

Anomalous ocean conditions in 2015: impacts on spring Chinook salmon and their prey field

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ABSTRACT: In the northern California Current, Columbia River Chinook salmon *Oncorhynchus tshawytscha* that return as adults in spring are primarily hatchery-produced, though they include natural-origin fish listed under the US Endangered Species Act. Anomalous warm ocean conditions persisted in the California Current during 2015 (>2.5°C above normal) through the winter period when fish prey resources of juvenile salmon develop and during spring as salmon enter the ocean. The biomass of ichthyoplankton in winter 2015 was the 4th highest of our 18 yr time-series (1998–2015), predicting good food conditions for salmon and high adult salmon returns several years later. The larval composition of 2015 ichthyoplankton included abnormally large amounts of the warm-water taxa northern anchovy *Engraulis mordax* and rockfish *Sebastes* spp. When the composition of ichthyoplankton is dominated by warm-water taxa in winter, we would predict poor returns of salmon. May diets of juvenile Chinook salmon collected in coastal waters reflected high proportions of juvenile rockfish, no evidence of northern anchovy, and most closely resembled those of other warm years. June diets also reflected a warm prey community being consumed, predicting poor returns of salmon. Chinook salmon had high percentages of empty stomachs and were small and thin in 2015, with fish weighing 17.6% less than the same-length fish in a cold year (2008). Lower condition of juvenile Chinook salmon related to decreased returns of adult salmon. Overall, all but one biological predictor (biomass of prey) suggests that the prospects for the 2015 ocean-entry smolts were not favorable for survival.

KEY WORDS: Warm anomaly · Ichthyoplankton · Salmon feeding · Salmon condition · Ocean survival

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INTRODUCTION

In 2014, anomalous atmospheric forcing in the northeast Pacific Ocean caused lower-than-normal oceanographic rates of heat loss in addition to relatively low cold-water advection in the upper ocean, which led to ocean sea-surface temperature (SST) anomalies of >2.5°C (Di Lorenzo & Mantua 2016). This large, warm body of water named the 'Blob' (Bond et al. 2015) persisted through 2015 from

Alaska to Mexico (Zaba & Rudnick 2016). Biological responses in the southern California Current in 2015 ranged from lower trophic-level changes, such as decreases in chlorophyll *a* (fluorescence), to mass strandings and mortality of California sea lion (*Zalophus californianus*) pups at the upper trophic levels (Kintisch 2015, Zaba & Rudnick 2016). The warm 'Blob' moved into the coastal waters of the northern California Current (NCC) in mid-September 2014 (Peterson et al. 2015) and remained through late 2015

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[§]Corrections were made to Fig. 4 in the online version after publication. For details see www.int-res.com/abstracts/meps/v566/c_p169-182
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(Peterson et al. 2016). The warm 'Blob' had a dramatic effect on the biological communities in the NCC. Marine life sampled in 2015 appears to have moved to a condition that was considerably different from long-term data sets, both in composition and abundance, for the copepod, ichthyoplankton, pelagic fish, and invertebrate communities (Leising et al. 2015).

Pacific salmon *Oncorhynchus* spp. are an anadromous species with high interannual variability in survival, and there are numerous salmon stocks that are listed as threatened or endangered under the US Endangered Species Act (ESA). In the US Pacific Northwest, salmon have great economic, social, and cultural importance to the region. During spring, millions of juvenile spring-run Chinook salmon *O. tshawytscha* exit the Columbia River into the NCC to eat and grow (Tomaro et al. 2012, Miller et al. 2014, Daly & Brodeur 2015). There is a short window of time for this early marine growth to occur, and if food resources are insufficient, there is evidence that size-selective mortality occurs (Claiborne et al. 2011) and that the returns of the adult spring-run Chinook salmon to the river system 2 yr later are suppressed. The return of adult Chinook salmon to the Columbia River 2 yr later is particular to yearling stocks of Chinook salmon that return as adults in the spring (Ruzicka et al. 2016). The number of winters that spring-run Chinook salmon spend in the ocean prior to their return to the Columbia River can be extrapolated from retrospective scale-aging analysis made by the Columbia River Inter-Tribal Fish Commission of the returning adults (e.g. CRITFC 2015). The majority (77.7 ± 6.4%) of spring-run Chinook salmon returned on average after 2 ocean winters from the out-migration years of 1998–2012. While the life-histories of Chinook salmon are highly variable at the population level in terms of age and timing of their ocean entry (Rich 1920, Healey 1991, Waples et al. 2001), spring-run Chinook salmon are typically yearlings and rapidly migrate north after exiting the ocean (Fisher et al. 2014, Teel et al. 2015).

In 2005, the most recent non-El-Niño-related anomalously warm ocean year, impacts were observed throughout the food web: die-offs of planktivorous birds (Sydemann et al. 2006), pelagic nekton displacements and reductions of larval and juvenile nekton (Brodeur et al. 2006), and changes in the plankton (Mackas et al. 2006) and primary production (Kudela et al. 2006). The Sacramento River fall-run Chinook salmon population that out-migrated into the ocean in 2005 and which failed to return as adults 3 yr later caused the most restrictive salmon

fisheries in the history of the west coast (Lindley et al. 2009). The year 2005 was the 3rd and most extreme warm year in a row in the NCC, which may have reduced the fitness of the fish and birds and their tolerance to adverse ocean conditions.

With 5 populations of Columbia River Chinook salmon listed as part of the ESA, it is of critical importance to understand the impact of extreme ocean conditions, as were observed in 2005 and 2015, so that fisheries managers may take appropriate actions to protect the returning adult populations. Long-term time-series have been used to predict fluctuations in population abundance of salmon over the last 10 yr, such as northern copepod biomass (Peterson et al. 2014), ichthyoplankton biomass (Daly et al. 2013), otolith structural and chemical analysis (Miller et al. 2014), diet, stomach fullness, condition (Daly & Brodeur 2015), and growth (Burke et al. 2013). The purpose of the present study was to examine the marine feeding ecology and body condition of the juvenile Chinook salmon that entered the ocean in 2015, along with the availability of their potential prey resources, and to compare the 2015 biological characteristics within multiple time-series in order to estimate the potential impact of ocean warming on the Chinook salmon that out-migrated during the 'Blob', and predict how this may affect future returns of adults.

