

Defining marine habitat of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, and coho salmon, *O. kisutch*, in the northern California Current System

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Abstract We investigated habitat use by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) to identify environmental characteristics that may define their optimal marine habitat. We utilized physical and biological data from four cruises in the northern California Current system from Newport, Oregon, to Crescent City, California, in June and August 2000 and 2002. A non-parametric statistical method was used to analyze and select environmental parameters that best defined ocean habitat for each species. Regression trees were generated for all cruises combined to select the most important habitat variables. Chlorophyll *a* concentration best defined habitat of yearling Chinook salmon, while decapod larvae, salinity, and neuston biovolume

defined habitat of yearling coho salmon. Using criteria from the regression tree analysis, GIS maps were produced to show that the habitat of yearling Chinook salmon was widespread over the continental shelf and the habitat of yearling coho salmon was variable and mainly north of Cape Blanco.

Keywords Regression trees · GIS · Coho salmon · Chinook salmon · California Current · Habitat

Introduction

Examination of the factors leading to variation in early marine survival of juvenile Pacific salmon (*Oncorhynchus* spp.) in the northern California Current System (CCS) is currently an area of active research (Brodeur et al. 2000, 2003; Hobday and Boehlert 2001; Mueter et al. 2002, 2005; Grimes et al. 2007). Upon ocean entrance, juvenile salmon need to adapt to and inhabit highly dynamic ocean conditions in the northern CCS, and the first few months at sea are considered critical in determining survival and ultimate run size of adult salmon (Pearcy 1992). Variable ocean conditions in the CCS complicate assessment of environmental characteristics that define marine habitat and influence survival of juvenile salmon. For example, changes in the strength of coastal upwelling may influence primary and secondary productivity (Checkley and Barth 2009), which in turn may have consequences for higher trophic levels

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by expanding or contracting the inhabitable areas for juvenile salmon in the ocean (Bi et al. 2008).

Off the Washington and Oregon coasts, research surveys have captured juvenile Chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) and measured and collected environmental data for more than a decade (Peterson et al. 2010). This work has provided insight into the marine survival of these salmonids as mediated through predation, prey availability, diet, and growth (Fisher and Pearcy 1995; Brodeur et al. 2004; Emmett et al. 2006). Fisher and Pearcy (1995) showed that juvenile Chinook salmon (≤ 400 mm FL) occurred at a median distance of 13 km from shore. Small juvenile Chinook salmon (≤ 130 mm FL) were caught mainly in relatively warm ($\geq 15^\circ\text{C}$) and low salinity (≤ 17 psu) waters, such as those in the Columbia River plume, while large juvenile Chinook salmon (> 130 mm FL) were found in cooler and more saline waters (Fisher and Pearcy 1995). Conversely, Brodeur et al. (2004) showed that juvenile salmon occupy upwelling areas with cool temperature and high salinity off southern Oregon and northern California. Juvenile Chinook salmon were caught mainly inshore of the 100-m isobath, whereas juvenile coho salmon tended to be farther offshore (Brodeur et al. 2004). Peterson et al. (2010), analyzing catches from purse seine catches from the 1980s and more recent (1998–2007) catches from trawl surveys off Oregon and Washington found that salmon were patchily distributed with Chinook salmon juveniles again found closer to shore than coho salmon juveniles.

While our understanding of juvenile salmon marine habitat in the CCS is increasing, explanatory variables have generally been limited to a few physical characteristics (i.e., temperature, salinity, water depth) and chlorophyll *a* and copepod biomass as the only biological variables (Brodeur et al. 2004; Bi et al. 2007, 2008, 2011; Peterson et al. 2010). Information is lacking on whether other physical or ocean processes also play a role and to what extent they influence the relative abundance of juvenile salmon. Juvenile salmon generally do not consume copepods and the small nets used to sample these zooplankton do not adequately collect what salmon feed upon (see Brodeur et al. 2011 and references therein). Hence, an expanded definition of marine habitat that juvenile salmon are found in is needed that considers the dominant prey items of juvenile salmon.

We investigated habitat use by juvenile Chinook salmon and coho salmon using data collected during four mesoscale cruises in 2000 and 2002 from Newport, Oregon, to Crescent City, California. A non-parametric statistical method was used to analyze and select which environmental parameters defined the ocean habitat of each species. Regression trees were generated to select the most important variables for all cruises combined. The resulting subset of variables and their criteria (i.e., splitting values) were overlaid with actual catches in a geographic information system (GIS). The primary objective was to understand which environmental characteristics may define optimal marine habitat using relative abundance of juvenile salmon catches in the northern California Current.

Materials and methods

Sample collection

Four mesoscale cruises were conducted on 29 May–11 June 2000, 28 July–12 August 2000, 1–18 June 2002, and 1–17 August 2002 (hereafter called Jun 2000, Aug 2000, Jun 2002, and Aug 2002, respectively). The sampling area was between Newport, Oregon (44.7°N) and Crescent City, California (41.9°N) over the continental shelf and slope and further west to 126.0°W (Fig. 1). Stations were sampled based upon a predetermined grid but many sampling locations were also added adaptively during the cruise depending on physical features (fronts and eddies) detected by biophysical and acoustical sampling from additional oceanographic vessels working in the same area (Brodeur et al. 2004). Physical water characteristics were measured with a conductivity-temperature-depth profiler (CTD) which was deployed to a maximum depth of 100 m or within 10 m of the bottom in shallower water. For measurements of chlorophyll *a* concentrations, water samples were collected from the 3-m depth and then processed using the cold-acetone extraction method (Arar and Collins 1997).

