Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: a shift to gelatinous food sources

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ABSTRACT: Forage fish play a central role in the transfer of energy from lower to higher trophic levels. Ocean conditions may influence this energy pathway in the Northern California Current (NCC) ecosystem, and we may expect it to differ between warm and cold periods in the northeast Pacific Ocean. The recent unprecedented warming in the NCC provides a unique opportunity to better understand the connection between ocean conditions and forage fish feeding habits and the potential consequences for predators that depend on them for sustenance. Here we present findings from gut content analysis to examine food sources of multiple forage fishes (northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, jack mackerel *Trachurus symmetricus*, Pacific herring *Clupea pallasii*, surf smelt *Hypomesus pretiosus*, and whitebait smelt *Allosmerus elongatus*) off the Washington and Oregon coasts. Analyses were applied to fish collected in May and June during recent warm years (2015 and 2016) and compared to previous collections made during cool (2011, 2012) and average (2000, 2002) years. Results of the diet analysis indicate that fish feeding habits varied significantly between cold and both average and warm periods. Euphausiids, decapods, and copepods were the main prey items of the forage fishes for most years examined; however, gelatinous zooplankton were consumed in much higher quantities in warm years compared to cold years. This shift in prey availability was also seen in plankton and trawl surveys in recent years and suggests that changing ocean conditions are likely to affect the type and quality of prey available to forage fish. Although gelatinous zooplankton are generally not believed to be suitable prey for most fishes due to their low energy content, some forage fishes may utilize this prey in the absence of more preferred prey resources during anomalously warm ocean conditions.

KEY WORDS: Warm anomaly · Forage fishes · Feeding ecology · Feeding intensity · Gelatinous zooplankton

INTRODUCTION

Eastern boundary upwelling regions make up a small percentage of the world's oceans but account for a large proportion of the annual fish catch. Much of this biomass in the pelagic zones of these regions is comprised of small pelagic fishes, also called forage fishes. In addition to being commercially valuable, these fishes serve as an important trophic link between the primary and secondary producers and the top trophic levels (Pikitch et al. 2012). This dual function (of providing services to both the ecosystem and humans) performed by forage species has led to concerns about the proper way to manage them in many ecosystems (Pikitch et al. 2012, Engelhard et al. 2014, Peck et al. 2014) and has stimulated some active debate about the need to limit fishing to conserve these stocks for other components of the ecosystem (Cury et al. 2011, Walters et al. 2016, Hilborn et al. 2017).

An important characteristic of these pelagic fishes is their marked response to changes in oceanographic conditions leading to interannual and decadal-scale variability in their population sizes on a world-wide basis (Schwartzlose et al. 1999, Chavez et al. 2003). In the California Current upwelling region, these fluctuations are recorded to have occurred well before the onset of industrial fishing, which implies that they are likely caused by climate variability (Baumgartner et al. 1992, Field et al. 2009), although food web processes may attenuate these fluctuations (Cury et al. 2005). Fish production in this region, as in other mid-latitude regions, is believed to be controlled by phytoplankton production through bottom-up mechanisms (Ware & Thomson 2005), perhaps operating over different trophic levels (Miller et al. 2010). Small pelagic forage fish taxa are important conduits for transferring this production up to higher trophic levels in the California Current, including piscivorous fishes, seabirds and marine mammals (Brodeur et al. 2014, Szoboszlai et al. 2015), as documented in regional ecosystem models (Ruzicka et al. 2012, Kaplan et al. 2013, Koehn et al. 2016, 2017).

Due to large-scale environmental drivers such as the Pacific Decadal Oscillation and El Niño/Southern Oscillation (ENSO) dynamics, the California Current undergoes dramatic environmental variability on interannual and interdecadal time scales (Checkley & Barth 2009). Evidence suggests that recent decades have witnessed extreme variability (Sydeman et al. 2013) based on changes in temperature, salinity, oxygen, and other system properties. Superimposed on this long-term variability, the northeast Pacific Ocean and particularly the California Current has experienced an unprecedented environmental perturbation caused by changes in atmospheric circulation beginning in 2014. A lack of the usual deep-water mixing in the Gulf of Alaska resulted in a large, anomalously warm water mass which has been termed the 'Blob' (Bond et al. 2015). This water mass persisted through 2015 affecting much of the North Pacific and led to ocean sea-surface temperature anomalies of >2.5°C (Di Lorenzo & Mantua 2016). The 'Blob' moved onto the shelf in the Northern California system in September 2014 and remained through late 2015 (Peterson et al. 2017). There have been numerous biological anomalies associated with these changes including occurrences of unusual taxa, widespread toxic algal blooms, and extreme mortality events of higher trophic level organisms (Leising et al. 2015, Cavole et al. 2016, Sakuma et al. 2016).

