 | Fine Gravel |
| 20 | 9.8 | Medium Gravel | 20 | 10.7 | Medium Gravel |
| 25 | 6.7 | Medium Gravel | 25 | 7.9 | Coarse Gravel |
| 30 | 3.7 | Medium Gravel | 30 | 5.5 | Medium Gravel |
| 35 | 0.9 | Sand | 35 | 2.4 | Medium Gravel |
| 40 | 0.3 | Medium Gravel | 40 | 0.3 | Medium Gravel |

Table A3 continued: Site 2 SCUBA transect substrate classification.

| Site 2 | | | | | |
|--------------------------|-----------|---------------------|--------------------------|-----------|---------------------|
| Distance on Transect (m) | Depth (m) | Substrate Type | Distance on Transect (m) | Depth (m) | Substrate Type |
| Transect 3 | | | Transect 4 | | |
| 0 | 20.4 | Silt/Organic debris | 0 | 20.1 | Silt/Organic debris |
| 5 | 19.8 | Silt/Organic debris | 5 | 20.1 | Silt/Organic debris |
| 10 | 18.9 | Silt/Organic debris | 10 | 19.5 | Silt |
| 15 | 16.2 | Silt | 15 | 15.5 | Silt |
| 20 | 13.1 | Silt | 20 | 14.0 | Silt/Organic debris |
| 25 | 10.1 | Organic debris | 25 | 11.3 | Organic debris |
| 30 | 6.7 | Organic debris | 30 | 8.8 | Large Gravel/Sand |
| 35 | 4.3 | Organic debris | 35 | 6.1 | Medium/Large Gravel |
| 40 | 1.5 | Fine Gravel | 40 | 3.4 | Medium Gravel |
| 45 | 0.3 | Fine/Medium Gravel | 45 | 0.9 | Fine Gravel |
| | | | 50 | 0.3 | Fine/Medium Gravel |
| Transect 5 | | | | | |
| 0 | 17.7 | Silt | | | |
| 5 | 17.4 | Silt | | | |
| 10 | 17.4 | Silt | | | |
| 15 | 16.8 | Silt | | | |
| 20 | 13.1 | Silt/Organic debris | | | |
| 25 | 10.1 | Organic debris | | | |
| 30 | 7.0 | Organic debris | | | |
| 35 | 4.3 | Sand/Large Gravel | | | |
| 40 | 1.2 | Medium Gravel | | | |
| 45 | 0.3 | Medium Gravel | | | |

Table A4: Site 3 SCUBA transect substrate classification.

| Site 3 | | | | | |
|--------------------------|-----------|----------------|--------------------------|-----------|----------------|
| Distance on Transect (m) | Depth (m) | Substrate Type | Distance on Transect (m) | Depth (m) | Substrate Type |
| Transect 6 | | | Transect 7 | | |
| 0 | 3.4 | Silt | 0 | 7.0 | Silt |
| 5 | 3.0 | Silt | 5 | 6.1 | Silt |
| 10 | 3.0 | Silt | 10 | 5.2 | Silt |
| 15 | 2.7 | Silt | 15 | 4.6 | Silt |
| 20 | 2.7 | Silt | 20 | 4.0 | Silt |
| 25 | 2.7 | Silt | 25 | 3.7 | Silt |
| 30 | 2.7 | Silt | 30 | 3.4 | Silt |
| 35 | 2.7 | Silt | 35 | 2.7 | Silt |
| 40 | 2.7 | Silt | 40 | 2.7 | Silt |
| 45 | 2.4 | Silt | 45 | 2.1 | Silt |
| 50 | 2.4 | Silt | | | |
| 55 | 2.4 | Silt | | | |

Table A4 continued: Site 3 SCUBA transect substrate classification.

| Site 3 | | | | | |
|--------------------------|-----------|----------------|--------------------------|-----------|----------------|
| Distance on Transect (m) | Depth (m) | Substrate Type | Distance on Transect (m) | Depth (m) | Substrate Type |
| Transect 8 | | | Transect 9 | | |
| 0 | 4.6 | Silt | 0 | 3.7 | Silt |
| 5 | 4.0 | Silt | 5 | 3.7 | Silt |
| 10 | 3.7 | Silt | 10 | 3.4 | Silt |
| 15 | 3.4 | Silt | 15 | 3.4 | Silt |
| 20 | 3.0 | Silt | 20 | 3.0 | Silt |
| 25 | 3.0 | Silt | 25 | 3.0 | Silt |
| 30 | 2.7 | Silt | 30 | 3.0 | Silt |
| 35 | 3.0 | Silt | 35 | 3.0 | Silt |
| 40 | 2.7 | Silt | 40 | 3.0 | Silt |
| 45 | 2.7 | Silt | 45 | 3.0 | Silt |
| 50 | 2.7 | Silt | 50 | 2.7 | Silt |
| 55 | 2.4 | Silt | 55 | 2.7 | Silt |
| 60 | 2.7 | Silt | 60 | 2.7 | Silt |
| 65 | 2.7 | Silt | 65 | 2.7 | Silt |
| 70 | 2.4 | Silt | 70 | 2.7 | Silt |
| 75 | 2.4 | Silt | 75 | 1.5 | Silt |
| 80 | 2.4 | Silt | | | |
| 85 | 2.4 | Silt | | | |
| 90 | 2.4 | Silt | | | |
| Transect 10 | | | | | |
| 0 | 4.0 | Silt | | | |
| 5 | 4.0 | Silt | | | |
| 10 | 3.7 | Silt | | | |
| 15 | 3.7 | Silt | | | |
| 20 | 3.4 | Silt | | | |
| 25 | 3.4 | Silt | | | |
| 30 | 3.0 | Silt | | | |
| 35 | 3.0 | Silt | | | |
| 40 | 3.0 | Silt | | | |
| 45 | 3.0 | Silt | | | |
| 50 | 3.0 | Silt | | | |
| 55 | 2.7 | Silt | | | |
| 60 | 2.7 | Silt | | | |
| 65 | 2.4 | Silt | | | |
| 70 | 2.4 | Silt | | | |
| 75 | 1.5 | Silt | | | |

