Ontogenetic shifts in the diets of juvenile Chinook Salmon: new insight from stable isotopes and fatty acids

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Abstract Variations in marine prey availability and nutritional quality can affect juvenile salmon growth and survival during early ocean residence. Salmon growth, and hence survival, may be related to the onset of piscivory, but there is limited knowledge on the interplay between the prey field, environment, and salmon ontogeny. Subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) and their potential prey were sampled in coastal waters off Willapa Bay, USA to explore this issue. Three seasonal prey assemblages were identified, occurring in spring (May), early summer (June – July), and late summer (August – September). The onset of piscivory, based on salmon stomach contents, fatty acids, and stable isotopes occurred later in 2011 compared to 2012, and coincided with the appearance of Northern Anchovy (*Engraulis mordax*). Salmon fork length (FL) and carbon isotope values (δ^{13}C) increased with a fatty acid biomarker for marine phytoplankton and decreased with a freshwater marker, indicating dietary carbon sources changed as salmon emigrated from the Columbia River. Salmon FL also increased with nitrogen isotope ratios (δ^{15}N), trophic position, and a fatty acid marker for piscivory – a consequence of the ontogenetic shift in diet to fish. Salmon grew faster and obtained larger size and condition by September 2011 compared to 2012, which was related to inter-annual differences in ocean conditions and the duration over which Northern Anchovy were available. Our results support the idea that juvenile salmon growth depends on the onset and duration of piscivory, suggesting both of these factors may be important components of lifetime growth and fitness.

Keywords Juvenile salmon · Salmon prey · Salmon growth · Trophic ecology · Stable isotopes · Lipids · Fatty acids

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Introduction

The occurrence of ontogenetic, or size-related, shifts in diet or habitat are prevalent in nature and important in shaping species interactions and community structure (Werner and Gilliam 1984). Pacific salmon (*Oncorhynchus* spp.) populations undergo ontogenetic shifts in both diet and habitat as they migrate from freshwater to saltwater, and research suggests that year class strength is determined during this critical period (Pearcy 1992; Beamish et al. 2004; Pearcy and McKinnell 2007). A suite of environmental factors during early marine residence (e.g., physical conditions, plankton and predator abundance) have recently been shown to correlate with salmon survival (Burke et al. 2013; Miller et al. 2013, 2014), but identifying specific mechanisms that account for juvenile salmon mortality in the ocean remains a challenge. Because predation pressure and selective mortality may be higher in smaller or slower growing fish, rapid growth may provide a survival advantage during ontogeny (Zabel and Williams 2002; Claiborne et al. 2011; Duffy and Beauchamp 2011). Rapid growth may reduce the potential pool of competitors, predators, and pathogens, as well as provide sufficient energetic stores needed to survive the first winter at sea (Beamish and Mahnken 2001).

Across several taxa of fish that become piscivorous during ontogeny, many experience dramatic increases in growth following the onset of piscivory (i.e. when fish become mostly piscivorous; see reviews by Juanes 1994; Mittelbach and Persson 1998). Variations in the timing of the onset of piscivory are related to predator size, prey availability, and environmental variability (Juanes et al. 2002; Hansen et al. 2013). Bigger juveniles have larger gape widths, more developed jaw structures, larger reaction distances, better visual acuity, and swim faster than smaller conspecifics. Collectively, these attributes allow fish of a certain size expand their trophic niche. Predator and prey phenologies may also determine the onset of piscivory (Juanes 1994). Predators and prey respond differently to environmental cues across species and life stages. For example, anomalously high temperatures that shift the timing of predator migration (Anderson et al. 2013) may lead to temporal or spatial mismatches between predator and prey (Cushing 1972) and advance or delay the onset of piscivory.

For juvenile Chinook Salmon (*Oncorhynchus tshawytscha*), whose diets during early marine residence have been extensively studied (Peterson et al. 1982; Emmett et al. 1986; Brodeur et al. 2007), there is clear support for an ontogenetic shift from invertebrate and terrestrial insect prey to piscivory of larval and young-of-the-year (YOY) marine fishes (Brodeur 1991; Daly et al. 2009; Duffy et al. 2010). Despite this, quantitative estimates of potential prey fields, relationships between prey community and environmental variables, information on the timing and size at the onset of piscivory, and the effects of prey quality on salmon growth remain understudied (but see Schabetsberger et al. 2003; Brodeur et al. 2011; Wells et al. 2012). Juvenile salmon size and survival are related to climate across broad scales (Beamish and Bouillon 1993; Mantua et al. 1997) and expected to increase when conditions during the first few months of ocean residence are favorable (i.e. during cool, productive, upwelling conditions) and when lipid-rich prey are plentiful (Peterson et al. 2014). Therefore the onset of piscivory might occur earlier when ocean conditions are favorable.

Tracking ontogenetic shifts in diet from salmon stomach contents alone has its inherent limitations. While providing considerable taxonomic resolution, observations are temporally limited to the most recent meal, and interpretations based on quantitative measures can be biased by differences in digestion rates (Rindorf and Lewy 2011). A more informative approach combines stomach content analysis with chemical analyses of trophic biomarkers from lipids (fatty acids) and stable isotopes. Fatty acids and bulk stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) measured in the muscle tissue of consumers reflect diet integrated over weeks to months (Fry 2006; Copeman et al. 2016; Vander Zanden et al. 2015). While carbon isotopes and some fatty acid biomarkers generally reflect sources of primary production (Peterson and Fry 1987; Budge and Parrish 1998; Parrish 2013), nitrogen isotopes and other fatty acid biomarkers vary with nutrient source and consumer trophic position (Post 2002; El-Sabaawi et al. 2009; Daly et al. 2010). When combined, stomach content and trophic biomarker analyses provide a more robust method for recent (weeks to months) diet reconstruction than either method alone. The goal of our study was to identify and evaluate the timing and size at the onset of piscivory in a population of juvenile Chinook Salmon using a combination of field sampling of potential prey with measurements of salmon size, growth, stomach

contents, stable isotopes, and fatty acids. We defined the onset of piscivory as the timing or size when salmon consumed more fish prey by wet weight than any other prey category.

Our study was divided into three parts. First, we characterized seasonal and annual variations in the salmon prey field by sampling potential prey over two years and identifying environmental variables associated with prey community composition. Next, we developed metrics to account for variation in juvenile salmon size, growth, and body condition. For this analysis, we selected an abundant stock group of upper Columbia summer-fall Chinook Salmon (UCSF) that was repeatedly sampled through time and identified using genetics. Subyearlings from the UCSF stock group have been detected exiting the Columbia River from May through November, with abundance peaking in July (Weitkamp et al. 2015). Because UCSF subyearlings remain concentrated nearshore along the Oregon and Washington coasts during their first few months at sea (Fisher et al. 2014; Teel et al. 2015) this stock group is ideal for a longitudinal foraging study. Lastly, we evaluated ontogenetic changes in salmon diet using direct observations (stomach content analysis), stable isotopes, and fatty acids. In response to the ontogenetic shift in habitat from freshwater to saltwater, we expected changes in salmon carbon stable isotopes and phytoplankton fatty acid biomarkers, indicating changes in the carbon pool at the base of the food web. We hypothesized that the onset of piscivory would be related to the availability of marine fish prey and that piscivorous salmon would be larger, in better condition, and grow faster than salmon feeding on invertebrates. Compared to invertebrate feeders, we also expected that piscivores would have higher stable nitrogen isotope and fatty acid marker values related to trophic position but that there would be a lag of at least a month between consumption of fish prey and expression of diet in consumer tissues (Copeman et al. 2013; Heady and Moore 2013; Vander Zanden et al. 2015). This is the first study to quantify seasonality in the salmon prey field using a trawling method designed to sample micronekton upon which juvenile salmon feed. It is also the first study to present information on ontogenetic shifts in juvenile Chinook Salmon diets using an integrative approach that combines stomach content, stable isotopes and fatty acid analyses.

Methods

Field collections

We sampled two stations located off Willapa Bay, Washington, USA (46° 40′ N) a total of 52 times during monthly cruises from late-May through late-September 2011 and 2012 (Fig. 1). Each station was sampled 2–4 times per cruise. The first station was located 9 nautical miles (nm) offshore (16.7 km) and the second station was located 14 nm (26.0 km) offshore. Sampling occurred during daylight hours when juvenile salmon feed (Brodeur et al. 2011). There was no cruise in June 2012 due to difficulties chartering a vessel. We collected animals used in this study under Scientific Research Permit 1410 issued to the Northwest Fisheries Science Center under the authority of Section 10(a)(1)(A) of the Endangered Species Act, Scientific Taking Permit 17,203 issued by Oregon Department of Fish and Wildlife, and Washington State Scientific Collection Permit 12–128.

We fished for salmon and their potential prey by deploying a 264 Nordic rope trawl (NET Systems Bainbridge Island, Washington) for 15 min at an average speed of 5.7 km hr.$^{-1}$ from the chartered commercial fishing vessel *F/V Miss Sue*. The trawl had variable mesh sizes (162.6 cm at the mouth to 8.9 cm at the cod end), with a 6.1 m long, 0.3 cm knotless liner sewn into the cod end. This gear has been used to successfully sample micronekton at mid-water (30 m) depths (Phillips et al. 2009) and was the type of gear recommended by Brodeur et al. (2011) to best sample all potential salmon prey types. We recorded GPS locations at the start and end of each haul and estimated volume swept (m^3) by multiplying distance trawled (m) by the mouth area of the net (336 m^2). Hydrographic information was collected to within 5 m from the bottom by deploying a Seabird SBE 25 conductivity, temperature, and depth (CTD) profiler at each station. The CTD recorded water temperature (°C), salinity (psu), density (kg m^{-3}), turbidity (mg m^{-3}), fluorescence (mg m^{-3}), dissolved oxygen concentration (ml l^{-1}), and dissolved oxygen saturation (%).

Analysis of the prey field

All potential prey items collected in the trawl were sorted by size (<80 mm total length; TL and <3.0 g), frozen, and transported back to the laboratory. Up to 30

individuals per taxon and station were measured (nearest mm) and weighed (nearest 0.01 g). Prey field biomass estimates were calculated for each prey type and station by dividing the total mass of the prey by the volume of water sampled by the trawl net, standardized to µg m^{-3} by multiplying by 1000, and averaged by cruise (Appendix).

Size at and timing of ocean entry varies considerably for populations of salmon originating from the Columbia River basin (Weitkamp et al. 2015). Development of the prey field is also highly variable and dependent on environmental conditions, thus contributing to potential variability in the prey field juvenile salmon first encounter. We tested for seasonal variation in the salmon prey field by conducting ecological analyses on the community structure of catch data. Data were evaluated using nonparametric multi-response permutation procedures (Mielke and Berry 2001) and nonmetric multidimensional scaling (NMS; Kruskal 1964) with the Sørensen distance measure in the statistical package PC-ORD v. 6.07 (MjM Software Design). Because we were interested in seasonality of the prey field, we used nonparametric multi-response permutation tests to test the hypothesis of no difference in prey field community by month across years. We used NMS to ordinate sample units (biomass by haul) in species space to identify sample unit clusters with similar prey field community compositions. Biomass estimates were normalized using a generalized logarithmic transformation [log($x + x_{min}$) − log(x_{min})] to reduce bias from overly abundant species and to account for zero truncation in the data (McCune and Grace 2002).

In NMS, the most dissimilar samples are farthest apart and the most similar samples closest together. To measure the success of the prey community ordination, we calculated a stress value from 250 runs of real data starting from a random configuration (Mather 1976). Monte Carlo simulations were conducted with an additional 250 runs of randomized data, which were then compared to the real data. Statistical significance (α = 0.05) was calculated as the proportion of randomized runs with stress less than or equal to the observed stress.

Indicators of the physical ocean environment such as temperature and salinity are related to salmon recruitment (Peterson et al. 2014). We hypothesized that coastal ocean environmental variables would also be related to the salmon prey community so we evaluated associations between prey community NMS ordinations and

the physical environment with correlation analyses using in situ measurements of 1 m sea surface temperature (SST), salinity, turbidity, fluorescence (a proxy for chlorophyll-*a* concentration), and dissolved oxygen concentration collected by the CTD. We also selected two of the regional physical variables that positively correlate with Chinook Salmon adult returns (Burke et al. 2013; Miller et al. 2013), Columbia River plume volume (www.stccmop.org) and coastal upwelling (www.pfeg.noaa.gov), for inclusion in the analysis. We obtained estimates of the three-dimensional volume (km^3) of the Columbia River plume (salinity cutoff 28 PSU) using simulation database DB31 of the "Virtual Columbia River" modeling system generated by the Center for Coastal Margin Observation and Prediction (Zhang and Baptista 2008). For upwelling, we used indices from daily averages of offshore Ekman transport driven by geostrophic wind stress between 45°N and 48°N and 125°W.