As the ecosystem effects of the 'Blob' were ongoing, the California Current received an additional perturbation from a major El Niño arriving from the tropics and affecting the region in 2015 and 2016 (McClatchie et al. 2016), albeit initially not to the extent that some previous events of similar magnitude had on the ecosystem (Jacox et al. 2016). Overall, the combined effects of the 'Blob' and El Niño reduced the productivity and altered the community structure of the ecosystem over several years in a way not seen in recent history (McClatchie et al. 2016, Peterson et al. 2017, Auth et al. 2018).

Previous warm periods in the Northern California Current mainly associated with El Niño events have altered the species composition and biomass of zooplankton, leading to changes in the feeding of intermediate and higher trophic levels including the pelagic fishes (Brodeur & Pearcy 1992, Lee & Sampson 2009, Francis et al. 2012). Although some diet information existed for the major 1983/1984 El Niño that affected much of the northeast Pacific Ocean (Brodeur et al. 1987, Brodeur & Pearcy 1992), our ability to make detailed comparisons with normal, or even cool, high-productivity conditions was limited. Most recent diet studies on forage fishes in this region have been conducted mainly in cooler or highly productivity years (Miller & Brodeur 2007, Miller et al. 2010, Hill et al. 2015).

Here we analyze forage fish diets collected during this recent marine heatwave and make comparisons to diet data available from previous surveys to assess the impacts of this anomalous event on the trophic ecology of these important fishes. The focal species of this study include northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, surf smelt *Hypomesus pretiosus*, whitebait smelt A*llosmerus elongatus*, Pacific herring *Clupea pallasii*, and jack mackerel *Trachurus symmetricus*. These species dominate the catch of pelagic trawls in most years in this region (Brodeur et al. 2005, Litz et al. 2014), and all are major forage species in the California Current (Brodeur et al. 2014, Szoboszlai et al. 2015). We hypothesize that the anomalous warming that occurred during 2015 and 2016 would have altered the prey available to this forage assemblage, leading to changes in the diet composition of these species.

MATERIALS AND METHODS

Characterization of ocean conditions

In order to classify the time periods for which we had diet data in their respective regimes, we examined 4 different regional or basin-scale environmen-

tal variables. For the regional variable, we included the monthly sea surface temperature (SST) averaged over the first 6 mo of the year for a box centered off the central coast of Oregon (44.0° to 46.0° N, 124.0° to 125.0° W) based upon the NCEP reanalysis downloaded from the NOAA/ESRL PSD website (www. esrl.noaa.gov/psd/data/timeseries/). For the basin-scale variables, we calculated averages for Pacific Decadal Oscillation (PDO), Multivariate ENSO Index (MEI) and North Pacific Gyre Oscillation (NPGO).

The PDO is a major basin-wide mode of variability, and is defined as the first principal component of sea surface temperature in the North Pacific Ocean between 20° and 65° N (http://jisao.washington.edu/pdo; Mantua et al. 1997). In the positive phase of the PDO, low pressure in the North Pacific is associated with cyclonic winds along the west coast of North America. Poleward alongshore winds drive increased onshore transport of surface water creating anomalously high SST. The ENSO is one of the dominant high-frequency environmental drivers in the Pacific Ocean, although it originates in the tropical Central Pacific. MEI values available from the Earth System Research Laboratory, National Oceanic and Atmospheric Administration (https://www.esrl.noaa.gov/psd/enso/mei/table.html) were averaged for January through March to account for the lag in response from the tropics.

The NPGO index is defined as the principal component of the second EOF of sea surface height in the North Pacific (www.o3d.org/npgo; Di Lorenzo et al. 2008). The positive phase of the NPGO is reflected in a strengthening of the North Pacific Current and leads to upwelling-favorable conditions in the CCS (Di Lorenzo et al. 2008).

We used cluster analysis to objectively group our years into different environmental regimes. Prior to running the cluster analysis, we adjusted for negative values (PDO, etc.) by adding a constant equal to the maximum negative value within each column. We then standardized all variables based on the maximum of the data. Cluster analysis was performed using Euclidean Distance measure and a group average clustering strategy. Significant cluster groups were determined through a similarity profile analysis (SIMPROF; Clarke et al. 2008) performed in PRIMER v.7 (Clarke & Gorley 2015).

