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NOTE

Microtrolling: an Economical Method to Nonlethally Sample and Tag Juvenile Pacific Salmon at Sea

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Abstract

Mortality of juvenile Pacific salmon *Oncorhynchus* spp. in their first marine year is hypothesized to be a primary driver of variable recruitment in a changing ocean. Much contemporary research focuses on diet, distribution, growth, and survival during this period; however, existing methods of capturing juvenile salmon at sea are expensive and may be limited by topography and tidal currents. We assessed the feasibility of using a small vessel and modified recreational fishing gear (microtrolling) to nonlethally capture, sample, and tag juvenile Chinook Salmon *O. tshawytscha* during their first marine summer. Sampling was conducted in the Strait of Georgia, British Columbia, from August to October 2014. We captured 168 Chinook Salmon, 13 Coho Salmon *O. kisutch*, and 1 Chum Salmon *O. keta* in 72 h of active fishing; Chinook Salmon CPUE was greatest between 6 and 19 m and increased late in the afternoon and on the flood tide. To assess short-term mortality related to capture, PIT tagging, and sampling, we maintained 66 microtroll-captured Chinook Salmon (41 of which were PIT-tagged) overnight in a net pen; only one mortality and one incidence of tag loss were observed. Microtrolling proved effective for systematically sampling juvenile Chinook Salmon across depths and habitats. Unlike alternative methods of sampling juvenile Pacific salmon (trawling and purse seining), the utility of microtrolling is likely limited to studies of Chinook Salmon and possibly Coho Salmon. The low cost of this method has potential to facilitate participation of frequently excluded stakeholders, including First Nations and community groups, in marine research on juvenile Pacific salmon.

Early marine residence is widely considered to be a period of high and variable mortality for juvenile Pacific salmon *Oncorhynchus* spp., with implications for both interannual variation and long-term trends in recruitment (Parker 1965; Beamish and Mahnken 2001; Wells et al. 2012, 2016). The mechanisms underlying this mortality are a major focus of contemporary research, much of which involves the capture and sampling of juvenile salmon. Long-term monitoring studies annually measure abundance, distribution, diet, size, and condition of juvenile salmon at sea (Beamish et al. 2000; Brodeur et al. 2003); in some cases, these data contribute directly to the forecasting of future returns (Karpenko et al. 1998; Wertheimer et al. 2013). Ocean sampling of juvenile salmon also facilitates investigations of how size, condition, pathogen or parasite load, ontogenetic patterns in habitat use, and trophic position may relate to growth and survival (Duffy et al. 2010; Duffy and Beauchamp 2011; Miller et al. 2013, 2014; Kemp 2014; Godwin et al. 2015; Hertz et al. 2015). Tagging studies seek to directly measure marine mortality (Furey et al. 2015) and in some cases to localize mortality in space and time (Melnychuk et al. 2013) or to link mortality to a proximate cause (Berejikian et al. 2016).

Juvenile Pacific salmon in their first marine year are seldom encountered by commercial fisheries. Most of the research focusing on early marine residence and mortality of Pacific salmon therefore relies on fishery-independent sampling methods. Many gear types have been used to sample juvenile salmon in the marine environment; these include beach seines, purse seines, gill nets, dip nets, traps, surface trawls, and midwater trawls of various types (reviewed by Beamish et al. 2003; Brodeur et al. 2003; Karpenko 2003). The primary contemporary methods that are used to capture juvenile Pacific salmon for research are rope trawling and purse seining. Rope trawling involves a large, powerful vessel towing a net with a very large opening (often >1,000 m^2) at high speed (up to 9 km/h). This method can sample at all depths and under most weather conditions and is nonselective, capturing both juvenile and adult salmon of all species (Beamish et al. 2003).

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Rope trawling also allows for large volumes of water to be sampled at a given depth stratum and large numbers of juvenile salmon to be obtained for sampling. Disadvantages of rope trawling are that the large vessels involved cannot operate close to shore or in narrow passages, nets cannot be deployed safely in shallow water, and fish are killed during capture and cannot be used for tagging studies. In addition, scales are typically rubbed off during capture, thus limiting age and growth rate analyses to more labor-intensive otolith processing. Given the relatively high tow speed, the distance covered per tow is typically greater than 2 km (Beamish et al. 2000; Duffy and Beauchamp 2011), limiting the scale at which juvenile salmon distribution patterns can be resolved. Vessel availability also presents major challenges for trawl sampling programs due to the high costs of chartering capable vessels and the multipurpose-use requirements of government agency vessels.

Unlike trawling, purse seining allows for fine-scale point sampling of juvenile salmon distribution. In addition, the fish are landed alive, meaning that they can be used for tagging studies (e.g., Chittenden et al. 2009; Neville et al. 2015). Purse seines can also be deployed close to shore and in confined areas. However, major problems with purse seines include the following: (1) the small mesh needed to retain juveniles restricts where and when the sets can be made, resulting in a nonrandom survey (D. Beamish, Department of Fisheries and Oceans Canada, personal communication); (2) depth-stratified fishing is not possible; and (3) sorting salmon from the bycatch can be time consuming and can result in mortality (for example, if the bycatch consists of large jellyfish). Purse seining also samples far less water than trawling and may not be an economical method of sampling juvenile salmon at low densities, particularly as vessels that are capable of deploying a large purse seine are expensive to charter. Smaller, hand-hauled purse seines have been used effectively from small vessels, but they are only suitable for use in shallow water (e.g., Healey 1980) or for sampling surface-oriented juvenile salmon (e.g., Godwin et al. 2015).

Hook-and-line methods have been used infrequently to sample juvenile salmon at sea. Rich (1920) used hook-and-line sampling, primarily from cannery wharves, as part of an investigation of juvenile Chinook Salmon *O. tshawytscha* life history in the Columbia River and Sacramento River estuaries. Orsi (1987) assessed whether a commercial troller with scaled-down hooks and lures could be used to effectively sample juvenile Chinook Salmon and Coho Salmon *O. kisutch* in Southeast Alaska. Building on the success of that trial, Orsi and Wertheimer (1995) used trolling to study the vertical distribution of juvenile Coho Salmon and Chinook Salmon with respect to season and physical oceanography, and Orsi and Jaenicke (1996) investigated temporal and spatial patterns of age and origin for pre-recruit Chinook Salmon in Southeast Alaska. Despite the success of those studies, trolling has not become more common as a sampling method for juvenile salmon.

Marine survival of Chinook Salmon and Coho Salmon in the Strait of Georgia, British Columbia, and Puget Sound, Washington, has declined dramatically since the 1980s (Beamish et al. 1995, 2010; Zimmerman et al. 2015). This decline provided the impetus for an ongoing binational research initiative, the Salish Sea Marine Survival Project. This initiative includes projects that investigate spatiotemporal patterns in diet, growth, and predation exposure of juvenile salmon and tagging studies that seek to identify potential critical mortality periods. As part of this work, we identified the need for a low-cost method that could be used to capture, biologically sample, and apply PIT tags to juvenile Chinook Salmon and Coho Salmon during the latter part of their first summer at sea. We therefore investigated the feasibility of using modified recreational fishing gear deployed from a small vessel (microtrolling) to nonlethally capture juvenile salmon. Specifically, we (1) assessed the utility of microtrolling for investigating fine-scale patterns in distribution, (2) compared the sizes of fish that were captured by microtrolling and alternative methods, and (3) investigated short-term (overnight) mortality resulting from hook-and-line capture in conjunction with sampling and tagging.