Analysis of juvenile salmon

We transported juvenile salmon frozen at sea back to the laboratory where they were identified to species, measured for fork length (FL; nearest mm), and weighed (nearest 0.1 g). To estimate genetic stock of origin, we extracted fin clips from 288 juvenile Chinook Salmon and genotyped them at 13 microsatellite DNA loci following Teel et al. (2015). Salmon were assigned to stock groups using a standardized genetic database (Seeb et al. 2007), the likelihood model of Rannala and Mountain (1997), and the program ONCOR (Kalinowski et al. 2007). Based on genetic information, we assigned 61% ($n = 175$) of juvenile Chinook Salmon to the UCSF genetic stock group with mean ± standard error (SE) probability of assignment of 89.1 ± 1.0%. Our analysis focused on subyearlings (0-age; 96% of UCSF fish), which we classified by length (Weitkamp et al. 2015): ≤120 mm FL in May (0% of catch), ≤140 mm FL in June (1% of catch), ≤180 mm FL in July (49% of catch), ≤210 mm FL in August (21% of catch), and ≤250 mm FL in September (25% of catch). Of these fish, 40% had an adipose fin clip, passive integrated transponder (PIT), or coded wire tag (CWT), indicating likely hatchery origin. The UCSF stock group is composed of fish originating in main stem and tributary sources east of the Cascade Mountains, although both hatchery and natural production of the stock also occurs in

Fig. 1 Map of study area showing the two stations repeatedly sampled on the continental shelf off of Willapa Bay, Washington from May through September in 2011 and 2012
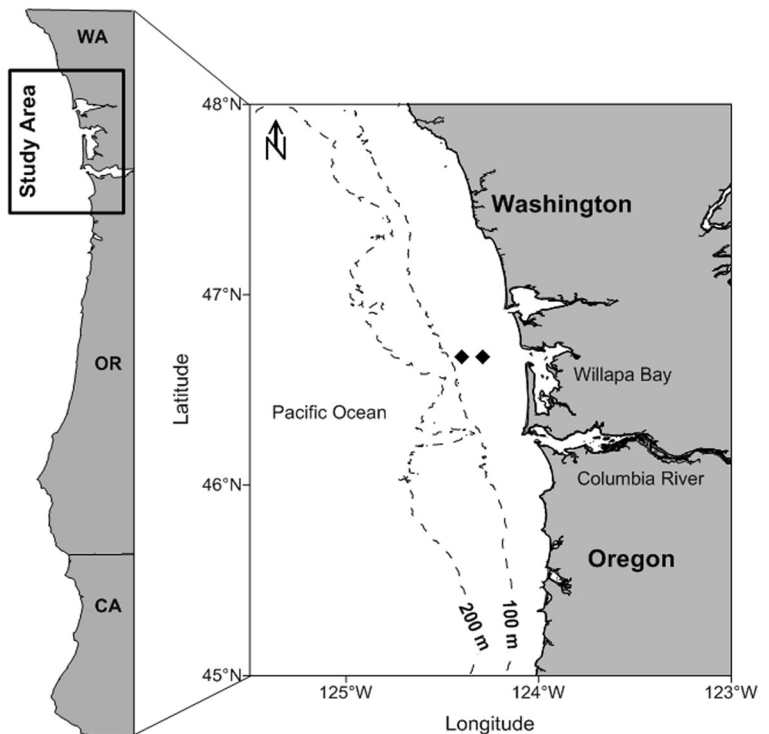
the mid-Columbia River (Miller et al. 2013; Teel et al. 2014).

To evaluate salmon size, we compared FL and mass by month between 2011 and 2012 using Student's t-tests. We developed a condition index for UCSF subyearlings using residuals from the linear regression of ln-transformed FL and mass ($r^2 = 0.99$, $p < 0.001$; Jakob et al. 1996; Brodeur et al. 2004), and compared condition by month within years using analysis of variance (ANOVA) followed by Tukey's Honestly Significant Difference (HSD). We increased the sample size of UCSF subyearlings used for size, growth, and condition calculations from 168 to 518 by including salmon from two other studies that used the same genetic and life history identification methods. The first study sampled UCSF subyearlings ($n = 201$) as they exited the Columbia River (Weitkamp et al. 2015). The second study sampled salmon ($n = 149$) in coastal waters from central Oregon to northern Washington (Teel et al. 2015). We included only individuals that were collected May through September in 2011 and 2012 from the mouth of the Columbia River north along the shelf to Willapa Bay. Inclusion of these additional samples did not change our results but increased statistical power to detect differences in size, growth, and condition by sampling period.

Monthly estimates of early ocean growth (G_L in mm d^{-1}) in UCSF subyearlings were calculated from differences in FL between ocean and estuary-caught individuals, assuming a uniform size and time of entry for each month:

$$G_L = \frac{(L_o - L_e)}{(t_o - t_e)},$$

where L_o is individual FL at capture in the ocean at time t_o and L_e is the mean monthly FL at capture in the estuary the prior month at mean time t_e. We also estimated specific growth rates (SGR in% body weight [BW] d^{-1}) from changes in salmon weight as:

$$SGR = \frac{(\ln[W_o] - \ln[W_e])}{(t_o - t_e)} \times 100,$$

where W_0 is individual mass at capture in the ocean at time t_o and W_e is the mean mass at capture in the estuary the prior month at mean time t_e. Even though we did not know which month the fish entered the ocean, we considered growth estimates to be valid based on evidence that abundances of UCSF subyearlings exiting the estuary are normally distributed around June and August (Weitkamp et al. 2015) and observations that average

estuary residence times for this stock are low (<1 week, Claiborne et al. 2014). We compared monthly estimates of G_L and SGR between years using t-tests.

Dietary analysis and comparison with the prey field

An integrative approach for assessing salmon foraging ecology includes stomach content analysis conducted alongside salmon stable isotope and fatty acid analyses. We identified stomach contents from a subsample of 229 UCSF subyearlings collected in the lower estuary and ocean from June through September in both years. Prey items were identified to the lowest possible taxa under a dissecting scope using methods described by Brodeur et al. (2007). To quantify stomach contents, we weighed the entire stomach contents and individual prey items (nearest 0.001 g), enumerated all of the prey, and measured the total length of up to 10 prey per taxon per stomach (nearest mm).

To standardize stomach fullness, we calculated mean stomach fullness as a percent of total body weight:

Stomach Fullness (%)

$$= \frac{\text{stomach content weight } (g)}{\text{total fish weight}(g) - \text{stomach content weight}(g)} \times 100.$$

We defined stomachs as empty when fullness <0.05% according to Weitkamp and Sturdevant (2008). Stomach fullness was compared by month within years using ANOVA followed by Tukey HSD tests. To visually represent diet composition, prey taxa were grouped into 14 categories that contributed ≥2% of salmon diets by weight: nonfood (e.g., Plantae), insects (Insecta), pteropods (Pteropoda), cladocerans (Cladocera), ostracods (Ostracoda), copepods (Copepoda), isopods (Isopoda), amphipods (Amphipoda), mysids (Mysidacea), krill (Euphausiidae), shrimp larvae (Pandalidae), crab larvae (*Metacarcinus magister* and *Cancer productus* zoea and megalopae), YOY Northern Anchovy (*Engraulis mordax*; hereafter referred to as anchovy), and unidentified fish (Osteichthyes). Average size at the onset of piscivory was compared between years using t-tests.

Stable isotope and lipid analysis

To address ontogenetic changes in diet, we sub-sampled ($n = 29$, 3–6 fish per month) UCSF subyearlings for bulk stable isotopes of nitrogen and carbon, total lipids, and fatty acids. For isotopes, we sampled dorsal muscle tissue with skin removed from the right side just under the dorsal fin (average = 0.32 g wet weight). For lipids, we sampled dorsal muscle from the left side (average = 0.54 g wet weight). In addition, we processed a representative sample of Dungeness crab megalopae collected from May through July in each year ($n = 5$–6 per year) for nitrogen stable isotopes. This was done to establish a trophic baseline to estimate salmon trophic position as megalopae are primary consumers and the salmon prey item with the lowest trophic position as determined by Miller et al. (2010). We also measured fatty acids from a subsample of invertebrate prey ($n = 32$) and fish prey ($n = 144$) collected from May through September in each year to develop a piscivory biomarker based on fatty acid differences between these two main prey types.

We processed bulk stable isotopes of carbon and nitrogen at Oregon State University (College of Earth, Ocean, and Atmospheric Sciences Stable Isotope Laboratory). Dried tissue was ground into a fine powder and 1.0 ± 0.1 mg of powder packed into a tin capsule. Prepared samples and international standards (USGS40, ANU Sucrose, and IAEA-N2) were combusted at >1000 °C using a Carlo Erba NA1500 elemental analyzer. The resulting CO_2 and N_2 were measured by continuous-flow mass spectrometry using a DeltaPlus isotope ratio mass spectrometer. Stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) were expressed in the delta notation:

$$\text{Stable Isotopes} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000,$$

where R is $^{15}N{:}^{14}N$ or $^{13}C{:}^{12}C$. Instrument error was ± 0.1‰ for carbon and ± 0.2‰ for nitrogen. Because no samples had atomic C:N ratios >3.5, they were not lipid-corrected as suggested by Post et al. (2007).

We converted all $\delta^{15}N$ values to trophic position (TP) using the notation of Post (2002):

$$TP = \lambda + \frac{\delta^{15}N_{salmon} - \delta^{15}N_{base}}{\Delta_n},$$

where λ is the trophic position of Dungeness crab megalopae used to establish the $\delta^{15}N_{base}$ relative to $\delta^{15}N_{salmon}$, and Δ_n ($\Delta\delta^{15}N$) is the enrichment in $\delta^{15}N$ per trophic level. For $\Delta\delta^{15}N$ we used the value of 3.4‰ per trophic level from Post (2002). The $\delta^{15}N_{base}$ in this case was estimated each year from the average $\delta^{15}N$ value determined for Dungeness crab megalopae sampled in 2011 ($\delta^{15}N = 10.3 \pm 0.3$ SE) and 2012 ($\delta^{15}N = 10.2 \pm 0.6$ SE) and setting $\lambda = 2.1$ according to Miller et al. (2010). We assumed a one-month lag between consumption of prey and expression of trophic position in tissues of the consumer based on the turnover model of Vander Zanden et al. (2015).

We extracted lipids in chloroform and methanol according to Parrish (1999) using a modified Folch procedure (Folch et al. 1957). To calculate fatty acid concentration (μg mg^{-1}), a constant amount of internal standard (23:0) was added to each sample. We prepared fatty acid methyl esters (FAME) by transesterification using sulfuric acid according to Budge et al. (2006) and analyzed FAME on an HP 7890 GC FID equipped with an autosampler and a DB wax + GC column (Agilent Technologies, Inc., USA) according to Copeman et al. (2016). The column temperature began at 65 °C for 0.5 min and was increased to 195 °C (40 °C min^{-1}), held for 15 min then increased again (2 °C min^{-1}) to a final temperature of 220 °C. Final temperature was held for 1 min. The carrier gas was hydrogen, flowing at a rate of 2 ml min^{-1}. Injector temperature was set at 250 °C and the detector temperature was constant at 250 °C. We identified peaks using retention times based upon Supelco standards (37 component FAME, BAME, PUFA 1, and PUFA 3). We used Nu-Check Prep GLC 487 quantitative fatty acid mixed standard to develop correction factors for individual fatty acids and integrated chromatograms using Chem Station (version A.01.02, Agilent).

Analysis of trophic markers

Fatty acids and stable isotopes integrate information about dietary history over a period of weeks to months (Fry 2006; Copeman et al. 2016; Vander Zanden et al. 2015). We used correlation analyses to compare salmon stable isotopes and fatty acids to assess their coherence as trophic biomarkers. Trophic biomarkers were selected a priori from existing literature (Table 1). The piscivory marker (the ratio of docosahexaenoic acid to eicosapentaenoic acid, DHA:EPA) was selected based on initial observations by Daly et al. (2010) that fish prey contains higher proportions of DHA relative to EPA than invertebrate prey and later confirmed by fatty analysis of prey items collected in this study (fish prey DHA:EPA = 1.6 ± 0.1 SE and invertebrate prey = 0.9 ± 0.1 SE). To evaluate the relationship between environmental variability and salmon foraging ecology, we used regression analysis to estimate the relative importance of biological and physical factors in explaining variation in trophic position. Explanatory variables included measures of salmon size (FL and condition), measures of prey availability (proportion of fish in the diet and anchovy biomass), and

Table 1 Summary of trophic biomarkers analyzed in this study, including stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) and fatty acid biomarkers (based on percent of total fatty acids)

Biomarker	Indicator Type	Reference
$\delta^{13}C$	Carbon source	Peterson and Fry (1987)
$\delta^{15}N$	Trophic position	Vander Zanden and Rasmussen (1999)
18:3n-3 + 18:2n-6[a]	Freshwater/Nearshore	Budge and Parrish (1998); Copeman et al. (2009)
16:18 PUFA[b]	Diatoms:Flagellates	Budge and Parrish (1998)
DHA:EPA[c]	Piscivory	Daly et al. (2010); this study

[a] Freshwater/Nearshore sources of phytoplankton in the food web indicated by the sum of linolenic (18:3n-3) and linoleic (18:2n-6) fatty acids

[b] Proportion of marine diatoms to flagellates indicated by the ratio of all polyunsaturated fatty acids (PUFA) containing 16 carbon atoms to all PUFA containing 18 carbon atoms

[c] Piscivory indicated by the ratio of docosahexaenoic (22:6n-3) to eicosapentaenoic fatty acid (20:5n-3)

environmental conditions measured in the coastal environment (SST, fluorescence, upwelling, and Columbia River plume volume). We lagged all explanatory variables except FL by one month to account for tissue turnover and conducted all statistical analyses using R (R Core Team 2015).