Neustonic zooplankton were collected with a 333- μm neuston net with a 1-m wide by 0.3-m high mouth (Reese et al. 2005; Pool and Brodeur 2006). A General Oceanics flowmeter was attached in the mouth of the net to measure the volume of water sampled. The net was towed off to the side of the vessel, outside of its

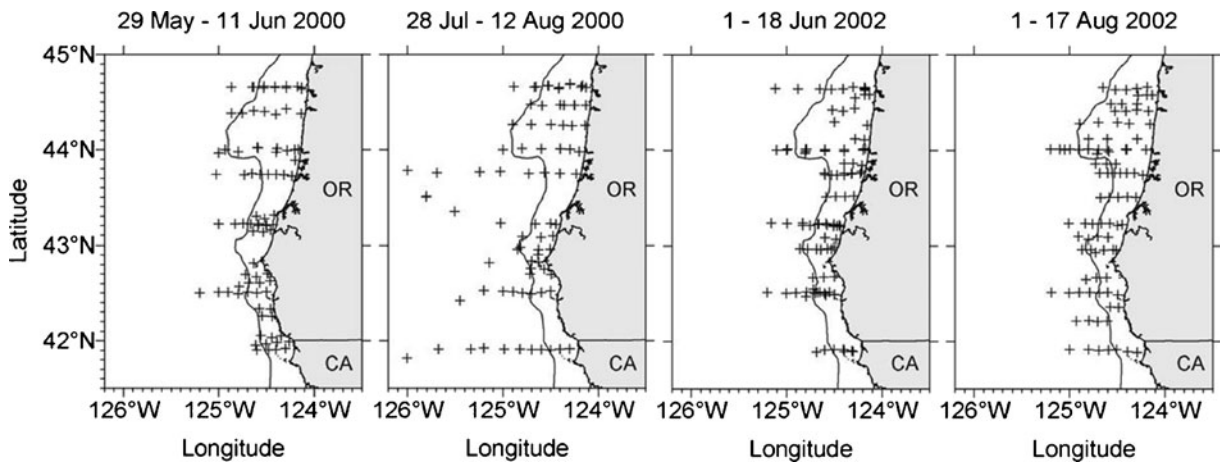


Fig. 1 Trawl sampling stations (plus signs) in June and August of 2000 and 2002

wake for 5 min at about 3.7 km h^{-1} (2 knots). In the laboratory, biovolumes were obtained prior to removing large zooplankton ($\geq 5 \text{ mm}$) for enumeration and identification.

Juvenile salmon were captured with a Nordic 264 rope trawl (Nor'Eastern Trawl Systems, Inc., Bainbridge Island, WA) with meshes ranging from 162.6 cm near the mouth to 8.9 cm in the cod end. The cod end was lined with 0.8-cm knotless mesh to retain small fish. The trawl mouth was generally 30-m wide by 18-m deep and spread apart by a pair of 3.0-m Lite foam-filled trawl doors. The trawl was then towed at the surface for 30 min, except on a few occasions when it filled prematurely with large schools of epipelagic fish or high abundance of jellyfish. Average trawling speed was 6.3 km h^{-1} . Juvenile salmon captured in the trawl were identified to species, measured to fork length, and frozen for laboratory analysis. Most sampling occurred during daylight hours.

Data analysis

Based on past and current studies, we selected environmental variables that may define potential marine habitat of juvenile salmon (Table 1). The strengths of coastal upwelling at the time of salmon capture, 6-h upwelling indices at 45°N , 125°W were obtained from an online database (http://las.pfeg.noaa.gov/las6_5/servlets/dataset). Temperature ($^\circ\text{C}$) and salinity (psu) from the 3-m depth were selected, and their gradients from 3 to 20 m were included as proxies for strength of the thermoclines and haloclines

and depth of the surface mixed layer. Density (σ_t ; kg m^{-3}) and its gradient were not used because of a high correlation between salinity and density ($n=364$, $r^2=0.90$, $P<0.001$). As indicators of primary and secondary productivity, we used chlorophyll *a* concentration ($\mu\text{g l}^{-1}$) and total neuston ($>333 \mu\text{m}$) biovolume ($\text{ml} \cdot 100 \text{ m}^{-3}$), respectively. Remaining variables were concentration (number $\cdot 100 \text{ m}^{-3}$) of all large ($\geq 5 \text{ mm}$) neuston, as well as concentrations of hyperiid amphipods, fishes, decapod larvae (zoal and megalopal stages), and euphausiids. These four taxonomic groups are numerically and gravimetrically dominant prey of juvenile salmon caught off Washington and Oregon (Brodeur et al. 2007; Daly et al. 2009). Although we were able to identify individuals of these groups down to species in all cases (Pool and Brodeur 2006), the digestive state of prey in most stomachs precluded identification beyond these higher taxonomic categories (Baldwin et al. 2008).

For each haul, catch per unit effort (CPUE) was calculated by dividing the number of juvenile salmon captured by the total volume sampled: trawl speed ($\text{m} \cdot \text{sec}^{-1}$) \times duration fished (sec) \times footrope depth (m) \times headrope width (m) and expressed as number $\cdot 10^6 \text{ m}^{-3}$. Salmonids that were captured in the trawls were separated into age classes based on length-frequency distributions, coded-wire tagging studies, and scale analysis (J. Fisher, pers. comm., 2007). Our analysis was limited to yearling Chinook salmon and yearling coho salmon. Subyearling Chinook salmon were not included because they were caught in $<4\%$ of all trawls.

