NRC Research Press

ARTICLE

The effects of early sandbar formation on the abundance and ecology of coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*) in a central California coastal lagoon

Ann-Marie K. Osterback, Cynthia H. Kern, Emerson A. Kanawi, Jeffrey M. Perez, and Joseph D. Kiernan

Abstract: We investigated how extreme drought conditions influenced the abundance, growth, movement, and seawater readiness of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*) in a small central California coastal lagoon. In 2015, the seasonal sandbar at the mouth of Scott Creek formed over 2 months earlier than average, effectively trapping fish in the lagoon for 7 additional months (mid-May through December) before outmigration opportunities eventually resumed. Monthly mark–recapture sampling demonstrated that juvenile coho salmon and steelhead were able to persist in the lagoon during extended periods of high water temperature and low dissolved oxygen concentration. Both salmonid species exhibited similar temporal trends in abundance, growth, and Na^+-K^+-ATPase activity levels during lagoon residence; however, abundance and growth rates were consistently higher for steelhead. Stationary passive integrated transponder tag antenna detections revealed recurrent movement of individuals between the warm lagoon and cooler lower mainstem creek, suggesting individuals regulated key physiological processes by moving between the adjacent habitats. Our study provides new insight concerning the consequences of drought for imperiled salmonid populations and underscores the importance of life-history diversity during extreme climatic events.

Résumé : Nous avons étudié l'influence de conditions de sécheresse extrême sur l'abondance, la croissance, les déplacements et la préparation à l'entrée en mer de saumons cohos (*Oncorhynchus kisutch*) et de truites arc-en-ciel (*Oncorhynchus mykiss*) juvéniles dans une petite lagune côtière du centre de la Californie. En 2015, la barre de sable saisonnière à l'embouchure du ruisseau Scott s'est formée plus de 2 mois plus tôt qu'à l'habitude, piégeant ainsi les poissons dans la lagune pour 7 mois supplémentaires (de la mi-mai à la mi-décembre) avant que ne se représentent des occasions de migration vers l'extérieur. L'échantillonnage mensuel de poissons marqués démontre que les saumons cohos et truites arc-en-ciel juvéniles étaient capables de persister dans la lagune durant des périodes prolongées de haute température de l'eau et de faibles concentrations d'oxygène dissous. Les deux espèces de salmonidés présentaient des tendances temporelles semblables de l'abondance, de la croissance et de l'activité de la Na^+-K^+-ATPase durant la résidence dans la lagune, l'abondance et les taux de croissance étant toutefois uniformément plus élevés pour les truites arc-en-ciel. Les détections avec des antennes stationnaires d'étiquettes à transpondeur intégré passif révèlent des déplacements récurrents d'individus entre la lagune chaude et le bras principal du ruisseau plus frais, donnant à penser que les individus régulaient des processus physiologiques clés en se déplaçant entre les habitats attenants. L'étude fournit de nouveaux renseignements sur les conséquences de la sécheresse pour des populations de salmonidés en péril et souligne l'importance de la diversité des cycles biologiques durant des épisodes climatiques extrêmes. [Traduit par la Rédaction]

Introduction

The impacts of hydrological drought and reduced surface flows can be especially severe for diadromous fishes that require connectivity among freshwater, estuarine, and marine habitats at multiple life stages (Lake 2011; Woelfle-Erskine et al. 2017). In many coastal areas worldwide, drought conditions can extend the closure of seasonal sandbar-built estuaries (Rustomji 2007), thus affecting the migration of fish populations to and from the marine environment (Gillanders et al. 2011) and disrupting characteristic life-history patterns. In California (USA), many at-risk populations of anadromous Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (anadromous *Oncorhynchus mykiss*) must contend with seasonal sandbars at their river mouths (Kraus et al. 2002; Heady et al. 2014), which constrain migration opportunities for both outmigrating juveniles and returning adults (Shapovalov and Taft 1954). During very low water years, barrier sandbars can form during the typical spring juvenile (smolt) outmigration period and effectively trap substantial numbers of salmon in the estuary or in freshwater habitat where they must persist for many months until the onset of winter rain reconnects the creek to the ocean (Smith 1990; Hayes et al. 2008).

While oversummer use of small sandbar-built estuaries and seasonal lagoons has been well-documented for juvenile steel-

Received 15 October 2017. Accepted 12 February 2018.

A.-M.K. Osterback. University of California, Santa Cruz, affiliated with Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA; University of California, Santa Cruz, Institute of Marine Sciences, 1156 High Street, Santa Cruz, CA 95064, USA.

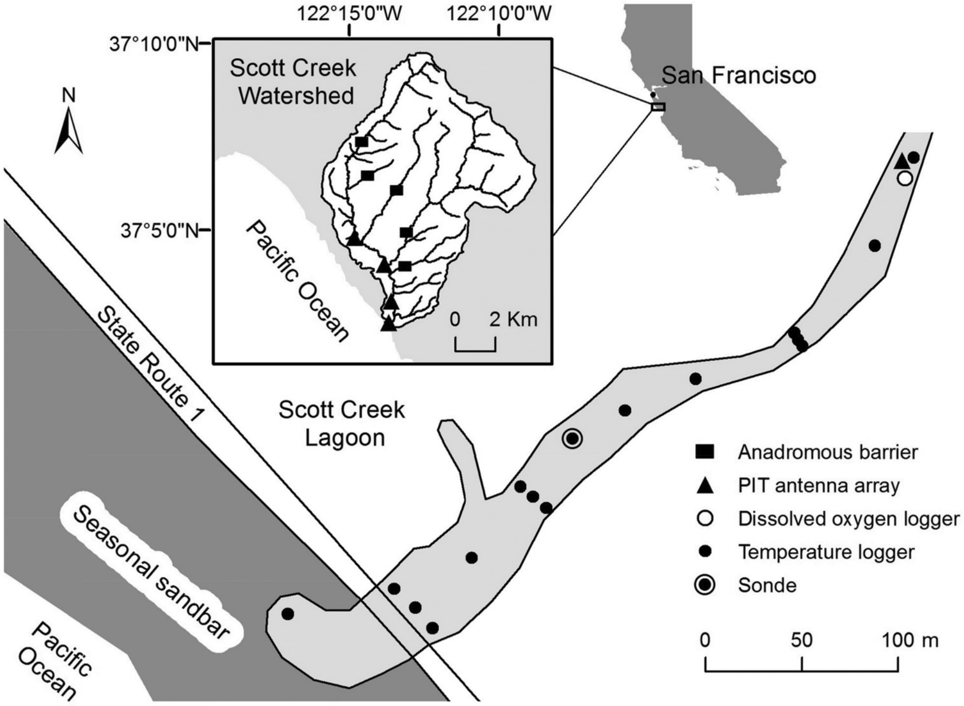
C.H. Kern, E.A. Kanawi, and J.M. Perez. University of California, Santa Cruz, affiliated with Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA.

J.D. Kiernan. Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA; University of California, Santa Cruz, Institute of Marine Sciences, 1156 High Street, Santa Cruz, CA 95064, USA.

Corresponding author: Joseph D. Kiernan (email: joseph.kiernan@noaa.gov).

Can. J. Fish. Aquat. Sci. **75**: 2184–2197 (2018) dx.doi.org/10.1139/cjfas-2017-0455

Fig. 1. Location map of the Scott Creek watershed and a detailed view of the lagoon study area (Santa Cruz County, California, USA).



head in California (e.g., Hayes et al. 2008; Bond et al. 2008; Osterback et al. 2014), it has rarely been reported for juvenile coho salmon (*Oncorhynchus kisutch*). The ability of steelhead to utilize seasonal lagoons is largely attributed to their remarkable early life-history diversity and plasticity (Thorpe 2007; Moore et al. 2014; Hall et al. 2016), which permit individuals to adjust their behavior and (or) physiology to adapt to variable environments. For example, steelhead in seasonal lagoons have been shown to regulate enzyme activity levels (e.g., gill Na^+-K^+-ATPase; hereinafter NKA) in response to changing environmental conditions (Hayes et al. 2011), modify movement and migration patterns to manage fitness trade-offs between favorable foraging opportunities and physiologically stressful abiotic conditions (Hayes et al. 2008, 2011) and alter age at outmigration based on individual growth (Satterthwaite et al. 2012). Furthermore, it has been demonstrated that lagoon-rearing steelhead often exhibit increased growth rates and subsequent marine survival relative to conspecifics that rear higher in the drainage network (Hayes et al. 2008; Bond et al. 2008).

In contrast with steelhead, juvenile coho salmon in California typically exhibit less life-history variability, with rearing occurring principally in upstream riverine habitats and nearly all individuals emigrating to sea as yearling (age-1+) smolts (Shapovalov and Taft 1954; Moyle 2002). While age-1+ coho salmon are known to utilize estuaries as temporary (stopover) habitats during seaward migration in the spring (Sandercock 1991; Moore et al. 2016), reports of subyearling (age-0+) and (or) age-1+ individuals rearing in small estuaries and seasonal lagoons are scarce, particularly during the summer and fall. During annual sampling of the Scott Creek lagoon conducted between 2002 and 2014 (e.g., Bond et al. 2008; Hayes et al. 2008; Frechette et al. 2016), juvenile coho salmon were infrequently observed as part of the resident fish assemblage after sandbar formation. Hayes et al. (2008) hypothesized that the absence of juvenile coho salmon from the Scott Creek lagoon, despite their presence in the upper watershed, was due to unsuitable water quality during the summer months. Given the paucity of information concerning oversummer use of seasonal lagoons by coho salmon in California and elsewhere, the ability of these habitats to support juvenile growth and production remains poorly understood.

Here we report on the abundance, behavior, and performance of juvenile coho salmon and steelhead in a small central California coastal lagoon during an extreme climatic event. Our study took place during the final year of a multiyear drought (2012–2015), when early sandbar formation precluded the outmigration of many ocean-ready coho salmon and steelhead. This occurrence provided a unique opportunity to investigate oversummer lagoon use by juvenile coho salmon, in particular, and assess whether environmental conditions in the lagoon remained suitable for salmonids throughout the period of sandbar closure. Our primary objectives were to (*i*) characterize spatial and temporal patterns of water quality during the period of lagoon formation; (*ii*) quantify the abundance and growth of lagoon-rearing juvenile coho salmon and steelhead across all months of the dry season; (*iii*) determine whether juvenile salmonids reared in the lagoon exclusively or moved between the lagoon and upstream riverine habitats; and (*iv*) assess temporal patterns in seawater readiness during extended lagoon residency.