MATERIALS AND METHODS

Ichthyoplankton samples were collected from 5 stations spaced 9 km apart, 9–46 km offshore, along the southern transect of the Newport Hydrographic (NH) line at 44.65° N, approximately every 2 wk, January–March in 1998–2015 (Fig. 1; 'NH line'). Sampling was primarily conducted at night using either a 1 m diameter ring net with 333 µm mesh or a 60 cm diameter bongo net with 333 µm mesh (200 µm before 2005). The net was fished as an oblique tow within the upper ~20 m of the water column at a retrieval rate of ~30 m min⁻¹ and a ship speed of 2–3 km h⁻¹ (1.1–1.6 knots; see Auth et al. 2015 for detailed methodology). Ichthyoplankton samples were preserved at sea and sorted, counted, measured, and converted to biomass as described in Daly et al. (2013). Total biomass of ichthyoplankton that are important prey of juvenile salmon *O. tshawytscha* were calculated for each station as the sum of the carbon weights of individuals per m³, expressed as mg C 1000 m⁻³, and averaged for the year. Ichthyoplankton biomass values for all years used in this study are

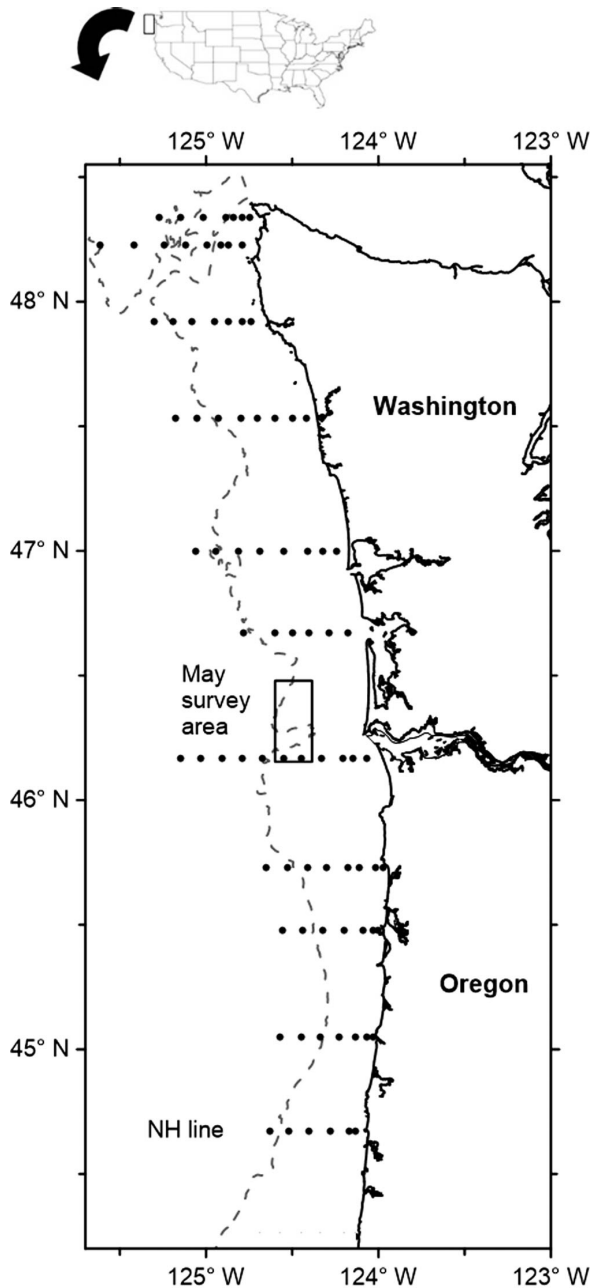


Fig. 1. Sampling stations (●) off the coast of Washington and Oregon, USA. Samples of winter ichthyoplankton were taken at stations on the Newport Hydrographic (NH) line (44.65° N). May Chinook salmon *Oncorhynchus tshawytscha* were sampled in the area of the small box ('May survey area'). Included in the May survey were 2 stations that had been sampled consistently during the long-term study (1998–2015). The June sampled area for Chinook salmon ranged from the northern coastal region of Washington at 48.5° N south to the NH line

available at: www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/eg-winter-ichthyoplankton.cfm.

This annual winter ichthyoplankton biomass was used as an index of food conditions for salmon prior

to their ocean entry in the spring (Daly et al. 2013). The important ichthyoplankton salmon prey were Pacific sand lance *Ammodytes hexapterus*, rockfishes *Sebastes* spp., smelts (Osmeridae), sculpins (Cottidae), and northern anchovy *Engraulis mordax*. The lag-time from winter to spring is approximately the time that these winter-spawned larval fish would take to grow to the juvenile fish that the salmon consume when they enter the ocean. In addition to the biomass of prey available, we also considered whether the species composition of the winter ichthyoplankton biomass was important to the juvenile salmon. The maximum variance of a principal coordinate analysis (PCO) based on annual average values of winter ichthyoplankton biomass composition was aligned along Axis 1, and the Axis 1 PCO values were used as a univariate value to test for annual ichthyoplankton composition differences and other environmental or biological impact factors. Lastly, to identify the larvae which contributed to any significant composition differences, we utilized SIMPER analysis. To test for significant differences between years, we used the ANOSIM test, with station larval compositions nested within each year and a significance level of $p < 0.05$. Only the annual differences relative to 2015 were reported. All PCO, ANOSIM, and SIMPER analyses were carried out using PRIMER6+ software (Clarke & Gorley 2006).

Surface-trawl surveys to collect juvenile salmon have been conducted from 1998 to 2015 by the Estuarine and Ocean Ecology Program of NOAA in Oregon and Washington coastal waters (Fig. 1). Sampling occurred at the end of May (except in 1998, 2012, and 2013) and June, for a total of 33 surveys. Transects ran perpendicular to the coast and were spaced ~30–50 km apart. Predetermined stations spaced 5–8 km apart were sampled along these transects, running from inshore starting at 30–40 m bottom depth and out to the shelf break. Transects and stations were primarily located between 44–48.5° N and 124–125° W. Not all transects were sampled every survey, and some surveys included specially designed repeated sampling efforts in focused geographic areas to answer specific questions regarding salmon ocean ecology, as was the case in May 2015. In order to compare the salmon collected in May 2015 with the fish sampled in previous May surveys without this geographic bias, we limited all data analyses in May to the same limited geographic range directly off the Columbia River (46.1–46.5° N, 124.4–124.3° W) as was sampled in May 2015. No salmon were collected in May 2005 within this restricted geographic region. Sampling efforts in

June 2015 were consistent with previous survey years, and all transects were included in these comparisons.

Juvenile Chinook salmon were collected using a Nordic 264 pelagic rope trawl with a mouth opening of 30 m wide and 20 m deep and a 0.8 cm cod-end liner, which was towed during daylight hours for 30 min at a ship speed of $\sim 6 \text{ km h}^{-1}$ (3.2 knots). Captured juvenile salmon were identified, fork length (FL) was measured, and fish were individually tagged and then frozen immediately. In the laboratory, all salmon were weighed and stomachs were removed and placed into a preservative solution (10% formaldehyde prior to 2008, and a non-formaldehyde fixative called Prefer [Anatech] from 2008 onward) for trophic analysis. Yearling Chinook salmon were the only juvenile salmon used for our study, and their age-class was based upon FL criteria from Pearcy & Fisher (1990), with May yearling Chinook salmon being 121–250 mm, while in June the range was 141–280 mm. Statistical analysis of the variation in salmon FL between years was conducted using the non-parametric Kruskal-Wallis test statistic due to the non-normality of the data. The May yearling Chinook salmon were 82% spring-run fish from the Columbia River, while 98% of the fish collected in June were from the Columbia River, with 54% being spring-run stocks. Upper Columbia River summer-fall yearling Chinook salmon comprised 31% of the June fish (Teel et al. 2015).