A non-parametric statistical method, regression tree analysis, was used to analyze and identify which

Table 1 List of predictor variables selected for analysis of marine habitat of juvenile Chinook salmon and coho salmon

Predictor	Depth or size fraction	Unit
Temperature	3 m	°C
Salinity	3 m	psu
Temperature gradient	3–20 m	°C
Salinity gradient	3–20 m	psu
Upwelling index		$\text{m}^3 \cdot \text{s}^{-1} \cdot 100 \text{ m}^{-1}$ coastline
Chlorophyll <i>a</i> concentration	3 m	$\mu\text{g l}^{-1}$
Neuston biovolume	>333 μm	$\text{ml} \cdot 100 \text{ m}^{-3}$
Total neuston concentration	$\geq 5 \text{ mm}$	$\text{number} \cdot 100 \text{ m}^{-3}$
Hyperiid amphipod concentration	$\geq 5 \text{ mm}$	$\text{number} \cdot 100 \text{ m}^{-3}$
Fish juvenile concentration	$\geq 5 \text{ mm}$	$\text{number} \cdot 100 \text{ m}^{-3}$
Decapod larval concentration	$\geq 5 \text{ mm}$	$\text{number} \cdot 100 \text{ m}^{-3}$
Euphausiid concentration	$\geq 5 \text{ mm}$	$\text{number} \cdot 100 \text{ m}^{-3}$

of these environmental parameters defined the ocean habitat of each salmon species. Although ocean conditions differed by cruise, all cruises were combined for analyses to provide insight into the range of conditions to which juvenile salmon may adapt. Regression trees are generated through recursive partitioning of data into subgroups that clarify non-linear relationships between a response and its associated predictors (Breiman et al. 1984; Therneau and Atkinson 1997; De'ath and Fabricius 2000). Data are divided by a predictor variable (e.g., temperature, neuston volume) where its value splits a group of response data (i.e., salmon CPUE) into two. Each division is determined by minimization of the sum of squares within two subgroups, and division continues until subgroups are relatively homogeneous. Graphically, the base of the tree begins at the top with the predictor that first divides a group of data and that explains most of the variation in the data, and subsequent splits and associated predictors are added that explain progressively less variation in the data. These subsequent splits end with terminal nodes or leaves which contain the final, relatively homogeneous subgroups. The length of each branch or vertical line represents the proportion of the total sum of squares explained by a split. A predictor variable can be reused for subsequent splits and can be used as a surrogate to handle missing cases of a predictor. After a full regression tree is generated, it is pruned to a smaller, visually interpretable tree. The pruning follows a minimum rule based on a set of fifty 10-fold cross validations so that a pruned tree minimizes relative error (Breiman et al. 1984; De'ath

and Fabricius 2000). Cross validation is a process in which ten random subgroups of data are used to calculate the prediction error. Using fifty cross validations, the minimum rule determines the most frequently occurring number of splits where the cross-validation error is at a minimum. The tree is then pruned to where the number of splits is the most frequent. Trees were generated in and analyzed using the *rpart* package, version 3.1–43 in R, a statistical software program (R Development Core Team 2006; Therneau and Atkinson 2006).

In the regression tree analysis, log-transformed CPUE of salmon species per age class (yearling Chinook salmon and coho salmon) was the response, and environmental variables were the predictors. Because CPUE was considered a count or discrete variable, we used the Poisson method of the regression tree analysis. For all cruises combined, full regression trees were generated until a complexity parameter of 0.001 was reached, and then trees were pruned.

To spatially display the results of the regression tree analysis, we used ArcGIS version 9.1 (ESRI, Redlands, CA) to map prominently utilized and non-utilized habitats of juvenile salmon. To accomplish this, we used geostatistical modeling techniques to geographically represent the spatial extent of the dominant habitat variables obtained at each sampling station throughout the study region (Johnston et al. 2001). This method provides a means to interpolate predicted values between sampled stations (no extrapolations were used). It has been used previously to determine the spatial distributions of various species and community characteristics within this study region

and is described in detail by Reese and Brodeur (2006). Habitat maps of dominant environmental predictors found for each salmon species were combined within the GIS using the Spatial Analyst extension and then salmon catches at each station were overlaid on the dominant habitat variables.

Results

Yearling Chinook salmon

Yearling Chinook salmon were captured in 67 of 366 total hauls (Table 2). The initial regression tree selected 8 predictors with 18 terminal nodes. The tree was pruned to 1 predictor and 2 terminal nodes (Fig. 2). Most yearling Chinook salmon were captured from stations with chlorophyll *a* concentrations of more than $1.4 \mu\text{g} \cdot \text{l}^{-1}$. In the full regression tree, total neuston concentration was the second predictor with a split at $2.5 \cdot 100 \text{ m}^{-3}$ and temperature was the third predictor with a split of 10.1°C . However, standard pruning rules precluded use of more than one variable in the final tree.

The area of defined habitat for yearling Chinook salmon was most similar among the June cruises (Fig. 3). During the June cruises, chlorophyll concentrations were highest near shore and decreased with distance from shore, and nearly all catches of yearling Chinook salmon were made within the defined habitat and relatively close to shore, with none found beyond the shelf break (200-m isobath). During the August cruises, yearling Chinook salmon were found further offshore in 2002 than in 2000, even at few stations beyond the shelf break coincident with the high chlorophyll concentrations extending further offshore at this time of the year.