Field and laboratory sampling

Stomach collections for this study were made during several cruises conducted during June 2015 and May and June of 2016 off the entire coast of Wash-
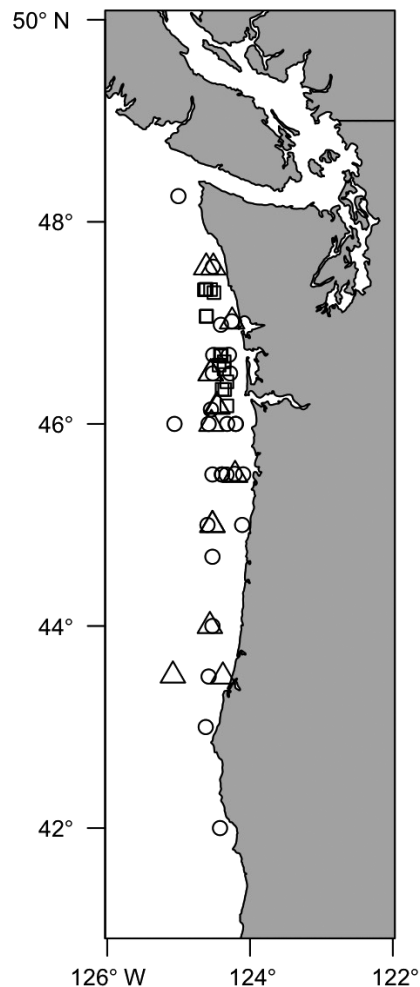

Fig. 1. Stations where forage fish were collected during 2015 (May: squares, June: triangles) and 2016 (June: circles)

ington and Oregon (Fig. 1). During all 3 time periods, stations were sampled from northern Washington (48.5° N) to Newport, Oregon (44.7° N) as part NOAA's juvenile salmon survey using a Nordic 226 rope trawl towed at the surface (Brodeur et al. 2005). Stations were in areas of high expected salmon abundance off the mouth of the Columbia River in May, and more broadly distributed along several transects that spanned the survey area. Additional collections were made during a juvenile fish survey conducted during June of both years. Collections were made along 10 transects from the Oregon-California border (42° N) up to Willapa Bay, Washington (46.5° N) using a Cobb trawl with a fine mesh liner fished with the headrope at 30 m (R. D. Brodeur unpubl.). The overall latitudinal and longitudinal range of sampling overlapped that of the earlier studies which we used as representative of cooler ocean conditions (Miller et al. 2010, Hill et al. 2015).

Forage fishes were identified and measured at sea, and then frozen for later dissection and stomach removal in the laboratory. Detailed stomach processing methods are given by Hill et al. (2015). Briefly, the fish were thawed and weighed (±0.01 g) and fork length (±0.1 mm) was remeasured before the stomachs were excised and preserved in Prefer (Anatech) for later stomach content analysis. Diet analysis was performed under a dissecting microscope. For each individual stomach, the overall fullness, and number of prey were quantified and classified to lowest discernable taxa. The damp weight of prey items was measured using an analytical balance (±0.001 g) after absorbing the excess moisture with blotting paper. Prey items were individually counted unless they were too numerous, in which case a subsample was taken, enumerated and the total number in the stomach was extrapolated from the damp weight. The number of stomachs examined per year and month is given in Table 1 by species.

Data analysis

Diet data for each fish were summarized by major prey groups based on 2 main indices: Percent frequency of occurrence of a prey group (%FO) and percent by weight (%W) and averaged within a station, and these station means were compared by month across years. There were fewer May cruises with only 2000, 2011, 2012, and 2016 available, whereas all 6 years had stomach collections available in June for most species.

Multivariate statistics were used to compare community-level and species-level diet relationships among periods of warm, cool, and average ocean conditions or regimes. First, we analyzed and visually represented the relationships with Nonmetric Multidimensional Scaling (NMDS) ordinations. A random starting location was used with all runs with up to 500 iterations per run. The data matrix included the station-specific %W of prey groups for each forage species (arcsine square root transformed) as well as collection data for grouping purposes, including sample year and month. A dispersion ellipse was used to visually simplify the diet data using the standard deviation of the average spatial scores (Oksanen et al. 2012). We fit basin-scale environmental indices, including the PDO, MEI, and NPGO, to the ordinations to identify whether they correlated well with shifts in diet relationships between regimes.

Next, we tested for similarity in forage fish diets between the different ocean regimes using a multi-response permutation procedure (MRPP) of the %W data. For this analysis, we used a Bray-Curtis distance measure appropriate for community analyses (McCune & Grace 2002). MRPP tests the null hypothesis of no difference between groups, and generates an *A*-statistic that represents the effect size and ranges from 0 to 1, with 1 representing complete within-group agreement and 0 representing within group heterogeneity being equal to chance. Similar to Hill et al. (2015), we defined an *A*-statistic ≥ 0.3 as strong differences between grouping (McCune & Grace, 2002), between 0.2 and 0.3 as moderately strong differences, between 0.1 and 0.2 as moderate differences, while < 0.1 is weak to no difference. Because diet information was not available for the month of May in all survey years, we limited our NMDS and MRPP analyses to June data only. In addition, species-level comparisons among ocean regimes were made for northern anchovy *Engraulis mordax*, Pacific herring *Clupea pallasii* and surf smelt *Hypomesus pretiosus*; however, Pacific sardine *Sardinops sagax*, whitebait smelt *Allosmerus elongatus* and jack mackerel *Trachurus symmetricus* had insufficient sample sizes for at least one of the regimes to make meaningful comparisons. All multivariate analyses were conducted with the Vegan, MASS, and labdsv packages in R v. 3.3.3 (R Development Core Team 2014, Oksanen et al. 2012, Wood 2012).