Materials and methods

Study system

Scott Creek is a small (drainage area 78 km^2) central California coast watershed located approximately 90 km south of San Francisco in Santa Cruz County, California, USA (37°02′26″N, 122°13′44″W; Fig. 1). The catchment is predominantly a mixed-conifer forest composed of coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*). Red alder (*Alnus rubra*), tanoak (*Notholithocarpus densiflorus*), bay laurel (*Umbellularia californica*), and bigleaf maple (*Acer macrophyllum*) become increasingly abundant in the lower basin. Dominant land uses include small-scale timber harvest and agriculture, and housing density is very low. The climate is cool Mediterranean, and localized climatic conditions in the watershed vary with many factors, including distance from the coast, elevation, and aspect. Mediterranean climate regions are characterized by a distinct wet season between November and April, followed by a lengthy dry season with little to no precipitation. While the onset of rain is seasonally predictable, the amount is highly variable among years and routinely results in episodic disturbance events that range from extreme floods to prolonged drought (Grantham et al. 2010; Kiernan and Moyle 2012). Peak discharge in mainstem Scott Creek can exceed 65 $m^3 \cdot s^{-1}$ during storm events and summer base flow declines to <0.1 $m^3 \cdot s^{-1}$ in a typical water year. Mean air temperatures during the winter and summer are approximately 10 and 17 °C, respectively, with the latter influenced by the onshore movement of marine fog most mornings and evenings. Mean monthly stream temperatures typically range from 9.0 to 17.0 °C (January and August, respectively), and instantaneous temperature values rarely vary by more than 1.5 °C between upstream and downstream locations (Sogard et al. 2012). Conversely, the small exposed estuary at the terminus of the watershed is prone to summer heating following sandbar formation, and water temperatures can exceed 24 °C (Hayes et al. 2008).

The Scott Creek watershed supports sympatric populations of coho salmon (Central California Coast evolutionarily significant unit) and steelhead trout (Central California Coast distinct population segment), which are listed as endangered and threatened species, respectively, under the US Endangered Species Act (NMFS 2005, 2006). The Scott Creek coho salmon population is of special management concern because it represents the southernmost extant population of this species in North America and the only persistent population south of San Francisco Bay (NMFS 2012). A small conservation fish hatchery is operated in the Scott Creek basin to aid regional coho salmon recovery efforts and periodically supplement steelhead populations. Prior to our study, 14 674 hatchery-origin coho salmon smolts (age-1+) were released within the Scott Creek watershed across four dates during the spring of 2015: 19 March (n = 3490); 3 April (n = 3567); 9 April (n = 4526); and 13 April (n = 3091). All hatchery-origin coho salmon were coded wire-tagged, and 85% (n = 12 441) were also issued a passive integrated transponder (PIT) tag prior to release. No hatchery-origin steelhead were outplanted to the Scott Creek basin during the spring of 2015. Natural instream production of smolts (and presmolts) during the same period was estimated to be 4722 steelhead and 264 coho salmon (Kiernan et al. 2016).

Scott Creek is representative of many coastal California watersheds in that its small estuary transitions to a freshwater lagoon each year during the dry season. This change occurs when reduced stream flows coincide with increased sediment deposition from coastal wave action, and a sandbar (barrier beach) forms across the creek mouth, blocking connectivity between the creek and the Pacific Ocean (Fig. 1). Continued inflows from the watershed are subsequently impounded behind the sandbar and create the freshwater lagoon. The Scott Creek lagoon typically forms in midsummer (average date of sandbar formation from 2002 to 2014 = 27 July) and persists until late fall or early winter when storms produce sufficient streamflow to erode the sandbar and reconnect the creek to the ocean (average date of sandbar opening from 2002 to 2014 = 29 November). Connectivity between the creek and ocean from late November through July is necessary for anadromous coho salmon and steelhead to complete their life cycles, as this time period encompasses both immigration of adults and outmigration of smolts (Fig. 2). Extreme drought conditions throughout California between 2012 and 2015 (Griffin and Anchukaitis 2014) progressively reduced the duration of connectivity between Scott Creek and the Pacific Ocean and restricted migration opportunities for both returning adults and outmigrating juveniles (Fig. 2). In 2015, the sandbar at the mouth of Scott Creek formed over 2 months earlier than average (i.e., on 16 May 2015), thus requiring smolts that had not yet emigrated to rear for at least an additional 7 months in fresh water before migration opportunities resumed the following winter (i.e., on 21 December 2015).

Spatiotemporal patterns of abiotic conditions

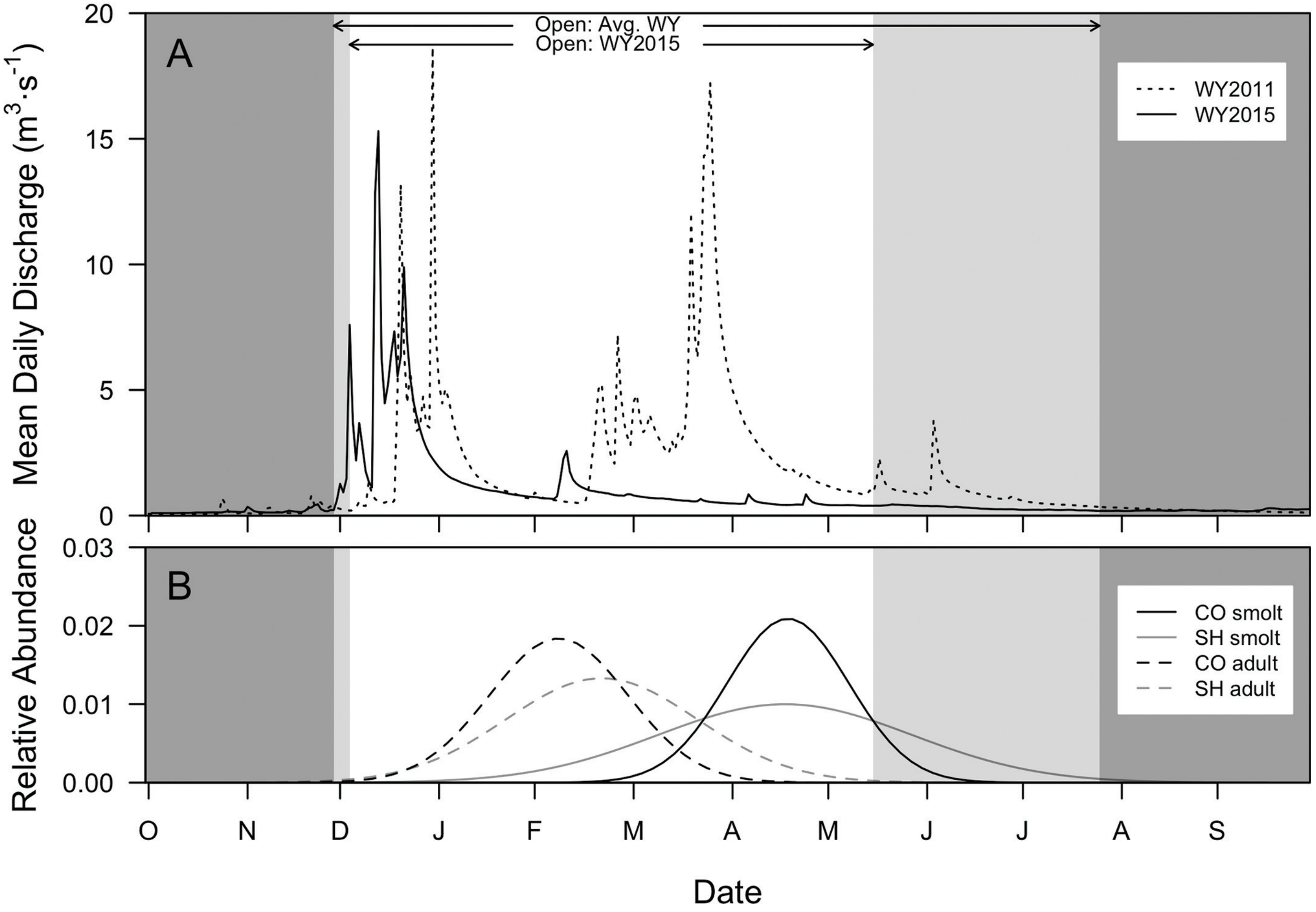
We defined the Scott Creek lagoon as the area of inundation extending from the sandbar (river kilometre (rkm) 0) upstream to where adjacent wetland vegetation transitioned from emergent marsh to riparian species, predominantly willow (*Salix* spp.; approximately rkm 0.6). The size of the lagoon varied during the study period; however, habitat mapping conducted in June 2015 at a representative size indicated a lagoon surface area of approximately 8240 m^2, a mean depth of 1.01 m, and a maximum depth of 1.62 m. To characterize abiotic conditions in the lagoon, we collected water quality data from 1 June to 21 December 2015. Temporal trends in temperature (°C), dissolved oxygen ($mg \cdot L^{-1}$), and salinity (ppt) were quantified every 15 min using a MANTA2 multiprobe sonde (EUREKA Environmental Engineering, Austin, Texas, USA) located at rkm 0.4. The sonde was fixed in the water column at a height of 0.3 m above the bottom of the lagoon. Water depth at the sonde averaged 0.88 m (±1 standard deviation (SD) = 0.45 m) during the study period. We monitored vertical temperature stratification at the sonde location with a continuous temperature data logger (HOBO Pendant; Onset Computer Corp., Bourne, Massachusetts, USA) tethered to a surface buoy and maintained at a depth of 0.3 m below the water surface. Spatial variability in lagoon water temperature was assessed via a network of vertically paired continuous temperature data loggers positioned at 15 different sites throughout the lagoon (Fig. 1). At each site, an anchor and buoy system was used to maintain a temperature logger 0.3 m above the bottom of the lagoon (near-bottom) and a top logger suspended 0.3 m below the water surface (near-surface). During periods when the lagoon was shallow (mid-August through October), a YSI 556 handheld multiprobe system (Yellow Springs Instruments Inc., Yellow Springs, Ohio, USA) was periodically used to generate vertical temperature profiles (10 cm intervals) and assess thermal stratification. We also deployed a second dissolved oxygen sensor (HOBO U26 data logger; Onset Computer Corp.) 0.3 m from the bottom of the lagoon at the upstream extent of the study area (rkm 0.6) to assess longitudinal variability in dissolved oxygen concentration.

Principal component analysis (PCA) was used to assess spatiotemporal patterns in water temperature across the entire lagoon study area. PCA, frequently termed empirical orthogonal function analysis when applied to time series data, helps identify dominant modes of variation in time series data generated at multiple locations (Preisendorfer 1988; Hannachi et al. 2007). Our input matrix consisted of mean daily water temperature values (MDT; rows) measured at the sonde location and at each of the 15 buoy sites (columns). Two separate PCAs were performed, each using the covariation matrix, to assess near-bottom and near-surface MDT values. Of the 30 buoy temperature loggers deployed, 15 loggers (n = 8 near-bottom, n = 7 near-surface) were missing between 3% and 35% of the MDT values due to hardware malfunction. To include all temperature sites in each PCA, we used the EM algorithm (Beale and Little 1975; Dempster et al. 1977) to interpolate missing MDT values based on their conditional expectations. Lastly, the relationship between mean daily dissolved oxygen (MDDO) concentrations measured at the sonde location and corresponding measurements generated at the upstream extent of our study area was tested using pairwise correlation analysis (Pearson's product-moment; $\alpha = 0.05$).