Results

Salmon prey field

During the two years of our study, we captured 22,661 potential juvenile salmon prey items representing 47 taxa (Appendix). Species richness was highest in May, with 22 taxa collected in each of 2011 and 2012, but on average, biomass estimates were lower in May (53.1 ± 26.3 µg m^{-3}) compared to other months. Lowest diversity (3 taxa) occurred in August 2012, but average biomass estimates were highest (2585 µg m^{-3}) during this sampling period because of large catches of anchovy, an important prey for subyearling Chinook Salmon in the California Current (Brodeur 1991; Daly et al. 2009; MacFarlane 2010). In fact, during both years of the study, highest prey biomass estimates coincided with large catches of anchovy, although the timing of peak anchovy biomass differed between years. In 2011, the highest average anchovy biomass estimates occurred in September (342 µg m^{-3}), whereas the highest anchovy biomass estimates in 2012 occurred in August (2577 µg m^{-3}). Over the whole study, average prey biomass estimates were lowest in September 2012 (1.8 µg m^{-3}). Interestingly, this was just one month after biomass estimates peaked for the study. Average anchovy biomass estimates in September 2012 were >450 times lower than they were in September 2011, representing a clear shift in prey phenology between the two years.

As expected, the prey field community transitioned throughout the sampling season as the coastal environment varied. Results of the multi-response permutation procedure comparing community composition revealed significant differences in the prey field by month ($p < 0.001$). Pairwise comparisons showed there was no difference in the prey field community between June and July or between August and September over the entire sampling period (both with $p > 0.100$), which justified combining months into three seasons over both years of the study (spring = May, early summer = June

and July, and late summer = August and September). A diverse, but low biomass community of invertebrate prey and YOY fishes (osmerids, flatfishes, and other groundfish in their pelagic phase) occurred in spring and early summer, which transitioned into a community dominated by anchovy by late summer.

The NMS ordination that best described the prey field dataset had three dimensions, Monte Carlo $p < 0.001$ and medium stress (12.5), suggesting little risk of drawing false inferences (Fig. 2, Table 2). The ordination represented 86.6% of the variation in the prey community. Axis 1 accounted for 55.5% of the variation and was positively associated with Dungeness Crab megalopae, smelt (Osmeridae), Pacific Sanddab (*Citharichthys sordidus*), Slender Sole (*Lyopsetta exilis*), and Sand Sole (*Psettichthys melanosticus*) during spring (May), when Columbia River plume volume was highest. Axis 1 was negatively associated with anchovy during late summer (August and September), when SST and fluorescence values were highest, indicating high productivity. Axis 2 accounted for 15.3% of the variation and separated coastal downwelling from upwelling conditions. Axis 3 accounted for 15.8% of the variation and was positively associated with rockfish (*Sebastes* spp.), negatively associated with California Market Squid (*Doryteuthis opalescens*), but was not associated with any environmental variables measured.

UCSF subyearlings

Subyearling UCSF Chinook Salmon was the most abundant genetic stock group sampled alongside the prey community from July through September in both years. We also collected juvenile Chinook Salmon from 14 other genetic stock groups, as well as juvenile Coho, Chum (*O. keta*), and Sockeye (*O. nerka*) Salmon, but they were not included in this analysis. Average size of UCSF subyearlings, including salmon sampled in the two other complementary studies, ranged from 89 mm FL and 6.9 g in May to 151 mm FL and 43.2 g in September (Fig. 3a, b). Salmon lengths (t-test, $p = 0.014$) and weights ($p = 0.002$) were significantly lower in June 2011 compared to June 2012, but were significantly larger by the end of September in 2011 compared to 2012 (length and mass both $p < 0.001$). Average early ocean growth rates were significantly
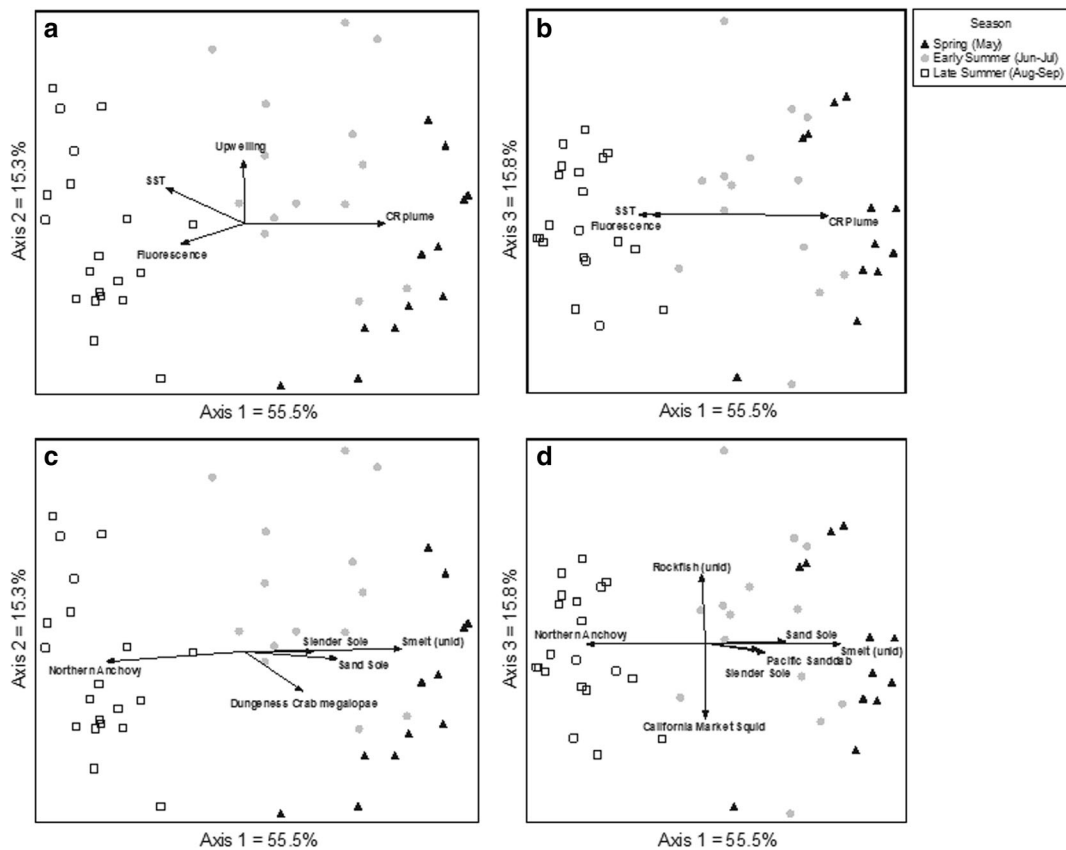
Fig. 2 Results of nonmetric multidimensional scaling analysis where each point represents the log-transformed biomass ($\mu g\ m^{-3}$) of invertebrate and marine fish prey sampled by haul and plotted in species space from May through September 2011 and 2012; top plots show joint plots of environmental variables (cut-off $r^2 = 0.30$ for inclusion) for **a** axes 1–2, and **b** axes 1–3; bottom plots show joint plots of species (cut-off $r^2 = 0.30$ for inclusion) for **c** axes 1–2, and **d** axes 1–3 (symbols are based on categorical groupings for season: spring = May, denoted by a filled *black triangle*, early summer = June–July, denoted by a *grey circle*, and late summer = August–September, denoted by an *open square*); abbreviations are 1 m sea surface temperature (SST), Columbia River plume volume (CR plume; km^3), and unidentified (unid)

($p = 0.005$) slower from June to July in 2011 (0.4 mm d^{-1}) than 2012 (0.6 mm d^{-1}), but significantly faster ($p < 0.001$) from August to September in 2011 (1.2 mm d^{-1}) compared to 2012 (0.9 mm d^{-1}; Fig. 3c). Average specific growth rates were also significantly ($p < 0.001$) faster from August to September 2011 (3.1% BW d^{-1}) compared to August to September 2012 (2.0% BW d^{-1}; Fig. 3d). As expected, UCSF subyearlings grew fastest when anchovy were most abundant in the field and consumed. Salmon condition was also significantly higher (ANOVA and Tukey HSD, $p < 0.05$) when anchovy biomass in the field was greatest (Fig. 4). Across years, mean salmon condition and anchovy biomass were significantly and positively correlated ($r = 0.900$, $p = 0.015$).

Stomach contents

Juvenile salmon stomach contents varied by month and year over the sampling period and reflected variations in the prey field (Fig. 5). Of the stomachs examined, 18 were considered empty. In general, proportions of fish increased in stomachs through time, except from August to September 2012, when proportions of fish in diet (and salmon growth rate) decreased. The onset of piscivory, which we defined as when diets contained more fish than any other prey category, occurred later in 2011 (September =62% of diet) than 2012 (August =50% of diet). Average salmon size at the onset of piscivory (Fig. 6) was significantly higher (t-test, $p < 0.01$) in 2011 (140–150 mm FL; 49% fish in diet) than in 2012

Table 2 Pearson's correlation coefficients for associations between nonmetric multidimensional scaling ordination axes and environmental variables or species, denoted by "*" where $r^2 > 0.30$

Factor	Axis 1	Axis 2	Axis 3
Environmental variables			
SST[a]	-0.61*	0.41	-0.07
Flu[b]	-0.55*	-0.31	-0.06
CR plume[c]	0.82*	-0.02	-0.09
Upwelling[d]	-0.06	0.55*	0.01
Species			
Dungeness Crab	0.53*	-0.43	0.23
California Market Squid	-0.01	-0.35	-0.65*
Northern Anchovy	-0.81*	-0.22	-0.05
Smelt (unid)[e]	0.86*	0.12	-0.07
Rockfish (unid)[e]	-0.13	-0.53	0.62*
Pacific Sanddab	0.55*	0.12	-0.19
Slender Sole	0.57*	-0.01	-0.23
Sand Sole	0.67*	-0.19	0.09

[a] Sea surface (1 m) temperature (°C)

[b] Fluorescence (mg m^{-3})

[c] Columbia River plume volume (km^3)

[d] Upwelling index

[e] Unidentified

(120–130 mm FL; 43% fish in diet). All salmon >150 mm were completely piscivorous in 2011 whereas proportions of fish in diet decreased rather than increased in fish >130 mm FL in 2012, indicating that the onset of piscivory was related more to prey availability than predator size. Prey-sized (<80 mm TL) anchovy were caught in the trawl in August and September 2011 and from July through September 2012. Stomach fullness (% of total body weight) was significantly higher (ANOVA and Tukey HSD, $p < 0.05$) when salmon ate more anchovy (mean ± SE = 2.2 ± 0.4% in September 2011 and 2.0 ± 1.2% in August 2012), compared to when anchovy were less abundant and overall prey biomass estimates were low (0.6 ± 0.3% in September 2012).

Salmon stable isotopes and lipids

Salmon stable isotopes, trophic position, and fatty acids varied by month and year (Table 3). Correlation analyses identified significant relationships among bulk stable isotopes of carbon and nitrogen, fatty acids, and salmon size (Table 4, Figs. 7 and 8). Values of δ^{13}C,

indicating carbon source at the base of the food web, were positively correlated with salmon FL ($r = 0.620$, $p < 0.001$) and a fatty acid biomarker for marine diatoms:flagellates (the ratio of all polyunsaturated fatty acids [PUFA] containing 16 carbon atoms to all PUFA containing 18 carbon atoms, $r = 0.730$, $p < 0.001$; Fig. 7a, c). Carbon isotopes and salmon FL were both negatively correlated (δ^{13}C $r = -0.700$ and FL $r = -0.560$, both $p < 0.002$) with a fatty acid biomarker for freshwater (the sum of linolenic and linoleic fatty acids [18:3n-3 + 18:2n-6]; Fig. 7b, d), indicating that the dietary carbon pools changed as salmon migrated from freshwater to saltwater. Values of δ^{15}N were positively correlated with salmon FL ($r = 0.460$, $p = 0.012$), δ^{13}C ($r = 0.690$, $p < 0.001$) and a fatty acid marker for piscivory (DHA:EPA, $r = 0.720$, $p < 0.001$; Fig. 8), which supports the observation that salmon diet shifted from invertebrate prey to piscine prey during early ocean residence as salmon grew (Fig. 9). Across years, salmon in September 2012 had the highest δ^{15}N, trophic position, and DHA:EPA, even though they were not the largest fish sampled and were not piscivorous at the time of collection. Due to the lag between when prey is consumed and expressed in salmon isotopes and fatty acids, we assumed that salmon biochemistry in September 2012 reflected fish prey consumed in August 2012, the sampling period when anchovy were most abundant in the field and when salmon first became piscivorous.