METHODS

Sampling.—Sampling occurred in the vicinity of Cowichan Bay, British Columbia, Canada (Figure 1), on 30 d between August 9 and October 3, 2014. Gear was deployed from an open, 4.9-m aluminum boat (37-kW outboard motor) using electric downriggers (Scotty Depthpower; Scott Plastics, Victoria, British Columbia) spooled with braided Dacron line (90-kg breaking strain) and weighted with a 6.8-kg lead ball. These downriggers are equipped with a switch that automatically stops retrieving when activated by a plastic stopper on the line. Stoppers were placed on the line at measured intervals to allow each piece of gear (hereafter, "leader") to be fished at a predetermined depth. Leaders consisted of a stainless-steel clip for attachment to the downrigger line, 2 m of monofilament (18-kg breaking strain), a stainless-steel swivel, and a piece of terminal gear attached with 50 cm of monofilament (2.4–3.6-kg breaking strain). This light line was used to allow any adult salmon encountering the gear to break free. Terminal gear consisted primarily of either a transparent, pink-and-purple, 2.5-cm Apex UV Trout Killer plastic lure (hereafter, "Apex"; Hot Spot Lures Ltd., Victoria, British Columbia) or a 2-cm fly consisting of red and pearlescent Mylar strands tied in with thread at the front end of a Mylar-wrapped hook (hereafter, "fly"). To impart erratic movement, flies were tied 50 cm behind a 7-cm gold-and-chrome Super Diamond salmon spoon (Gibbs-Delta Tackle, Delta, British Columbia), which was connected directly to the 2 m of heavy monofilament. Hooks for all gear types were number-12 fly-tying hooks with a 5-mm point-to-shank gap and a 1.5-cm shank length

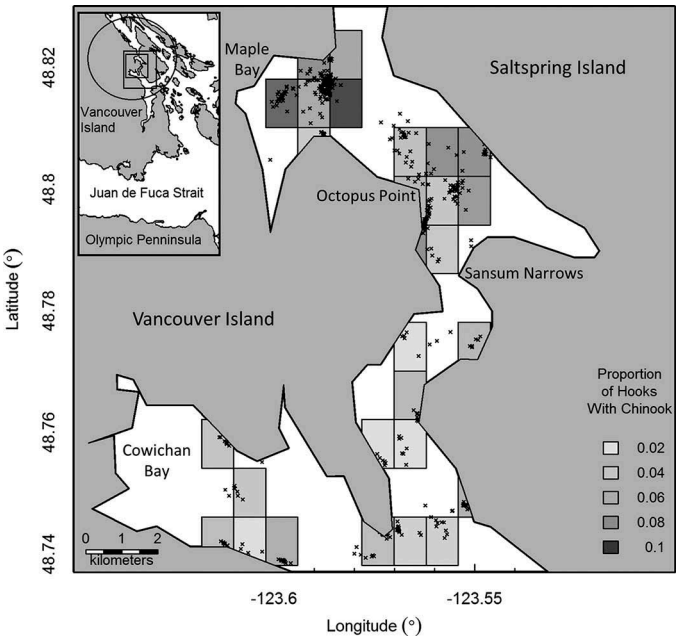

FIGURE 1. Fishing event locations (× symbols) and CPUE (proportion of hooks with Chinook Salmon; shaded rectangles represent CPUE on a continuous scale) for microtrolling conducted in the vicinity of Cowichan Bay, British Columbia, from August 9 to October 3, 2014. The inset map indicates expanded area (smallest rectangle), Canada Department of Fisheries and Oceans (DFO) purse seine sampling region (larger rectangle), and DFO rope trawl sampling region (ellipse). The CPUE is averaged by a 0.48′ × 0.48′ grid and is shown only for grid references containing 30 or more hook records.

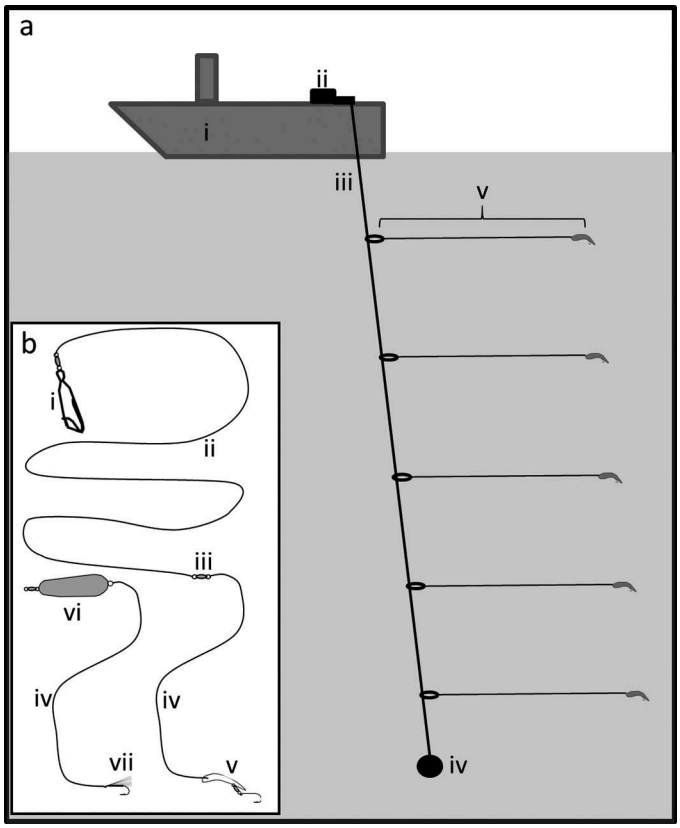

FIGURE 2. Schematic of microtrolling gear (not drawn to scale): **(a)** a 4.9-m, welded aluminum vessel (i) was equipped with two (only one side shown) Scotty Depthpower electric downriggers (ii) with a mainline of braided Dacron (iii; 90-kg breaking strain) weighted with a 6.8-kg lead ball (iv), and with leaders (v) deployed at measured intervals indicated by small plastic stoppers on the line; and **(b)** each leader consisted of a stainless-steel clip for attachment to the downrigger line (i) and 2 m of monofilament (ii; 18-kg breaking strain) connected to terminal gear consisting of either a stainless-steel swivel (iii) with 50 cm of monofilament (iv; 2.4–3.6-kg breaking strain) and a 2.5-cm Apex UV Trout Killer lure (v) or a 7-cm, gold-and-chrome Super Diamond salmon spoon (vi) to provide action to a 2-cm Mylar fly (vii).