Trophic analysis was conducted on up to 30 stomachs per station, with prey identified to the lowest possible taxonomic category and weighed to the nearest 1 mg (Daly & Brodeur 2015). Prey were grouped into the following trophic categories: northern anchovy, clupeids, cottids, flatfishes (*Pleuronectiformes*), osmerids, northern ronquils *Ronquilus jordani*, Pacific sand lance, rockfishes, rare fish (fish that made up <5% of diet composition in any year), *Cancer* spp. crab larvae, euphausiids, hyperiid amphipods, non-*Cancer* crab larvae, shrimp larvae, and other (i.e. cephalopods, cirripede larvae, copepods, insects, gelatinous zooplankton, mysids, non-hyperiid amphipods, pteropods, and polychaetes). Unidentified fish were re-proportioned at the station level according to the average proportion of the known fish prey similar to Beauchamp & Van Tassell (2001) and Daly et al. (2013) (see next paragraph regarding diet auto-correlation at sampling stations). If no known fish prey were consumed at a station, the unidentified fish were re-proportioned to the average survey ratio of the known fish proportion. The amount of unidentified fish in May diets was on aver-

age 31.7% (± 28.1 SD), whereas in June, unidentified fish was on average 37.7% (± 31.1).

Diets of juvenile salmon have been shown to be most similar to the salmon they are caught with in the same haul (Weitkamp & Sturdevant 2008). Yearling Chinook salmon diets were averaged at each station, and then averaged for the survey. This was done to eliminate any auto-correlation among individual fish that may occur at a station when the juvenile salmon feed concurrently on the prey that are present, resulting in most individuals having similar diets at a station. All diet analyses were calculated on the percentage of prey eaten by weight. May and June were evaluated separately and annual diet composition differences were visually presented using a Bray-Curtis similarity matrix to create a PCO. For each year, individual placement along the axes on the PCO plots represents the average annual diet composition relative to the other years. Maximum variance of the PCO was aligned along Axis 1, and PCO values from this axis were used as a univariate value to test for annual diet differences and other environmental or biological metrics.

Stomach fullness was calculated as: $(\text{Weight [g] of prey consumed}) / (\text{Total fish weight} - \text{Weight of prey consumed}) \times 100$. Salmon with stomach fullness <0.05% of their body weight were considered empty. There was a significant correlation between length and feeding intensity over the range of sizes examined ($\text{Stomach fullness} = 0.0135815 - 0.0000222084 \times \text{FL}$; $p = 0.0001$). Therefore, we used multifactor ANCOVA, with length as a covariate, to test for differences in feeding intensity between groups. When there were significant interannual differences in feeding intensity, we followed up the ANCOVA with Fisher's least significant difference multiple range test.

For an index of salmon growth, we calculated a length-weight condition factor in order to ascertain if the salmon were thin or fat for their length. We used the residuals from regression analysis on $\ln(\text{weight [g]})$ to $\ln(\text{FL [mm]})$ of the salmon to identify if they were in positive (fatter) or negative (thinner) condition for their size. Statistical analysis of the differences between salmon condition and year were tested using the Kruskal-Wallis test due to the non-normality of the data.

Using long-term time-series of various environmental and biological metrics, we attempted to predict what effect the warm 'Blob' might have on the juvenile salmon that out-migrated into such anomalously warm ocean conditions. Biological measures of prey biomass and composition based on the winter ichthyoplankton and salmon (i.e. diet composition,

stomach fullness, and condition factor) were related to environmental conditions and/or the marine survival of the salmon represented by counts of adult salmon that returned to the Columbia River 2 yr later. The most common life-history strategy of yearling spring-run Chinook salmon is to spend 2 yr in the ocean, and 2017 is the year that the majority of the juvenile salmon that out-migrated into the ocean in 2015 would return as adult salmon (see 'Introduction'). We used these biological metrics and the regressions to predict adult salmon returns to the Columbia River in 2017.

Environmental variables utilized for explanatory analyses were the Pacific Decadal Oscillation (PDO), which is an index based on the long-term variation in SST, with more positive values indexing warmer ocean conditions (<http://research.jisao.washington.edu/pdo/PDO.latest>; last accessed May 16, 2016), and the North Pacific Gyre Oscillation (NPGO), which is an index correlated with fluctuations in salinity, nutrients, and chlorophyll *a*, with positive NPGO values related to more productive, colder ocean conditions (www.o3d.org/npgo/npgo.php; last accessed May 16, 2016). Winter ichthyoplankton biomass and composition was related to winter October–December environmental conditions the prior year (Daly et al. 2013). Salmon biological characteristics of size, diet, fullness, and condition in May were compared to averaged spring PDO and NPGO values from March–May, and June salmon biological characteristics of size, diet, fullness, and condition were related to average spring/early summer April–June PDO and NPGO values as proxies of the physical

ocean conditions that the salmon and their prey were encountering. With the stable hatchery production of Chinook salmon in the Columbia River, the variability in return counts of adult salmon at Bonneville Dam was used as a proxy for marine survival (Columbia River Data Access in Real Time [DART]; www.cbr.washington.edu/dart/query/adult_daily/; last accessed Feb 9, 2017). We used counts of spring-run Chinook taken during March 15 to May 31 each year, and count data were lagged by 2 yr to reflect year of ocean entry for these adults.

RESULTS

Environmental conditions in late spring 2015, and the previous winter (October–December 2014), were highly anomalous. PDO values have been calculated going back to 1900, and only one other winter (1937) in the 115 yr time-series was more positive (warmer) on average than 2015. March–May spring PDO conditions were 7th most positive (2005 was 10th), and April–June were 11th most positive of the entire time-series (2005 was 12th). For 1998–2015, the time-series of our study, each of these blocks of time were the most positive of the 18 yr, with 2005 almost as positive (Fig. 2a). In late 2014, the NPGO was average for the entire time-series dating back to 1950 (31st most negative), with the values becoming more negative into the spring of 2015. March–May and April–June average NPGO values in 2015 were 8th most negative (less productive) in the 65 yr time-series, and were 6th most negative in the 18 yr time-series in