Table 1. Percent frequency of occurrence of gelatinous material in diets of forage fishes during variable oceanographic conditions: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, surf smelt *Hypomesus pretiosus*, whitebait smelt *Allosmerus elongatus*, Pacific herring *Clupea pallasii*, and jack mackerel *Trachurus symmetricus*. Temperature regimes: average, cool, warm. –: No samples of that species were collected during that particular year. Parentheses: sample sizes for each year

	Average		Cool		Warm	
	2000	2002	2011	2012	2015	2016
Northern anchovy	0 (4)	0 (95)	0 (27)	5.3 (19)	30.0 (10)	80.8 (78)
Pacific herring	0 (126)	12.0 (248)	0 (43)	0 (9)	62.5 (17)	71.4 (52)
Pacific sardine	16.7 (95)	45.7 (98)	0 (14)	0 (10)	66.7 (12)	100.0 (11)
Surf smelt	40.6 (246)	1.0 (105)	0 (34)	30.0 (10)	66.7 (9)	100.0 (28)
Whitebait smelt	0 (89)	0 (101)	0 (30)	–	45.4 (11)	100.0 (41)
Jack mackerel	0 (86)	0 (241)	–	–	44.7 (39)	76.5 (28)

Description of the primary taxa contributing to the observed dietary differences between forage species within a regime or within a species between regimes was done using indicator species analysis (ISA) (Dufrene & Legendre 1997). ISA examines the fidelity of occurrence of a species within a particular group, which is based on the combined proportional measurements of the abundance of each particular species in a group relative to its abundance in all groups, and the percent frequency of that species in each group (McCune & Grace 2002). The statistical significance of each group is examined by a Monte Carlo test, such that sample units are randomly reassigned n times to test if the indicator species values are higher than would be expected by chance. For this study, 1000 runs were applied to each Monte Carlo simulation using PC-ORD v.4.25 (McCune & Mefford 1999).

Body condition

We also examined within-species potential size (length and weight) and fish body condition differences between years to assess potential ontogenetic factors driving diet and affecting nutritional condition and growth. For body condition, residuals of the length–weight relationship of the predators were used as a measure of the relative condition of the fish between years (Daly & Brodeur 2015). This condition factor was calculated as the residual of the regression analysis of ln-transformed weight and length. Regression analysis was performed separately for the months of May and June in cold and warm years to observe possible variations in growth in conjunction with varying oceanographic conditions. All size (length and weight) and body condition comparisons between years were performed using a Mann-Whitney U test for differences between warm, average, and cold years. All tests were performed using the software R v.2.15.1 (R Development Core Team 2014).

RESULTS

Environmental conditions

Sea surface temperatures (SST) off Oregon were extremely warm in 2015 and 2016, and those were the only 2 years to

exceed 1 SD above the mean for the 22 yr period examined (Fig. 2). In contrast, the spring SSTs in 2011 and 2012 were at or below 1 SD of the mean. SST in 2000 was close to the long-term average whereas 2002 was below average but not as extreme as 2011 and 2012. The mean March–May PDO pattern followed closely that of the surface SSTs, and the NPGO had the same pattern as the other indices with the exception that 2000 was much more extreme and 2016 was less extreme compared to SST or PDO (Fig. 2). The January–March MEI showed that 2016 could be classified as a relatively strong El Niño event, almost as strong as the major 1998 event (Fig. 2). The MEI values for 2015 and 2016 were well above average, whereas the other 4 years considered were all below average with the most extreme La Niña seen in 2011. A hierarchical cluster analysis revealed that the 2011 and 2012 conditions grouped closely with other cool years in the Northern California Current (NCC) such as 1999 and 2008, whereas 2015 and 2016 were grouped with other warm years (2005) and the El Niño years of 1998 and 2010 (Fig. 3). The other years for which we have diet data (2000 and 2002) fell into a large group of years with more average conditions (Fig. 3).
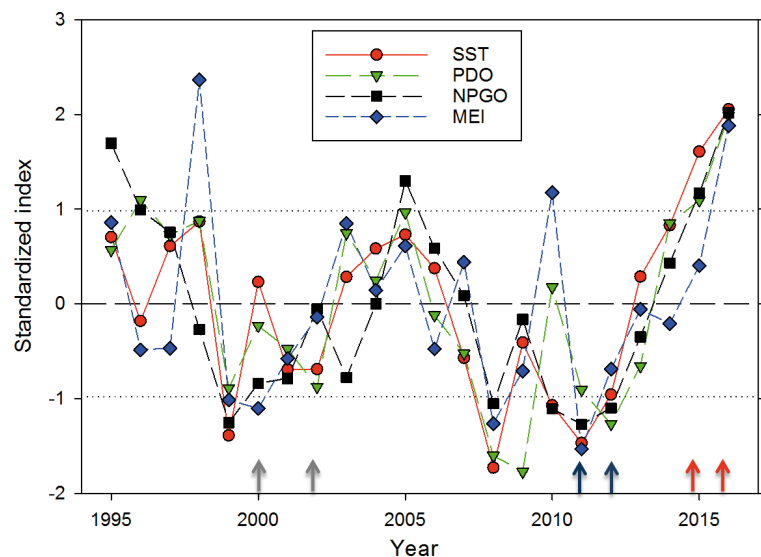