Table 2 Number of hauls deployed and number of positive hauls for yearling Chinook salmon and coho salmon by cruise

Cruise	Total deployed	Yearling Chinook salmon	Yearling Coho salmon
June 2000	84	7	14
August 2000	79	17	18
June 2002	104	27	27
August 2002	99	16	18
Total	366	67	77

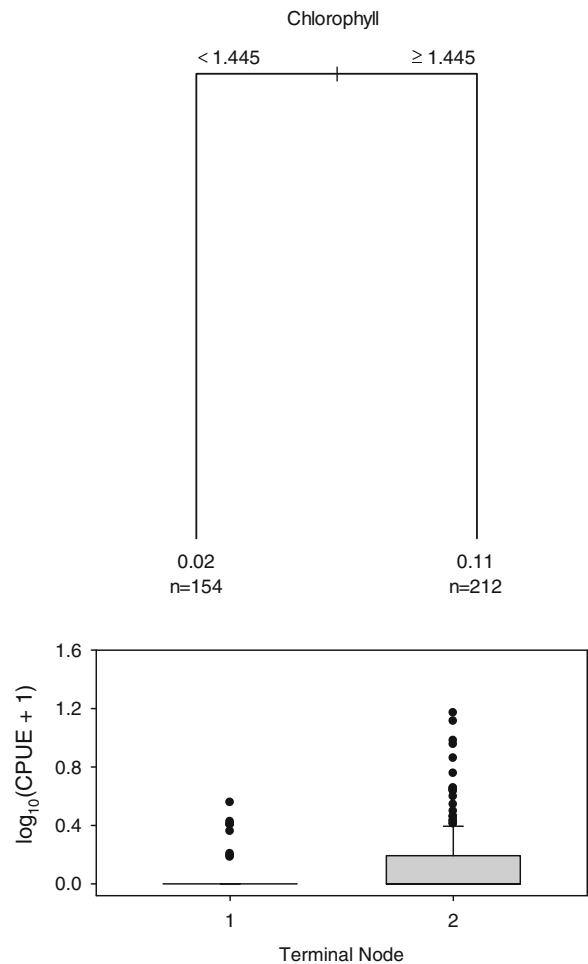


Fig. 2 Pruned regression tree (top) showing environmental variables and splitting values to define preferred and non-preferred habitats of yearling Chinook salmon. Under each terminal node, the mean CPUE is followed by the number of hauls. The variable unit is: chlorophyll *a* = $\mu\text{g} \cdot \text{l}^{-1}$. The box plot (bottom) shows log-transformed CPUE per terminal node. The boxes denote the 75th (top end of box) and 90th (whisker) percentiles with outliers (dots)

Yearling coho salmon

Yearling coho salmon were captured in 77 of 366 total hauls (Table 2). The initial regression tree selected 11 predictors with 20 terminal nodes, and the tree was pruned to 3 predictors and 4 terminal nodes (Fig. 4). Most yearling coho salmon (in terms of CPUE) were captured at stations with larval decapod concentrations $\geq 0.74 \cdot 100 \text{ m}^{-3}$ and salinity < 33.55 psu. Some yearlings were also captured at stations with neuston biovolumes $< 76.42 \text{ ml} \cdot 100 \text{ m}^{-3}$.