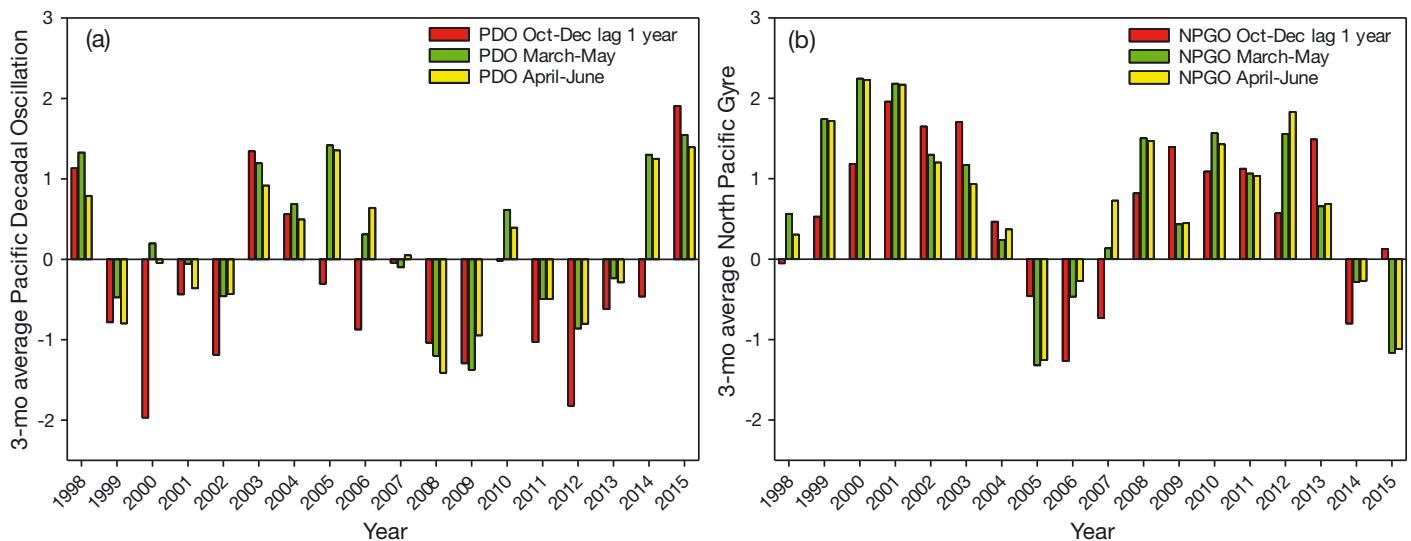


Fig. 2. Average 3 mo values for (a) Pacific Decadal Oscillation (PDO) and (b) North Pacific Gyre Oscillation (NPGO) for 3 time periods: Oct–Dec lagged 1 yr, Mar–May, and Apr–Jun

winter, and 2nd most negative in spring 2015, behind 2005 (Fig. 2b). Generally, if PDO was positive (or negative) in the prior winter, it was positive (or negative) in spring, respectively. Exceptions to this were: 2000, 2005, 2010, and 2014 (Fig. 2a). There were exceptions to the NPGO as well, when winter was different from spring, such as in 1998, 2007, and 2015 (Fig. 2b).

The biomass of fish larvae in January–March 2015 off the NH line (Fig. 1), which is an index of the amount of food that could be available to the juvenile salmon when they enter the ocean in spring, was 4th highest in the time-series, which predicted good food conditions for the salmon in 2015 (Burke et al. 2013, Daly et al. 2013). The biomass of salmon prey in winter was negatively related to prior winter PDO conditions (regression; $p = 0.02$; $R^2 = 0.31$). However, with the PDO conditions in late 2014 being almost double (warmer) than those of any year in our 18 yr time-series, we considered the 2014 PDO an outlier, as it was >2 Studentized residuals different from all of the other years of data. In juxtaposition to the high biomass was the type of prey, which were taxa that are typically available in warm ocean years (e.g. rockfishes and northern anchovy larvae; Brodeur et al. 2008, Daly et al. 2013). Winter ichthyoplankton composition, based on PCO analysis, showed 2015 on the negative side of Axis 1, along with several other warm ocean years that had similar ichthyoplankton composition (2004–2005; Fig. 3). The larval composition was significantly different from 10 out of the 18 yr (ANOSIM; pairwise; $p < 0.05$), and larval rockfishes (66.6%) and northern anchovy (26.4%; SIMPER) contributed the most to the significant differences. The winter ichthyoplankton composition based on Axis 1 values was negatively related to the prior winter PDO (regression; $p = 0.03$; $R^2 = 0.27$).

In the small geographic area sampled in May (Fig. 1, small box; 'May survey area'), a total of 2120 juvenile yearling Chinook salmon were captured over the 14 yr, with 214 captured in 2015 (Table 1). Chinook salmon FLs were slightly smaller than average (152.2 vs. 160.5 mm) in May 2015, and were significantly less for fish captured in 1999–2002, 2009, and 2012 (Kruskal-Wallis test; $p < 0.0001$), but not significantly different from the other years. May FL was positively related to spring NPGO (regression; $p = 0.02$; $R^2 = 0.40$). In June, 2488 yearling Chinook salmon were captured over the 18 survey years

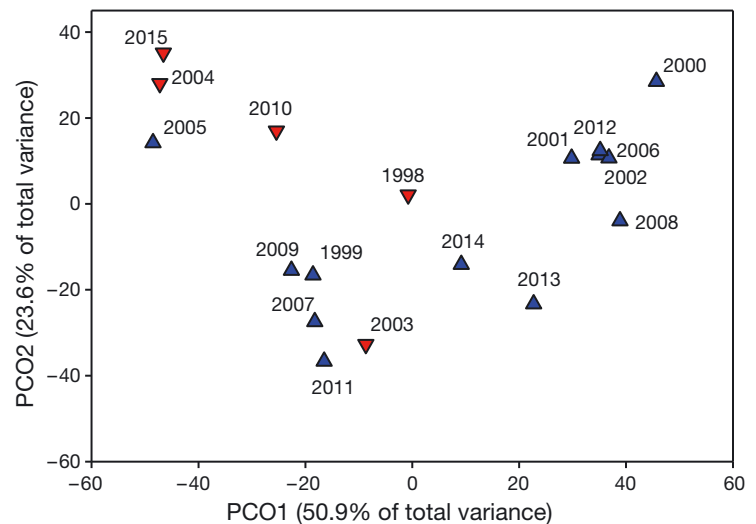


Fig. 3. Principal coordinate analysis (PCO) of winter ichthyoplankton composition of main prey taxa eaten by juvenile salmon *Oncorhynchus tshawytscha*: Pacific sand lance, osmerids, cottids, northern anchovy, and rockfishes. Blue: years when winter had negative Pacific Decadal Oscillation (PDO) conditions, and red: positive PDO conditions

(Fig. 1; 48.5° N to NH line), with 94 being caught in 2015 (Table 1). The average FL of the salmon in 2015 was tied for 3rd largest average size of the fish relative to the other June survey years (209.1 mm vs. 189.7 mm overall), and was significantly larger than for fish collected from 12 other years (Kruskal-Wallis test; $p < 0.0001$), but were not significantly different

Table 1. Annual sample size and fork length (FL) (\pm SD) of yearling Chinook salmon *Oncorhynchus tshawytscha* caught in May and June, and grand total with overall average size. Blanks: no cruises or salmon were available

Year	May		June	
	N	FL (mm)	N	FL (mm)
1998			32	217.7 \pm 39.4
1999	175	164.5 \pm 28.3	193	191.8 \pm 27.9
2000	60	169.0 \pm 25.5	93	200.0 \pm 32.4
2001	67	163.6 \pm 22.5	40	209.1 \pm 34.8
2002	838	165.4 \pm 29.6	131	194.1 \pm 33.9
2003	34	148.4 \pm 17.7	138	195.7 \pm 37.4
2004	228	155.3 \pm 18.6	85	201.8 \pm 37.7
2005			21	189.3 \pm 31.7
2006	7	146.4 \pm 16.7	91	189.5 \pm 27.6
2007	43	147.9 \pm 17.1	132	187.9 \pm 35.3
2008	139	155.4 \pm 26.2	467	187.3 \pm 29.1
2009	182	158.1 \pm 22.2	166	198.1 \pm 33.8
2010	20	150.8 \pm 16.7	160	188.8 \pm 32.3
2011	70	153.6 \pm 21.0	98	193.0 \pm 37.6
2012	43	166.4 \pm 23.4	206	194.9 \pm 30.3
2013			196	184.4 \pm 30.6
2014			145	223.8 \pm 35.0
2015	214	152.2 \pm 19.0	94	209.1 \pm 37.4
Total	2120	160.5 \pm 26.0	2488	189.7 \pm 33.0

from those caught in 1998, 2000, 2001, 2004, and 2014. Average size of yearling Chinook salmon in June did not relate to spring/early summer NPGO or PDO.