Models estimating trophic position

Regression analysis of average salmon trophic position and physical and biological factors showed salmon trophic position increased from July to September from 2.5 to 2.9 in 2011 and from 2.6 to 3.0 in 2012, reflecting prey consumed from approximately June through August in both years (Table 3, Fig. 9). Monthly and interannual variations in trophic position were best explained by differences in fluorescence (1-mo lag), Columbia River plume volume (1-mo lag), salmon FL, and proportion of fish in salmon diet (1-mo lag; Fig. 9). These results demonstrate that all fish were transitioning from being zooplantivorous to piscivorous through time as they increased in size. Associations between trophic position and the physical environment also highlights the potential role of bottom-up productivity in regulating the timing of the onset of piscivory.
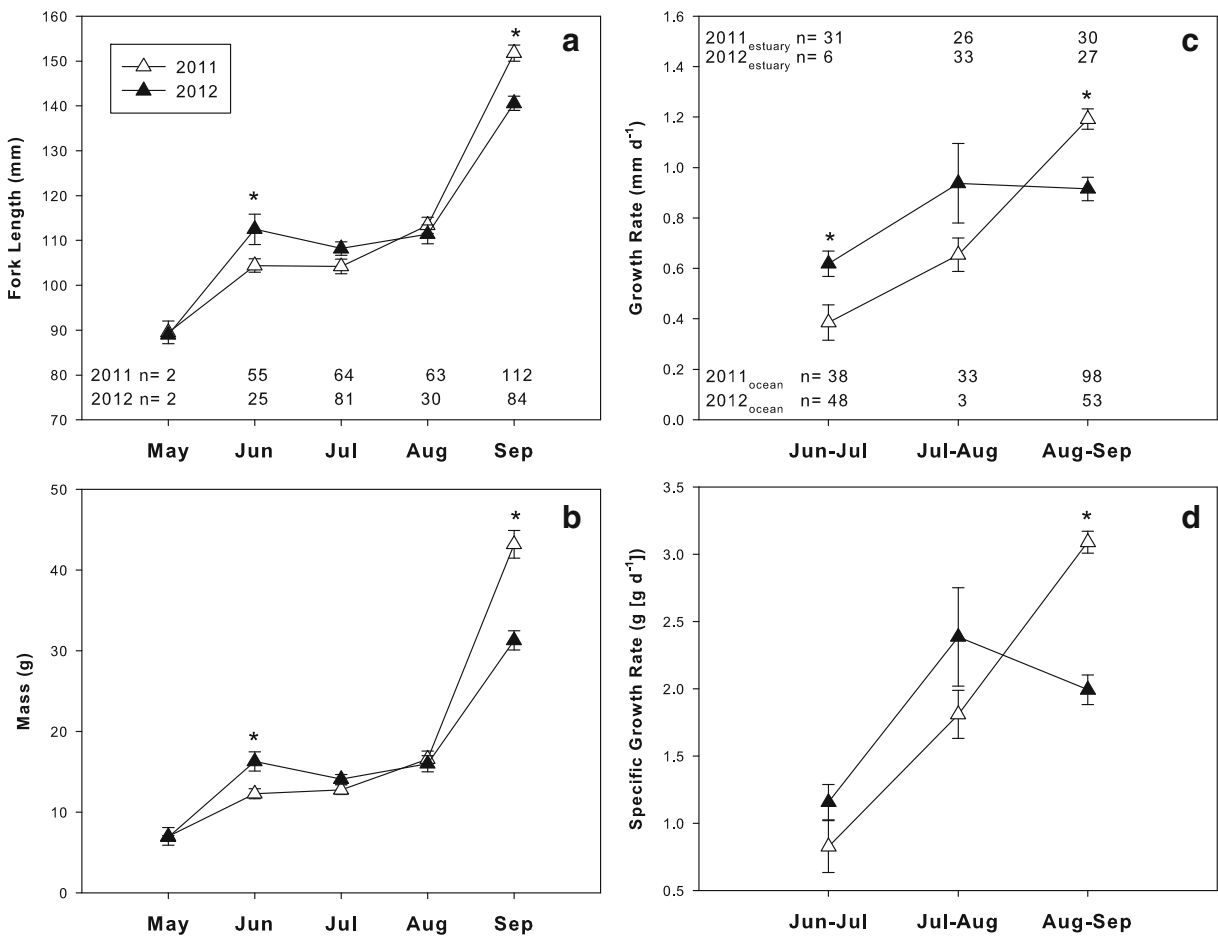
Fig. 3 Plots of average ± SE **a** fork length **b** mass, **c** growth rates, and **d** specific growth rates of subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) assigned to the upper Columbia summer-fall genetic stock group in 2011 and 2012 (*indicates significance [Student's t-test, $p < 0.05$])

Discussion

Our analyses showed that inter-annual differences in timing and size at the onset of piscivory in a population of Chinook Salmon were related to prey availability. Seasonal variation in the prey field during ontogeny has broad implications for early ocean foraging success, growth, and survival in UCSF subyearlings. The composition of the prey field is also important for other populations of Columbia River Pacific Salmon and Steelhead (*O. mykiss*) that have stock-specific differences in their size and timing of ocean entry (Weitkamp et al. 2015). Our results that UCSF subyearlings became piscivorous at a smaller size and earlier in 2012 than 2011, but that the earlier onset of

piscivory did not result in higher growth rates by the end of the sampling period in 2012, lends support to the idea that the total duration of piscivory, not just the onset, should be considered in terms of long-term fitness and survival. A longer period of piscivory in early marine life may increase survival by increasing salmon size at the end of the first summer at sea, as suggested by the critical size, critical period hypothesis (Beamish and Mahnken 2001). It may also be that Chinook Salmon size-at-maturity, fecundity, and fitness are related to the total duration of piscivory during marine life.

The spatial coverage of our study was limited through time therefore we do not know how representative our samples were of the prey community

Fig. 4 Scatterplots with separate scales on the y-axis for monthly mean ± SE condition of subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) assigned to the upper Columbia summer-fall genetic stock group (filled *triangles*) and mean ± SE biomass of Northern Anchovy (*Engraulis mordax*) measured in net tows (*open circles*) sampled July through September in **a** 2011 and **b** 2012 (different subscripts indicate months when salmon condition varied significantly [ANOVA and Tukey HSD; *p* < 0.05])
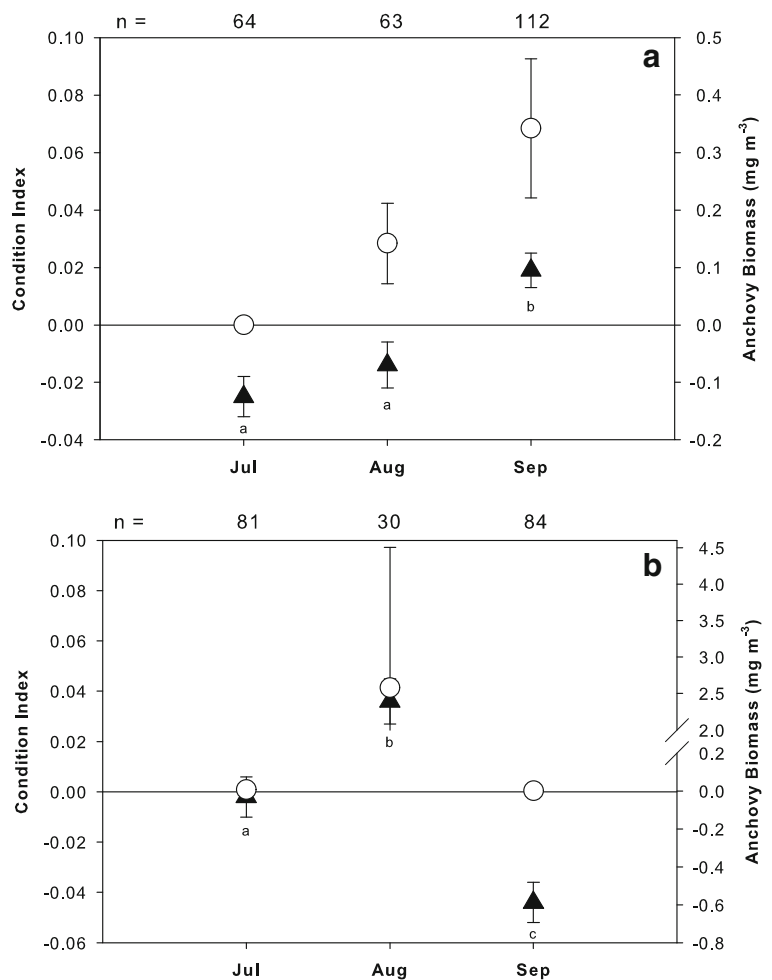
throughout salmon's range. We suspect that our samples represented available prey in the Northern California Current as previous surveys of zooplankton (Lamb 2011) and ichthyoplankton (Auth 2011) resources concluded that community structure was homogenous north and south of the region sampled. In June 2016, NOAA Fisheries conducted a coastwide (northern Washington to central California) survey of the salmon prey field in shelf waters using the same gear type as we did to further investigate this issue. That survey also used zooplankton net tows (bongo and Methot nets) to capture small marine invertebrate prey such as pteropods, ostracods, copepods, amphipods, and decapod larvae that our trawl gear was less effective at sampling. Future studies could also include image analysis (e.g. in situ ichthyoplankton imaging system [*IS*IIS], Cowen and Guigand 2008) or acoustics to provide a more complete quantitative estimate of the prey field, especially at

depths greater than we sampled where salmon might feed (Brodeur et al. 2011). This type of sampling could help better understand prey patchiness as it relates to fronts and other oceanographic features (Peterson and Peterson 2008; Ainley et al. 2009; Brodeur and Morgan 2016).