(Mustad and Sons, Inc., Doral, Florida). In general, barbs on hooks were crushed with pliers (to minimize hooking injury), and the two terminal gear types described above were fished on either side of the vessel. To assess the impact of barb removal on CPUE, we used only flies during the final eight sampling days (after September 16), with barbless hooks deployed on one side of the vessel and barbed hooks deployed on the other side. A schematic diagram of gear configuration is provided in Figure 2.

Gear was deployed in standardized fishing events. For each fishing event, the time of day was logged before gear deployment began, and the times required to lower the gear to the desired fishing depth and to retrieve the gear were measured with a stopwatch. When two crew members were available, the lines on both sides of the boat were dropped and retrieved simultaneously, and the gear was fished for 5 min. When only one person was available, the two lines were dropped and retrieved sequentially and were fished for only 4 min to compensate for the extra time required to lower and retrieve. The depth fished and the number of leaders deployed depended on the water depth; in general, up to five leaders were fished per side at 4–8-m intervals from depths of 2–34 m. At shallower bottom depths, fewer leaders were deployed. Latitude and longitude were recorded at the beginning and end of each fishing event by using a handheld Global Positioning System (GPS) unit. The course and amount of throttle applied during gear deployment were adjusted based on the topography and the prevailing wind and current to maintain a relatively constant forward motion through the water (~2.5 km/h). It was not possible to determine the lure speed by using GPS data, as prevailing currents could result in speed over ground that was substantially greater or less than the speed through water. We targeted a speed through water that would result in erratic action of our lures without making them too difficult to catch. As gear was retrieved, the presence (and species) or absence of fish on each hook was logged.

Some sampling effort (~12 d) focused on testing the feasibility of pseudo-systematic spatial sampling across different habitats, with one or more fishing events occurring at each of a series of predetermined waypoints between Cowichan Bay and

Maple Bay. These waypoints included sites in open water, close to shore, and adjacent to Sansum Narrows, a narrow (500 m) passage with tidal currents reaching more than 7.41 km/h (4 knots). Most of the balance of the sampling days focused on maximizing catch for the postrelease mortality assessment. Fishing effort on those days occurred primarily in Maple Bay within 3.5 km of the net-pen site at Octopus Point (Figure 1), and fishing events generally occurred consecutively without moving the boat to a different site. Some additional effort was expended on reconnaissance of other areas, particularly Saanich Inlet.

Fish processing.—Fish were lifted aboard and lowered directly into a 150-L cooler that was partially filled with seawater. Water in the cooler was periodically refreshed, and temperature was monitored to ensure that it did not exceed 17°C. All nonsalmonid fish were identified to species and immediately released. Using small mesh-bottomed containers, all juvenile salmon were gently transferred into an anaesthetic bath (tricaine methanesulfonate, 80 mg/L) for unhooking and sampling.

Juvenile salmon were examined for the presence of an adipose fin clip and were wanded with a metal detector (to assess coded wire tag presence) and a PIT tag reader. Nose-to-fork length was recorded to the nearest millimeter, and five scales (to be used for genetic stock identification; described below) were removed from the preferred area (just above the lateral line immediately posterior to the dorsal fin) using forceps and were transferred to a gummed scale card. To express stomach contents (i.e., gastric lavage), a section of 3-mm-diameter plastic tubing glued to the outlet of a 250-mL wash bottle was slid gently in and out of the stomach of the fish (held inverted above a plastic container) while seawater was continually expressed from the bottle. Chinook Salmon that did not exhibit sustained bleeding or hook damage to the eye had a 12.5-mm × 2.1-mm PIT tag (HPT12 FDX-B; Biomark, Boise, Idaho) injected intraperitoneally in a posterior direction approximately 5 mm off the dorsal midline and just anterior to the pelvic girdle. Total handling time from first placement in the anaesthetic bath was approximately 3 min. Fish were returned to the 150-L cooler and were allowed to regain equilibrium before being released near the site of capture.

Genetic stock identification.—To determine whether PIT-tagged Chinook Salmon originated from the Cowichan River and in turn to determine which tags should be included in an ongoing (from 2014 to at least 2019) investigation of Cowichan River Chinook Salmon survival, scale samples were submitted to the Molecular Genetics Laboratory at the Pacific Biological Station, Fisheries and Oceans Canada (DFO). Qiagen DNeasy kits were used for DNA extraction. Probabilities of belonging to 296 unique North American Chinook Salmon populations were assigned to each fish based on combinations of alleles at 15 highly variable microsatellite loci using methods similar to those described by Beacham et al. (2012).

Fish size in microtroll samples relative to other gear types.—To assess potential size bias relative to alternative sampling methods, we obtained FL data for juvenile Chinook Salmon captured in the same region by DFO researchers using (1) a chartered purse seiner that deployed a 300-m-long, 20-m-deep seine net with a 6-mm-mesh bunt and (2) the research trawler CCGS *W.E. Ricker* using gear as described by Beamish et al. (2000). Purse seine sampling occurred between May 8 and July 23, 2014, in the vicinity of Cowichan Bay; trawling occurred on June 10 and September 17, 2014, throughout the Southern Gulf Islands (Figure 1). There was little temporal overlap between microtrolling and other methods of sampling, and the FL of Chinook Salmon increased during the study period. As the sampling method was not independent of time, a statistical comparison of the sizes of Chinook Salmon captured by alternative methods was not possible. To facilitate qualitative assessment of size bias, we graphically report FL on each date for microtrolling and the alternative capture methods (Chinook Salmon >300 mm FL were assumed to be in their second marine year and were excluded).

Postrelease mortality assessment.—To assess short-term mortality related to capture, tagging, and handling, a subset of juvenile Chinook Salmon were maintained overnight in a net-pen (1.2 × 1.2 × 2.4 m) consisting of a wood frame that was covered with 2.5-cm, galvanized-wire mesh (to deter predators) and lined with 5-mm nylon netting. The net-pen was weighted and suspended just below the surface from a concrete dock at Octopus Point near Sansum Narrows (Figure 1). In our original study design, we sought to compare the mortality of fish subjected to tagging and all handling practices (gastric lavage and scale sampling) with mortality in a control group that was only anesthetized and measured. However, negligible mortality was observed in both groups, and logistical challenges limited the sample size; therefore, we switched to sampling and tagging all fish prior to transfer to the net-pen. We maintained a total of 66 juvenile Chinook Salmon overnight in the net-pen (4–11 fish/night over 8 nights); 41 of the 66 fish were anesthetized, PIT-tagged, subjected to gastric lavage, and sampled for scales. Of those 41 individuals, 10 were captured on barbed hooks, and 31 were captured on barbless hooks. The remaining 25 fish were anesthetized and measured only.

Statistical analyses.—All analyses were conducted in R (R Core Team 2015). Analysis of CPUE was based on whether an individual hook that was deployed for one fishing event did (value = 1) or did not (value = 0) catch a juvenile Chinook Salmon. Catches of other species were too low to permit meaningful analyses.