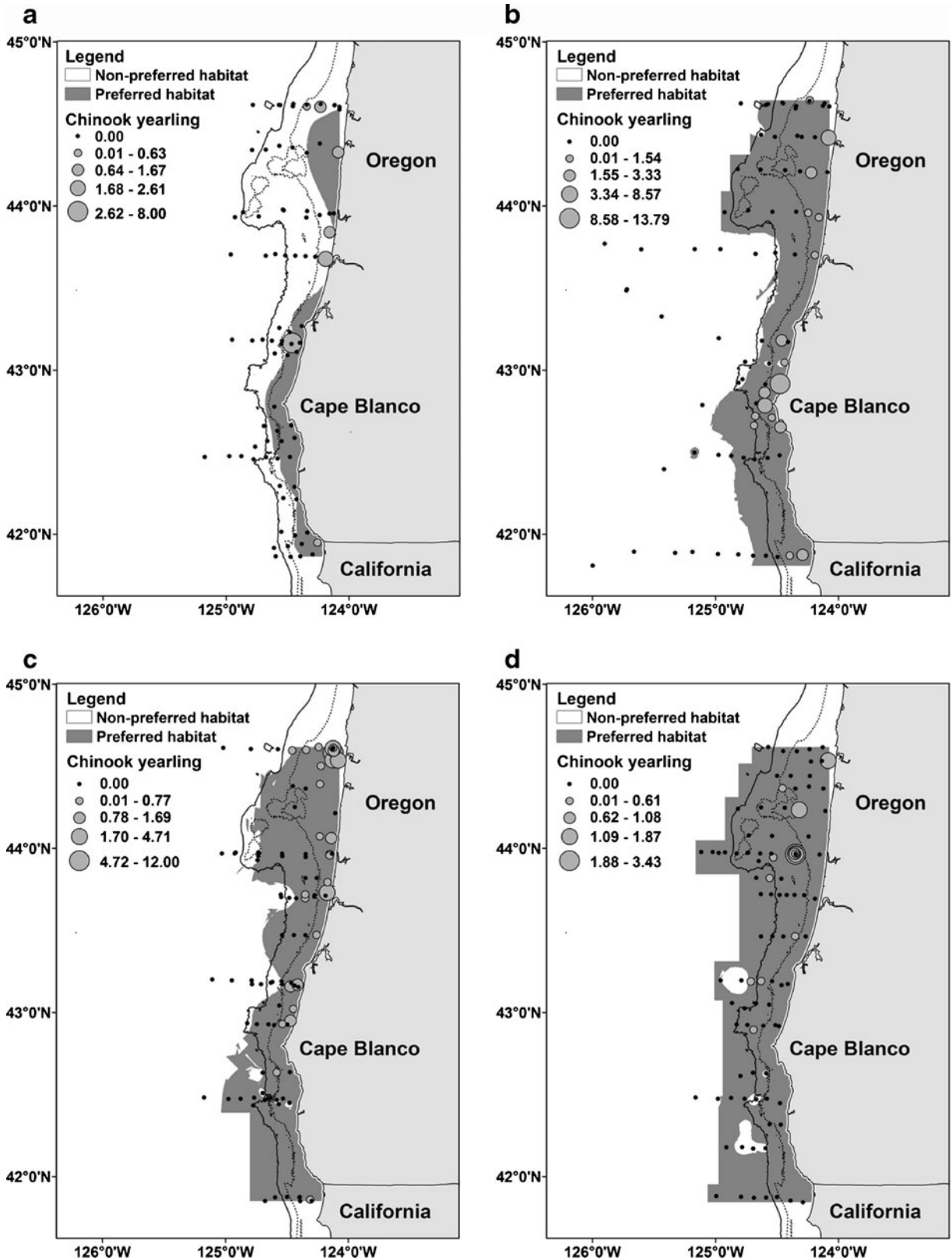


Fig. 3 Maps showing the preferred and non-preferred habitat of yearling Chinook salmon and its distribution in **a** June 2000, **b** August 2000, **c** June 2002, and **d** August 2002. The dotted and solid lines next to the coastline represent the 100- and 200-m isobaths, respectively. Salmon abundance is expressed in CPUE

The defined habitat of yearling coho salmon in terms of larval decapod concentrations ($\geq 0.74 \cdot 100 \text{ m}^{-3}$) and salinity ($< 33.55 \text{ psu}$) was more limited during the 2000 cruises than during the 2002 cruises. Yearling coho salmon catches were typically more

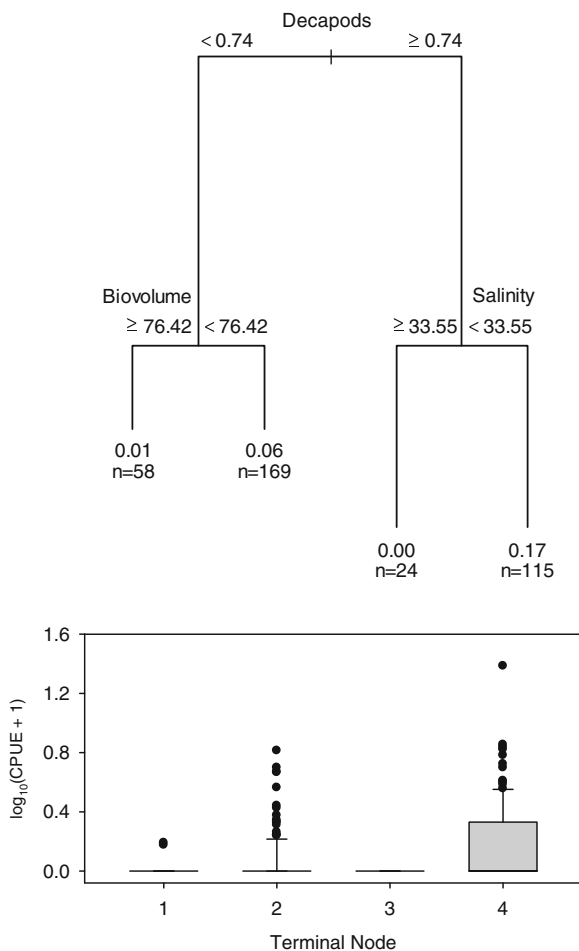


Fig. 4 Pruned regression tree (top) showing environmental variables and splitting values to define preferred and non-preferred habitats of yearling coho salmon. Under each terminal node, the mean CPUE is followed by the number of hauls. The variable units are: decapods = number $\cdot 100 \text{ m}^{-3}$, biovolume = $\text{ml} \cdot 100 \text{ m}^{-3}$, and salinity = psu. The box plot (bottom) shows log-transformed CPUE per terminal node. The boxes denote the median (line inside box), 75th (top end of box) and 90th (whisker) percentiles, and outliers (dots)

offshore compared to catches of yearling Chinook salmon (Figs. 3 and 5). Yearling coho salmon tended to be most abundant on the mid-shelf (100 m–200 m isobaths) during all cruises. In terms of suitable habitat based on model results, the August cruises showed a better fit to the catch data than did the June cruises. During June 2000, yearling coho salmon were mostly limited to relatively few stations close to shore and were within the modeled habitat conditions. An exception to this occurred at three neighboring stations on the northernmost transect line. These stations were sampled twice on different days resulting in either positive catches or no catches which introduced considerable variability in determining suitable habitat conditions there. At these stations, 4 positive catches had no decapod larvae in the neuston ($\geq 5\text{-mm}$ size fraction). During June 2002, suitable habitat conditions were found over most of the sampled region with the exception of the southern portion of the study that was close to shore. In addition, during August 2000, modeled conditions were met at several offshore stations, however, yearling coho salmon are typically not found this far offshore and no positive catches were obtained.

Discussion

This study identified the relative importance of environmental variables in defining preferred marine habitat for juvenile Chinook and coho salmon. Our analysis reduced a large number of potential habitat variables to a select few, and provided an optimal range of these variables with which to define habitat for juveniles of both species. In addition, we focused on bottom-up controls in terms of suitable habitat characteristics. Coastal upwelling occurs sporadically along the Oregon coast throughout the upwelling season (Checkley and Barth 2009). When these pulsed events occur, cooler, nutrient-rich water that is brought to the surface fuels primary productivity. This typically occurs close to shore, with higher chlorophyll concentrations occurring along the shore and decreasing with increased distance from shore. The upwelling and subsequent increased chlorophyll concentrations correspond with our results.