Fig. 2. Standardized time series of sea surface temperature (SST) for a fixed location off Newport, Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and Multivariate ENSO Index (MEI). See 'Materials and methods: Characterization of ocean conditions' for location, time period, and source for the different variables. The axis of the NPGO was reversed so that it aligned with the other indices. Dashed line: overall mean; dotted lines: ± 1 SD of the mean of the 22 yr represented. The arrows at the bottom of the figure show the years for which diet data are available. The color of the arrow corresponds to cool (blue), average (grey) and warm (red) years as determined by cluster analysis
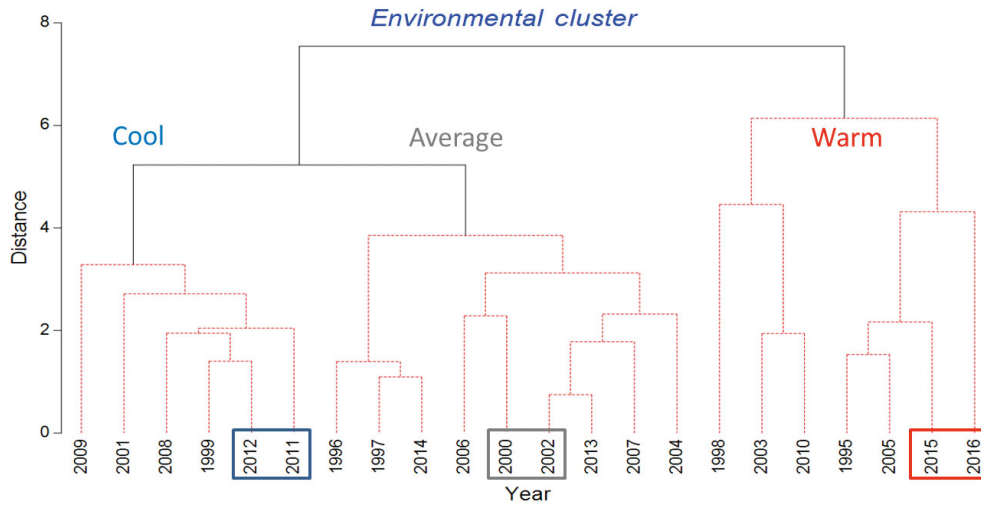
Fig. 3. Dendrogram resulting from cluster analysis of the 4 environmental variables by year. Dotted lines: groups of years that were not statistically different (p > 0.05) in the SIMPROF analysis. The years included in this study are enclosed in boxes color coded by the 3 regime types labeled

Diet composition

Comparisons of the diet composition for May by major prey categories between years indicated substantial shifts in the prey composition during May 2016 compared to the cool years of 2011 and 2012, and the relatively average year of 2000 (Fig. 4). For 4 of the 5 species (northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, surf smelt *Hypomesus pretiosus*, and whitebait smelt *Allosmerus elongatus*) for which data were available (no jack mackerel *Trachurus symmetricus* were analyzed for any of the May periods), the diets in 2016 showed a major fraction of the prey biomass (range 42 to 80%) was made up by gelatinous zooplankton, whereas this prey taxon did not show up in the previous May cold periods. The exception was Pacific herring *Clupea pallasii* which did not consume gelatinous material in May (Fig. 4). The diets in colder years were dominated by several crustacean taxa (39 to 99%) and pteropods (8 to 61%), with a lesser contribution by fish prey (3 to 18%).