To provide an example of how microtrolling could be applied to study spatiotemporal patterns in habitat use, we employed a generalized additive modeling (GAM) approach with a logit link function (binomial family) to describe how CPUE varied with hour of the day, tidal stage, and depth. Tidal

stage was defined as hours after the most recent low slack at Active Pass in the Southern Gulf Islands, as predicted by the Canadian Hydrographic Service. A GAM including all terms was fitted by using the unbiased risk estimator criterion and allowing for a maximum of 9 degrees of freedom for each covariate smooth term (i.e., basis dimension [k] = 10) in the mgcv package in R (Wood 2011). To account for a lack of independence among hooks within fishing events, a random effect structure was included in the model, with fishing event represented as a penalized regression term (Wood 2008), effectively resulting in a generalized additive mixed model (GAMM). A small number of hook deployments deeper than 35 m (n = 150, or 3% of the total) was excluded from the analysis, as such deployments did not occur throughout the study period. We assessed potential collinearity among covariates by using variance inflation factors calculated with the corvif function (available at www.highstat.com/Book2/HighstatLibV6.R). For all three predictor variables, the variance inflation factors were less than 1.5, suggesting no issues with multicollinearity.

To compare CPUEs between the two primary lure types (Apex and fly) and between barbed and barbless hooks, we generated subsets of data including only those fishing events in which either two lure types or the barbed and barbless hooks were fished simultaneously. We then fitted a GAMM to each data set as described above, with the addition of either lure type or hook status (barbed or barbless) as a parametric fixed factor.

RESULTS

Microtrolling

We conducted 557 fishing events on 30 d between August 9 and October 3, 2014, resulting in a total of 4,865 individual hook deployments. Straight-line distance between the starting and ending points for fishing events averaged 281 m (SD = 102 m; n = 496). Timed duration of fishing events, including gear deployment and retrieval, averaged 7.73 min (SD = 0.77 min; n = 471). Based on this average, we estimated a total gear deployment time of 71.8 h. We captured 182 juvenile Pacific salmon: 168 Chinook Salmon, 13 Coho Salmon, and 1 Chum Salmon *O. keta*. We also captured a single adult Coho Salmon (~45 cm). An additional four bent, broken, or missing hooks may have resulted from encounters with adult salmon. Bycatch was very limited, consisting of three Copper Rockfish *Sebastes caurinus*, three Pacific Sanddabs *Citharichthys sordidus*, and five juvenile Pacific Sandfish *Trichodon trichodon*. Approximately 46% of total microtrolling effort was devoted to repeated sampling of predefined waypoints, 13% was invested in reconnaissance outside the main survey area, and 41% was used to maximize catch for the postrelease mortality assessment. The Chinook Salmon CPUE (percentage of hooks with Chinook Salmon) during these activities was 3.0, 1.6, and 4.6%, respectively. This equated to approximately 1.9 Chinook Salmon per hour of active gear deployment time during the pseudo-systematic sampling portion of the study and 3.2 Chinook Salmon/h for the period during which we were attempting to maximize catch. Overall Chinook Salmon CPUE was higher north of Sansum Narrows (4.4%) than at sites south of Sansum Narrows (1.9%; see Figure 1).

Fish Sampling

Mean FL was 155 mm (range = 116–236 mm; n = 168) for microtroll-caught Chinook Salmon and 194 mm (range = 131–311 mm; n = 13) for Coho Salmon. A single adult Coho Salmon with a FL of approximately 450 mm was not measured; a single Chum Salmon captured on September 17 had a FL of 168 mm. The lengths of Chinook Salmon captured by microtrolling increased over the study period and were broadly consistent with the lengths of fish caught by purse seining and rope trawling (Figure 3). No PIT-tagged Chinook Salmon were detected during the study. All Coho Salmon were wild (adipose fins were intact and no coded wire tags were detected), whereas 18 Chinook Salmon had a clipped adipose fin, and coded wire tags were detected in 12 of those 18 fish. A coded wire tag was also detected in a single, non-adipose-clipped Chinook Salmon. This equated to a total hatchery Chinook Salmon proportion of 11.3%. The hatchery proportion in August (12.3%; N = 73) was similar to that in September (10.9%; N = 91); only four wild Chinook Salmon were caught during October. Gastric lavage was successful for sampling stomach contents; however, a discussion of the diet is beyond the scope of the present study, so those data are not presented here.

Scales were collected from 148 Chinook Salmon for genetic stock identification, and DNA was successfully amplified for all but two of those samples. Based on individual stock assignments, the majority of juvenile Chinook Salmon that were captured (64%) were from the Cowichan River. Other stock groups with significant representation were the lower Fraser River (Chilliwack and Harrison rivers; 18%) and other rivers on the east coast of Vancouver Island (Nanaimo, Puntledge, and Big Qualicum rivers; 10%). The remaining 8% consisted of west coast Vancouver Island, upper Fraser River, Howe Sound, and Puget Sound stocks.

We successfully PIT-tagged and released 138 Chinook Salmon, 89 of which were identified by genetic stock identification as being most likely of Cowichan River origin. One individual, which was tagged on September 17, 2014, in Maple Bay at 166 mm, was recorded on a PIT tag antenna at the fish fence in the lower Cowichan River on October 7, 2015 (Kevin Pellett, British Columbia Conservation Foundation [BCCF], personal communication). This fish returned as an age-1 jack.

Postrelease Mortality Assessment

The average duration for which juvenile Chinook Salmon (n = 66) were held in the net-pen was 21.6 h (SD = 2.8). A