Estimates of marine growth in UCSF subyearlings were based on the assumption that salmon caught in the estuary and ocean were representative of the entire population and that changes in size were due to ocean growth and not factors such as emigration, immigration, or size-selective mortality. We contend that this is a reasonable assumption as our estimates of growth (0.4 to 1.2 mm d^{-1} and 0.8 to 3.1% BW d^{-1}) were similar to estimates calculated for this stock based on otoliths (0.8 to 1.2 mm d^{-1} and 0.9 to 2.6% BW d^{-1}; Miller et al. 2013; Claiborne et al. 2014).
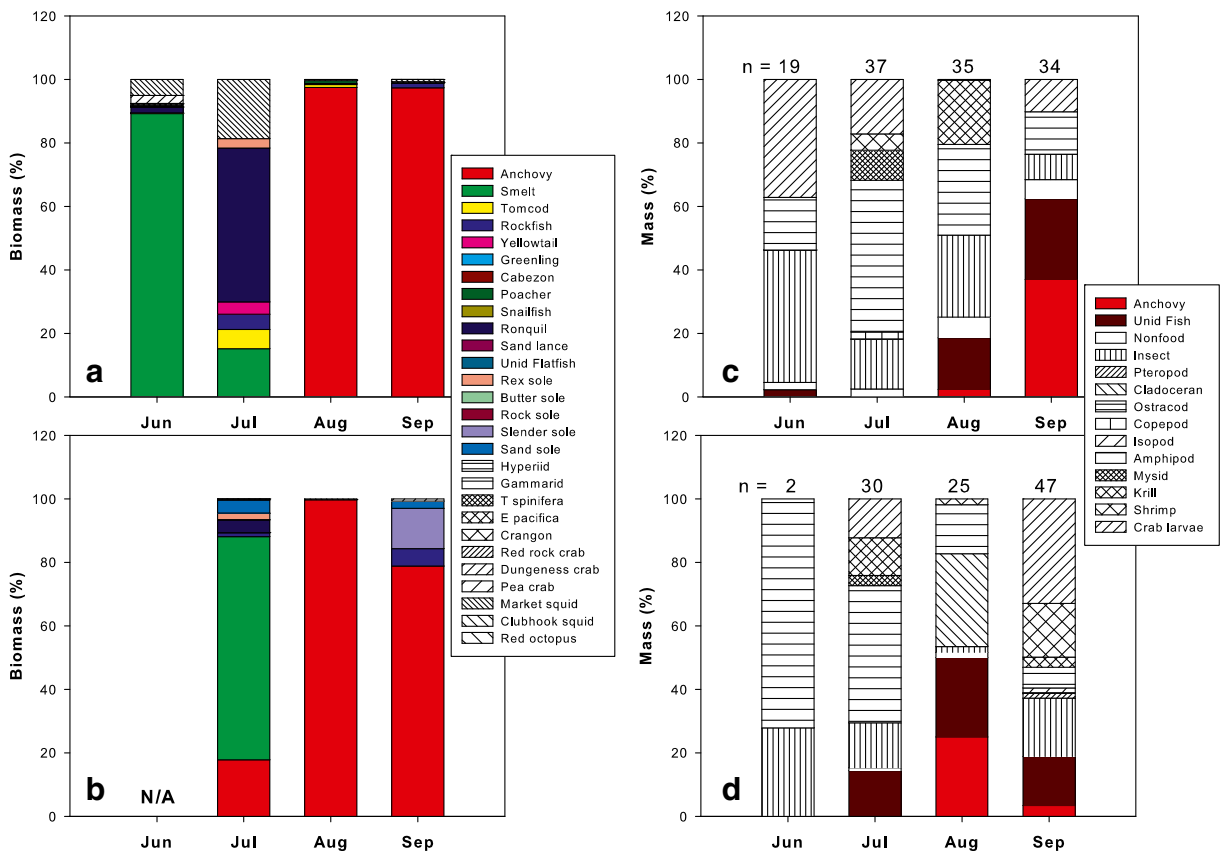
Fig. 5 Average percent biomass of potential prey measured from June through September in **a** 2011 and **b** 2012, and diet composition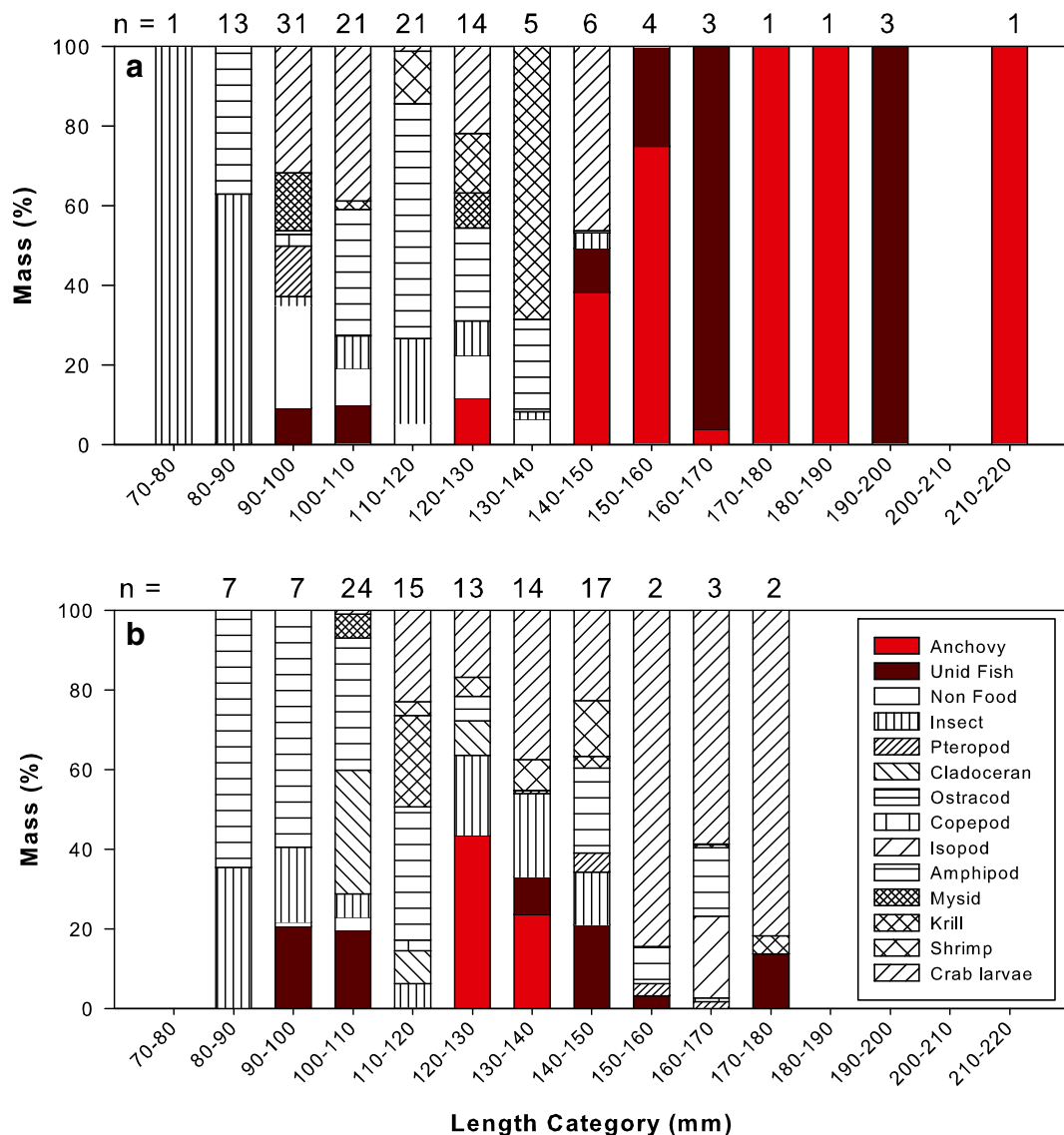 presented as percent wet mass of prey eaten by subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) in **c** 2011 (*n* = 125) and **d** 2012 (*n* = 104; fish prey indicated by *colored bars*, invertebrate prey indicated by *black* and *white bars*)

We suggest that foraging and growth patterns observed in UCSF subyearlings would be similar in salmon populations with similar life histories. One example is the Snake River fall population of Chinook Salmon, which was the second most abundant genetic stock group represented in our samples (14.2% of catch). Unlike the UCSF population, Snake falls are listed under the U.S. Endangered Species Act. These fish migrate to the ocean slightly earlier than UCSF subyearlings (Weitkamp et al. 2015), but have the same genetic lineage (Waples et al. 2004) and similar early marine distributions and growth rates (Teel et al. 2015; Weitkamp et al. 2015).

Combining stomach content analysis with stable isotope and fatty acid analyses is a powerful integrated approach for evaluating diet and for understanding biological processes. For example, carbon isotope values in fish, which represent primary producers at the base of the food web, can be difficult to interpret as fractionation of $\delta^{13}C$ in phytoplankton tends to vary positively with SST, cell size, and growth rate, and negatively with dissolved inorganic carbon pools (CO_2 and HCO_3^-) (Laws et al. 1995; Burkhardt et al. 1999). Combining stable isotopes with fatty acid biomarkers can help aid in $\delta^{13}C$ interpretation. The fatty acid biomarker approach is based on observations that phytoplankton produce essential fatty acids not biosynthesized by consumers that are then deposited in consumer tissue with minimal modification (Dalsgaard et al. 2003; Budge et al. 2006; Copeman et al. 2016). Freshwater biomarkers (18:2n-3 + 18:2n-6), likely originating from the Columbia River, varied inversely with $\delta^{13}C$ and salmon FL, whereas marine phytoplankton biomarkers (16:18 PUFA) varied positively with $\delta^{13}C$ and salmon FL. These results confirm

Fig. 6 Diet composition presented as percent of wet mass of prey by length category in **a** 2011 ($n = 125$) and **b** 2012 ($n = 104$; fish prey indicated by *colored bars*, invertebrate prey indicated by *black* and *white bars*)

a general pattern of enrichment of $\delta^{13}C$ in salmon tissue by up to 7.5‰ associated with the ontogenetic shift in diet and habitat from freshwater to saltwater. However, it varies from other interpretations of juvenile salmon $\delta^{13}C$ that consider there to be a gradient between enriched $\delta^{13}C$ waters onshore and depleted $\delta^{13}C$ values offshore within the marine realm (Miller et al. 2008). Salmon $\delta^{13}C$ may also vary along a SST gradient with lower $\delta^{13}C$ values at lower temperatures due to higher concentrations of dissolved CO_2 in cooler waters

(Hertz et al. 2015a), although we found no significant relationship between salmon $\delta^{13}C$ and SST ($r = 0.00$, $p = 0.99$).

Completely piscivorous fish should have a trophic position of 3.5–4.0, but by September our estimates for trophic position were 2.9 in 2011 and 3.0 in 2012. There are several explanations for this. The first is that piscivorous diets were not yet reflected in salmon tissue. We assumed a one-month lag between a diet shift and when tissue actually equilibrates with that value, but muscle

Table 3 Average ± SE subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) fork length (FL, mm), mass (g), stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$, ‰), trophic position, total fatty acids expressed as the amount per dry weight of each sample ($\mu g\ g^{-1}$),% fatty acids comprising >1% of total fatty acids, and biomarker * values for fatty acids from 29 samples collected July through September 2011 and 2012

	Jul 2011	Aug 2011	Sep 2011	Jul 2012	Aug 2012	Sep 2012
FL	107.8 ± 3.5	113.2 ± 3.5	164.4 ± 14.7	108.0 ± 2.8	134.7 ± 5.8	147.2 ± 0.9
Mass	13.5 ± 1.3	16.6 ± 1.5	58.5 ± 15.2	13.9 ± 0.9	27.3 ± 3.4	34.5 ± 1.6
$\delta^{13}C$	-23.0 ± 0.8	-21.0 ± 0.7	-19.8 ± 0.8	-23.2 ± 0.6	-23.3 ± 1.5	-20.6 ± 0.6
$\delta^{15}N$	11.7 ± 0.3	12.6 ± 0.4	13.0 ± 0.3	12.0 ± 0.3	12.3 ± 0.8	13.2 ± 0.5
Trophic position	2.5 ± 0.1	2.8 ± 0.1	2.9 ± 0.1	2.6 ± 0.1	2.7 ± 0.2	3.0 ± 0.2
Total fatty acids	10.1 ± 1.0	11.6 ± 2.1	11.4 ± 1.3	15.5 ± 1.7	16.7 ± 1.0	15.5 ± 1.7
14:0	1.1 ± 0.2	1.9 ± 0.2	1.2 ± 0.1	1.5 ± 0.2	1.7 ± 0.1	1.5 ± 0.2
16:0	23.2 ± 2.1	26.9 ± 2.5	27.4 ± 2.1	23.7 ± 0.6	21.0 ± 1.2	23.3 ± 0.9
18:0	6.8 ± 1.0	6.6 ± 1.1	4.8 ± 0.3	6.8 ± 0.4	5.2 ± 0.3	5.1 ± 0.3
22:0	1.6 ± 0.4	1.0 ± 0.7	0.8 ± 0.4	1.3 ± 0.7	0.7 ± 0.7	1.6 ± 0.7
$\sum$SFA[a]	34.8 ± 0.24	34.8 ± 0.29	34.8 ± 0.19	34.8 ± 0.14	34.8 ± 0.16	34.8 ± 0.14
16:1n-7	2.2 ± 0.3	3.3 ± 0.6	2.0 ± 0.4	3.3 ± 0.5	2.3 ± 0.2	2.2 ± 0.4
18:1n-9	6.3 ± 0.5	6.6 ± 0.8	6.0 ± 0.3	7.4 ± 0.4	7.1 ± 0.4	9.2 ± 1.0
18:1n-7	3.2 ± 0.3	3.2 ± 0.2	2.4 ± 0.6	3.5 ± 0.2	2.4 ± 0.1	2.4 ± 0.2
$\sum$MUFA[b]	14.5 ± 0.1	17.8 ± 0.2	13.2 ± 0.1	17.7 ± 0.1	14.1 ± 0.1	17.2 ± 0.2
18:2n-6	1.6 ± 0.2	1.3 ± 0.1	0.6 ± 0.1	1.6 ± 0.2	1.1 ± 0.1	1.1 ± 0.2
18:3n-3	1.3 ± 0.4	1.0 ± 0.2	0.6 ± 0.2	1.4 ± 0.4	1.2 ± 0.4	1.0 ± 0.3
20:4n-6	2.4 ± 0.4	1.4 ± 0.2	1.3 ± 0.2	2.2 ± 0.3	2.0 ± 0.5	1.3 ± 0.3
20:5n-3 (EPA)	11.4 ± 0.3	10.3 ± 1.1	11.7 ± 0.8	11.5 ± 0.6	11.7 ± 0.6	8.9 ± 0.8
22:5n-3	3.9 ± 0.3	3.0 ± 0.3	3.1 ± 0.5	3.6 ± 0.2	4.0 ± 0.5	2.9 ± 0.2
22:6n-3 (DHA)	24.4 ± 2.8	23.3 ± 3.5	31.1 ± 2.4	23.4 ± 1.8	32.7 ± 4.2	31.4 ± 2.9
$\sum$PUFA[c]	50.6 ± 0.2	43.6 ± 0.2	51.1 ± 0.2	47.2 ± 0.1	50.6 ± 0.2	49.3 ± 0.2
16:18 PUFA	0.2 ± 0.0	0.4 ± 0.1	0.5 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.4 ± 0.1
18:3n-3 + 18:2n-6	2.9 ± 0.6	2.3 ± 0.4	1.2 ± 0.3	3.0 ± 0.5	2.2 ± 0.5	2.0 ± 0.5
DHA:EPA	2.2 ± 0.3	2.3 ± 0.4	2.7 ± 0.2	2.1 ± 0.2	2.8 ± 0.4	3.7 ± 0.5
N	5	5	5	6	3	5