A similar pattern was observed during the more extensive comparisons for the June surveys (Fig. 5). For all 6 species (adding jack mackerel), the diets contained a substantial proportion of gelatinous material (range from 13 to 88%) in both June 2015 and 2016. However, in the case of Pacific sardine and surf smelt, some of the cool or average years also had a smaller fraction (<10%) of the diet made up by gelatinous material (Fig. 5). The diets in the cool or average years were made up of mainly copepods, euphausiids, phytoplankton, and to a lesser extent pteropods and decapod larvae. Teleost prey were consumed in at least some of the years by all forage fishes but were only a major proportion (58%) of the

diet in jack mackerel in 2016. Some crustacean prey were consumed during the recent warm years, but generally in differing proportions from the earlier average or cold years (e.g. northern anchovy consumed more euphausiids compared to copepods; Fig. 5).

Although we did not conduct a detailed analysis of the taxonomic composition of the prey consumed in this study, several prominent trends were observed between the prey taxa consumed in the warm period compared to the normal or cold periods. One notice-
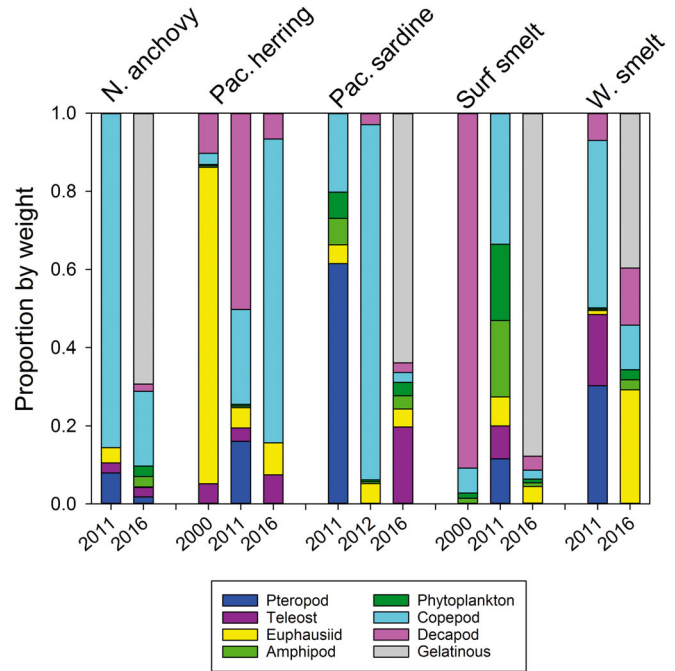

Fig. 4. May diet composition by proportion wet weight of dominant forage fishes by year for the major taxonomic categories
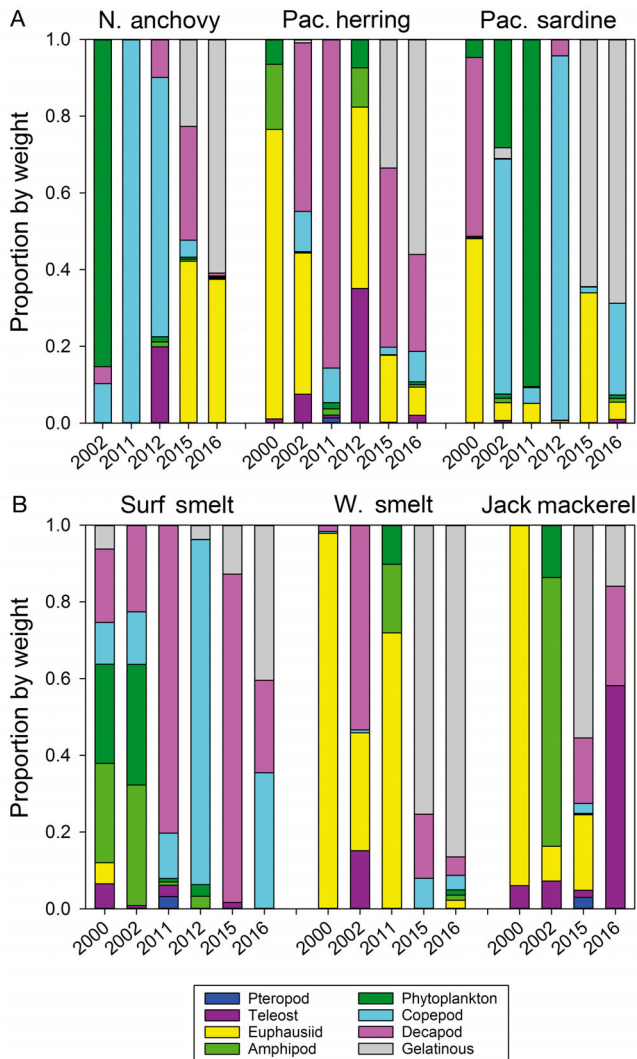
Fig. 5. June diet composition by proportion wet weight of dominant forage fishes by year for the major taxonomic categories

of their biomass importance, we also examined the frequency of occurrence of gelatinous material in the diets. Although gelatinous material was detected in the stomachs of all forage species except jack mackerel and whitebait smelt during the earlier average years, and to a lesser extent, in the cool years, the levels of occurrence increased dramatically in 2015 and 2016 (Table 1). In fact, we detected at least some gelatinous material in all of the Pacific sardine, whitebait and surf smelt examined in 2016 (Table 1).