In terms of diet (Figs. 4 & 5), the juvenile Chinook salmon collected in May 2015 ate high amounts of juvenile rockfishes, flatfishes, and *Cancer* crab megalopae and had a complete absence of euphausiids in their diets (Fig. 4a). These salmon diets were closest to 2010 and 2006, 2 other positive (warmer) PDO years, both with high amounts of juvenile rockfish in their diets. This is illustrated in the PCO plot (Fig. 5a), with May 2015 diets being the most negative along PCO Axis 1. Annual diets were significantly different (ANOSIM; global R = 0.56; p < 0.001), with pairwise tests showing that 2015 was significantly different from the other years except 2010 and 2006 (ANOSIM; p < 0.05). The 2015 diets were different from the other years primarily due to high amounts of juvenile rockfish in the diets. This prey contributed to 77.6% of the diet differences (SIMPER). Flatfish was the other prey of significance, which contributed to 17.6% of the significant annual diet differences (SIMPER). May diet composition, based on Axis 1 PCO values, related positively to spring NPGO (regression; p = 0.01; R² = 0.40).

The diets of the salmon collected in June 2015 were grouped with other warm ocean years, with the primary prey consumed being juvenile rockfish, northern anchovies, and flatfish (Fig. 4b). In ordination space, June 2015 salmon diets clustered with the

other positive (warmer) PDO ocean years, which were aligned on the negative side of Axis 1 (Fig. 5b). Exceptions to this pattern were 2014, a positive spring/early summer PDO year (yet a negative winter PDO year; Fig. 2) which was not in this warm ocean cluster, and 2007, a neutral PDO year which was in the warm ocean group. Again there was highly significant interannual differences in June salmon diets (ANOSIM; global R = 0.19; p < 0.0001; Fig. 5). June 2015 diets were significantly different than the previous sampling years, with the exception of 2003, 2005, and 2010 (ANOSIM, pairwise; p < 0.05). Prey eaten in June 2015 that contributed to the significant annual differences were juvenile rockfishes (63.3%), flatfishes (13.4%), and northern anchovy (13.2%; SIMPER). June diet composition, based on Axis 1 PCO values, related negatively to spring/early summer PDO (regression; p = 0.003; R² = 0.44), and positively to NPGO (regression; p = 0.006; R² = 0.38). Other fish prey that are common in the diets of juvenile Chinook salmon in cold years, such as Pacific sand lance and sculpins, were nearly if not completely absent in 2015 (Fig. 3). In addition to the changes in fish prey composition, other anomalies were evident, such as a complete absence of euphausiids in May, and abnormally high abundances of gammarid amphipods (the pelagic taxa *Atylus tridens*) and ruby octopus *Octopus rubescens* in June, which are part of the 'other' prey category (Fig. 4b).

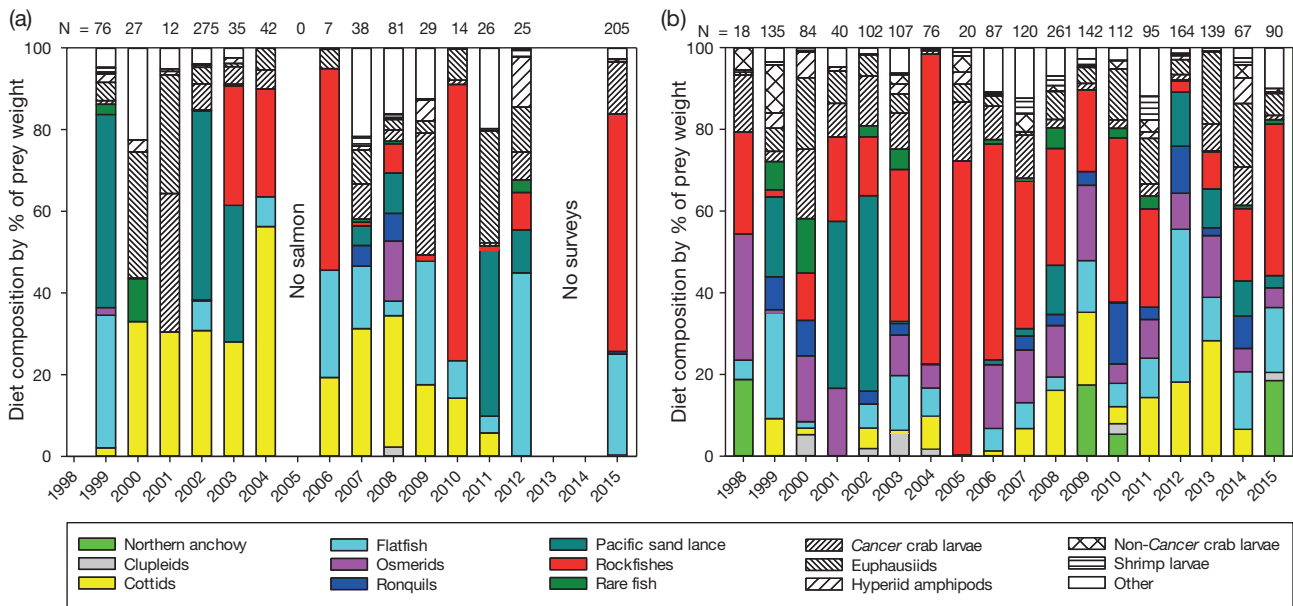


Fig. 4. Diet composition of (a) May and (b) June yearling Chinook salmon *Oncorhynchus tshawytscha* by weight of prey consumed. Sample sizes are shown at the top of each bar plot, fish prey are in color, and invertebrates are in black and white with differing patterns. Unidentified fish were re-proportioned to the proportion of known fish prey