We assumed a one-month lag between diet and expression of diet in salmon biochemistry

*See Table 1 for explanation of trophic biomarkers

[a] Also contains < 1% of i-15:0, ai15:0, 15:0, i16:0, ai16:0, i17:0, ai17:0, 17:0, 19:0, 20:0, 21:0, 24:0

[b] Also contains < 1% of 14:1, 15:1, 16:1n-5, 17:1, 18:1n-11, 18:1n-6, 18:1n-5, 20:1n-9, 20:1n-11, 20:1n-7, 22:1n-11, 22:1n-9, 22:1n-7, 24:1

[c] Also contains < 1% of 16:2n-4, 16:3n-4, 16:4n-3, 16:4n-1, 18:2n-4, 18:3n-6, 18:3n-4, 18:4n-3, 18:4n-1, 20:2a, 20:2b, 20:2n-6, 20:3n-6, 20:3n-6, 20:3n-3, 20:4n-3, 21:5n-3, 22:4n-6, 22:5n-6, 22:4n-3

may take longer to equilibrate than other tissues (Heady and Moore 2013). Anchovy consumed in August may not have been reflected in salmon muscle by September. A two-month lag would suggest that September $\delta^{15}N$ values reflected zooplanktivorous diets consumed in July. We also may have overestimated the trophic discrimination factor of 3.4‰ given that our $\delta^{15}N$ baseline values

for crab megalopae were near 10‰. Recent analyses (Hussey et al. 2014; Hertz et al. 2016) show that turnover can complicate interpretation of ontogeny in salmon. We also may have inadequately captured the trophic baseline by integrating megalopae values across season and space. A final possibility is that UCSF juveniles never became completely piscivorous, an observation supported

Table 4 Significant ($p < 0.05$) Pearson's correlation coefficients for comparisons between carbon and nitrogen stable isotopes (δ^{13}C and δ^{15}N) and fatty acid biomarkers[a] from 29 subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) muscle tissue samples collected July through September 2011 and 2012

Biomarker	δ^{13}C	δ^{15}N	18:3n-3 + 18:2n-6	16:18 PUFA	DHA:EPA
δ^{13}C	1.00				
δ^{15}N	0.69	1.00			
18:3n-3 + 18:2n-6	-0.70*	-0.56	1.00		
16:18 PUFA	0.73*	0.72	-0.82	1.00	
DHA:EPA	0.60	0.72*	-0.58	0.64	1.00

*Strongest correlations

[a] See Table 1 for explanation of trophic biomarkers

by stomach content data and consistent with the notion that Chinook Salmon are generalist foragers that feed upon a variety of prey types (Gregory and Northcote 1993).

The use of DHA:EPA as a biomarker of piscivory is based on observations that DHA is conserved in higher trophic levels in marine eco-systems (Dalsgaard et al. 2003; Parrish 2013) and
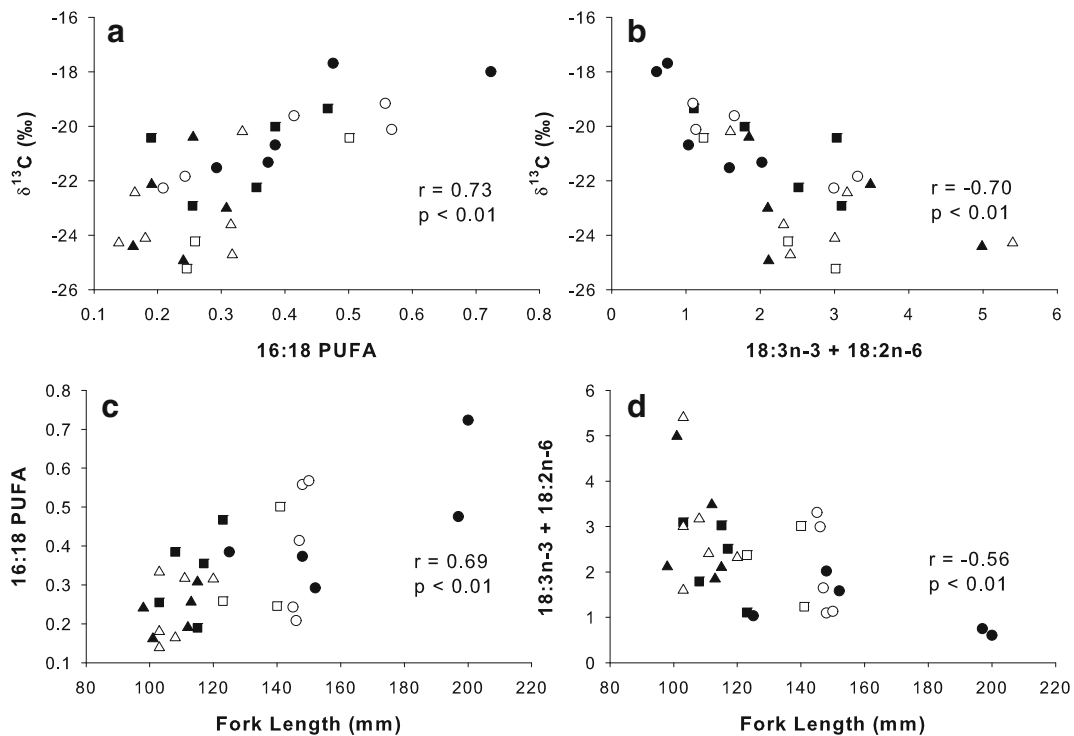
Fig. 7 Correlations between subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) carbon stable isotope values (δ^{13}C), fatty acids biomarkers (based on percent total fatty acids), and size: **a** the relationship between diatom to flagellate markers indicated by the ratio of all polyunsaturated fatty acids (PUFA) containing 16 carbon atoms to all PUFA containing 18 carbon atoms and δ^{13}C, **b** the relationship between freshwater markers indicated by the sum of linolenic acid (18:3n-3) and linoleic acid (18:2n-6) and δ^{13}C, **c** the relationship between salmon fork length (FL) and 16:18 PUFA, and **d** the relationship between salmon FL and 18:3n-3 + 18:2n-6 (symbols are based on categorical groupings for year and month: 2011 = filled symbols, 2012 = open symbols; July values are denoted by a *triangle*, August by a *square*, and September by a *circle*)
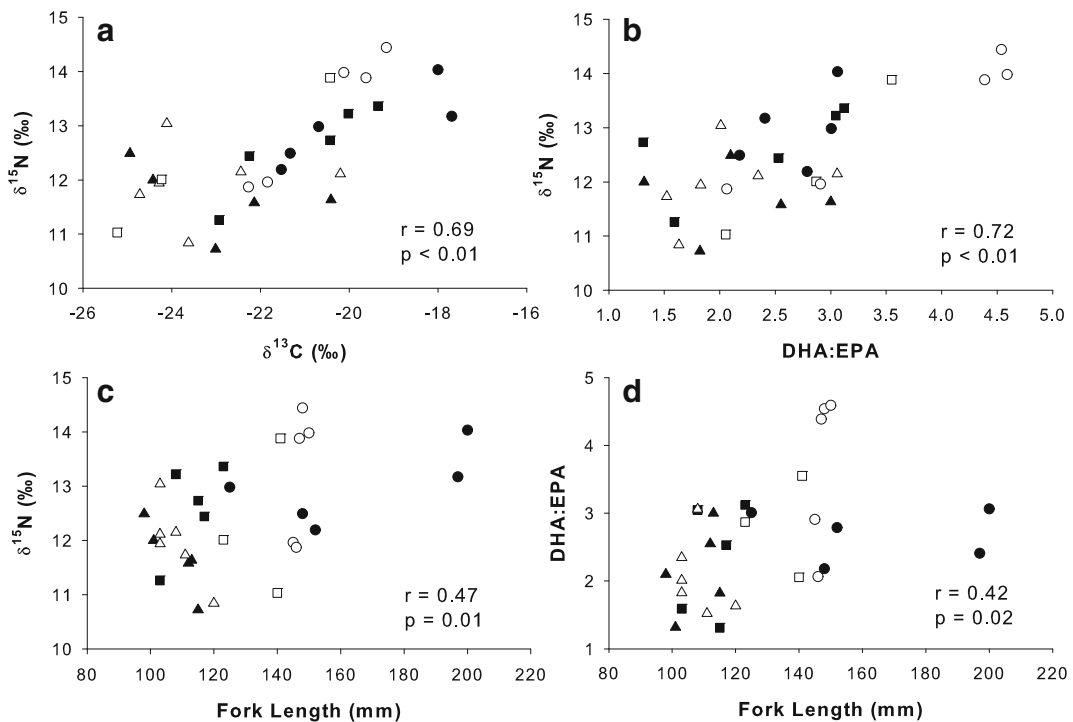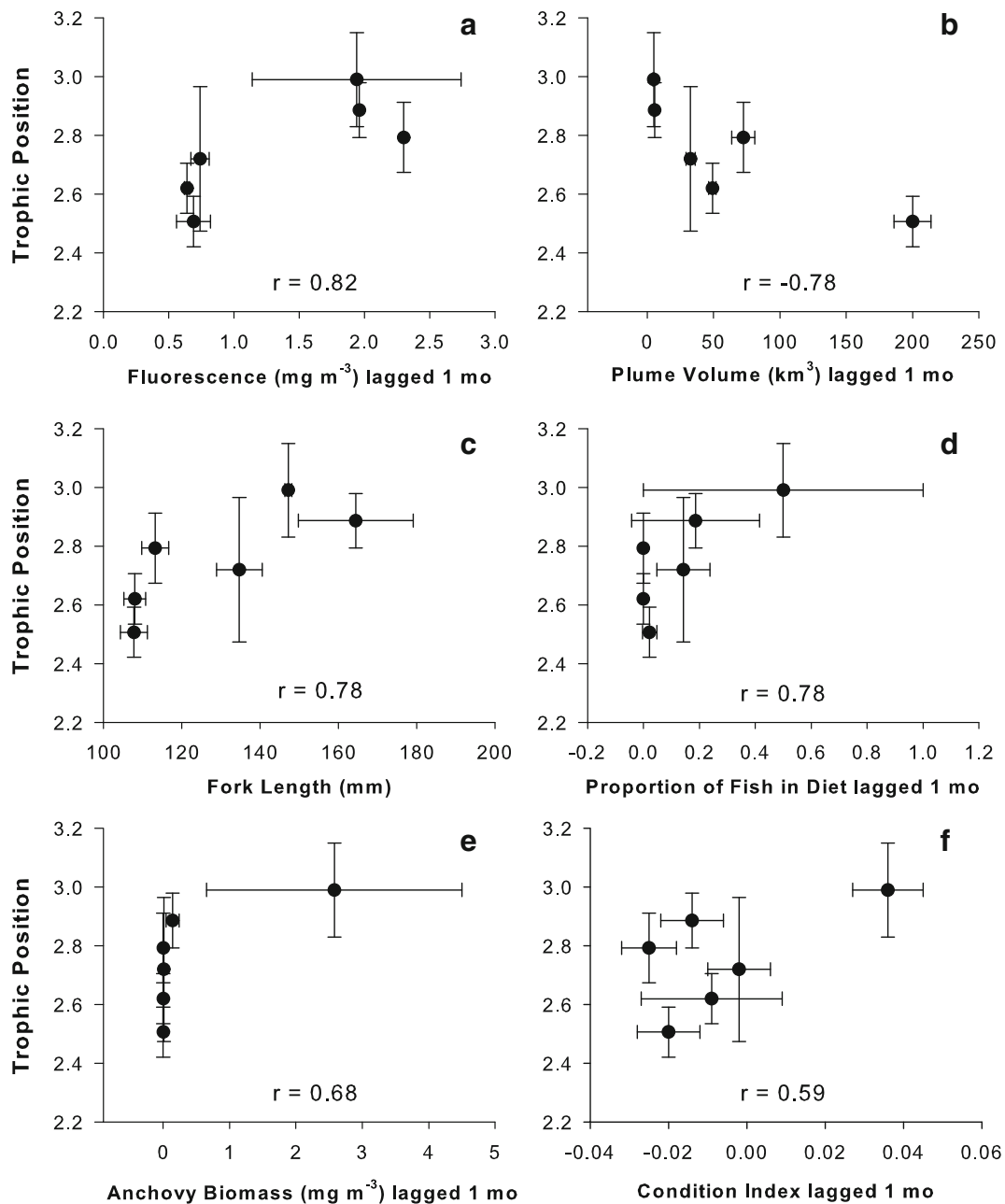
Fig. 8 Correlations between subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) isotope values, fatty acid biomarkers (based on percent of total fatty acids), and size: **a** the relationship between carbon and nitrogen stable isotope values ($\delta^{13}C$ and $\delta^{15}N$), **b** the relationship between the ratio of docosahexaenoic acid to eicosapentaenoic acid (DHA:EPA) and $\delta^{15}N$, **c** the relationship between salmon fork length (FL) and $\delta^{15}N$, and **d** the relationship between salmon FL and DHA:EPA (symbols are based on categorical groupings for year and month: 2011 = filled symbols, 2012 = open symbols; July values are denoted by a *triangle*, August by a *square*, and September by a *circle*)

found in higher concentrations in marine fish prey relative to invertebrate prey (Daly et al. 2010; this study). Increases in the DHA:EPA ratio may also indicate a decrease in juvenile salmon condition as lipid classes get utilized differently for energy under poor feeding conditions. Storage lipids (triacylglycerides) contain small amounts of DHA, but are mobilized more readily than polar lipids, which contain proportionally higher amounts of DHA. Similarly, fasting has been shown to increase $\delta^{15}N$ signatures by up to 0.5‰ in juvenile Chinook Salmon (Hertz et al. 2015b). Future applications of DHA:EPA and $\delta^{15}N$ as trophic markers must consider salmon condition in addition to stomach content data, as poor feeding conditions may cause these biomarkers to increase even though no fish prey has been consumed.