Salmonid abundance and growth

To estimate the abundance and growth of juvenile coho salmon and steelhead in the Scott Creek lagoon, we conducted monthly mark–recapture sampling between June and December 2015. Sampling occurred on 2 consecutive days each month (Day 1 = mark event, Day 2 = recapture event), resulting in 14 sampling occasions over the 7-month study period. Fish were sampled using a nylon beach seine (35 m long × 2.0 m deep (8.0 mm mesh), with a 2.0 m^2 bag (4.0 mm mesh)) that was pulled by hand perpendicular to the

Fig. 2. Hydrology, sandbar dynamics, and historical migration timing of salmonids in Scott Creek, California (USA). Panel A contrasts the annual hydrograph of a wet water year (WY2011) with the drought conditions that occurred during the year of our study (WY2015). Panel B shows the historical distribution of migration timing for coho salmon (CO) and steelhead (SH) smolts and adults, averaged from 2002 to 2014. In both panels, the unshaded and light gray shaded regions together identify the period the creek mouth is typically open (241 days; 29 November – 27 July based on WY2002–WY2014), whereas dark gray shading denotes the period the sandbar is typically present and the lagoon is closed. The unshaded region, exclusively, represents the truncated period the creek mouth was open in WY2015 (165 days; 3 December – 16 May) immediately preceding this study.



stream channel and circled-closed in shallow water. Multiple seine hauls were conducted during each sampling occasion (range = 7–10 hauls; effort dictated by lagoon volume) to sample all major habitat regions between the sandbar and the upstream extent of the study area. All captured salmonids were identified (species and origin (natural or hatchery)) and individuals ≥ 65 mm fork length (FL) were scanned for the presence of a PIT tag. Some individuals were tagged prior to our study, either at the hatchery or during life cycle monitoring activities (e.g., electrofishing surveys and downstream migrant trapping) conducted elsewhere in basin. Untagged individuals were anesthetized with tricaine methanesulphonate (MS-222; Western Chemical Inc., Ferndale, Washington, USA), measured for FL (±1.0 mm) and mass (±0.1 g), and PIT-tagged (12 mm HDX tag; Oregon RFID Inc., Portland, Oregon, USA). Captured salmonids too small to receive a PIT tag (<65 mm FL) were enumerated on each sampling occasion, but otherwise excluded from all analyses in this study. All handled fish were released back into the lagoon. PIT-tagged individuals captured on consecutive sampling months were used to calculate specific growth rates (SGR; %·day^{-1}) using the formula SGR = $[(\ln M_2 - \ln M_1)/t] \times 100$, where M_2 is the final mass (g), M_1 is the initial mass (g), and t is the growth interval (days).

We used PIT tag capture histories to estimate $N_{g,t}$, the abundance N for a given group g at time t (i.e., sampling occasion), using the POPAN formulation of the Cormack–Jolly–Seber model within Program MARK (White and Burnham 1999). The subscript g indicates species-specific abundance estimates (CO = coho salmon and SH = steelhead), and the subscript t indicates occasion-specific abundance estimates, specified by the first three letters of the month and the sampling occasion within that month (e.g., AUG2 = the second sampling occasion in August). The parameters included in POPAN to estimate abundance were (*i*) probability of survival (ϕ); (*ii*) probability of capture (p); (*iii*) super-population size (N^*); and (*iv*) the probability of entry (b) (Schwarz and Arnason 1996; Williams et al. 2002; Amstrup et al. 2006). Our modeling approach followed that of Frechette et al. (2016) with two exceptions. First, species was used as the grouping variable in the model, such that parameters could be estimated separately for steelhead and coho salmon. Second, the relatively small sample size of captured coho salmon required that both origins (i.e., hatchery and natural) be combined and precluded the use of a fully time- and group-dependent model to estimate survival and capture probability for both salmonid species. Therefore, we developed eight candidate POPAN models that limited the number of parameters yet allowed for species-specific estimates.

The suite of eight candidate models allowed for the probability of survival to either remain constant ($\phi_{(.)}$) or vary with time ($\phi_{(t)}$) when estimated for both species combined (i.e., one group) or remain constant ($\phi_{(g)}$) or vary with time with a constant offset between species ($\phi_{(g+t)}$; i.e., two groups). The probability of capture was estimated for both species combined and was allowed to vary with time ($p_{(t)}$), as probability of capture can vary significantly between sampling occasions (Frechette et al. 2016), and thus variation was more likely driven by differences among occasions than between species. The probability of entry was always allowed to vary with time and was either estimated for both species combined ($b_{(t)}$) or separately for each species with a constant offset between species ($b_{(g+t)}$). The super-population size was always estimated separately for each species ($N^*_{(g)}$). We used a model selection approach to identify the model that best fit the data by receiving the lowest Akaike information criterion score, corrected for small sample sizes (AIC$_c$; Burnham and Anderson 2002). We applied a χ^2 goodness-of-fit test using Program RELEASE within Program MARK to assess model fit. If lack of fit was detected, we applied a variance inflation factor ($\hat{c}$) to the model set and used quasi-Akaike information criterion (QAIC$_c$) for model comparisons (Lebreton et al. 1992).

Directional movement of PIT-tagged individuals

We operated a paired instream PIT tag antenna array (Multi-Antenna HDX Reader; Oregon RFID Inc.) at the upstream extent of the study area (rkm 0.6; hereinafter called the Lagoon antenna) to examine the movement of PIT-tagged individuals in and out of the Scott Creek lagoon. The array consisted of two (i.e., upstream and downstream) swim-through antennas that were separated by ~3.0 m, oriented perpendicular to stream flow, and spanned the entire wetted width of the channel (12.1 m). We concurrently operated four analogous paired PIT tag antenna arrays upstream of the lagoon study area (rkms 1.7, 1.8, 3.7, and 6.4; Fig. 1) to identify individuals initially encountered in the lagoon during one or more sampling occasions that subsequently emigrated to riverine habitat elsewhere in the Scott Creek basin. All paired antenna arrays were synchronized to permit inference of movement directionality based on the temporal sequence of upstream versus downstream detections.

Assessing directional movement at the Lagoon antenna was challenging due to its physical location near the head of the estuary where water velocity is slow to negligible. Lentic conditions can promote milling behavior and haphazard movement by juvenile salmonids and result in a large number of PIT tag detections that hinder interpretation of movement patterns. To protect against producing inflated estimates of directional movement at this location, PIT tag detection data were screened to identify movement patterns indicative of milling behavior and residency, rather than true migration in or out of the lagoon. We categorized a movement event as directional (upstream or downstream) when it was derived from serial PIT tag detections at both the upper (U) and lower (L) antennas of a paired antenna array (i.e., U-L or L-U) and occurred within an arbitrary 30 min time interval (to traverse a longitudinal distance of ~3 m). Conversely, PIT tag detections that (*i*) occurred on only one antenna of a paired antenna array (i.e., U or L only); (*ii*) were not directional (e.g., circular U-L-U type events); or (*iii*) were directional (i.e., U-L or L-U) but exceeded 30 min to complete passage were all categorized as ambiguous movement events (unknown directionality). As a final constraint, multiple serial detections attributed to the same individual at a given antenna array and not separated by ≥3 h were pooled into a single movement event for analysis. Note that due to variable detection efficiencies at each instream PIT tag antenna array, estimates of fish movement were conservative.

Temporal patterns in seawater readiness (gill NKA activity)

To examine changes in seawater readiness during lagoon residence, we collected nonlethal gill clips from a subset of age-1+ coho salmon and steelhead captured during the first sampling occasion of each month to characterize NKA activity levels. Increased gill NKA activity by salmonids is a necessary physiological adaptation for saltwater survival and is considered a reliable indicator of smoltification (i.e., seawater readiness; Folmar and Dickhoff 1980; Ewing et al. 1984). In the field, gill samples (five to six gill filaments) were taken from the first gill arch below the septum, placed in 100 μL of ice-cold SEI buffer (250 mmol·L^{-1} sucrose, 10 mmol·L^{-1} Na$_2$EDTA, and 50 mmol·L^{-1} imidazole), flash frozen using liquid nitrogen, and transported to the laboratory for storage at −80 °C. In the laboratory, gill NKA activity was quantified using an adaptation of McCormick (1993). Buffered gill samples were thawed, homogenized, and centrifuged, and the supernatant from each sample was pipetted into six wells of a 96-well microplate. Assay mixture (50 mmol·L^{-1} imidazole, 2.9 mmol·L^{-1} phosphoenolpyruvate, 0.26 mmol·L^{-1} NADH, 0.73 mmol·L^{-1} ATP, 4.6 U·mL^{-1} lactic dehydrogenase, and 5.1 U·mL^{-1} pyruvate kinase) containing a salt solution (50 mmol·L^{-1} imidazole, 189 mmol·L^{-1} NaCl, 10.5 mmol·L^{-1} MgCl$_2$, and 42 mmol·L^{-1} KCl) was added to all six replicates, and three of the replicates also received NKA inhibitor (ouabain; 0.7 mmol·L^{-1}). Assays were carried out at 25 °C in an Ultramark Microplate Imaging System (Bio-Rad Laboratories, Hercules, California, USA), and enzymatic activity measurements occurred within 30 min of tissue homogenization. Protein concentration was determined using the bicinchoninic acid method (BCA Protein Assay Kit; Pierce, Rockford, Illinois, USA). NKA activity was expressed in units of micromoles ADP per milligram protein per hour (μmol ADP·mg protein^{-1}·h^{-1}).