The NMDS ordination ellipses revealed at least some overlap among all the forage fish diets during June 2015 and 2016 (Fig. 6). Surf smelt showed the most differences from the other species in terms of its diet composition, consuming mainly decapods, copepods, and gelatinous material, and showed the greatest overlap with herring. Our community-level comparisons of diet composition between the 3 different ocean regimes showed moderate differences between warm and cold conditions (A = 0.14, p = 0.001) and weak to no differences between the other regimes (A < 0.05, p = 0.001; Fig. 7; Table 2). The indicator species analysis (ISA) showed that phytoplankton was a significant (p < 0.001) indicator taxa for northern anchovy, amphipods (p = 0.032) and copepods (p = 0.015) for whitebait smelt, decapods (p = 0.043) and gelatinous material (p = 0.047) for surf smelt, and teleosts (p = 0.024) for jack mackerel. No significant indicator taxa were found for either Pacific sardine or Pacific herring.

able difference for the prey identified to species is that there was a general shift from the nearshore species of euphausiid (*Thysanoessa spinifera*) in cool years to the offshore species (*Euphausia pacifica*) in the more recent warm period. Among the species which consumed fishes (e.g. Pacific herring and jack mackerel), there was a major change in that almost all of the fish prey were offshore juvenile rockfishes *Sebastes* spp. (standard length 30–48 mm) in 2015 and 2016, whereas in cooler years, the fish prey were mostly sand lance *Ammodytes* and other generally nearshore juvenile fishes such as sculpins (Cottidae).

Since gelatinous zooplankton are known to digest rapidly in fish stomachs compared to other chitinous invertebrate or fish prey, leading to an underestimate
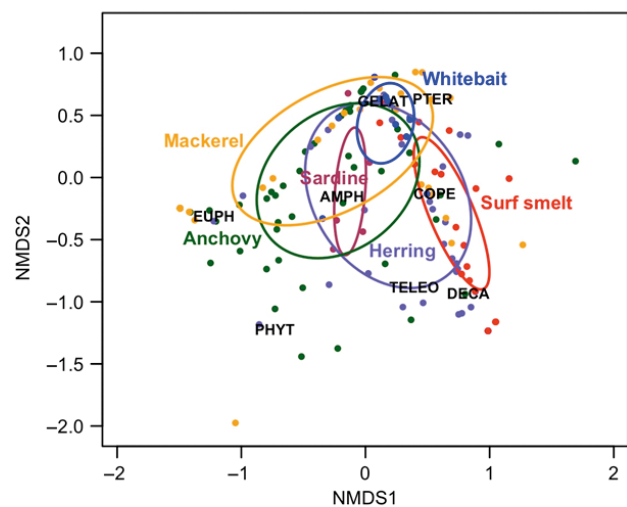