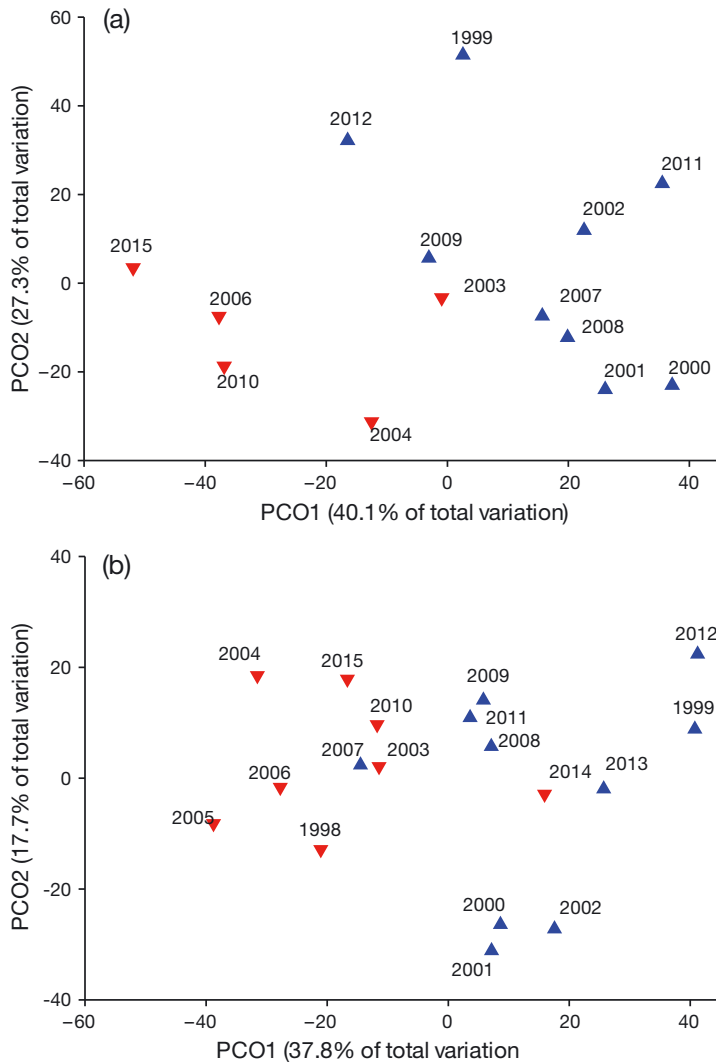


Fig. 5. Principal coordinate analysis (PCO) of (a) May and (b) June juvenile Chinook salmon (*Oncorhynchus tshawytscha*) diet composition. Blue: years with negative Pacific Decadal Oscillation (PDO) conditions in spring, and red: positive PDO conditions

Stomach fullness as a percentage of the salmon body weight was average in May 2015 (Fig. 6a). Only during 2004 and 2010 did salmon have significantly fuller stomachs than the salmon in 2015, and 2015 salmon ate significantly more food than the salmon examined in 2001 and 2012 (ANCOVA; $p < 0.0001$). What was anomalous was the higher percentage of empty stomachs (25%) observed in May 2015 relative to the other years, and when the salmon did eat prey, their stomachs were full (Fig. 6a). Stomach fullness was significantly positively related to spring PDO: in warmer years they ate more food (regression; $p = 0.04$; $R^2 = 0.30$). In June 2015, salmon had one of the lowest average stomach fullness values of the time-series (Fig. 6b), with 2015 stomachs being

significantly more full than just 2012, and significantly less full than in 1998, 2000, 2002–2008, and 2010 (ANCOVA; $p < 0.0001$; Fig. 6b). There were also high amounts of empty stomachs in June 2015 (23%), with just 2012 salmon having as many empty stomachs, while for most other years, just 5–10% of the Chinook salmon juveniles had empty stomachs in June (Fig. 6b). Stomach fullness was not related to any of the environmental variables in June.

The condition of the salmon in May 2015 was on average the 2nd thinnest of all study years, with only fish collected in 2004 being significantly thinner (Kruskal-Wallis; $p = 0.001$). The salmon in 2015 were thinner than the fish in 2003 and 2006, but not significantly, and fish in all other years were in significantly better condition (Kruskal-Wallis; $p = 0.001$; Fig. 7a). Yearling Chinook salmon condition in May related negatively to spring PDO, with thinner fish observed when the PDO was positive (regression; $p = 0.001$; $R^2 = 0.61$). In practical terms, how much heavier were fish in a cold ocean year, such as 2008, versus 2015? Fish in the size range of 148–152 mm, which is the length range of highest frequency, were on average 17.5% heavier in May 2008 (35.9 g) than fish in May 2015 (29.6 g). In June 2015, salmon were also thin, with just 2 years when they were significantly thinner for their size (i.e. 2001 and 2007; Kruskal-Wallis; $p < 0.0001$; Fig. 7b). Condition of fish in June did not relate significantly to spring/early summer PDO or NPGO.

Biological metrics of prey and juvenile Chinook salmon from 1998–2014 were related to spring-run Chinook salmon adult returns in order to predict, based on 2015 characteristics of the salmon and their prey, what effect the ocean condition could have on salmon returns in 2017. When salmon were larger in May of a given year, there was a significantly higher return of spring-run Chinook salmon adults 2 yr later (regression; $p = 0.01$; $R^2 = 0.48$). Moreover, when they were in better condition (fatter for their FL), there were higher returns of adults 2 yr later (regression; $p = 0.01$; $R^2 = 0.49$). June diet composition of juvenile Chinook salmon related positively to adult salmon returns 2 yr later (regression; $p = 0.01$; $R^2 = 0.39$). In addition, adult salmon returns related positively to both winter ichthyoplankton biomass (regression; $p = 0.003$; $R^2 = 0.48$) and composition (regression; $p = 0.001$; $R^2 = 0.54$).

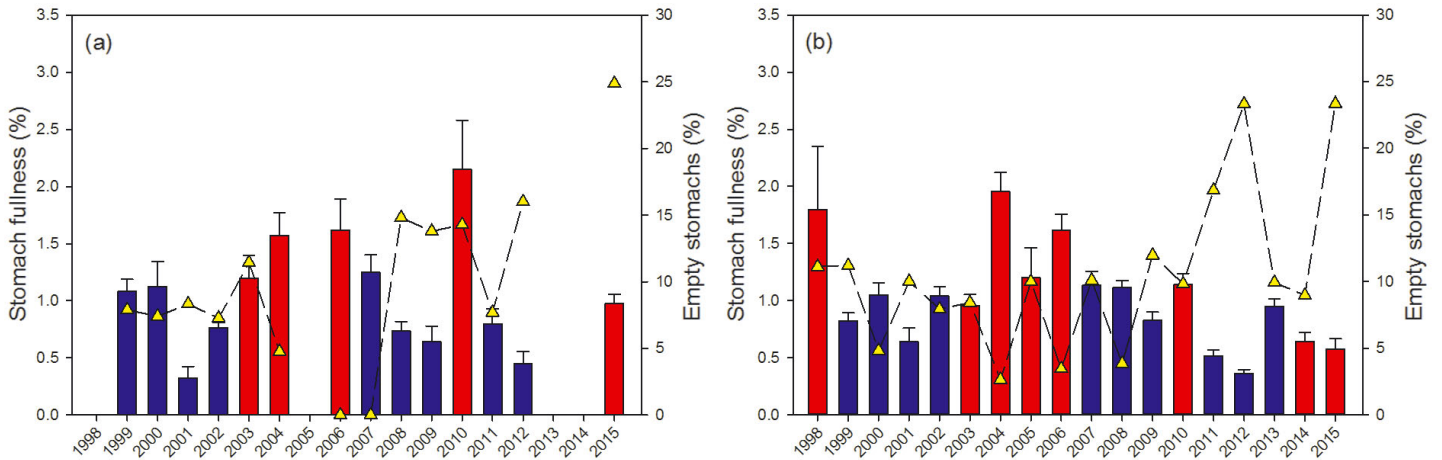


Fig. 6. Average annual stomach fullness (error bars: SD) for yearling Chinook salmon *Oncorhynchus tshawytscha* in (a) May and (b) June. Blue: years with spring in negative Pacific Decadal Oscillation (PDO) conditions, and red: positive PDO conditions. Annual percentage of empty stomachs (right-hand vertical axis) is represented by dashed line with yellow triangle

The year 1999 was removed as an outlier for all these analyses, as it was >2 Studentized residuals removed from all the years of data in the tested relationships, due to the higher adult salmon returns.