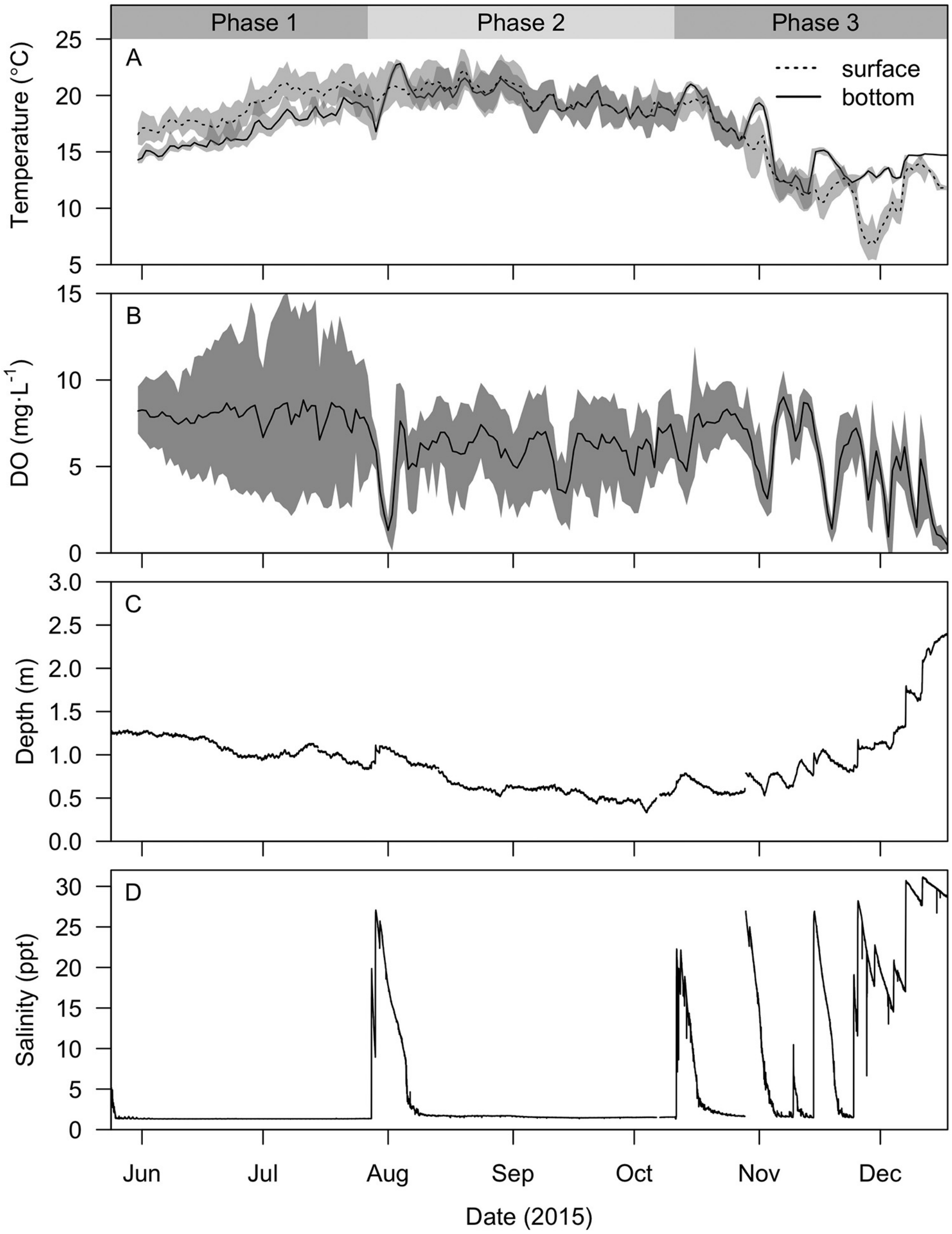
Results

Spatiotemporal patterns of abiotic conditions

Spatial patterns of temperature and dissolved oxygen within the lagoon were well represented by conditions quantified at the primary sonde location (rkm 0.4). The first PCA axis explained 96% (near-surface) and 89% (near-bottom) of the variation in MDT, providing strong evidence that temperature patterns were relatively homogeneous across all sites. Similarly, pairwise correlations between MDDO collected at the sonde location and at the upstream extent of the study area (rkm 0.6) were significantly correlated (r = 0.83, $p < 0.01$).

Three distinct environmental phases were identified (nonquantitatively) based on salient changes in abiotic conditions during the 7-month study period (Fig. 3). The first phase immediately followed sandbar formation on 16 May and was characterized by progressively increasing lagoon water temperature and minor thermal stratification. MDT (±1 SD) near the bottom of the lagoon was 16.9 ± 1.6 °C and consistently ~2.0 °C cooler than near-surface temperatures (18.9 ± 1.5 °C; Fig. 3A). MDDO (±1 SD) was high (8.0 ± 0.5 mg·L^{-1}) with broad diel variability (maximum 1-day range = 2.5 to 15.1 mg·L^{-1} on 7 July; Fig. 3B), water depth generally exceeded 1.0 m (mean ± SD = 1.0 ± 0.1 m; Fig. 3C), and the lagoon remained fresh (mean ± SD salinity = 0.2 ± 0.01 ppt; Fig. 3D). The second environmental phase began 72 days after sandbar formation (27 July) and was characterized by lower dissolved oxygen concentrations (mean ± SD = 5.9 ± 1.2 mg·L^{-1}; Fig. 3B) and warmer water temperature with no evidence of thermal stratification (mean ± SD near-bottom = 19.7 ± 1.2 °C, mean ± SD near-surface = 19.9 ± 1.0 °C; Fig. 3A). Environmental conditions during Phase 2 were driven by large episodic coastal wave (i.e., swell) events that delivered seawater into the lagoon and temporarily increased both salinity and depth (Figs. 3C and 3D). As salt water settled to the bottom of the lagoon, dissolved oxygen concentration in the lower water column declined abruptly (instantaneous minimum on 2 August = 0.1 mg·L^{-1}; Fig. 3B) and water temperature in-

Fig. 3. Abiotic conditions in the Scott Creek lagoon during three different environmental phases (bars atop panel A). All parameters were measured near the midpoint of the study area (~rkm 0.4) at a depth of 0.3 m from the bottom of the lagoon, except for the surface temperature in panel A (dotted line), which was measured 0.3 m below the lagoon surface. Temperature and dissolved oxygen (DO) are depicted as lines and reflect mean daily temperature (MDT) and mean daily dissolved oxygen concentration (MDDO); shading around means reflects daily maximum and minimum values (A and B). Lagoon depth (C) and salinity (D) are from data recorded at 15 min intervals. Short breaks in the time series occurred during equipment maintenance.



creased, thus eliminating thermal stratification. Following inputs of salt water, the lagoon returned to a freshwater state (mean ± SD salinity = 2.4 ± 5.6 ppt; Fig. 3D) and began to shallow (mean ± SD depth = 0.6 ± 0.2 m; Fig. 3C), whereupon wind-induced mixing kept the water column unstratified. The third environmental phase coincided with the onset of fall storms (148 days after sandbar formation; 11 October), where high surf and swell resulted in frequent wash-over of seawater into the lagoon and episodically increased salinity concentrations (mean ± SD salinity = 13.7 ± 11.8 ppt; Fig. 3D). Seawater inputs coupled with the onset of fall precipitation during this period progressively filled the lagoon and increased depth (mean ± SD = 1.1 ± 0.6 m; Fig. 3C). Additionally, the combination of shorter days, cooler weather, and increased lagoon depth contributed to decreased water temperatures. The persistence of a saline layer at the bottom of the lagoon during Phase 3 kept near-bottom temperatures (mean ± SD = 15.3 ± 2.6 °C) higher than near-surface temperatures (mean ± SD = 13.4 ± 3.5 °C; Fig. 3A), and bottom dissolved oxygen concentrations low (mean ± SD = 5.3 ± 2.5 mg·L^{-1}; Fig. 3B).

Salmonid abundance and growth

While age-0+ coho salmon were present in the Scott Creek lagoon following sandbar formation in June and July (Phase 1), they were largely absent from the lagoon fish assemblage thereafter (Fig. A1). Conversely, age-l+ coho salmon and multiple age classes of steelhead were present in the lagoon during all months of the

Table 1. Comparison of eight candidate POPAN models used to estimate the probability of survival (ϕ), probability of capture (p), probability of entry (b), super-population size ($N^* \pm 1$ standard error (SE)), and the ratio of steelhead N^* to coho salmon N^* (SH:CO) for juvenile steelhead and coho salmon in the Scott Creek lagoon in 2015, corrected for overdispersion ($\hat{c} = 1.273$).

Model[a]	QAIC$_c$	ΔQAIC$_c$	Model weight	Steelhead (N^* ± SE)	Coho salmon (N^* ± SE)	SH:CO
$\phi_{(g)}p_{(t)}b_{(t)}N^*_{(g)}$	3782.58	0.00	0.94	764.4±20.2	274.5±18.2	2.8
$\phi_{(g+t)}p_{(t)}b_{(t)}N^*_{(g)}$	3789.06	6.48	0.04	761.1±25.4	301.5±24.4	2.5
$\phi_{(t)}p_{(t)}b_{(g+t)}N^*_{(g)}$	3789.72	7.14	0.03	818.6±29.9	213.4±10.4	3.8
$\phi_{(.)}p_{(t)}b_{(g+t)}N^*_{(g)}$	3807.40	24.82	0.00	829.6±24.7	201.5 ± 8.5	4.1
$\phi_{(g+t)}p_{(t)}b_{(g+t)}N^*_{(g)}$	3811.52	28.94	0.00	813.5±27.5	244.1±21.2	3.3
$\phi_{(t)}p_{(t)}b_{(t)}N^*_{(g)}$	3862.19	79.61	0.00	819.1±28.4	218.5±10.8	3.7
$\phi_{(.)}p_{(t)}b_{(t)}N^*_{(g)}$	3879.60	97.02	0.00	816.7±23.7	217.9 ± 9.9	3.7
$\phi_{(g)}p_{(t)}b_{(g+t)}N^*_{(g)}$	4421.48	638.90	0.00	889.0±36.1	241.6±15.6	3.7

[a] Key to model subscripts: (g) = parameter was estimated separately for each species and held constant over time; (t) = parameter was combined for both species and allowed to vary with time; (g+t) = parameter was estimated separately for each species with a constant offset between species and shared variation over time; and (.) = only one parameter was estimated, combined for both species and held constant over time.

study (Fig. A1). We captured a total of 159 PIT-tagged coho salmon (85 hatchery-origin age-1+, 19 natural-origin age-1+, and 55 natural-origin age-0+) and 510 PIT-tagged steelhead during the study period. However, many individuals were captured during multiple sampling occasions, resulting in 1674 total captures of PIT-tagged individuals. Owing to logistical constraints, we also captured a small subset of individuals ≥65 mm FL that were released without PIT tags (n = 11 coho salmon and n = 126 steelhead), which represented 7.6% of the total capture events. These untagged individuals were included in the POPAN model as "losses on capture" and were not expected to bias our estimates of abundance (Schwarz and Arnason 1996; Frechette et al. 2016).

We compared eight possible POPAN models and chose the best-approximating model to estimate super-population size (N^*) and species-specific abundances at each occasion ($N_{g,t}$) in the Scott Creek lagoon (Table 1; Fig. 4A). The best-approximating model had the lowest QAIC$_c$ score, received 93.7% of the model support, and had a group-dependent probability of survival ($\phi_{(g)}$), a time-dependent probability of capture ($p_{(t)}$), a time-dependent probability of entry ($b_{(t)}$), and a group-dependent estimate for super-population size ($N^*_{(g)}$) (model{$\phi_{(g)}p_{(t)}b_{(t)}N^*_{(g)}$}; Table 1). The goodness-of-fit test revealed a slight lack of model fit to the data (Program RELEASE: χ^2 = 119.70, df = 94, p = 0.04); therefore, we applied a variance inflation factor ($\hat{c}$ = 1.273) to the model set to correct for overdispersion in the data.

The estimated total steelhead abundance (N^*, across the entire study period) was approximately 2.8 times larger than the estimated total coho salmon abundance in the lagoon (Table 1); however, both species exhibited similar temporal patterns of abundance during the study period. Specifically, we observed an increase of both juvenile coho salmon and steelhead immediately following lagoon formation (i.e., June to July), followed by a decline in the abundances of both species throughout the remainder of the study period (Fig. 4A). Although the abundances of both species declined from July ($N_{\mathrm{CO,JUL1}}$ = 180.3, 95% confidence interval (CI) = 144.5–224.8; $N_{\mathrm{SH,JUL1}}$ = 529.7, 95% CI = 446.6–628.2) through December ($N_{\mathrm{CO,DEC2}}$ = 26.6, 95% CI = 18.7–37.8; $N_{\mathrm{SH,DEC2}}$ = 337.3, 95% CI = 303.1–375.5), the percent decline in abundance over this period was substantially larger for coho salmon (85.2%) than for steelhead (36.3%). The largest declines in abundance for both species occurred during the second environmental phase (27 July – 10 October) when water temperatures were highest and dissolved oxygen concentrations were consistently low (Figs. 3 and 4).