One possible explanation for higher catches of yearling Chinook salmon at the nearshore, southernmost stations is that this location is in an area known for

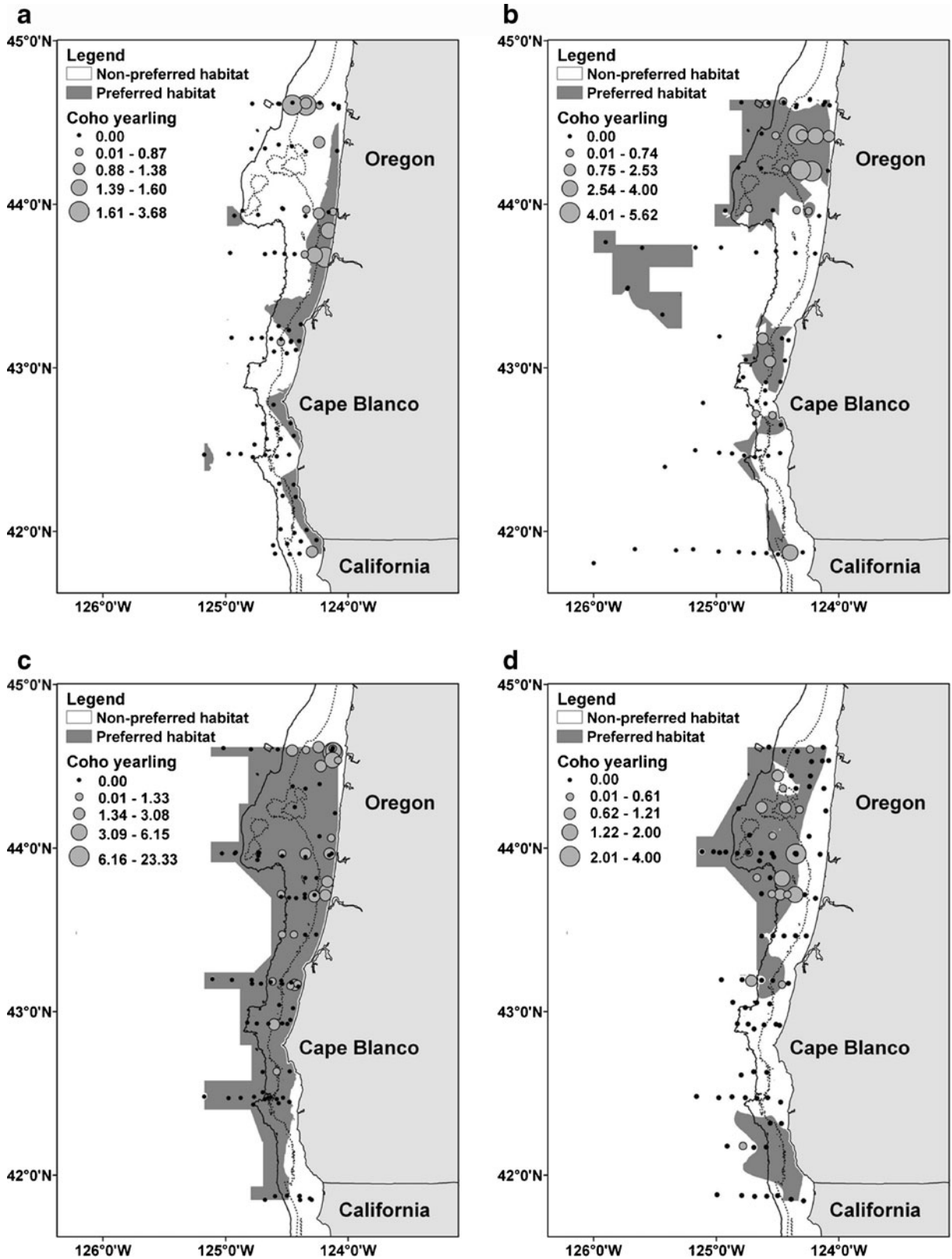


Fig. 5 Maps showing the preferred and non-preferred habitat of yearling coho salmon and its distribution in **a** June 2000, **b** August 2000, **c** June 2002, and **d** August 2002. The dotted and solid lines next to the coastline represent the 100- and 200-m isobaths, respectively. Salmon abundance is expressed in CPUE

upwelling and a persistent biological hotspot (Reese and Brodeur 2006). Moreover, juvenile Chinook salmon from Oregon coastal rivers south of Cape Blanco ($\sim 42.8^\circ\text{N}$) tend to migrate southward and mature in waters off southern Oregon and northern California (Nicholas and Hankin 1989; Myers et al. 1998). Based on genetic analysis of juvenile Chinook salmon captured between Cape Blanco and California in August 2000, 53% were from the Rogue, Chetco, and Winchuck rivers south of the cape, and a considerable proportion of the other salmonids caught originated from rivers in California (Brodeur et al. 2004). The location of these natal streams, direction of ocean migration, and relatively strong upwelling conditions in this area likely contributed to the catches of yearling Chinook salmon on the southernmost transect.

The increase in yearling coho salmon catches from south to north corresponded with higher concentrations of decapod larvae except in June 2002, when decapod larvae also were concentrated south of areas designated as preferred habitat. During all four cruises, Dungeness crab (*Cancer magister*) megalopae were the most abundant and frequently occurring decapods in the neustonic mesozooplankton, followed by Oregon and red rock crab (*C. oregonensis/C. productus*) megalopae (Reese et al. 2005; Pool and Brodeur 2006). In addition, each of these taxa was one of the ten most abundant mesozooplankton in the neuston, was more abundant in June than in August, and was more abundant in 2002 than in 2000. Juvenile coho salmon normally consume *Cancer* spp. megalopae and appear to selectively feed upon them relative to their availability in the plankton (Schabetsberger et al. 2003). In diets of salmon examined during this study, decapod larvae were more abundant in June than in August, especially in 2002 (Miller and Brodeur 2007; Baldwin et al. 2008), and this may be a function of their life history in which the megalopal stage settles between June and August.