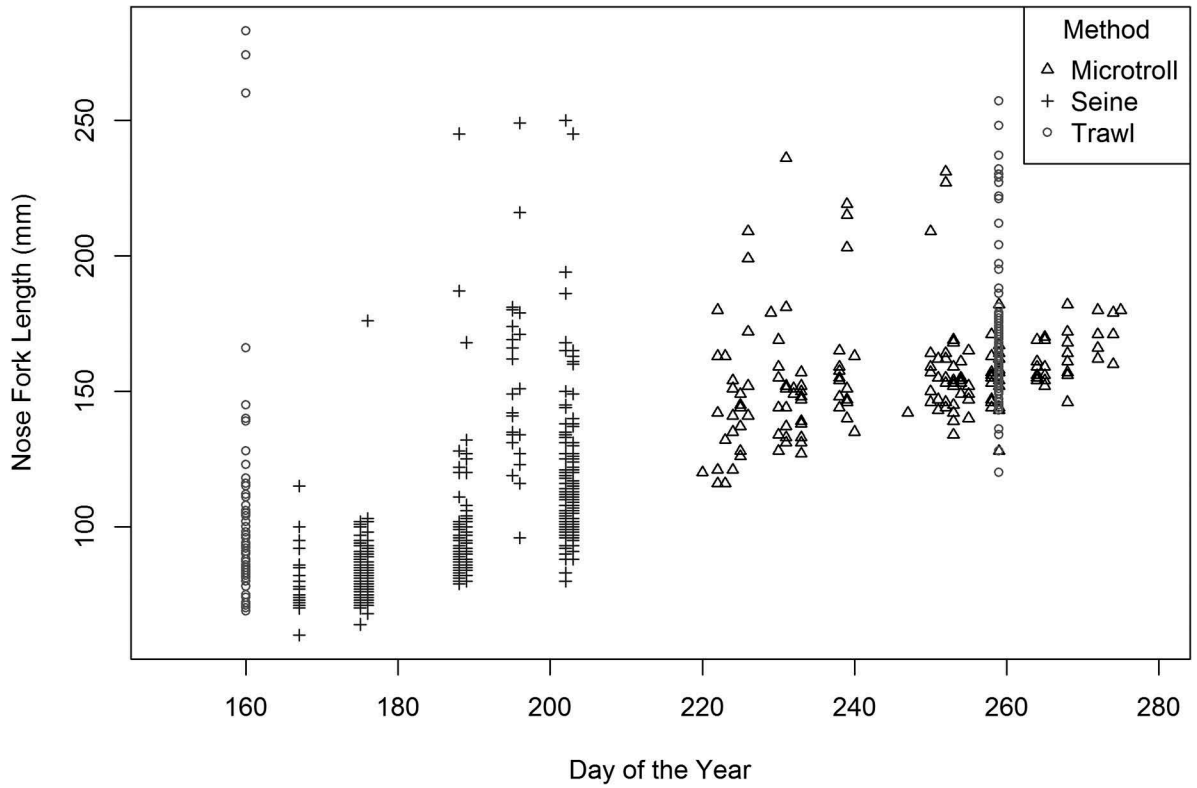

FIGURE 3. Nose-to-fork length (mm) for juvenile Chinook Salmon that were sampled by purse seining, rope trawling, or microtrolling in the Southern Gulf Islands region from June 10 to October 3, 2014, with sampling date presented as the day of the year.

single PIT-tagged fish that had been captured on a barbless hook died in the net-pen; one additional PIT-tagged fish lost its tag prior to release. All other fish were observed to be active and apparently in good condition at release.

Generalized Additive Modeling of CPUE

A GAMM including smooth terms relating the log odds of catching a juvenile Chinook Salmon to depth, hour of the day, and tidal stage and with fishing event included as a random effect explained 14% of the deviance in the data. Smooth terms for depth (estimated degrees of freedom [edf] = 4.19, χ^2 = 29.05, $P < 0.001$) and hour of the day (edf = 3.27, χ^2 = 13.54, P = 0.009) significantly reduced the deviance of the model. Tidal stage (edf = 2.70, χ^2 = 7.51, P = 0.082) marginally reduced the model deviance (Figure 4). Reported P-values are approximate and are based on χ^2 tests of whether each smooth term significantly reduced model deviance. The CPUE was lower through the morning and increased in the late afternoon; CPUE was highest during the first half of the flood tide and then declined to a minimum in the middle of the ebb tide. The additive effect of hook depth on the log odds of catching a Chinook Salmon was positive for depths between 6 and 19 m and was negative at shallower and deeper depths; the modeled peak CPUE occurred at 12 m. The decline in modeled CPUE with depth appeared to level off below 25 m (Figure 4).

We fished with both of the primary gear types on 17 d during the study period, with a total of 2,759 hook deployments (1,306 Apex and 1,453 fly). The percentage of hooks that caught Chinook Salmon was 4.0% (52 of 1,306) for Apex lures and 3.2% (46 of 1,453) for fly. A GAMM (see above) that was fitted to this subset of data and that included lure type as a parametric fixed effect did not detect a significant effect of lure type on CPUE (P = 0.267). During the final 8 d of the study period, we completed 177 fishing events (1,742 hook deployments) using flies with barbed hooks and barbless hooks on opposite sides of the vessel; 30 Chinook Salmon were captured on barbed hooks (3.4% of hooks), and 21 were captured on barbless hooks (2.4% of hooks). When barb status was incorporated as a parametric fixed effect in a GAMM for this subset of data, a significant effect of barb status was not detected (P = 0.216). In total, 3 (2.2%) of 138 juvenile Chinook Salmon that were landed on barbless hooks and 3 (10%) of 30 juveniles that were landed on barbed hooks had hooking injuries that precluded tagging (3.6% total); this difference was marginally nonsignificant (Fisher's exact test: df = 1, P = 0.07).

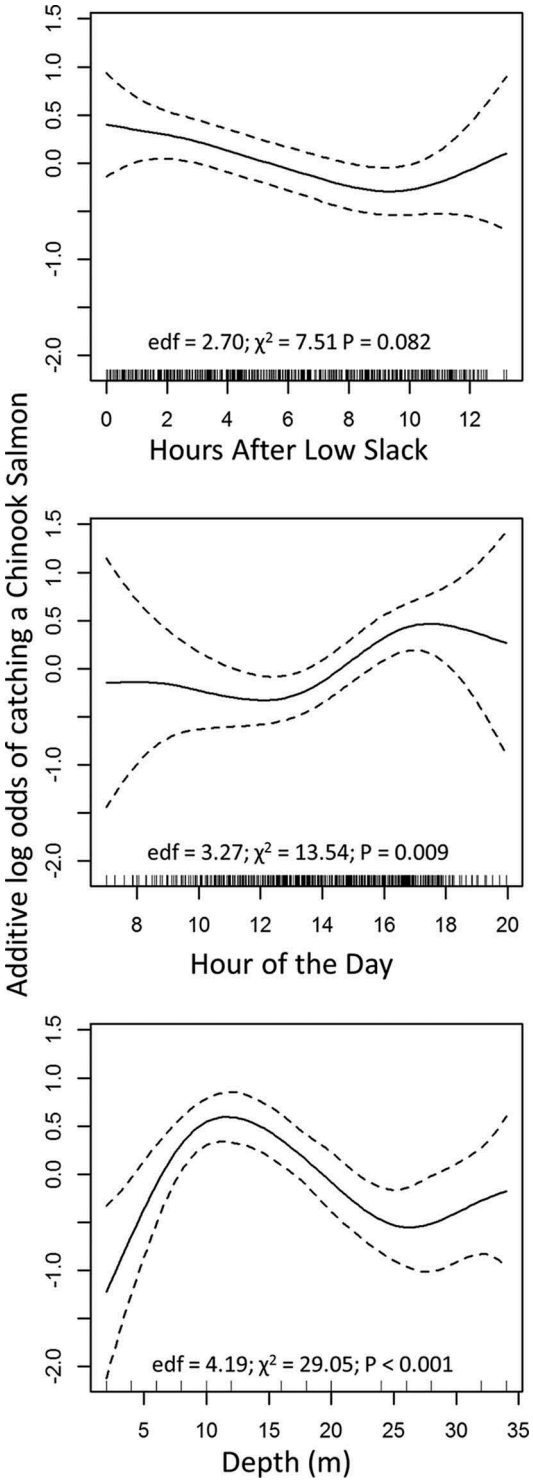

FIGURE 4. Additive log odds of catching a Chinook Salmon on an individual hook with respect to tidal stage, time of day, and depth, as predicted by a generalized additive mixed model fitted with the unbiased risk estimator criterion (default maximum df = 9) and with fishing event included as a random effect. Dashed lines indicate 2 SEs from the estimate; rug plots on the *x*-axis indicate the distribution of predictors. Estimated degrees of freedom (edf), chi-square statistics, and *P*-values for the reduction in model deviance for each smooth term are provided.