As far as predicting adult returns for 2017 adults based on 2015 metrics, the prey field in 2015 was composed of taxa typically observed in poor survival years (2017 prediction = 84 720). The salmon in 2015 were small (2017 prediction = 140 276), thin (2017 prediction = 91 674), and also consumed prey taxa typically found in low survival years (2017 prediction = 130 762). Only the biomass of prey provided a favorable prediction for the juvenile salmon survival with predicted returns of 213 126 in 2017. The 5 sig-

nificant predictors, when averaged together would predict $132\ 111 \pm 51\ 267$ (SD) adult salmon to return in 2017 from the ocean out-migration year of 2015, with predicted returns ranging from 45% higher than the 10 yr mean (biomass ichthyoplankton) to 42% lower than the 10 yr mean (ichthyoplankton composition).

DISCUSSION

Smolt-to-adult return rates for hatchery coho *Oncorhynchus kisutch* and Chinook salmon from southern British Columbia to California have typi-

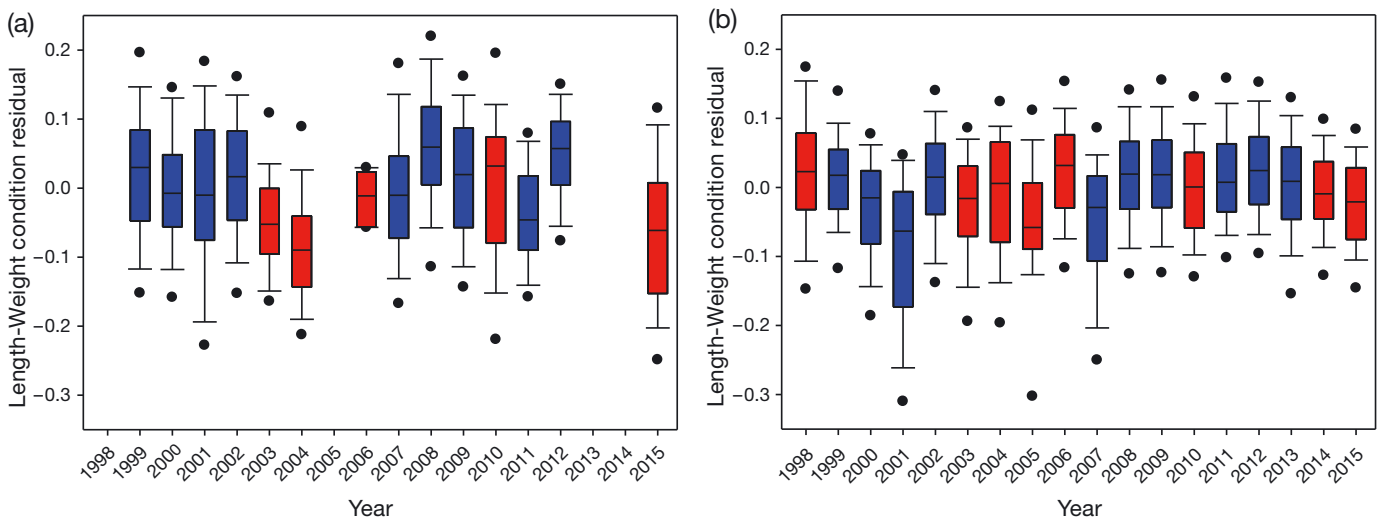


Fig. 7. Average annual length-weight condition residuals for (a) May and (b) June yearling Chinook salmon *Oncorhynchus tshawytscha*. Blue: years with spring in negative Pacific Decadal Oscillation (PDO) conditions, and red: positive PDO conditions. Boxplots include the median (lines in boxes), 25th and 75th percentiles (lower and upper ends of boxes), 10th and 90th percentiles (error bars), and 5th and 95th percentiles (black filled circles) for each year

cally been higher in periods of cold ocean temperatures along the west coast of North America (Mantua et al. 1997, Logerwell et al. 2003, Burke et al. 2013, Daly & Brodeur 2015, Kilduff et al. 2015, Mantua 2015). With such a warm coastal region in 2015, we would predict poor adult salmon returns over the next few years. Juvenile Chinook salmon exhibited poor growth in 2015 based upon the small average FL of the population that was sampled in May, their overall poor body condition, the high percentage of empty stomachs, and the type of prey eaten (warm-water taxa). Overall, biological characteristics of juvenile salmon and their prey were significantly poorer when the PDO was positive (warmer ocean) or the NPGO was negative (less productive ocean). Salmon and prey biological characteristics (low prey biomass, warm-water taxa in prey field and diets, and thin small salmon) related negatively to adult returns. Only stomach fullness was positively related to PDO, when the salmon had significantly more food in their stomachs when the ocean was warmer.

Physical changes in coastal waters can have a dramatic cascading effect throughout the ecosystem (Schwing et al. 2010). The prey base for upper trophic levels is closely tied with physical oceanographic changes, and when dramatic temperature changes occur, a highly reactive prey community will force predators into a physiological and biological response that may not be sufficient for their growth and survival (Siddon et al. 2013). Long-term studies in the NCC have documented the close ties between lower trophic levels and early-life history stages of higher trophic levels with physical oceanographic changes (Peterson & Schwing 2003, Brodeur et al. 2008, Hannah 2010, Daly et al. 2013, Shanks 2013). The prey base for both salmon and marine birds (Gladics et al. 2015) in the NCC has been shown to be closely linked to ocean temperatures several months prior to larval development (Daly et al. 2013). The dramatic temperature increase in late 2014 would have predicted a prey biomass significantly lower than the amount that was actually sampled in 2015 (95% lower). In spring and summer 2015, salmon were small, thin, and had high numbers of empty stomachs (the present study), and there were mass die-offs of marine birds in the region (Cavole et al. 2016), which is counterintuitive to the high biomass of the fish prey base observed in winter 2015.

Increased biomass of rockfish larvae in the winter 2015 ichthyoplankton samples during warm ocean conditions were not unexpected, as this was also seen in 2003–2005 and 2010 (Daly et al. 2013), although the biomass of rockfish was higher than

expected. What was unusual in winter 2015 was the high biomass of northern anchovies. Only in one other study year (the strong El Niño year of 1998) had there been any northern anchovies sampled in winter, and they were present in low concentrations. Previous sampling along the NH line showed relatively early spawning of northern anchovies in April 1983, which up to that time was the strongest El Niño ever recorded (Brodeur et al. 1985). Northern anchovies are heavily utilized as prey by juvenile Chinook salmon later in the summer, especially in the Columbia River plume region of the NCC (Brodeur & Pearcy 1990, Dale et al. 2017, Litz et al. in press), but the typical period when larval anchovies appear in the plankton is May–July (Brodeur et al. 2008, Parnel et al. 2008, Auth 2011). Salmon have been shown to be opportunistic predators (Brodeur 1989, Brodeur & Pearcy 1990, Schabetsberger et al. 2003), and have the potential to shift to eating prey resources that have spawned earlier in the season due to anomalously warm ocean temperatures, such as northern anchovies in 2015. Scenarios examining climate change impacts need to consider shifting prey phenologies (Albouy et al. 2014).