Table A5: Site 4 SCUBA transect substrate classification.

| Site 4 | | |
|--------------------------|-----------|--------------------|
| Distance on Transect (m) | Depth (m) | Substrate Type |
| Transect 11 | | |
| 0 | 7.9 | Silt |
| 5 | 6.7 | Silt/Organics |
| 10 | 4.3 | Organics |
| 15 | 1.8 | Medium Gravel |
| 20 | 1.8 | Fine/Medium Gravel |

Appendix 3: Coordinates and substrate classification for benthic grab sample transects in areas of lower fish use, 2012.

| Transect Number | Distance on Transect (m) | Depth (m) | Substrate Type | Transect Number | Distance on Transect (m) | Depth (m) | Substrate Type |
|---|--------------------------|-----------|---------------------|--|--------------------------|-----------|------------------|
| Transect 1 58.385469 -134.637644 | 0 | 2.06 | veg mat/silt | Transect 7 58.387145 -134.639149 | 0 | 2.40 | veg mat/silt |
| | 5 | 4.43 | silt | | 5 | 4.30 | silt |
| | 10 | 5.10 | silt | | 10 | 5.27 | silt |
| | 15 | 5.95 | silt | | 15 | 5.65 | silt |
| | 20 | 6.92 | silt | | 20 | 6.34 | silt |
| | 25 | 8.65 | silt | | 25 | 6.52 | silt |
| Transect 2 58.385638 -134.63800 | 0 | 2.60 | organic debris/silt | Transect 8 58.38756 -134.639076 | 0 | 2.24 | veg mat/silt |
| | 5 | 4.14 | organic debris/silt | | 5 | 4.09 | silt/fine gravel |
| | 10 | 4.85 | silt | | 10 | 4.89 | silt |
| | 15 | 5.27 | silt | | 15 | 5.15 | silt |
| | 20 | 5.85 | silt | | 20 | 5.93 | silt |
| | 25 | 6.31 | silt | | 25 | 6.53 | silt |
| Transect 3 58.385714 -134.638585 | 0 | 2.35 | organic debris/silt | Transect 9 58.38694 -134.639062 | 0 | 1.50 | veg mat |
| | 5 | 5.03 | organic debris/silt | | 5 | 3.10 | silt/sand |
| | 10 | 5.66 | silt | | 10 | 3.75 | silt |
| | 15 | 5.90 | silt | | 15 | 4.00 | silt |
| | 20 | 6.56 | silt | | 20 | 4.20 | silt |
| | 25 | 7.15 | silt | | 25 | 4.62 | silt |
| Transect 4 58.386086 -134.638896 | 0 | 2.65 | veg mat/silt | Transect 10 58.391803 -134.62740 | 0 | 2.50 | veg mat/sand |
| | 5 | 4.38 | silt | | 5 | 4.00 | silt |
| | 10 | 5.30 | silt | | 10 | 5.25 | silt |
| | 15 | 5.80 | silt | | 15 | 6.10 | silt |
| | 20 | 6.39 | silt | | 20 | 6.80 | silt |
| | 25 | 6.74 | silt | | 25 | 7.45 | silt |
| Transect 5 58.386402 -134.638908 | 0 | 2.21 | veg mat/silt | Transect 11 58.392149 -134.626778 | 0 | 1.85 | veg mat |
| | 5 | 3.91 | silt/medium gravel | | 5 | 4.30 | silt |
| | 10 | 4.40 | silt | | 10 | 4.60 | silt |
| | 15 | 5.39 | silt | | 15 | 6.85 | silt |
| | 20 | 5.40 | silt | | 20 | 7.75 | silt |
| | 25 | 5.72 | silt | | 25 | 8.40 | silt |
| Transect 6 58.386713 -134.638978 | 0 | 2.78 | organic debris/silt | Transect 12 58.392166 -134.62618 | 0 | 1.10 | veg mat/silt |
| | 5 | 4.06 | organic debris/silt | | 5 | 4.00 | silt |
| | 10 | 4.41 | silt | | 10 | 6.30 | silt |
| | 15 | 4.89 | silt | | 15 | 8.20 | silt |
| | 20 | 5.47 | silt | | 20 | 9.30 | silt |
| | 25 | 5.50 | silt | | 25 | 9.66 | silt |