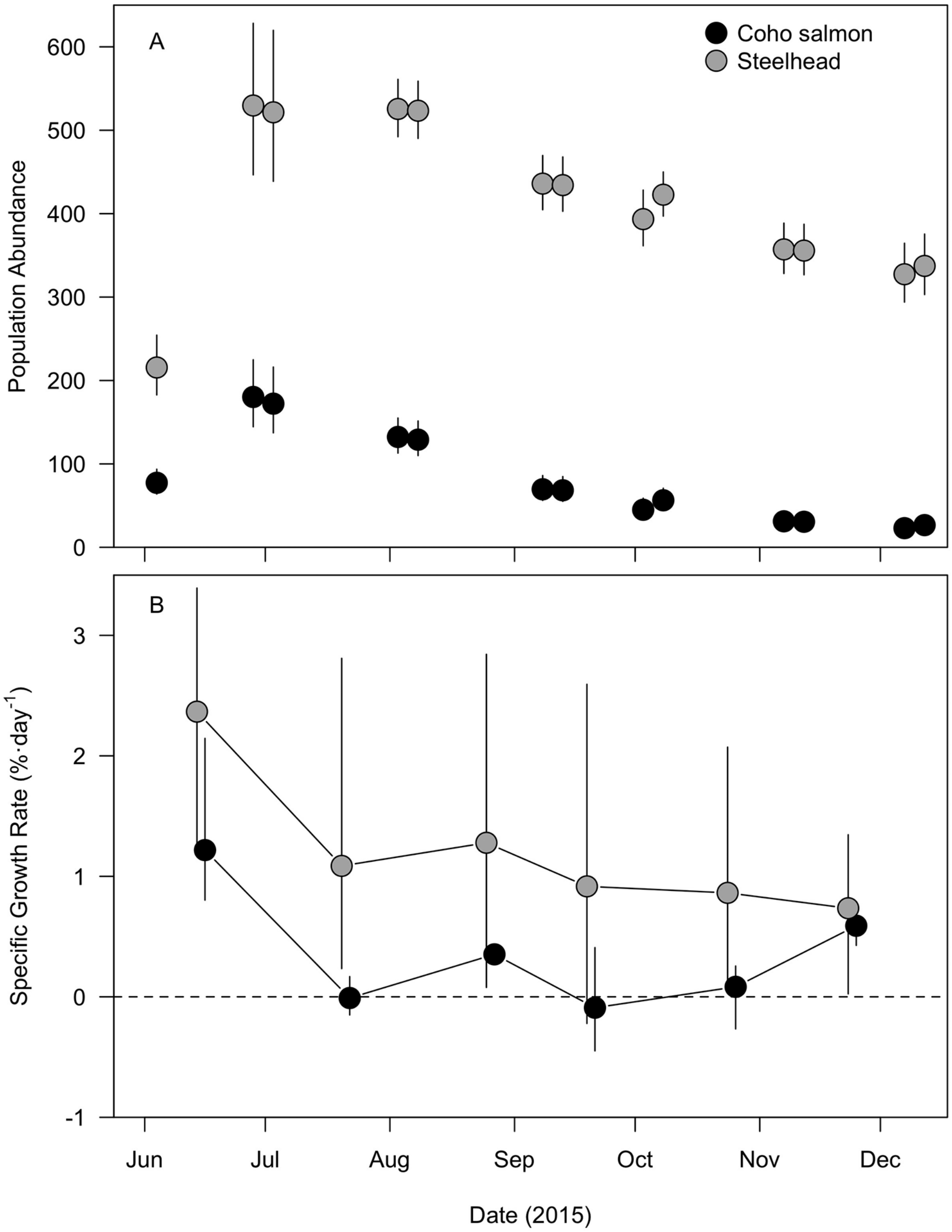
Although coho salmon and steelhead exhibited similar temporal patterns in growth during the study period, specific growth rates were significantly higher for steelhead than for coho salmon during all months (Welch's two-sample t test, p < 0.01; Fig. 4B), except for the November to December growth interval when growth rates were not significantly different (Welch's two-sample t test, p = 0.06; Fig. 4B). Mean specific growth rates were highest from June to July (coho salmon = 1.22%·day^{-1}, 95% CI = 0.80–2.14%·day^{-1}; steelhead = 2.37%·day^{-1}, 95% CI = 1.19–3.39%·day^{-1}) and declined rapidly starting in July. Steelhead growth from July to August was 1.09%·day^{-1} (95% CI = 0.23–2.81%·day^{-1}), whereas growth rates for coho salmon were ≤0.0%·day^{-1} from July to August and likewise from September to October. Steelhead exhibited positive mean growth rates during all months of the study period, while coho salmon only exhibited positive mean growth during four of the six monthly growth intervals (Fig. 4B).

Directional movement of PIT-tagged individuals

We identified a total of 11 836 unique movement events generated by 545 distinct individuals (n = 124 coho salmon, n = 421 steelhead) across our 7-month study period. The majority of movement events occurred at the Lagoon antenna (99.4%, n = 11 768) when compared with all other upper watershed antenna arrays combined (0.6%, n = 68). Although both coho salmon and steelhead exhibited directional movement at the Lagoon antenna, the timing and relative direction of movement varied between species (Fig. 5). Of the 11 768 movement events identified at the Lagoon antenna, 1512 (12.8%) were upstream (i.e., moving out of the lagoon), 930 (7.9%) were downstream (i.e., moving into the lagoon), and 9326 (79.2%) were classified as unknown (ambiguous) directionality. From June to October, the ratio of upstream to downstream movement events was higher for coho salmon (2.06) than for steelhead (1.36), indicating more net upstream movement by coho salmon (Fig. 5). Steelhead exhibited directional movement during nearly all months of the study, while movement by coho salmon primarily occurred from June through September, with peak upstream movement occurring in July (Fig. 5). Periodic increases in fish movement at the Lagoon antenna coincided with sampling (seining) occasions in the lagoon, indicating that some movement was triggered by human disturbance (Fig. 5).

Few individuals were detected at upper watershed PIT tag antenna arrays (>rkm 1.7) during the period of lagoon formation, indicating most fish movement occurred over a limited spatial scale between the lagoon and lower main stem of Scott Creek. Nonetheless, 65 PIT-tagged individuals initially captured in the lagoon were subsequently detected in the upper watershed during the study period (n = 8 coho salmon, 6.5%; n = 57 steelhead, 13.5%). Upstream movement of PIT-tagged individuals beyond rkm 1.7 was identified in July, August, and December for coho salmon and in July, November, and December for steelhead. None of the fish that migrated to the upper watershed were detected returning downstream to either the lagoon or lower main stem of

Fig. 4. Monthly abundance estimates from the best-approximating POPAN model {$\phi_{(g)}p_{(t)}b_{(t)}N^*_{(g)}$} (A) and mean specific growth rates (B) for juvenile coho salmon and steelhead in the Scott Creek lagoon. Population estimates are only presented for 13 of the 14 sampling occasions because abundance cannot be estimated for the first sampling occasion when the probability of capture is time-dependent. Specific growth rates were plotted at the midpoint between sampling occasions to indicate average growth within that time interval. All point estimates are presented with 95% confidence intervals.



Scott Creek as of the end of the study in December. Antenna detection efficiencies among upstream (riverine) antenna arrays averaged 76% during the study period. However, we were unable to assess the efficiency of the Lagoon antenna because a substantial number of detections occurred on only a single antenna of the paired array due to milling behavior. This circumstance violates the assumption of continuous movement across both antennas, which must be met to accurately quantify detection efficiency (e.g., Zydlewski et al. 2006).

Temporal patterns in seawater readiness

We collected 491 gill samples for NKA activity (*n* = 117 coho salmon, *n* = 374 steelhead) across the 7-month study period. Overall temporal trends for expression of NKA activity were similar for both species (Fig. 6). The highest mean NKA activity levels were observed during the first sampling event following sandbar formation (i.e., June: coho salmon = 6.5 μmol ADP·mg protein^{-1}·h^{-1}, 95% CI = 1.8–14.2 μmol ADP·mg protein^{-1}·h^{-1}; steelhead = 6.1 μmol ADP·mg protein^{-1}·h^{-1}, 95% CI = 0.9–9.2 μmol ADP·mg protein^{-1}·h^{-1}), and levels declined steadily for the next 3 months to their lowest mean levels in September (coho salmon = 1.1 μmol ADP·mg protein^{-1}·h^{-1}, 95% CI = 0.8–1.4 μmol ADP·mg protein^{-1}·h^{-1}; steelhead = 1.5 μmol ADP·mg protein^{-1}·h^{-1}, 95% CI = 0.7–3.0 μmol ADP·mg protein^{-1}·h^{-1}). NKA activity steadily increased from October to December, when levels reached their second highest values for both species over the duration of the study (coho salmon = 5.6 μmol ADP·mg protein^{-1}·h^{-1}, 95% CI = 3.8–7.7 μmol ADP·mg

Fig. 5. The number of upstream (positive values; black bars) and downstream (negative values; gray bars) movement events exhibited by PIT-tagged coho salmon (A) and steelhead (B) at the lagoon PIT tag antenna array (~rkm 0.6) during lagoon closure in 2015. Asterisks (*) denote the dates of lagoon sampling occasions.

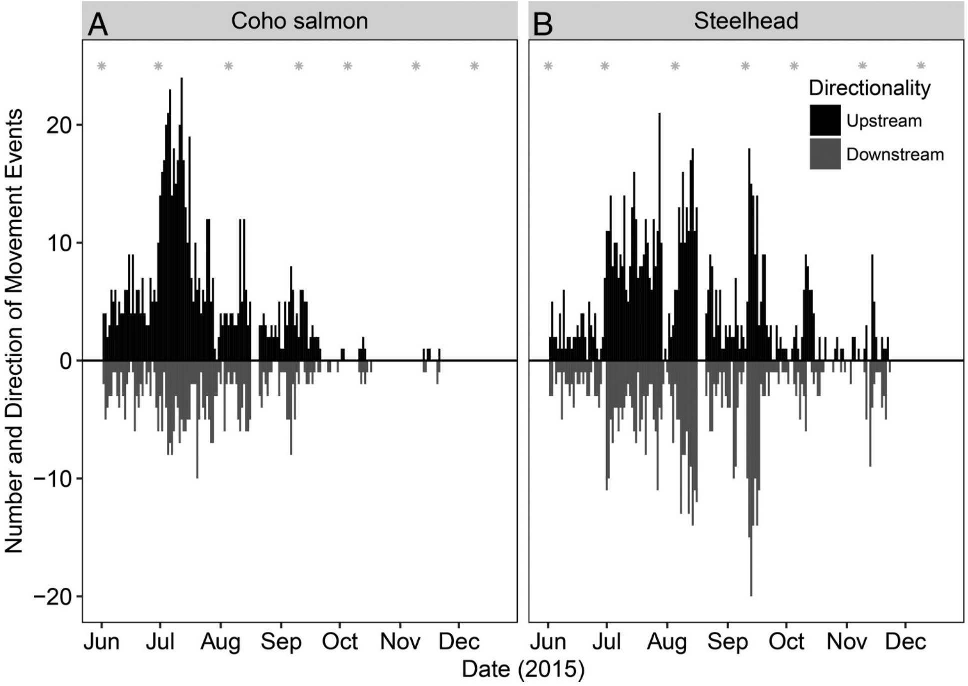
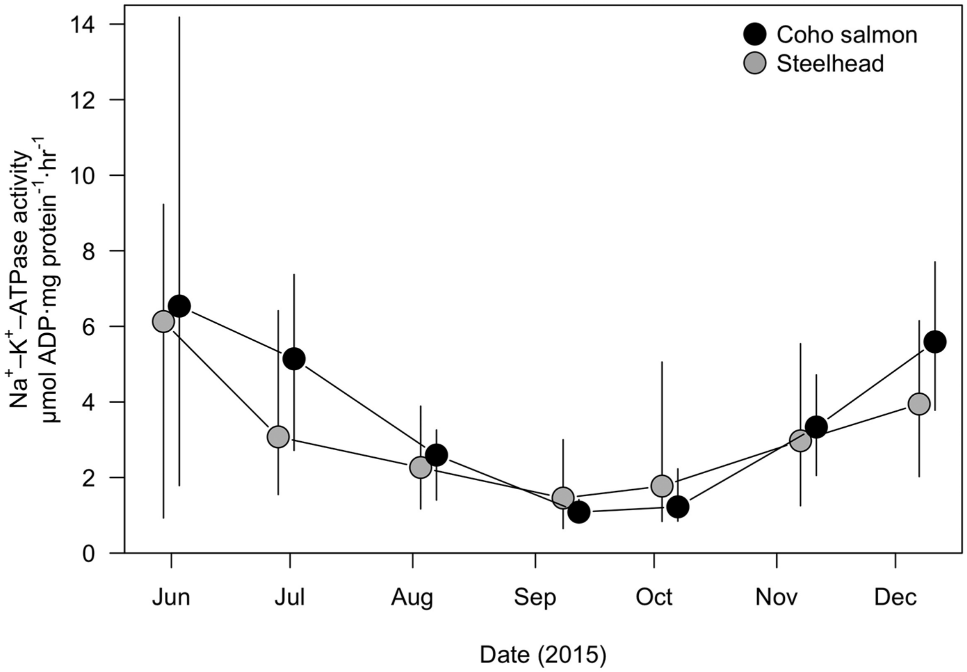