However, there was little evidence that the high biomass of northern anchovies in winter translated to food for the juvenile salmon during their early out-migration. There were no observed feeding occurrences on northern anchovies in May 2015, and they made up <20% of the diets in June 2015. We do not have corresponding prey availability estimates for May or June 2015, as the common prey at this time of year (juvenile fishes) are extremely unlikely to be caught in plankton gear or in our large-mesh trawls (Brodeur et al. 2011). We do have data from another cruise from a 5 yr time-series, which surveyed for juvenile fishes in late May and early June 2015, and did catch age-0 anchovies, but few juvenile rockfishes and very low concentrations of euphausiids compared to the previous years (R. Brodeur, NWFSC, Newport, OR, unpubl. data). The high larval rockfish biomass in winter 2015 but low catches of juvenile rockfish in early summer 2015, in addition to thin, small salmon with high amounts of empty stomachs, suggests that the rockfish were available to the salmon as prey in relatively low amounts in 2015. There are several possibilities for what happened to the winter larval rockfish: earlier-than-normal settlement and/or advection offshore of the rockfish, thus making these rockfish less available to the coastal and surface dwelling salmon, or a high mortality due to increased predation and/or starvation leading to recruitment failure in early

spring. Northern anchovies are serial batch spawners, and we have indications from plankton collections that larvae were present throughout the summer in 2015 (T. D. Auth et al. unpubl.). However, we have no data to confirm whether the individuals that were spawned during the winter survived to an age that they could have been consumed by the juvenile salmon. Although northern anchovy larvae were extremely abundant at the southern end of our sampling region (NH line) early in the year, we lack data to confirm that they also were abundant off the Columbia River at that time. Therefore, our restricted sampling area in May 2015 may not have reflected the coast-wide salmon feeding environment. Although, as seen in Daly & Brodeur (2015) when the entire survey area of May was utilized (1999–2011), similar patterns as identified in this study were observed during warm spring ocean conditions in that there were small, thin salmon in May that ate more juvenile rockfish.

Chinook salmon in June 2015 were the third longest on average in the 18 yr time-series. Was this increased size due to high growth rates, or size-selective mortality? Of the 5 years (including 2015) when the salmon were the longest in June, 2 were from high-survival, cold-ocean years (2000 and 2001), and 2 were from low-survival, warm-ocean years (1998 and 2004). With these mixed results of good growth years potentially leading to longer fish in June, and poor growth years potentially leading to longer fish in June due to the small fish being consumed, we cannot conclude which of these occurred in 2015. While there was higher biomass of winter fish larvae (potential food for growth), the juvenile salmon were thin in both May and June and there were high rates of empty stomachs. In the NCC, piscivorous predators have been shown to increase in abundance during warm ocean conditions (Emmett et al. 2006), and concurrent marine bird observations made during our June salmon ocean surveys (the present study) showed that piscivorous birds in June 2015 had the highest overall densities observed since bird observations began in 2003 (J. Zamon, NWFSC, Hammond, OR, unpubl. data). Warm ocean conditions, thin salmon, and higher-than-usual marine bird densities are evidence that the above-average size of the Chinook salmon in 2015 may have resulted from size-selective predation (Claiborne et al. 2011, Miller et al. 2013, Sabal et al. 2016).

The juvenile salmon in 2015 did not follow the stomach fullness patterns as observed in a recently published study of long-term data by Daly & Brodeur (2015), which showed significantly fuller stomachs

and higher estimated caloric values per meal during warm ocean conditions, even with a reduction in prey resources in the environment. Fergusson et al. (2013) reported that there was a temperature effect on stomach fullness of juvenile salmon off southeast Alaska, with a slight increase in fullness during cold versus warm ocean conditions. Bachiller et al. (2016) also showed that several forage fishes in the Norwegian Sea had fuller stomachs during cold conditions. Both these studies occurred at much more northern latitudes than our study, where temperature may be a more limiting factor physiologically. Further exploration of the relationships between temperature, prey availability, and predator stomach fullness is warranted. Regardless of the overall effect of temperature on feeding, stomach fullness is regulated in part by the availability of prey. Stomach fullness was low in June 2015, with high percentages of empty stomachs observed in Chinook salmon, whereas in May, stomach fullness was average, still with high percentages of empty stomachs. Small size and thinness of the salmon would indicate that there was little food in the environment for the salmon to consume. While the biomass of ichthyoplankton prey was high in winter, the salmon do not appear to have been able to take advantage of a higher-than-usual prey biomass. Several studies have documented biological changes in the northeast Pacific Ocean due to the warm 'Blob', including starvation and mass death of marine animals in 2015 (Leising et al. 2015, Zaba & Rudnick 2016). Environmental temperatures can rise with low consequences for the growth productivity of juvenile salmon if there are sufficient food resources (Beauchamp et al. 2007, Handeland et al. 2008), but there is little evidence of this in 2015, even with a high biomass of ichthyoplankton in winter.

In September 2014, the warm water mass commonly referred to as the 'Blob' uniformly moved onshore from British Columbia to Oregon, where SST increased by 6°C during a 6 h period off of Newport, Oregon (Peterson et al. 2016). This warm water mass that pressed into the coastal waters of the northeast Pacific Ocean persisted throughout 2015, and completely overlapped with the out-migration period of juvenile salmon from the Columbia River. Warm water persisted well into summer 2016, due to the arrival in the California Current of a strong El Niño. Observing and predicting the long-term effects of such an anomalous ocean temperature increase on the biological community can help fisheries managers understand recruitment variability in fisheries, as well as how systems may react to global climate change.

CONCLUSIONS

Ocean conditions in the northeast Pacific Ocean, including the shelf and shelf-break waters we sampled in the NCC, were highly anomalous in 2015. We have described the biological response of juvenile spring-run Chinook salmon and their prey in 2015 relative to a long time-series. Almost all of the data from the juvenile salmon that out-migrated in spring and early summer 2015 into anomalously warm ocean conditions (i.e. small size, poor condition, overall diet composition, and high percentage of empty stomachs), along with the prey fish composition from the 2015 winter ichthyoplankton community, suggest that the adult returns of spring-run Chinook salmon are expected to be low in 2017. The biomass of potential fish prey based on the 2015 winter ichthyoplankton was the only variable that would predict high returns of spring-run Chinook salmon in 2017. With numerous distinct population segments of Chinook salmon currently listed as threatened or endangered, it is critical for fisheries managers to mitigate for potential population disasters like the Sacramento River fall Chinook salmon population that out-migrated into the ocean in 2005 (Lindley et al. 2009) as soon as possible. Understanding the implications of changing trophic pathways on recruitment variability for salmon populations (Wells et al. 2012) will aid in more accurate assessments of the health of ecosystems and the sustainability of fisheries.

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