From June to August, a proportion of yearling coho salmon migrates to the north of their natal streams, but many originate in coastal rivers of Oregon and remain off the Oregon coast during the

entire summer (Pearcy and Fisher 1988; Peterson et al. 2010). Indeed, genetic analysis of the coho salmon collected in our sampling in 2000 confirmed that they mostly originated from central Oregon and northern California rivers (Brodeur et al. 2004). This region is somewhat influenced by freshwater discharge from the Columbia River which produces a distinct low salinity plume that typically moves south in the summer and is often found offshore in the northern part of the study region (Hickey and Banas 2003). Our analysis suggests that yearling coho salmon were more likely to be found in lower than normal salinity waters that likely originated from the Columbia River.

The analytical techniques and potential habitat variables generated in the present study expanded the existing definition of optimal marine habitat for juvenile Chinook and coho salmon using the distribution of both physical factors and the food resources that are the major prey resources of juvenile coho and Chinook salmon in coastal waters (Baldwin et al. 2008; Daly et al. 2009; Brodeur et al. 2011). Using these techniques, we showed that several environmental and biological variables did appear to be related to juvenile salmon distribution to a limited extent. In addition, other physical or biological variables that we were not able to measure (horizontal gradients such as temperature or salinity fronts, larval decapod concentrations) may also be important to the distribution of these fish (Emmett et al. 2004; DeRobertis et al. 2005). Salmon are patchily distributed in the ocean environment (Peterson et al. 2010) and our tows which extended over several km in length may have integrated across multiple ‘microhabitats’ that we were not able to detect. Also, the relatively low number of positive catches of juvenile Chinook and coho salmon likely limited our ability to determine the precise habitat characteristics for both species. To increase our sample size, we combined data from all cruises to determine habitat characteristics that each species are likely to be associated with, and this is a potential reason for the suboptimal fit in some of the mapped representations of modeled results. Nonetheless, our results support previous findings relating to the distribution of these two species and provide additional and valuable information on the habitat characteristics important to both species.

Regression tree analysis has only recently been used in oceanographic work, but has been applied to studies ranging from sessile species such as corals

(De'ath and Fabricius 2000; Fabricius and McCorry 2006) to migratory species such as sharks and whales (Friedlaender et al. 2006; Goetz et al. 2007; Froeshke et al. 2010). Applications of this methodology to fish species are rare (Norcross et al. 1997; Gutiérrez et al. 2007; Haynes et al. 2008) but could yield some useful information of fish habitat preferences. While our analytical approach to juvenile salmon habitat in the ocean had not been done before, it clearly described environmental characteristics that may make some habitats more attractive for juvenile salmon.

Zero-inflated counts are common in ecological studies of species abundance and distribution (Bi et al. 2007). Because we were interested in defining preferred as well as non-preferred marine habitat, it was necessary to include the zero observations of juvenile salmon catches. However, juvenile salmon may have avoided the trawl and vessel in locations of preferred marine habitat, or they may not have reached these locations by the time of trawling due to migration timing, particularly from areas of great distance from the natal streams.

In conclusion, this study led to an increased understanding of which environmental characteristics may play a role in the marine habitat of juvenile salmon in the CCS. Other variables that we did not measure may play a more important role than, or work in conjunction with, the variables indicated here. The regression tree analysis and GIS mapping were useful in producing visually interpretable habitats which changed in size and area between cruises.

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References

Arar EJ, Collins GB (1997) Method 445.0: *In vitro* determination of chlorophyll *a* and pheophytin *a* in marine and freshwater algae by fluorescence. Revision 1.2. U.S. Environmental Protection Agency, Cincinnati, Ohio

Baldwin RE, Miller TW, Brodeur RD, Jacobson KC (2008) Expanding the foraging history of juvenile salmon: combining stomach-content and macroparasite-community analyses for studying marine diets. *J Fish Biol* 72:1268–1294

Bi H, Ruppel RE, Peterson WT (2007) Modeling the pelagic habitat of salmon off the Pacific Northwest (USA) coast

using logistic regression. *Mar Ecol Prog Ser* 336:249–265

Bi H, Ruppel RE, Peterson WT, Casillas E (2008) Spatial distribution of ocean habitat of yearling Chinook salmon (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon off Washington and Oregon, USA. *Fish Oceanogr* 17:463–476

Bi H, Peterson WT, Lamb J, Casillas E (2011) Copepods and salmon: characterizing the spatial distribution of juvenile salmon along the Washington and Oregon coast, USA. *Fish Oceanogr* 20:125–138

Breiman L, Friedman JH, Olshen RA, Stone CJ (1984) Classification and regression trees. Chapman and Hall, New York

Brodeur RD, Boehlert GW, Casillas E, Eldridge MB, Helle JH, Peterson WT, Heard WR, Lindley ST, Schiewe MH (2000) A coordinated research plan for estuarine and ocean research on Pacific salmon. *Fisheries* 25:7–16

Brodeur RD, Myers KW, Helle JH (2003) Research conducted by the United States on the early ocean life history of Pacific salmon. *North Pacific Anad Fish Comm Bull* 3:89–131

Brodeur RD, Fisher JP, Teel DJ, Emmett RL, Casillas E, Miller TW (2004) Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the Northern California Current. *Fish Bull* 102:25–46

Brodeur RD, Daly EA, Sturdevant MV, Miller TW, Moss JH, Thiess M, Trudel M, Weitkamp LA, Armstrong J, Norton EC (2007) Regional comparisons of juvenile salmon (*Oncorhynchus* spp.) feeding in coastal marine waters off the west coast of North America. In: Grimes CB, Brodeur RD, Halderson LJ, McKinnell SM (eds) *The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons*. American Fisheries Society, Symposium 57, Bethesda, Maryland, pp 183–203