Fig. 6. Monthly mean Na⁺-K⁺-ATPase activity levels for age-1+ coho salmon and steelhead captured in the Scott Creek lagoon during the summer and fall of 2015. Error bars represent 95% confidence intervals.



protein^{-1}·h^{-1}; steelhead = 3.9 μmol ADP·mg protein^{-1}·h^{-1}, 95% CI = 2.0–6.1 μmol ADP·mg protein^{-1}·h^{-1}). Although NKA activity was not significantly different between species for three of the months (June, August, and November; Welch's two-sample *t* test, $p > 0.20$; Fig. 6), coho salmon exhibited significantly higher mean NKA activity levels than steelhead near the beginning (July) and end (December) of the study (Welch's two-sample *t* test, $p < 0.02$; Fig. 6) and had significantly lower levels of activity than steelhead in the middle of the study period (September and October; Welch's two-sample *t* test, $p < 0.01$; Fig. 6).

Discussion

Our study describes extended use of the Scott Creek lagoon by juvenile coho salmon and steelhead during a year in which extreme drought conditions substantially truncated the typical smolt outmigration window. We found that both salmonid species were present in the lagoon from June through December, despite protracted periods of unfavorable environmental conditions. Steelhead were consistently more abundant than coho salmon in the Scott Creek lagoon and also experienced significantly higher growth rates during nearly all months. Movement patterns derived from PIT tag detections provided evidence that connectivity between the lagoon and the lower mainstem river likely facilitated persistence of both species by permitting individuals to exploit both abundant food resources in the lagoon and more thermally favorable conditions in the lower mainstem river. While extended lagoon use by steelhead has been previously reported (Bond et al. 2008; Hayes et al. 2008, 2011), this study provides novel information on oversummer lagoon use by age-1+ coho salmon beyond the traditional late spring migration window and demonstrates that juvenile coho salmon in California are more plastic than previously recognized.

The coho salmon life cycle has traditionally been considered fairly rigid and characterized by juveniles spending approximately 1 year in fresh water before emigrating to the ocean as age-1+ smolts (Sandercock 1991; Brown et al. 1994; Moyle 2002). However, recent studies have highlighted considerable variability in coho salmon life-history strategies, especially with respect to estuary residence and use during juvenile life stages. Research conducted in the Pacific Northwest revealed use of estuarine habitats by subyearling (age-0+) coho salmon for several months before subsequently retreating back upstream and later returning downstream to outmigrate as smolts (e.g., Miller and Sadro 2003; Koski 2009). Jones et al. (2014) reported a range of early life-history rearing strategies in the Salmon River basin (north-central Oregon, USA), including age-0 individuals rearing for a full year in the estuary before emigrating to sea as age-1+ smolts. Several other studies have highlighted short-term estuary use by older age-1+ coho salmon, where mean residence time ranged from 15 to 40 days prior to outmigration to the ocean (Hoem Neher et al. 2013; Jones et al. 2014; Moore et al. 2016). To our knowledge, only Wallace et al. (2015) have described protracted estuary use by age-1+ coho salmon in California, where mean residence times in the stream–estuary ecotone of several Humboldt Bay tributaries ranged from 14 to 50 days, and a few individuals remained for more than 8 months. However, age-1+ coho salmon in this extremely large estuarine system were mostly present during winter and spring (with peak abundance occurring during the spring smolt outmigration period) and rarely observed beyond July (Wallace et al. 2015). In contrast, we found limited use of the Scott Creek lagoon by age-0+ coho salmon beyond July (end of Phase 1; Fig. 3), but that age-1+ coho salmon persisted and reared in the lagoon throughout the summer and fall dry period (June through December). Owing to early sandbar formation that precluded seaward migration of age-1+ smolts after mid-May, a portion of the Scott Creek coho salmon population was denied the opportunity to emigrate and remained in the watershed until age-2.

Despite ostensibly stressful abiotic conditions (i.e., elevated water temperature and low dissolved oxygen concentration) in the Scott Creek lagoon across much of the study period, juvenile coho salmon and steelhead were present during all sampling events and exhibited positive mean specific growth rates during many sample intervals. The presence and growth of age-1+ coho salmon is particularly interesting because coho salmon are generally considered less tolerant of warm water temperatures than steelhead. In a review of published temperature studies, Richter and Kolmes (2005) reported that optimal growth occurs below 15 °C for juvenile coho salmon and below 19 °C for steelhead. Water temperatures in the Scott Creek lagoon during our study were only below these thresholds during the June and December sampling occasions, whereupon growth rates were positive for both salmonid species (Figs. 3 and 4). Nonetheless, we found no consistent relationship between lagoon water temperature and fish growth, as both coho salmon and steelhead also exhibited positive growth rates in August (specific growth interval = 7 August – 10 September) when mean daily water temperatures averaged >20 °C and thus exceeded optimal temperature thresholds for growth, particularly for coho salmon. It is instructive to note, however, that the period with the highest observed water temperatures during our study (~late July to mid-October; Phase 2) was coincident with extremely high standing stocks of invertebrate prey in the lagoon (J.D. Kiernan, unpublished data). Both high acclimation temperatures (Myrick and Cech 2000) and abundant food resources (Bisson et al. 1988) can potentially reduce the adverse effects of elevated water temperature on salmonid performance, and these factors may explain the increase in growth rates observed for both species between August and September. Furthermore, juvenile salmonids in other study systems have persisted in water temperatures warmer than those documented in our study, including field observations of steelhead in stream temperatures reaching 30 °C for steelhead (Sloat and Osterback 2013) and 29 °C for coho salmon (Bisson et al. 1988). Thus, while lagoon water temperatures did not exceed lethal limits during our study, abiotic conditions were nonetheless stressful and likely contributed to declines in abundance and reduced growth rates during warmer months, except perhaps during periods of very high prey availability.

Both coho salmon and steelhead exhibited bidirectional movement between the lagoon and lower mainstem river throughout the study; however, the timing and frequency of movement varied between the two species (Fig. 5). Lagoons and estuaries in small coastal watersheds are typically productive habitats that provide enhanced growth opportunities for juvenile salmonids relative to upstream (riverine) rearing (Hayes et al. 2008; Jones et al. 2011), and thus lagoon residence has been linked to increased survival to adulthood (Bond et al. 2008). Nevertheless, lagoons and estuaries can also present risks such as high mortality rates (Satterthwaite et al. 2012), potentially from increased predator densities (Frechette et al. 2013; Osterback et al. 2013) or stressful abiotic conditions such as warm water temperature (Boughton et al. 2017) and low dissolved oxygen concentration. Consequently, some juvenile salmonid populations are known to exhibit frequent movement between proximate habitats that provide abundant food and high growth potential and habitats that allow for predator avoidance (Scheuerell and Schindler 2003) or provide water temperatures that aid in regulating physiological processes (Armstrong et al. 2013; Brewitt et al. 2017). We observed recurrent movement of individuals between the prey-rich lagoon and the lower main stem of Scott Creek where water temperatures were on average >2.5 °C cooler than thermal conditions in the lagoon. While it remains unknown which factors prompted movement in and out of the lagoon, a recent study demonstrated that different abiotic factors influenced species-specific presence in a small California intermittent stream, where low dissolved oxygen concentration limited the presence of coho salmon and temperature limited the presence of steelhead (Woelfle-Erskine et al. 2017). A higher sensitivity to low dissolved oxygen by coho salmon may explain the marked decline in coho salmon movement events (Fig. 5) following the abrupt decrease in dissolved oxygen concentration in early August (Fig. 3), whereas the frequency of steelhead movement events remained relatively consistent into the fall (Fig. 5).

While movement by both salmonid species was predominantly localized and occurred between the lagoon and lower main stem of Scott Creek, a number of coho salmon initially captured in the lagoon were subsequently detected moving considerable distances upstream (i.e., >1.7 rkm) in July, August, and December. Whereas the warmest lagoon water temperatures and lowest dissolved oxygen concentrations occurred during July and August (Fig. 3), we propose that upstream movement during this period was chiefly in search of more favorable abiotic conditions. However, factors driving upstream movement in December are more unclear. In general, upstream movement during December was coincident with increased stream flow and initiated by individuals that had earlier moved out of the lagoon (i.e., during the preceding months) to occupy habitat in the lower main stem of Scott Creek. The timing of outmigration for juvenile salmonids has evolved to occur during spring upwelling, when the marine environment is most productive (Spence and Hall 2010); thus, we posit that upstream movement in December may have been to avoid displacement into the ocean and delay outmigration until the following spring. Previous research in Scott Creek has documented an upstream retreat of lagoon-reared steelhead in the fall due to declining water quality and eventual outmigration the ensuing spring (Hayes et al. 2011); however, this is the first report of age-1+ coho salmon potentially exhibiting similar behavior patterns.

Coho salmon and steelhead demonstrated comparable temporal patterns of NKA activity over the study period, where activity was elevated at both the beginning and end of the 7-month study period (i.e., Phases 1 and 3), and lowest during the middle of lagoon residence (i.e., Phase 2; Fig. 5). Up-regulation of NKA activity is a widely used metric to indicate physiological changes in salmonids as they prepare to live in a saline environment (Björnsson and Bradley 2007). Therefore, elevated expression was expected immediately following sandbar formation, since most individuals were presumably physiologically preparing (or fully prepared) to enter the ocean when the sandbar at the mouth of Scott Creek prematurely closed. Our observation of an incremental decline in NKA activity with increasing lagoon residence time (i.e., during August through October) is a new finding for coho salmon, but consistent with previous observations for steelhead in the Scott Creek watershed (Hayes et al. 2011). While we cannot identify the precise mechanism for reduced NKA activity during Phase 2, warm water temperatures, low salinity, and advanced photoperiod are known to inhibit NKA expression in salmonids (Zaugg 1981; Morgan and Iwama 1998; McCormick et al. 1999).