Availability of anchovy prey appears to have important consequences for the onset of piscivory and growth in UCSF subyearlings. Anchovy are an abundant forage fish in the northern California

Current (Litz et al. 2008) and the timing and duration over which they spawn is related to physical factors such as SST and river plume dynamics (Richardson 1973; Parnel et al. 2008). Coastal ocean conditions were similar in the two years of our study and ecosystem indicators of ocean conditions related to salmon recruitment such as Pacific Decadal Oscillation (Mantua et al. 1997), winter SST, and copepod community structure (Peterson et al. 2014) were all considered favorable. Notably, mean volume of the Columbia River plume was 4 times larger in June 2011 (200 km^3) compared to June 2012 (49 km^3). June and July have been identified as important months for spawning anchovy that utilize plume fronts during reproduction (Richardson 1973; Auth 2011). There was also a difference in the intensity of upwelling favorable winds during July of 2011 relative to 2012; wind speed cubed ([m s^{-1}]^3) was 2.4 times lower in July 2011 (50.5) compared to 2012 (122.5; www.pfeg.noaa.gov). Differences

Fig. 9 Associations between mean ± SE subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) trophic position and **a** fluorescence (1-mo lag), **b** Columbia River plume volume (1-mo lag), **c** salmon fork length, **d** proportion of fish measured in salmon diet (1-mo lag), **e** biomass of juvenile Northern Anchovy (*Engraulis mordax*) measured in the field (1-mo lag), and **f** salmon condition (1-mo lag)

in plume size and wind strength may have contributed to inter-annual differences in the timing and magnitude of anchovy recruitment, which occurred later and persisted longer in 2011 than 2012. A less windy surface layer, as was observed in June and July 2011, is hypothesized to benefit first feeding anchovy during early life (Lasker 1978).

Yearling Chinook and Coho Salmon (juveniles that enter the ocean as 1.0 age fish) and juvenile Steelhead originating from the Columbia River are typically larger, migrate to the ocean earlier (April–May), and become piscivorous sooner than subyearlings (Daly et al. 2014; Weitkamp et al. 2015). Marine YOY fishes may contribute as much as 50 to 90% of the mass of larger juvenile diets during spring and early summer (Brodeur et al. 2007; Daly et al. 2009), but have been previously sampled in the field with limited success (Schabetsberger et al. 2003; Brodeur et al. 2011; Brodeur and Morgan 2016). Yearling Chinook, Coho, and Steelhead consume smelt, rockfishes, greenlings (Hexagramidae), sculpin (Cottidae), Pacific Sand Lance (*Ammodytes hexapterus*), and flatfishes (Pleuronectiformes, Brodeur et al. 2007; Daly et al. 2010, 2014). These prey items were well represented in our samples, but mainly collected in May when average biomass estimates were low (57.0 ± 26.3 $\mu g\ m^{-3}$ SE). It is currently unknown whether the observed low biomass estimates of fish prey measured in May was related to predator density, but hypotheses addressing prey limitation and predator density dependence could be further explored by comparing yearling densities, diets (including stomach fullness), condition, and composition of the prey field. Intra- and interspecific competition among outmigrating juvenile salmon is a topic that has received considerable attention in the North Pacific Ocean and Bering Sea (see Ruggerone and Nielsen 2004 for a review), but has not been extensively investigated for fish exiting the Columbia River.

Understanding variability in feeding ecology of juvenile salmon first entering the marine environment, and in particular identifying factors relating to their ontogenetic diet shift, is important for understanding future salmon survival. Chinook Salmon from the UCSF population typically spend 2–4 years in the ocean before returning to spawn, with the majority returning after three ocean winters. Adult passage of summer and fall Chinook Salmon at Priest Rapids Dam on the Upper Columbia River (www.cbr.washington.edu) after three years in the ocean provides a measure of relative survival (Miller et al. 2013; Losee et al. 2014). Juveniles from the same year class as fish sampled in this study in 2011 and 2012 predominantly returned during summer and fall of 2014 and 2015. Adult returns of UCSF

salmon was high in 2014 (198,341) – almost twice the ten-year average from 2004 to 2013 (111,008). Adult returns in 2015 were also unexpectedly high (167,440) despite a large developing El Niño (www.elnino.noaa.gov) and unprecedented warming in the Northeast Pacific known as the "The Blob" (Bond et al. 2015). Hatchery production of UCSF subyearlings has been similar over the last two decades (www.fpc.org) therefore the high returns in 2014 and 2015 were not due to increased hatchery production. Because El Niño and warm ocean temperatures are typically associated with poor salmon survival (Mantua et al. 1997; Meuter et al. 2002), high returns of 2011 and 2012 outmigrants suggests that UCSF salmon may have benefitted from favorable ocean conditions and abundant anchovy prey during early ocean residence. Comparison of salmon prey, diet, trophic biomarkers, and growth during years of poor survival could be used to test this hypothesis. During a warm and unproductive outmigration year, we might expect changes in the overall composition and abundance of salmon prey, earlier or later shifts in prey phenology and the onset of piscivory, lower growth rates, condition, and adult returns. Our integrated approach that combines sampling of salmon prey with estimates of salmon growth, stomach contents, stable isotopes, and fatty acids provides a useful framework for assessing bottom-up regulatory mechanisms impacting foraging ecology during a critical period in salmon life history.

Appendix

Table 5 Average biomass of the juvenile salmon prey by cruise (month) estimated as wet weight (μg m^{-3}) from May through September 2011 and 2012

Common Name	Scientific Name	2011					2012			
		May	Jun	Jul	Aug	Sep	May	Jul	Aug	Sep
Pteropod	Limacinidae	0.06								
Hyperiid Amphipod	Hyperiidea					0.07	0.01	0.004		
Gammarid Amphipod	Gammaridea							0.01		
Caprellid Amphipod	Caprelloidea						0.01			
Krill	*Thysanoessa spinifera*	2.14	0.54			0.73	0.12			
North Pacific Krill	*Euphausia pacifica*		0.04				0.18			
Pandalid Shrimp	Pandalidae	0.01								
Crangon Shrimp	Crangonidae		0.02							
Red Rock Crab	*Cancer productus*		0.07				0.001	0.09		
Dungeness Crab	*Metacarcinus magister*	2.10	2.40		0.06	0.02	0.41	0.04		0.01
Pea Crab	*Pinnotheres pisum*		0.003							
Squid (unid)	Cephalopoda									0.84
California Market Squid	*Doryteuthis opalescens*		4.79	1.52	0.09	2.59	2.21		6.28	
Boreopacific Armhook Squid	*Gonatopsis borealis*	1.51								
Magister Armhook Squid	*Berryteuthis magister*						0.14			
Boreal Clubhook Squid	*Onychoteuthis borealijaponica*				0.29					
East Pacific Red Octopus	*Octopus rubescens*					0.11				
Northern Anchovy	*Engraulis mordax*				142.29	341.79		6.97	2577.22	0.72
Smelt (unid)	Osmeridae	8.47	84.31	1.23			64.74	27.62	1.73	
Cod (unid)	Gadidae						0.02			
Pacific Tomcod	*Microgadus proximus*		0.12	0.48	1.26		0.99			
Rockfish (unid)	*Sebastes* spp.	3.31	0.08	0.07	0.45	5.25	0.16	0.48		0.05
Yellowtail Rockfish	*Sebastes flavidus*			0.32						
Greenling (unid)	Hexagrammidae	0.06								
Kelp Greenling	*Hexagrammos decagrammus*						4.86			
Lingcod	*Ophiodon elongatus*	0.07								
Painted Greenling	*Oxylebius pictus*					0.54				
Calico Sculpin	*Clinocottus embryum*	0.03								
Brown Irish Lord	*Hemilepidotus spinosus*	0.51								
Pacific Staghorn Sculpin	*Leptocottus armatus*						0.05			
Cabezon	*Scorpaenichthys marmoratus*					0.06				
Poacher (unid)	Agonidae	0.02								
Starsnout Poacher (unid)	*Bathyagonus* spp.				1.34					
Snailfish (unid)	Liparididae	0.29	0.09			0.04		0.03		
Northern Ronquil	*Ronquilus jordani*	0.05	1.68	3.93	0.18	0.07	0.13	1.57		
Bluebarred Prickleback	*Plectobranchus evides*	0.02								
Pacific Sand Lance	*Ammodytes hexapterus*	0.22					0.07	0.02		
Pacific Sanddab	*Citharichthys sordidus*						3.55			

Table 5 (continued)

Common Name	Scientific Name	2011					2012			
		May	Jun	Jul	Aug	Sep	May	Jul	Aug	Sep
Speckled Sanddab	*Citharichthys stigmaeus*						0.39			
Flatfish (unid)	*Pleuronectidae*	0.71				0.01				
Arrowtooth Flounder	*Atheresthes stomias*	2.11								
Rex Sole	*Glyptocephalus zachirus*			0.24			0.24	0.78		
Butter Sole	*Isopsetta isolepis*	0.04	0.03				0.05	0.02		
Rock Sole	*Lepidopsetta bilineata*	1.27	0.14							
Slender Sole	*Lyopsetta exilis*		0.04				1.16			0.12
English Sole	*Parophrys vetulus*	0.04								
Sand Sole	*Psettichthys melanostictus*	2.41	0.22			0.03	1.17	1.65		0.02

References

Ainley DG, Dugger KD, Ford RG, Pierce SD, Reese DC, Brodeur RD, Tynan CT, Barth JA (2009) Association of predators and prey at frontal features in the California current: competition, facilitation, and co-occurrence. Mar Ecol Prog Ser 389:271–294

Anderson JJ, Gurarie E, Bracis C, Burke BJ, Laidre KL (2013) Modeling climate change impacts on phenology and population dynamics of migratory marine species. Ecol Model 264: 83–97

Auth TD (2011) Analysis of the spring-fall epipelagic ichthyoplankton community in the northern California current in 2004-2009 and its relation to environmental factors. Calif Coop Ocean Fish Invest Rep 52:148–167

Beamish RJ, Bouillon DR (1993) Pacific salmon production trends in relation to climate. Can J Fish Aquat Sci 50:1002–1016

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49: 423–437

Beamish RJ, Sweeting RM, Neville CM (2004) Improvement of juvenile Pacific salmon production in a regional ecosystem after the 1998 climatic regime shift. Trans Am Fish Soc 133: 1163–1175

Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys Res Lett 42:3414–3420

Brodeur RD (1991) Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and Chinook, *O. tshawytscha*, salmon. Environ Biol Fish 30: 303–315

Brodeur RD, Morgan CA (2016) Influence of a coastal riverine plume on the cross-shelf variability in hydrography, zooplankton, and juvenile salmon diets. Estuar Coasts 39: 1183–1198

Brodeur RD, Fisher JP, Teel DJ, Emmett RL, Casillas E, Miller TW (2004) Juvenile salmonid distribution, growth, condition, origin, 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 ME, Trudel M, Weitkamp LA, Armstrong J, Norton EC (2007) Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. In: Grimes CB, Brodeur RD, Haldorson LJ, McKinnell SM (eds) The ecology of juvenile salmon in the Northeast Pacific Ocean: regional comparisons. American Fisheries Society, Bethesda, 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