Brodeur RD, Daly EA, Benkwitt CE, Morgan CA, Emmett RL (2011) Catching the prey: sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook salmon during their early marine residence. *Fish Res* 108:65–73

Checkley DA Jr, Barth JA (2009) Patterns and processes in the California Current system. *Prog Oceanogr* 83:49–64

Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: important for marine survival? *Trans Amer Fish Soc* 138:1420–1438

De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192

DeRobertis A, Morgan CA, Schabetsberger RA, Zabel RW, Brodeur RD, Emmett RL, Knight CM, Krutzikowsky GK, Casillas E (2005) Frontal regions of the Columbia River plume fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon. *Mar Ecol Prog Ser* 299:33–44

Emmett RL, Brodeur RD, Orton PM (2004) The vertical distribution of juvenile salmon (*Oncorhynchus* spp.) and associated fishes in the Columbia River plume. *Fish Oceanogr* 13:392–402

Emmett RL, Krutzikowsky GK, Bentley P (2006) Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer

- 1998–2003: Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. *Prog Oceanogr* 68:1–26
- Fabricius KE, McCorry D (2006) Changes in octocoral communities and benthic cover along a water quality gradient in the reefs of Hong Kong. *Mar Poll Bull* 52:22–33
- Fisher JP, Pearcy WG (1995) Distribution, migration, and growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, off Oregon and Washington. *Fish Bull* 93:274–289
- Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Mar Ecol Prog Ser* 317:297–310
- Froeshke J, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. *Mar Ecol Prog Ser* 407:279–292
- Goetz KT, Rugh DJ, Read AJ, Hobbs RC (2007) Habitat use in a marine ecosystem: beluga whales *Delphinapterus leucas* in Cook Inlet, Alaska. *Mar Ecol Prog Ser* 330:247–256
- Grimes CB, Brodeur RD, Halderson LJ, McKinnell SM (eds) (2007) The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland
- Gutiérrez M, Swartzman G, Bertrand A, Bertrand S (2007) Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983–2003. *Fish Oceanogr* 16:155–168
- Haynes TB, Robinson CKL, Dearden P (2008) Modelling nearshore intertidal habitat use of young-of-the-year Pacific sand lance (*Ammodytes hexapterus*) in Barkley Sound, British Columbia, Canada. *Env Biol Fish* 83:487–498
- Hickey BM, Banas NS (2003) Oceanography of the US Pacific Northwest coastal ocean and estuaries with application to coastal ecology. *Estuaries* 26:1010–1031
- Hobday AJ, Boehlert GW (2001) The role of coastal ocean variation in spatial and temporal patterns in survival and size of coho salmon (*Oncorhynchus kisutch*). *Can J Fish Aquat Sci* 58:2021–2036
- Johnston K, Ver Hoef JM, Krivoruchko K, Lucas N (2001) Using ArcGIS geostatistical analyst. ESRI, Redlands
- Miller TW, Brodeur RD (2007) Diet of and trophic relationships among dominant marine nekton within the Northern California Current ecosystem. *Fish Bull* 105:548–559
- Mueter FJ, Ware DM, Peterman RM (2002) Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific Ocean. *Fish Oceanogr* 11:205–218
- Mueter FJ, Pyper BJ, Peterman RM (2005) Relationships between coastal ocean conditions and survival rates of Northeast Pacific salmon at multiple lags. *Trans Amer Fish Soc* 134:105–119
- Myers JM, Kope RG, Bryant GJ, Teel D, Lierheimer LJ, Wainwright TC, Grant WS, Waknitz FW, Neely K, Lindley ST, Waples RS (1998) Status review of chinook salmon in Washington, Idaho, Oregon, and California. U S Dept Commer, NOAA Tech Memo NMFS-NWFSC-35
- Nicholas JW, Hankin DG (1989) Chinook salmon populations in Oregon coastal river basins: description of life histories and assessment of recent trends in run strengths. Oregon Dept Fish Wild, Fish Division, Info Rpt 88–1
- Norcross BL, Muter FJ, Holladay BA (1997) Habitat models for juvenile pleuronectids around Kodiak Island, Alaska. *Fish Bull* 95:504–520
- Pearcy WG (1992) Ocean ecology of North Pacific salmonids. Washington Sea Grant Program, University of Washington Press, Seattle, WA
- Pearcy WG, Fisher JP (1988) Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean. *Fish Bull* 86:173–195
- Peterson WT, Morgan CA, Fisher JP, Casillas E (2010) Ocean distribution and habitat associations of yearling coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) in the northern California Current. *Fish Oceanogr* 19:508–525
- Pool SS, Brodeur RD (2006) Neustonic mesozooplankton abundance and distribution in the northern California Current, 2000 and 2002. U S Dept Commer, NOAA Tech Memo NMFS-NWFSC-74
- Reese DC, Brodeur RD (2006) Identifying and characterizing biological hotspots in the Northern California Current. *Deep-Sea Res II* 53:291–314
- Reese DC, Miller TW, Brodeur RD (2005) Community structure of near-surface zooplankton in the northern California Current in relation to oceanographic conditions. *Deep-Sea Res II* 52:29–50
- R Development Core Team (2006) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Schabetsberger R, Morgan CA, Brodeur RD, Potts CL, Peterson WT, Emmett RL (2003) Prey selectivity and diel feeding chronology of juvenile chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. *Fish Oceanogr* 12:523–540
- Therneau TM, Atkinson EJ (1997) An introduction to recursive partitioning using the RPART routines. Technical report series no 61, Department of Health Sciences Research, Mayo Clinic, Rochester, Minnesota
- Therneau TM, Atkinson B (2006) rpart: Recursive partitioning. R package version 3.1-33. S-PLUS 6.x original at <http://mayoresearch.mayo.edu/mayo/research/biostat/splusfunctions.cfm>