A remarkable finding during our study was the increase in NKA activity during Phase 3 of lagoon residence for both salmonid species, suggesting physiological preparation for saltwater entry during late fall. However, PIT tag detections at stationary antennas located throughout the watershed provided clear evidence that a substantial number of fish remained in fresh water rather than emigrated out to sea after connectivity between the creek and ocean was reestablished. Specifically, over 5% of coho salmon and 46% of steelhead captured and PIT-tagged in the Scott Creek lagoon during the period of sandbar formation were passively detected elsewhere in the Scott Creek watershed ≥14 days following sandbar erosion. Since stationary PIT tag antenna detections represent a minimum estimate of movement, it is probable that many more individuals either remained in the lower basin or retreated upstream and went undetected. Because elevated NKA can be triggered by abiotic conditions such as increased salinity (Morgan and Iwama 1998) and lower water temperature (Adams et al. 1975), elevated NKA levels do not always correlate with life-history pathways such as outmigration (Hayes et al. 2011). Our results suggest that despite an extra season of obligatory freshwater residence, many coho salmon and steelhead detected in the lagoon further delayed their outmigration, possibly to time their ocean entry with more favorable marine conditions (Spence and Hall 2010).

The importance of life-history diversity in contributing to salmonid population stability and resilience has gained increasing attention (Schindler et al. 2010; Carlson and Satterthwaite 2011; Moore et al. 2014) and will undoubtedly be critical as imperiled salmonid populations respond to the uncertainties of future climate change (Katz et al. 2013; Moyle et al. 2013; Manhard et al. 2017). Our results demonstrate that juvenile coho salmon can exhibit plastic responses and persist during challenging climatic events and highlight that connectivity and preservation of diverse habitats is critical for the persistence of salmonid populations. Lagoon-type estuaries such as Scott Creek represent the majority of California's estuaries known to support anadromous salmonids (Hughes et al. 2014), and the frequency, intensity, and duration of drought events are expected to increase in the near future (Garssen et al. 2014; Diffenbaugh et al. 2015; Mann and Gleick 2015). Therefore, results of this study provide important insight into how many of California's imperiled coastal salmonid populations may be affected by future climate change and the likely importance of seasonal lagoons and habitat connectivity to their long-term viability.

Acknowledgements

We thank C. Attias, R. Bond, P. Doughty, S. Figueroa, A. Frederick, A. Ganley, R. Howard, K. Kobayashi, C. Nicol, N. Retford, T. Ryan, R. Tallman, C. Young, the Early Life History Team at NOAA Fisheries Southwest Fisheries Science Center, and an army of UC Santa Cruz undergraduate volunteers for field support. We also thank R. Bond for creating the location map and accommodating our countless revisions. Early drafts of this manuscript were substantially improved with recommendations from E. Anderson, R. Bond, D. Frechette, S. Munch, S. Sogard, W. Satterthwaite, and two anonymous reviewers. We are especially grateful to Big Creek Lumber Company and California Polytechnic State University's Swanton Pacific Ranch for continued support of our monitoring and research activities and for providing access to the Scott Creek watershed. Financial support for this project was provided, in part, by NOAA Fisheries California Coastal Office and the California Department of Fish and Wildlife (Fisheries Restoration Grant Program Awards P1330409 and P1330415). Capture of ESA-listed salmonids was authorized by National Marine Fisheries Service under Section 10(a)(1)(A) permit No. 17292. All animals were handled according to Institutional Animal Care and Use Protocols (IACUC UC Santa Cruz, No. KIERJ1604_A1).

References

Adams, B.L., Zaugg, W.S., and McLain, L.R. 1975. Inhibition of salt water survival and Na-K-ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Trans. Am. Fish. Soc. **104**(4): 766–769. doi:10.1577/1548-8659(1975)104<766:IOSWSA>2.0.CO;2.

Amstrup, S., MacDonald, L., and Manly, B. 2006. Handbook of capture–recapture analysis. Princeton University Press, Princeton, N.J.

Armstrong, J.B., Schindler, D.E., Ruff, C.P., Brooks, G.T., Bentley, K.E., and Torgersen, C.E. 2013. Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. Ecology, **94**(9): 2066–2075. doi:10.1890/12-1200.1. PMID:24279277.

Beale, E.M.L., and Little, R.J.A. 1975. Missing values in multivariate analysis. J. R. Stat. Soc. Ser. B Methodol. **37**(1): 129–145. Available from http://www.jstor.org/stable/2984998.

Bisson, P.A., Nielsen, J.L., and Ward, J.W. 1988. Summer production of coho salmon stocked in Mount St. Helens streams 3–6 years after the 1980 eruption. Trans. Am. Fish. Soc. **117**(4): 322–335. doi:10.1577/1548-8659(1988)117<0322:SPOCSS>2.3.CO;2.

Björnsson, B.T., and Bradley, T.M. 2007. Epilogue: past successes, present misconceptions and future milestones in salmon smoltification research. Aquaculture, **273**(2–3): 384–391. doi:10.1016/j.aquaculture.2007.10.020.

Bond, M.H., Hayes, S.A., Hanson, C.V., and MacFarlane, R.B. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Can. J. Fish. Aquat. Sci. **65**(10): 2242–2252. doi:10.1139/F08-131.

Boughton, D., Fuller, J., Horton, G., Larson, E., Matsubu, W., and Simenstad, C. 2017. Spatial structure of water-quality impacts and foraging opportunities for steelhead in the Russian River estuary: an energetics perspective. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-569. doi:10.7289/V5/TM-SWFSC-569.

Brewitt, K.S., Danner, E.M., and Moore, J.W. 2017. Hot eats and cool creeks: juvenile Pacific salmonids use mainstem prey while in thermal refuges. Can. J. Fish. Aquat. Sci. **74**(10): 1588–1602. doi:10.1139/cjfas-2016-0395.

Brown, L.R., Moyle, P.B., and Yoshiyama, R.M. 1994. Historical decline and current status of coho salmon in California. N. Am. J. Fish. Manage. **14**(2): 237–261. doi:10.1577/1548-8675(1994)014<0237:HDACSO>2.3.CO;2.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Carlson, S.M., and Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed salmon population complex. Can. J. Fish. Aquat. Sci. **68**(9): 1579–1589. doi:10.1139/f2011-084.

Dempster, A.P., Laird, N.M., and Rubin, D.B. 1977. Maximum likelihood from incomplete data via the EM algorithm. J. R. Stat. Soc. Ser. B Methodol. **39**(1): 1–38. Available from http://www.jstor.org/stable/2984875.

Diffenbaugh, N.S., Swain, D.L., and Touma, D. 2015. Anthropogenic warming has increased drought risk in California. Proc. Natl. Acad. Sci. **112**(13): 3931–3936. doi:10.1073/pnas.1422385112. PMID:25733875.

Ewing, R.D., Evenson, M.D., Birks, E.K., and Hemmingsen, A.R. 1984. Indices of parr-smolt transformation in juvenile steelhead trout (*Salmo gairdneri*) undergoing volitional release at Cole Rivers Hatchery, Oregon. Aquaculture, **40**(3): 209–221. doi:10.1016/0044-8486(84)90188-1.

Folmar, L.C., and Dickhoff, W.W. 1980. The parr–smolt transformation (smoltification) and seawater adaptation in salmonids: a review of selected literature. Aquaculture, **21**(1): 1–37. doi:10.1016/0044-8486(80)90123-4.

Frechette, D.M., Collins, A.L., Harvey, J.T., Hayes, S.A., Huff, D.D., Jones, A.W., Retford, N.A., Langford, A.E., Moore, J.W., Osterback, A.-M.K., Satterthwaite, W.H., and Shaffer, S.A. 2013. A bioenergetics approach to assessing potential impacts of avian predation on juvenile steelhead during freshwater rearing. N. Am. J. Fish. Manage. **33**(5): 1024–1038. doi:10.1080/02755947.2013.816395.

Frechette, D., Satterthwaite, W.H., Osterback, A.-M.K., and Hayes, S.A. 2016. Steelhead abundance in seasonally closed estuaries estimated using mark recapture methods. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-555 U.S.: 1-34. doi:10.7289/V5/TM-SWFSC-555.

Garssen, A.G., Verhoeven, J.T.A., and Soons, M.B. 2014. Effects of climate-induced increases in summer drought on riparian plant species: a meta-analysis. Freshw. Biol. **59**(5): 1052–1063. doi:10.1111/fwb.12328. PMID:26180267.

Gillanders, B.M., Elsdon, T.S., Halliday, I.A., Jenkins, G.P., Robins, J.B., and Valesini, F.J. 2011. Potential effects of climate change on Australian estuaries and fish utilising estuaries: a review. Mar. Freshw. Res. **62**(9): 1115–1131. doi:10.1071/MF11047.

Grantham, T.E., Merenlender, A.M., and Resh, V.H. 2010. Climatic influences and anthropogenic stressors: an integrated framework for streamflow management in Mediterranean-climate California, U.S.A. Freshw. Biol. **55**(S1): 188—204. doi:10.1111/j.1365-2427.2009.02379.x.

Griffin, D., and Anchukaitis, K.J. 2014. How unusual is the 2012-2014 California drought? Geophys. Res. Lett. **41**: 9017–9023. doi:10.1002/2014GL062433.

Hall, J., Roni, P., Bennett, T., McMillan, J., Hanson, K., Moses, R., McHenry, M., Pess, G., and Ehinger, W. 2016. Life history diversity of steelhead in two coastal Washington watersheds. Trans. Am. Fish. Soc. **145**(5): 990–1005. doi:10.1080/00028487.2016.1194893.

Hannachi, A., Jolliffe, I.T., and Stephenson, D.B. 2007. Empirical orthogonal functions and related techniques in atmospheric science: a review. Int. J. Climatol. **27**: 1119–1152. doi:10.1002/joc.1499.

Hayes, S.A., Bond, M.H., Hanson, C.V., Freund, E.V., Smith, J.J., Anderson, E.C., Ammann, A.J., and MacFarlane, R.B. 2008. Steelhead growth in a small central California watershed: upstream and estuarine rearing patterns. Trans. Am. Fish. Soc. **137**(1): 114–128. doi:10.1577/T07-043.1.

Hayes, S.A., Bond, M.H., Hanson, C.V., Jones, A.W., Ammann, A.J., Harding, J.A., Collins, A.L., Perez, J., and MacFarlane, R.B. 2011. Down, up, down and "smolting" twice? Seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. Can. J. Fish. Aquat. Sci. **68**(8): 1341–1350. doi:10.1139/F2011-062.

Heady, W.N., O'Connor, K., Kassakian, J., Doiron, K., Endris, C., Hudgens, D., Clark, R.P., Carter, J., and Gleason, M.G. 2014. An inventory and classification of U.S. West Coast estuaries [online]. The Nature Conservancy, Arlington, Va. Available from https://www.scienceforconservation.org/products/inventory-and-classification-of-u.s.-west-coast-estuaries.