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter, and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29:1547–1559

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar. Mamm Sci 22:759–801

Burke BJ, Peterson WT, Beckman BR, Morgan CA, Daly EA, Litz MNC (2013) Multivariate models of adult Pacific salmon returns. PLoS One 8(1):e54134

Burkhardt S, Riebesell U, Zondervan I (1999) Effects of growth rate, CO_2 concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. Geochim Cosmochim Acta 63:3729–3741

Claiborne AM, Fisher JP, Hayes SA, Emmett RL (2011) Size at release, size-selective mortality, and age of maturity of Willamette River hatchery yearling Chinook Salmon. Trans Am Fish Soc 140:1135–1144

Claiborne AM, Miller JA, Weitkamp LA, Teel DJ (2014) Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type. Mar Ecol Prog Ser 515:187–202

Copeman LA, Parrish CC, Gregory RS, Jamieson RE, Wells J, Whiticar MJ (2009) Fatty acid biomarkers in coldwater eelgrass meadows: elevated terrestrial input to the food web of age-0 Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser 386: 237–251

Copeman LA, Laurel BJ, Parrish CC (2013) Effect of temperature and tissue type on fatty acid signatures of two species of

North Pacific juvenile gadids: a laboratory feeding study. J Exp Mar Biol Ecol 448:188–196

Copeman LA, Laurel BJ, Boswell KM, Sremba AL, Klinck K, Heintz RA, Vollenweider JJ, Helser TE, Spencer ML (2016) Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (Eleginus gracilis) from the Beaufort, Chukchi and Bering Seas. Polar Biol 39:1109–1126

Cowen RK, Guigand CM (2008) In situ ichthyoplankton imaging system (ISIIS): system design and preliminary results. Limnol Oceanogr-Meth 6:126–132

Cushing DH (1972) The production cycle and the numbers of marine fish. Symp Zool Soc Lond 29:213–232

Dalsgaard J, St. John MA, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340

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 Am Fish Soc 138:1420–1438

Daly EA, Benkwitt CE, Brodeur RD, Litz MNC, Copeman LA (2010) Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Mar Biol 157:1975–1987

Daly EA, Scheurer JA, Brodeur RD, Weitkamp LA, Beckman BR, Miller JA (2014) Juvenile steelhead distribution, migration, feeding, and growth in the Columbia River estuary, plume, and coastal waters. Mar Coast Fish 6:62–80

Duffy EJ, Beauchamp DA (2011) Rapid growth in the early marine period improves marine survival of Puget sound Chinook Salmon. Can J Fish Aquat Sci 68:232–240

Duffy EJ, Beauchamp DA, Sweeting RM, Beamish RJ, Brennan JS (2010) Ontogenetic diet shifts of juvenile Chinook Salmon in nearshore and offshore habitats of Puget sound. Trans Am Fish Soc 139:803–823

El-Sabaawi R, Dower JF, Kainz M, Mazumder A (2009) Characterizing dietary variability and trophic positions of coastal calanoid copepods: insight from stable isotopes and fatty acids. Mar Biol 156:225–237

Emmett RL, Miller DR, Blahn TH (1986) Food of juvenile Chinook, Oncorhynchus tshawytscha, and coho, O. kisutch, salmon off the northern Oregon and southern Washington coasts, may – September 1980. Calif Fish Game 72:38–46

Fisher JP, Weitkamp LA, Teel DJ, Hinton SA, Trudel M, Morris JFT, Theiss ME, Sweeting RM, Orsi JA, Farley EV Jr (2014) Early ocean dispersal patterns of Columbia River Chinook and Coho Salmon. Trans Am Fish Soc 143:252–272

Folch J, Lees M, Stanley GHS (1957) A simple method for the isolation and purification of total lipid from animal tissues. J Biol Chem 226:287–291

Fry B (2006) Stable isotope ecology. Springer, New York

Gregory RS, Northcote TG (1993) Surface, planktonic, and benthic foraging by juvenile Chinook Salmon (Oncorhynchus tshawytscha) in turbid laboratory conditions. Can J Fish Aquat Sci 50:233–240

Hansen AG, Beauchamp DA, Schoen ER (2013) Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size. Trans Am Fish Soc 142:854–867

Heady WN, Moore JW (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. Oecologia 172:21–34

Hertz E, Trudel M, Brodeur RD, Daly EA, Eisner L, Farley EV Jr, Harding JA, MacFarlane RB, Mazumder S, Moss JH, Murphy JM, Mazumder A (2015a) Continental-scale variability in the feeding ecology of juvenile Chinook Salmon along the coastal Northeast Pacific Ocean. Mar Ecol Prog Ser 537:247–263

Hertz E, Trudel M, Cox MK, Mazumder A (2015b) Effects of fasting and nutritional restriction on the isotopic ratios of nitrogen and carbon: a meta-analysis. Ecol Evol 8:4829–4839

Hertz E, Trudel M, El-Sabaawi R, Tucker S, Dower JF, Beachum TD, Edwards AM, Mazumder A (2016) Hitting the moving target: modelling ontogenetic shifts with stable isotopes reveals the importance of isotopic turnover. J An Ecol 85:681–691

Hussey NE, MacNeil MA, McMeans BC, Olin JA, Dudley SFJ, Cliff G, Wintner SP, Fennessy ST, Fisk AT (2014) Rescaling the trophic structure of marine food webs. Ecol Lett 17:239–250

Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: a comparison of body condition indices. Oikos 77:61–67

Juanes F (1994) What determines prey size selectivity in piscivorous fishes? In: Stouder DJ, Fresh KL, Feller RJ (eds) Theory and application in fish feeding ecology. University of South Carolina Press, Columbia, pp. 79–100

Juanes F, Buckel JA, Scharf FS (2002) Feeding ecology of piscivorous fishes. In: Hart PJB, Reynolds JB (eds) Handbook of fish biology and fisheries, volume 1: fish biology. Blackwell Scientific Publications, Oxford, pp. 267–283

Kalinowski ST, Manlove KR, Taper ML (2007) ONCOR: a computer program for genetic stock identification. Montana State University, Bozeman

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:115–129

Lamb J (2011) Comparing the hydrography and copepod community structure of the continental shelf ecosystems of Washington and Oregon, USA from 1998 to 2009: can a single transect serve as an index of ocean conditions over a broader area? MS thesis, Oregon State University, Corvallis, OR

Lasker R (1978) The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. Rapp P-V Reun Cons Int Explo Mer 173:212–230

Laws EA, Popp BN, Bidigare RR, Kennicutt MC, Macko SA (1995) Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: theoretical considerations and experimental results. Geochim Cosmochim Acta 59:1131–1138

Litz MNC, Emmett RL, Heppell SS, Brodeur RD (2008) Ecology and distribution of the northern subpopulation of northern anchovy (Engraulis mordax) off the U.S. west coast. Calif Coop Ocean Fish Invest Rep 49:167–182

Losee J, Miller JA, Peterson WT, Teel DJ, Jacobson KC (2014) Influence of ocean ecosystem variation on trophic interactions and survival of juvenile coho and Chinook Salmon. Can J Fish Aquat Sci 71:1747–1757

MacFarlane RB (2010) Energy dynamics and growth of Chinook Salmon (Oncorhynchus tshawytscha) from the Central Valley of California during the estuarine phase and first ocean year. Can J Fish Aquat Sci 67:1549–1565

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. Bull Am Meteorol Soc 78:1069–1079

Mather PM (1976) Computational methods of multivariate analysis in physical geography. J. Wiley and Sons, London

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach

Meuter FJ, Peterman RM, Pyper BJ (2002) Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Can J Fish Aquat Sci 59:456–463

Mielke PW Jr, Berry KJ (2001) Permutation methods: a distance function approach. Springer, New York

Miller TW, Brodeur RD, Rau G (2008) Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California current pelagic community. Limnol Oceanogr 53:1493–1503

Miller TW, Brodeur RD, Rau G, Omori K (2010) Prey dominance shapes trophic structure of the northern California current pelagic food web: evidence from stable isotopes and diet analysis. Mar Ecol Prog Ser 420:15–26

Miller JA, Teel DJ, Baptista A, Morgan CA (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook Salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70: 617–629

Miller JA, Teel DJ, Peterson WT, Baptista AM (2014) Assessing the relative importance of local and regional processes on the survival of a threatened salmon population. PLoS ONE 9: e99814

Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. Can J Fish Aquat Sci 55:1454–1465

Parnel MM, Emmett RL, Brodeur RD (2008) Ichthyoplankton community in the Columbia River plume off Oregon: effects of fluctuating oceanographic conditions. Fish Bull 106:161–173

Parrish CC (1999) Determination of total lipids, lipid classes and fatty acids in aquatic samples. In: Arts MT, Wainmann BC (eds) Lipids in freshwater ecosystems. Springer, New York, pp. 4–20

Parrish CC (2013) Lipids in marine ecosystems. ISRN Oceanography 2013 Article ID 604045, 16 pp

Pearcy WG (1992) Ocean ecology of North Pacific salmonids. Washington Sea Grant Program University of Washington Press, Seattle

Pearcy WG, McKinnell SM (2007) The ocean ecology of salmon in the Northeast Pacific Ocean – an abridged history. 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, Bethesda, pp. 7–30

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Peterson JO, Peterson WT (2008) Influence of the Columbia River plume (USA) on the vertical and horizontal distribution of mesozooplankton over the Washington and Oregon shelf. ICES J Mar Sci 65:477–483

Peterson WT, Brodeur RD, Pearcy WG (1982) Food habits of juvenile salmon in the Oregon coastal zone, June 1979. Fish Bull 80:841–851

Peterson WT, Fisher JL, Peterson JO, Morgan CA, Burke BJ, Fresh KL (2014) Applied fisheries oceanography: ecosystem indicators of ocean conditions inform fisheries management in the California current. Oceanography 27:80–89

Phillips AJ, Brodeur RD, Suntsov AV (2009) Micronekton community structure in the epipelagic zone of the northern California current upwelling system. Prog Oceanogr 80:74–92

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189

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

Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. P Natl Acad Sci USA 94:9197–9201

Richardson S (1973) Abundance and distribution of larval fishes in waters off Oregon, may-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish Bull 71:697–711

Rindorf A, Lewy P (2011) Bias in estimating food consumption of fish by stomach-content analysis. Can J Fish Aquat Sci 61: 2487–2498

Ruggerone GT, Nielsen JL (2004) Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. Rev Fish Biol Fish 14: 371–390

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

Seeb LW, Antonovich A, Banks MA, Beachem TD, Bellinger MR, Blankenshipp SM, Campbell MR, Decovich NA, Garza JC, Guthrie CM III, Lundrigan TA, Moran P, Narum SR, Stephanson JJ, Supernault KJ, Teel DJ, Templin WD, Wenburg JK, Young SF, Smith CT (2007) Development of a standardized DNA database for Chinook Salmon. Fisheries 32:540–549

Teel DJ, Bottom DL, Hinton SA, Kuligowski DR, McCabe GT, McNatt R, Roegner GC, Stamatiou LA, Simenstad CA (2014) Genetic identification of Chinook Salmon in the Columbia River estuary: stock-specific distributions of juveniles in shallow tidal and freshwater habitats. N Am J Fish Manag 34:621–641

Teel DJ, Burke BJ, Kuligowski DR, Morgan CA, Van Doornik DM (2015) Genetic identification of Chinook Salmon: stock-specific distributions of juveniles along the Washington and Oregon coasts. Mar Coast Fish 7:274–300

Vander Zanden MJ, Rasmussen JB (1999) Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80:1395–1404

Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS One 10(1): e0116182

Waples RS, Teel DJ, Myers J, Marshall A (2004) Life history divergence in Chinook Salmon: historic contingency and parallel evolution. Evolution 58:386–403

Weitkamp LA, Sturdevant MV (2008) Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of Southeast Alaska. Fish Oceanogr 17:380–395

Weitkamp LA, Teel DJ, Liermann M, Hinton SA, Van Doornik DM, Bentley PJ (2015) Stock-specific size and timing at ocean entry of Columbia River juvenile Chinook Salmon and steelhead: implications for early ocean growth. Mar Coast Fish 7:370–392

Wells BK, Santora JA, Field JC, MacFarlane RB, Marinovic BB, Sydeman WJ (2012) Population dynamics of Chinook Salmon *Oncorhynchus tshawytscha* relative to prey availability in the Central California coastal region. Mar Ecol Prog Ser 457:125–137

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425

Zabel RW, Williams JG (2002) Selective mortality in Chinook Salmon: what is the role of human disturbance? Ecol Appl 12:173–183

Zhang YL, Baptista AM (2008) SELFE: a semi-implicit Eulerian-Lagrangian finite-element model for cross-scale ocean circulation. Ocean Model 21:71–96