Appendix 3 continued: Coordinates and substrate classification for benthic grab sample transects in areas of lower fish use, 2012.

| Transect Number | Distance on Transect (m) | Depth (m) | Substrate Type | Transect Number | Distance on Transect (m) | Depth (m) | Substrate Type |
|--|--------------------------|-----------|---------------------|--|--------------------------|-----------|---------------------|
| Transect 13 58.392169 -134.625467 | 0 | 1.75 | veg mat | Transect 19 58.389669 -134.624925 | 0 | 1.65 | veg mat/silt |
| | 5 | 4.62 | silt | | 5 | 4.05 | silt/organic debris |
| | 10 | 7.50 | silt | | 10 | 6.00 | silt |
| | 15 | 9.25 | silt | | 15 | 7.05 | silt |
| | 20 | 9.50 | silt | | 20 | 7.50 | silt |
| | 25 | 10.00 | silt | | 25 | 8.00 | silt |
| Transect 14 58.392221 -134.625015 | 0 | 1.25 | veg mat/silt | Transect 20 58.386929 -134.627569 | 0 | 1.20 | veg mat/silt |
| | 5 | 4.10 | silt | | 5 | 4.40 | silt |
| | 10 | 5.95 | silt | | 10 | 6.60 | silt |
| | 15 | 7.50 | silt | | 15 | 9.00 | silt |
| | 20 | 9.20 | silt | | 20 | 12.20 | silt |
| | 25 | 9.30 | silt | | 25 | 15.25 | silt |
| Transect 15 58.390272 -134.62328 | 0 | 1.30 | veg mat/silt | Transect 21 58.385042 -134.628035 | 0 | 1.00 | organic debris/silt |
| | 5 | 3.35 | silt | | 5 | 6.50 | organic debris/silt |
| | 10 | 3.95 | silt | | 10 | 8.70 | silt |
| | 15 | 4.50 | silt | | 15 | 10.60 | silt |
| | 20 | 5.10 | silt | | 20 | 15.50 | silt |
| | 25 | 6.00 | silt | | na | na | na |
| Transect 16 58.390022 -134.623587 | 0 | 1.15 | veg mat/silt | Transect 22 58.387151 -134.627273 | 0 | 1.30 | organic debris/silt |
| | 5 | 3.10 | silt | | 5 | 5.40 | organic debris/silt |
| | 10 | 3.70 | silt | | 10 | 7.70 | silt |
| | 15 | 4.18 | silt | | 15 | 9.90 | silt |
| | 20 | 4.70 | silt | | 20 | 15.10 | silt |
| | 25 | 5.30 | silt | | 25 | 17.70 | silt |
| Transect 17 58.38999 -134.624031 | 0 | 1.10 | veg mat/silt | Transect 23 58.385311 -134.628074 | 0 | 1.00 | organic debris/silt |
| | 5 | 3.65 | silt/organic debris | | 5 | 5.60 | silt/sand |
| | 10 | 4.33 | silt | | 10 | 7.90 | silt |
| | 15 | 5.28 | silt | | 15 | 10.00 | silt |
| | 20 | 6.00 | silt | | 20 | 14.90 | silt |
| | 25 | 6.75 | silt | | 25 | 17.40 | silt |
| Transect 18 58.389885 -134.624445 | 0 | 1.50 | veg mat/sand | Transect 24 58.38477 -134.627969 | 0 | 1.45 | veg mat/silt |
| | 5 | 3.80 | silt/organic debris | | 5 | 4.70 | silt/fine gravel |
| | 10 | 4.50 | silt | | 10 | 6.70 | silt |
| | 15 | 5.50 | silt | | 15 | 9.10 | silt |
| | 20 | 6.40 | silt | | 20 | 12.00 | silt |
| | 25 | 7.15 | silt | | 25 | 15.20 | silt |

Appendix 3 continued: Coordinates and substrate classification for benthic grab sample transects in areas of lower fish use, 2012.

| Transect Number | Distance on Transect (m) | Depth (m) | Substrate Type | Transect Number | Distance on Transect (m) | Depth (m) | Substrate Type |
|--------------------|--------------------------|-----------|------------------|--------------------|--------------------------|-----------|----------------|
| Transect 25 | 0 | 1.25 | veg mat/silt | Transect 26 | 0 | 1.40 | veg mat/silt |
| 58.384495 | 5 | 4.75 | sand/fine gravel | 58.387409 | 5 | 4.50 | silt |
| -134.627871 | 10 | 6.45 | silt | -134.627117 | 10 | 6.60 | silt/sand |
| | 15 | 8.95 | silt | | 15 | 8.10 | silt |
| | 20 | 12.10 | silt | | 20 | 11.90 | silt |
| | 25 | 15.30 | silt | | 25 | 14.95 | silt |