Hoem Neher, T.D., Rosenberger, A.E., Zimmerman, C.E., Walker, C.M., and Baird, S.J. 2013. Estuarine environments as rearing habitats for juvenile coho salmon in contrasting South-Central Alaska watersheds. Trans. Am. Fish. Soc. **142**(6): 1481–1494. doi:10.1080/00028487.2013.815660.

Hughes, B.B., Levey, M.D., Brown, J.A., Fountain, M.C., Carlisle, A.B., Litvin, S.Y., Greene, C.M., Heady, W.N., and Gleason, M.G. 2014. Nursery functions of U.S. West Coast estuaries: the state of knowledge for juveniles of focal invertebrate and fish species. The Nature Conservancy, Arlington, Va. pp. 1–172.

Jones, K.K., Cornwell, T.J., Bottom, D.L., Stein, S., Kelly, H.W., and Campbell, L.A. 2011. Recovery of wild coho salmon in Salmon River basin, 2008–10. Monitoring Program Report Number OPSW-ODFW-2011-10. Oregon Dept. Fish and Wild., Salem, Ore.

Jones, K.K., Cornwell, T.J., Bottom, D.L., Campbell, L.A., and Stein, S. 2014. The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. J. Fish Biol. **85**(1): 52–80. doi:10.1111/jfb.12380. PMID:24766645.

Katz, J., Moyle, P.B., Quiñones, R.M., Israel, J., and Purdy, S. 2013. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. Environ. Biol. Fishes, **96**(10–11): 1169–1186. doi:10.1007/s10641-012-9974-8.

Kiernan, J.D., and Moyle, P.B. 2012. Flows, droughts, and aliens: factors affecting the fish assemblage in a Sierra Nevada, California, stream. Ecol. Appl. **22**(4): 1146–1161. doi:10.1890/11-1047.1. PMID:22827124.

Kiernan, J.D., Osterback, A.-M.K., Kern, C.H., Kanawi, E., and Gilbert-Horvath, L. 2016. Results of Scott Creek life-cycle monitoring station 2014-2015. Final Report. Fish. Restor. Grant Prog. Award #P1330409. Available from NOAA Fisheries, Southwest Fisheries Science Center, Santa Cruz, CA 95062, USA.

Koski, K.V. 2009. The fate of coho salmon nomads: the story of an estuarine-rearing strategy promoting resilience [online]. Ecol. Soc. **14**(1): 1–16. Available from http://www.ecologyandsociety.org/vol14/iss1/art4/ [accessed 24 September 2017].

Kraus, N.C., Militello, A., and Todoroff, G. 2002. Barrier breaching processes and barrier spit breach, Stone Lagoon, California. Shore and Beach, **70**(4): 21–28.

Lake, P.S. 2011. Drought and aquatic ecosystems: effects and responses. John Wiley & Sons, Ltd., Chichester, UK. doi:10.1002/9781444341812.

Lebreton, J.-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. **62**(1): 67–118. doi:10.2307/2937171.

Manhard, C.V., Joyce, J.E., and Gharrett, A.J. 2017. Evolution of phenology in a salmonid population: a potential adaptive response to climate change. Can. J. Fish. Aquat. Sci. **74**(10): 1519–1527. doi:10.1139/cjfas-2017-0028.

Mann, M.E., and Gleick, P.H. 2015. Climate change and California drought in the 21st century. Proc. Natl. Acad. Sci. **112**(13): 3858–3859. doi:10.1073/pnas.1503667112. PMID:25829537.

McCormick, S.D. 1993. Methods for nonlethal gill biopsy and measurement of Na^+, K^+-ATPase activity. Can. J. Fish. Aquat. Sci. **50**(3): 656–658. doi:10.1139/f93-075.

McCormick, S.D., Cunjak, R.A., Dempson, B., O'Dea, M.F., and Carey, J.B. 1999. Temperature-related loss of smolt characteristics in Atlantic salmon (*Salmo salar*) in the wild. Can. J. Fish. Aquat. Sci. **56**(9): 1649–1667. doi:10.1139/f99-099.

Miller, B.A., and Sadro, S. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. Trans. Am. Fish. Soc. **132**(3): 546–559. doi:10.1577/1548-8659(2003)132<0546:RTASMO>2.0.CO;2.

Moore, J.W., Yeakel, J.D., Peard, D., Lough, J., and Beere, M. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. J. Anim. Ecol. **83**(5): 1035–1046. doi:10.1111/1365-2656.12212. PMID:24673479.

Moore, J.W., Gordon, J., Carr-Harris, C., Gottesfeld, A.S., Wilson, S.M., and Russell, J.H. 2016. Assessing estuaries as stopover habitats for juvenile Pacific salmon. Mar. Ecol. Prog. Ser. **559**: 201–215. doi:10.3354/meps11933.

Morgan, J.D., and Iwama, G.K. 1998. Salinity effects on oxygen consumption, gill Na^+, K^+-ATPase and ion regulation in juvenile coho salmon. J. Fish Biol. **53**(5): 1110–1119. doi:10.1006/jfbi.1998.0780.

Moyle, P.B. 2002. Inland fishes of California. University of California Press, Berkeley, Calif.

Moyle, P.B., Kiernan, J.D., Crain, P.K., and Quiñones, R.M. 2013. Climate change vulnerability of native and alien freshwater fishes of California: a systematic assessment approach. PLoS ONE, **8**(5): e63883. doi:10.1371/journal.pone.0063883. PMID:23717503.

Myrick, C.A., and Cech, J.J. 2000. Temperature influences on California rainbow trout physiological performance. Fish Physiol. Biochem. **22**(3): 245–254. doi:10.1023/A:1007805322097.

NMFS. 2005. Endangered and threatened species: final listing determinations for 16 ESUs of west coast salmon, and final 4(d) protective regulations for threatened salmonid ESUs. National Marine Fisheries Service. Fed. Reg. **70**(123): 37009–37248.

NMFS. 2006. Endangered and threatened species: final listing determinations for 10 distinct population segments of west coast steelhead. National Marine Fisheries Service. Fed. Reg. **71**(3): 834–862.

NMFS. 2012. Final recovery plan for Central California Coast coho salmon Evolutionarily Significant Unit. National Marine Fisheries Service, Southwest Region, Santa Rosa, Calif.

Osterback, A.-M.K., Frechette, D.M., Shelton, A.O., Hayes, S.A., Bond, M.H., Shaffer, S.A., and Moore, J.W. 2013. High predation on small populations: avian predation on imperiled salmonids. Ecosphere, **4**(9): 1–21. doi:10.1890/ES13-00100.1.

Osterback, A.-M.K., Frechette, D.M., Hayes, S.A., Bond, M.H., Shaffer, S.A., and Moore, J.W. 2014. Linking individual size and wild and hatchery ancestry to survival and predation risk of threatened steelhead (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **71**(12): 1877–1887. doi:10.1139/cjfas-2014-0097.

Preisendorfer, R.W. 1988. Principal component analysis in meteorology and oceanography (Developments in Atmospheric Science). Book 17. Elsevier, New York.

Richter, A., and Kolmes, S.A. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Rev. Fish. Sci. **13**(1): 23–49. doi:10.1080/10641260590885861.

Rustomji, P. 2007. Flood and drought impacts on the opening regime of a wave-dominated estuary. Mar. Freshw. Res. **58**(12): 1108–1119. doi:10.1071/MF07079.

Sandercock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. UBC Press, Vancouver, B.C. pp. 396–445.

Satterthwaite, W.H., Hayes, S.A., Merz, J.E., Sogard, S.M., Frechette, D.M., and Mangel, M. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. Trans. Am. Fish. Soc. **141**(3): 781–794. doi:10.1080/00028487.2012.675912.

Scheuerell, M.D., and Schindler, D.E. 2003. Diel vertical migration by juvenile sockeye salmon: Empirical evidence for the antipredation window. Ecology, **84**(7): 1713–1720. doi:10.1890/0012-9658(2003)084[1713:DVMBJS]2.0.CO;2.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature, **465**(7298): 609–612. doi:10.1038/nature09060. PMID:20520713.

Schwarz, C.J., and Arnason, A.N. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics, **52**(3): 860–873. doi:10.2307/2533048.

Shapovalov, L., and Taft, A.C. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*). Calif. Dept. Fish Game Fish Bull. 98.

Sloat, M.R., and Osterback, A.-M.K. 2013. Maximum stream temperature and the occurrence, abundance, and behavior of steelhead trout (*Oncorhynchus mykiss*) in a southern California stream. Can. J. Fish. Aquat. Sci. **70**(1): 64–73. doi:10.1139/cjfas-2012-0228.

Smith, J.J. 1990. The effects of sandbar formation and inflows on aquatic habitat and fish utilization in Pescadero, San Gregorio, Waddell and Pomponio Creek estuary/lagoon systems, 1985–1989 [online]. Interagency Agreement 84-04-324, San Jose State University, prepared for California Department of Parks and Recreation. Available from http://cdm16658.contentdm.oclc.org/cdm/ref/collection/p267501ccp2/id/149.

Sogard, S.M., Merz, J.E., Satterthwaite, W.H., Beakes, M.P., Swank, D.R., Collins, E.M., Titus, R.G., and Mangel, M. 2012. Contrasts in habitat characteristics and life history patterns of *Oncorhynchus mykiss* in California's Central Coast and Central Valley. Trans. Am. Fish. Soc. **141**(3): 747–760. doi:10.1080/00028487.2012.675902.

Spence, B.C., and Hall, J.D. 2010. Spatiotemporal patterns in migration timing of coho salmon (*Oncorhynchus kisutch*) smolts in North America. Can. J. Fish. Aquat. Sci. **67**(8): 1316–1334. doi:10.1139/F10-060.

Thorpe, J.E. 2007. Maturation responses of salmonids to changing developmental opportunities. Mar. Ecol. Prog. Ser. **335**: 285–288. doi:10.3354/meps335285.

Wallace, M., Ricker, S., Garwood, J., Frimodig, A., and Allan, S. 2015. Importance of the stream–estuary ecotone to juvenile coho salmon (*Oncorhynchus kisutch*) in Humboldt Bay, California. Calif. Dept. Fish Game, **101**(4): 241–266.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study, **46**(S1): S120–S139. doi:10.1080/00063659909477239.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, Calif.

Woelfle-Erskine, C., Larsen, L.G., and Carlson, S.M. 2017. Abiotic habitat thresholds for salmonid over-summer survival in intermittent streams. Ecosphere, **8**(2): e01645. doi:10.1002/ecs2.1645.

Zaugg, W.S. 1981. Advanced photoperiod and water temperature effects on gill Na^+-K^+ adenosine triphosphatase activity and migration of juvenile steelhead (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. **38**(7): 758–764. doi:10.1139/f81-103.

Zydlewski, G.B., Horton, G.E., Dubreuil, T.L., Letcher, B.H., Casey, S., and Zydlewski, J. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries, **31**(10): 492–502. doi:10.1577/1548-8446(2006)31[492:RMOFIS]2.0.CO;2.

Appendix A

Appendix Fig. A1 appears on the following page.

Fig. A1. Length frequency histogram for all juvenile coho salmon (left column) and steelhead (right column) captured in the Scott Creek lagoon on the first occasion of each sampling month (June through December) in 2015. Only individuals ≥65 mm fork length were included in the population estimate generated by Program MARK.