DISCUSSION

Contemporary fishery-independent methods for sampling juvenile salmon represent trade-offs in terms of cost, flexibility, CPUE, and the condition of the catch. Our results suggest that microtrolling has potential as an economical and flexible tool for nonlethally capturing, sampling, and tagging Chinook Salmon—and possibly Coho Salmon—during the latter part of their first summer at sea.

Microtrolling CPUE

Our overall catch rate (168 Chinook Salmon in 30 d, or just under 6 Chinook Salmon/d) was relatively low. Our initial trial of a spatial sampling design involved the daily occupation of a number of predefined stations over a relatively large area (>10 km linear travel between the most distant waypoints). This proved somewhat impractical due to the time required to repeatedly mobilize and demobilize the gear, run between stations, and locate the vessel on station, combined with the low CPUE of an individual fishing event. Once we switched our focus to the postrelease mortality component of the study, we fished continuously within a given area, redeploying gear immediately after retrieval, which was more efficient. However, we stopped fishing soon after capturing juvenile Chinook Salmon (within 1–2 fishing events) to transport the fish approximately 3 km to the net-pen site. Collectively, these activities led to a misleadingly low total catch. The number of Chinook Salmon landed per hour of active gear deployment was a better reflection of CPUE (1.9 Chinook Salmon/h during pseudo-systematic sampling; 3.2 Chinook Salmon/h during the period when we attempted to maximize our catch). Indeed, in 2015, BCCF personnel working in the same area as the present study achieved a CPUE of approximately 7 fish/h for ocean age-0 (<300 mm FL) Chinook Salmon in 19 d of microtrolling to capture fish for PIT tagging (K. Pellett, BCCF, personal communication). Their gear differed from that used in the present study, as they deployed slightly larger barbed hooks (Gamkatsu Siwash Number 10005, size 10, 7-mm point-to-shank gap) and 10–20-cm plastic or metal flashers (designed to attract salmon and impart an erratic action to the lure) on all leaders.

It is unclear whether the very low observed CPUE for juvenile Coho Salmon reflected a lack of vulnerability to microtrolling gear or a low abundance of this species in the study area. Holtby et al. (1992) sampled juvenile salmon from the incidental catch obtained by sport fishers in Saanich Inlet through the summer and fall of 1985; they reported data for 331 Coho Salmon and 133 Chinook Salmon—catches that were roughly in proportion to seine catches obtained as part of the same study (3,117 Coho Salmon and 1,199 Chinook Salmon). This suggests similar vulnerability of the two species to hook-and-line gear. Despite the fact that juvenile Pink Salmon *O. gorbuscha*, Chum Salmon, and Sockeye Salmon *O. nerka* are present (the latter in very low numbers) in the

Gulf Islands during late summer and fall (Healey 1978), we caught only a single Chum Salmon and no Pink Salmon or Sockeye Salmon. Juvenile Pink Salmon, Chum Salmon, and Sockeye Salmon do not prey on fish to the same extent as Chinook Salmon and Coho Salmon (Healey 1978; Brodeur et al. 2007), potentially making those juveniles less vulnerable to microtrolling. Unlike rope trawling, which facilitates studies of the entire community of juvenile Pacific salmon and other pelagic species, we suspect that the potential applications of microtrolling will be limited to studies of Chinook Salmon and possibly Coho Salmon.

The lack of a significant difference in CPUE between the two primary gear types used (Apex and fly) suggests that juvenile Chinook Salmon were equally vulnerable to these gears during the study period. Small sample size was likely responsible for our failure to detect a significant effect of barb status on both CPUE and the frequency of serious hooking injury (we only evaluated the use of barbs toward the end of the study period). However, it is encouraging that even with barbed hooks, the incidence of serious hooking injuries was not more than 10%.

One drawback of the present study was a failure to measure or control for lure speed through the water. Accurate assessment of gear speed is challenging due to wind and tide, which can result in speed over ground that is very different from the speed through water. Future microtrolling work would benefit from the deployment of a flow logger to accurately measure the flow of water past the vessel and, in turn, the speed at which the gear passes through the water.

Fish Size in Microtroll Samples Relative to Other Gear Types

Qualitative assessment of the FLs of juvenile Chinook Salmon that were captured by microtrolling, trawling, and purse seining did not indicate an obvious size bias. Nevertheless, the size distribution of purse-seine- and trawl-caught Chinook Salmon in Figure 3 does suggest that fish below the minimum size captured by microtrolling (116 mm FL) were present in the study area during August. The size distribution of microtroll-caught Chinook Salmon prior to September (day of the year 244; Figure 3) also appears to be somewhat curtailed at the lower end. It is intuitive that there is some lower size below which juvenile Chinook Salmon are not vulnerable to hook-and-line sampling. The minimum fork length at which juvenile Chinook Salmon can be effectively sampled by microtrolling is likely somewhere between 120 and 150 mm.

Postrelease Mortality Assessment

Our short-term postrelease mortality assessment suggested that capture by microtrolling—combined with handling, PIT tagging, and gastric lavage—resulted in very low (<5%) short-term mortality of juvenile Chinook Salmon. Our holding period (mean = 21.6 h) was short; however, Wertheimer et al. (1989) maintained 363 sublegal-sized (<65 cm FL) Chinook Salmon in net-pens for 4–6 d after capture on troll gear and found that 89% of the total observed mortality (19%) occurred either immediately or on the first day. Their results suggest that extending the holding period would not have substantially changed our short-term mortality estimate. Our results contrast with those of Wertheimer et al. (1989), who estimated hooking mortality rates of 22.1–26.4% for sublegal Chinook Salmon captured in the commercial troll fishery, and Gjernes et al. (1993), who estimated a mortality rate of 30% for first-ocean-year Chinook Salmon that were captured and released in recreational fisheries. We suspect that the low mortality we observed was largely a consequence of using very small hooks that rarely penetrated the eye, gill, or other critical areas. Previous studies have suggested that the majority of short-term mortality for hook-and-line-captured salmon results from hooking injuries rather than capture or handling stress (Wertheimer et al. 1989; Cox-Rogers et al. 1999). Given the low sample size and the low overall mortality rate (1 out of 66 fish), the potential influences of handling, tagging, and gastric lavage on mortality could not be separated from the influence of capture alone. However, we believe that the potential for tagging- and gastric-lavage-related mortality was low. Dare (2003) observed a mortality rate of less than 1% for 145,000 PIT-tagged Chinook Salmon in the 28 d after tagging. Gastric lavage is also a minimally invasive procedure; Meehan and Miller (1978) found no effect of gastric lavage on the subsequent survival of juvenile Coho Salmon.

Assessment of postrelease predation risk or delayed mortality resulting from stress or infection was outside the scope of the present study. These factors and their potential interactions in released Pacific salmon were recently reviewed by Raby et al. (2015), who pointed out the difficulty of assessing delayed mortalities in the marine environment, where both tagging and extended net-pen-based holding approaches represent confounding stressors. Other methods of capturing juvenile salmon alive for sampling and tagging (e.g., purse seining) can also result in stressors (e.g., crowding in the bunt, pursuit with a dip net, and exposure to warm surface water during sorting) that are of equal or longer duration than the stressors experienced by microtroll-caught fish. We did not observe evidence of predation on microtrolled fish; however, in areas where predators may be habituated to recreational fishing vessels, predation on hooked or recently released fish might pose a significant problem for microtrolling-based studies.

Microtrolling as a Tool to Investigate Juvenile Salmon Ecology at Fine Spatiotemporal Scales

The relatively low percentage of deviance in the data (14%) explained by our GAMM approach was unsurprising given the low overall probability of catching a Chinook Salmon on any given hook (3.5%) and given the large role that was presumably played by stochasticity. The purpose of this exercise was not to predict CPUE, but rather to demonstrate the potential utility of microtrolling for investigations of fine-scale

spatiotemporal patterns in juvenile salmon distribution and feeding activity. To this end, GAMM results were informative, describing significant patterns in Chinook Salmon CPUE by depth and time of day. The positive effect of depth on CPUE between 9 and 19 m was consistent with September 2008 trawl surveys in the Southern Gulf Islands, where juvenile Chinook Salmon catches decreased by a factor of 3–4 with each increasing depth stratum (0–14, 15–29, and 30–44 m; Beamish et al. 2010). However, our results provided greater resolution of the depth distribution by revealing that the CPUE decreased sharply at depths shallower than 9 m (Figure 4). The greater CPUE we observed in the afternoon relative to the morning could reflect a resumption of feeding after the fish digested prey that were consumed during a crepuscular dawn feeding period. Schabetsberger et al. (2003) found that the stomach fullness of juvenile Chinook Salmon in the Columbia River plume peaked in mid-morning; those authors also reported that at offshore stations, the highest proportion of undigested stomach contents was observed early in the morning prior to peak fullness. Similarly, stomach fullness of juvenile Chinook Salmon in Puget Sound was greatest in the late morning (Duffy et al. 2010). For juvenile Chinook Salmon in freshwater, Sagar and Glova (1988) found that dawn was the most important feeding period, as indicated by stomach fullness, whereas late afternoon was the period of greatest feeding activity, with numerous small prey items consumed. Almost all of our fishing effort occurred after 0900 hours (Figure 4) and may therefore have missed a dawn feeding period. The observed patterns in CPUE by depth and time reflect both a strength and a weakness of hook-and-line sampling—namely, that CPUE represents both distribution and feeding activity rather than one or the other. This has potential to result in different spatiotemporal patterns in CPUE and different stomach fullness or diet composition for fish caught by microtrolling versus those caught by net-based gears. Microtrolling conducted in conjunction with net-based sampling or hydroacoustic surveys has the potential to elucidate spatiotemporal patterns in distribution and feeding activity and to reveal more than would be possible with any one method in isolation. Although we detected only a marginally significant effect of tidal stage on Chinook Salmon CPUE, our spatially and temporally unbalanced sampling prevented us from identifying the manner in which tide may have interacted with location to influence catch.

Equipment and vessel costs for microtrolling are low; outfitting a small vessel with downriggers and terminal gear should cost less than CAN$2,000, operators do not require advanced marine certification, and fuel costs should be moderate (<$40/d in the present study). In contrast, daily charter costs for purse seiners run as high as several thousands of dollars, and daily costs for chartering vessels that are capable of rope trawling exceed $10,000. For situations in which large sample sizes are required, potential capture-size biases cannot be tolerated, or the entire pelagic fish community must be sampled, trawling and purse seining remain the most robust methods for sampling juvenile salmon at sea. However, the low cost and flexibility of microtrolling make this method ideal for studies that require high-frequency sampling of juvenile Chinook Salmon in space or time. Nonlethal capture is also a benefit for tagging studies and where encounters with stocks of conservation concern are likely. Stakeholders, including First Nations and nonprofit stewardship groups, have long been involved in Pacific salmon research in freshwater habitats. However, with some exceptions (e.g., Carr-Harris et al. 2015), the very high costs associated with vessel time have generally precluded these groups from taking the lead in studies of juvenile Pacific salmon as they disperse into the marine environment. Microtrolling provides an example of a low-cost methodology with potential to enfranchise smaller stakeholders in the research process, thereby benefiting both fisheries science and fisheries management.

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REFERENCES

Beacham, T. D., K. Jonsen, and C. Wallace. 2012. A comparison of stock and individual identification for Chinook Salmon in British Columbia provided by microsatellites and single nucleotide polymorphisms (SNPs). Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 4:1–22.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Beamish, R. J., D. McCaughran, J. R. King, R. M. Sweeting, and G. A. McFarlane. 2000. Estimating the abundance of juvenile Coho Salmon in the Strait of Georgia by means of surface trawls. North American Journal of Fisheries Management 20:369–375.

Beamish, R. J., I. A. Pearsall, and M. C. Healey. 2003. A history of the research on the early marine life of Pacific salmon off Canada's Pacific coast. North Pacific Anadromous Fish Commission Bulletin 3:1–40.

Beamish, R. J., B. E. Riddell, C. M. Neville, B. L. Thomson, and Z. Zhang. 1995. Declines in Chinook Salmon catches in the Strait of Georgia in relation to shifts in the marine environment. Fisheries Oceanography 4:243–256.

Beamish, R. J., R. M. Sweeting, K. L. Lange, and D. J. Noakes. 2010. Early marine survival of Coho Salmon in the Strait of Georgia declines to very low levels. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 2:424–439.

Berejikian, B. A., M. E. Moore, and S. J. Jefferies. 2016. Predator–prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry. Marine Ecology Progress Series 543:21–35.

Brodeur, R. D., E. A. Daly, M. V. Sturdevant, T. W. Miller, J. H. Moss, M. E. Theiss, M. Trudel, L. A. Weitkamp, J. Armstrong, and E. C. Norton. 2007. Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. Pages 183–203 *in* C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Brodeur, R. D., K. W. Myers, and J. H. Helle. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 3:89–132.

Carr-Harris, C., A. S. Gottesfeld, and J. W. Moore. 2015. Juvenile salmon usage of the Skeena River estuary. PLOS (Public Library of Science) ONE [online serial] 10(3):e0118988.

Chittenden, C. M., R. J. Beamish, C. M. Neville, R. M. Sweeting, and R. S. McKinley. 2009. The use of acoustic tags to determine the timing and location of juvenile Coho Salmon migration out of the Strait of Georgia, Canada. Transactions of the American Fisheries Society 138:1220–1225.

Cox-Rogers, S., T. Gjernes, and E. Fast. 1999. A review of hooking mortality rates for marine recreational Coho and Chinook salmon fisheries in British Columbia. Canadian Stock Assessment Secretariat Research Document 99–127.

Dare, M. R. 2003. Mortality and long-term retention of passive integrated transponder tags by spring Chinook Salmon. North American Journal of Fisheries Management 23:1015–1019.

Duffy, E. J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook Salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Sciences 68:232–240.

Duffy, E. J., D. A. Beauchamp, R. M. Sweeting, R. J. Beamish, and J. S. Brennan. 2010. Ontogenetic diet shifts in juvenile Chinook Salmon in nearshore and offshore habitats of Puget Sound. Transactions of the American Fisheries Society 139:803–823.

Furey, N. B., S. P. Vincent, S. G. Hinch, and D. W. Welch. 2015. Variation in migration routes influences early marine survival of juvenile salmon smolts. PLOS (Public Library of Science) ONE [online serial] 10(10): e0139269.

Gjernes, T., A. R. Kronlund, and T. J. Mulligan. 1993. Mortality of Chinook and Coho salmon in their first year of ocean life following catch and release by anglers. North American Journal of Fisheries Management 13:524–539.

Godwin, S. C., L. M. Dill, J. D. Reynolds, and M. Krkošek. 2015. Sea lice, Sockeye Salmon, foraging competition: lousy fish are lousy competitors. Canadian Journal of Fisheries and Aquatic Sciences 72:1113–1120.

Healey, M. C. 1978. The distribution, abundance, and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. Fisheries and Marine Service, Technical Report 788, Nanaimo, British Columbia.

Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook Salmon, *Oncorhynchus tshawytscha*. U.S. National Marine Fisheries Service Fishery Bulletin 77:653–668.

Hertz, E., M. Trudel, R. D. Brodeur, E. A. Daly, L. Eisner, E. V. Farley Jr., J. A. Harding, R. B. MacFarlane, S. Mazumder, J. H. Moss, J. M. Murphy, and A. Mazumder. 2015. Continental-scale variability in the feeding ecology of juvenile Chinook Salmon along the coastal Northeast Pacific Ocean. Marine Ecology Progress Series 537:247–263.

Holtby, L. B., R. K. Kadowaki, and K. S. Simpson. 1992. Factors affecting the vulnerability of juvenile Coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) in a saltwater sport fishery. Canadian Journal of Fisheries and Aquatic Sciences 49:2164–2178.

Karpenko, V. I. 2003. Review of Russian marine investigations of juvenile Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 3:69–88.

Karpenko, V. I., V. G. Erokhin, and V. P. Smorodin. 1998. Abundance and biology of Kamchatkan salmon during the initial year of ocean residence. North Pacific Anadromous Fish Commission Bulletin 1:352–366.

Kemp, I. M. 2014. Spatial–temporal patterns in distribution and feeding of juvenile salmon and herring in Puget Sound, WA. Master's thesis. University of Washington, Seattle.

Meehan, W. R., and R. A. Miller. 1978. Stomach flushing: effectiveness and influence on survival and conditions of juvenile salmonids. Journal of the Fisheries Research Board of Canada 35:1359–1363.

Melnychuk, M. C., V. Christensen, and C. J. Walters. 2013. Meso-scale movement and mortality patterns of juvenile Coho Salmon and steelhead trout migrating through a coastal fjord. Environmental Biology of Fishes 96:325–339.

Miller, J. A., D. J. Teel, A. Baptista, and C. A. Morgan. 2013. Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook Salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 70:617–629.

Miller, K. M., A. Teffer, S. Tucker, S. Li, A. D. Schulze, M. Trudel, F. Juanes, A. Tabata, K. H. Kaukinen, N. G. Ginther, T. J. Ming, S. J. Cooke, J. M. Hipfner, D. A. Patterson, and S. G. Hinch. 2014. Infectious disease, shifting climates, and opportunistic predators: cumulative factors potentially impacting wild salmon declines. Evolutionary Applications 7:812–855.

Neville, C. M., R. J. Beamish, and C. M. Chittenden. 2015. Poor survival of acoustically-tagged Chinook Salmon in the Strait of Georgia, British Columbia, Canada. Transactions of the American Fisheries Society 144:25–33.

Orsi, J. A. 1987. Small versus large trolling lures for sampling juvenile Chinook Salmon and Coho Salmon. Transactions of the American Fisheries Society 116:50–53.

Orsi, J. A., and H. W. Jaenicke. 1996. Marine distribution and origin of prerecruit Chinook Salmon *Oncorhynchus tshawytscha*, in southeastern Alaska. U.S. National Marine Fisheries Service Fishery Bulletin 94:482–497.

Orsi, J. A., and A. C. Wertheimer. 1995. Marine vertical distribution of juvenile Chinook and Coho salmon in southeastern Alaska. Transactions of the American Fisheries Society 124:159–169.

Parker, R. R. 1965. Estimation of sea mortality rates for the 1961 brood-year Pink Salmon of the Bella Coola area, British Columbia. Journal of the Fisheries Research Board of Canada 22:1523–1554.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: www.R-project.org. (December 2016).

Raby, G. D., M. R. Donaldson, S. G. Hinch, T. D. Clark, E. J. Eliason, K. M. Jefferies, K. V. Cook, A. Teffer, A. L. Bass, K. M. Miller, D. A. Patterson, A. P. Farrell, and S. J. Cooke. 2015. Fishing for effective conservation: context and biotic variation are keys to understanding the survival of Pacific salmon after catch-and-release. Integrative and Comparative Biology 55:554–576.

Rich, W. H. 1920. Early history and seaward migration of Chinook Salmon in the Columbia and Sacramento rivers. Bulletin of the U.S. Bureau of Fisheries 37:73.

Sagar, P. M., and G. J. Glova. 1988. Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile Chinook Salmon (*Oncorhynchus tshawytscha* Walbaum). Journal of Fish Biology 33:643–653.

Schabetsberger, R., C. A. Morgan, R. D. Brodeur, C. L. Potts, W. T. Peterson, and R. L. Emmett. 2003. Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and Coho (*O. kisutch*) salmon in the Columbia River plume. Fisheries Oceanography 12:523–540.

Wells, B. K., J. A. Santora, J. C. Field, R. B. MacFarlane, B. B. Marinovic, and W. J. Sydeman. 2012. Population dynamics of Chinook Salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. Marine Ecology Progress Series 457:125–137.

Wells, B. K., J. A. Santora, I. D. Schroeder, N. Mantua, W. J. Sydeman, D. D. Huff, and J. C. Field. 2016. Marine ecosystem perspectives on Chinook Salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Marine Ecology Progress Series 552:271–284.

Wertheimer, A., A. Celewycz, H. Jaenicke, D. Mortensen, and J. Orsi. 1989. Size-related hooking mortality of incidentally caught Chinook Salmon, *Oncorhynchus tshawytscha*. U.S. National Marine Fisheries Service Review 51(2):28–35.

Wertheimer, A. C., J. A. Orsi, E. A. Fergusson, and M. V. Sturdevant. 2013. Forecasting Pink Salmon harvest in Southeast Alaska from juvenile salmon abundance and associated biophysical parameters: 2012 returns and 2013 forecast. North Pacific Anadromous Fish Commission, Document 1486, Vancouver.

Wood, S. N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical Society Part B 70:495–518.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society Part B 73:3–36.

Zimmerman, M. S., J. R. Irvine, M. O'Neill, J. H. Anderson, C. M. Greene, J. Weinheimer, M. Trudel, and K. Rawson. 2015. Spatial and temporal patterns in smolt survival of wild and hatchery Coho Salmon in the Salish Sea. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 7:116–134.