Fig. 6. Non-metric multidimensional scaling biplot of June diet composition of dominant forage fishes during the warm years of 2015 and 2016 combined for the major taxonomic categories. The individual stomachs are indicated as points color coded by species, and the ellipses indicate 1 standard deviation in the 2 main axes. Stress for ordination is 0.12
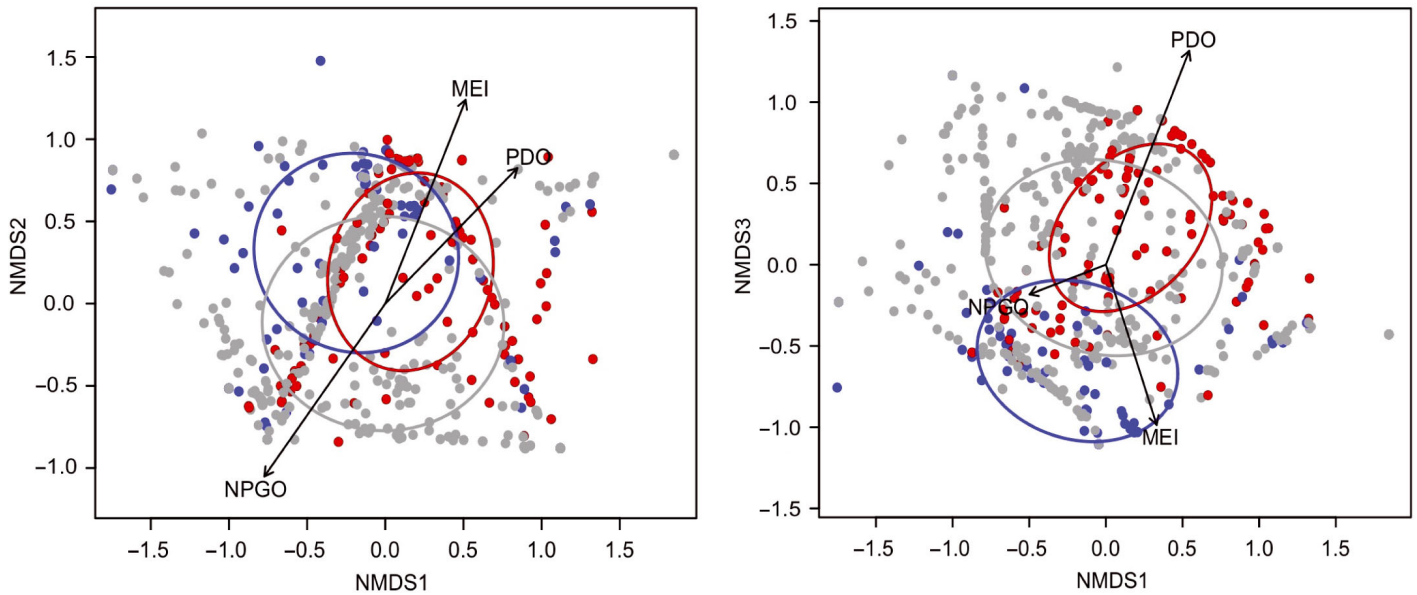
Fig. 7. Non-metric multidimensional scaling biplot of June diet composition for all dominant forage fishes combined (with the exception of jack mackerel *Trachurus symmetricus*) for the 3 regimes for the major taxonomic categories. Shown are the first versus the second NMDS axes (left) and the first versus the third (right). The individual stomachs are indicated as points color coded by regime (warm = red, average = grey, and cool = blue), and the ellipses indicate 1 standard deviation in the 2 main axes. The vectors represent the influence of the 3 major environmental variables on the prey taxa for the axes plotted. The coefficients of determination (R^2) were 0.46, 0.31, and 0.17 for the first 3 axes, respectively (cumulative $R^2 = 0.94$ for all 3)

At the species level, we found strong differences in northern anchovy diets between cool and average year conditions ($A > 0.30$, $p = 0.001$) and moderate differences were observed for warm versus cool and warm versus neutral conditions ($A = 0.20$ and 0.18, respectively; $p = 0.001$). The shift in diets from cool to warm regimes were positively correlated with the PDO ($R^2 = 0.73$, $p < 0.001$) and MEI ($R^2 = 0.65$, $p < 0.001$) and inversely correlated with the NPGO ($R^2 = 0.12$, $p < 0.001$; Fig. 8). There were significant but

Table 2. Results of the Multi-Response Permutation Procedure (MRPP) for June diet differences by species for the various regimes examined. Shown is the value for the MRPP *A*-statistic which is the chance-corrected within-group assignment. Also shown is the significance of the *A*-statistic (***$p \leq 0.001$; **$p \leq 0.01$; *$p \leq 0.05$; ns: not significant)

Species	Warm vs. Cool	Warm vs. Average	Cool vs. Average
Northern anchovy	0.20***	0.18***	0.35***
Pacific herring	0.09***	0.06***	0.02*
Pacific sardine	0.12***	−0.01 ns	−0.01 ns
Surf smelt	0.10***	0.0 ns	0.36***
Whitebait smelt	0.44***	0.19***	0.03 ns
Jack mackerel	–	0.17***	–
All species combined	0.14***	0.01***	0.02***

weak differences in diets of Pacific herring for all 3 regimes ($A = <0.10$, $p < 0.05$), which were also positively correlated with the PDO ($R^2 = 0.30$, $p < 0.001$) and MEI ($R^2 = 0.26$, $p < 0.001$) and inversely correlated with the NPGO ($R^2 = 0.34$, $p < 0.001$; Fig. 8). Surf smelt exhibited strong differences in diet composition between cool and average conditions, although differences between the other regimes were weak to none ($A \leq 0.10$, $p = 0.001$) and correlations with environmental indices were low ($R^2 < 0.05$). Jack mackerel showed moderate differences between warm and average ocean conditions ($A = 0.17$, $p = 0.001$). In terms of taxa indicative of the different regimes, copepods and pteropods were representative of the cool years (ISA both $p < 0.001$), amphipods, decapods, and euphausiids were indicative of average years, and gelatinous taxa were indicative of warm years ($p < 0.001$). Phytoplankton and teleosts were not significant indicators of any particular regime (both $p > 0.1$).

Body condition

Differences in size between years showed fishes were longest during cool or average years compared to the warm years in 5 of the 6 species, excluding
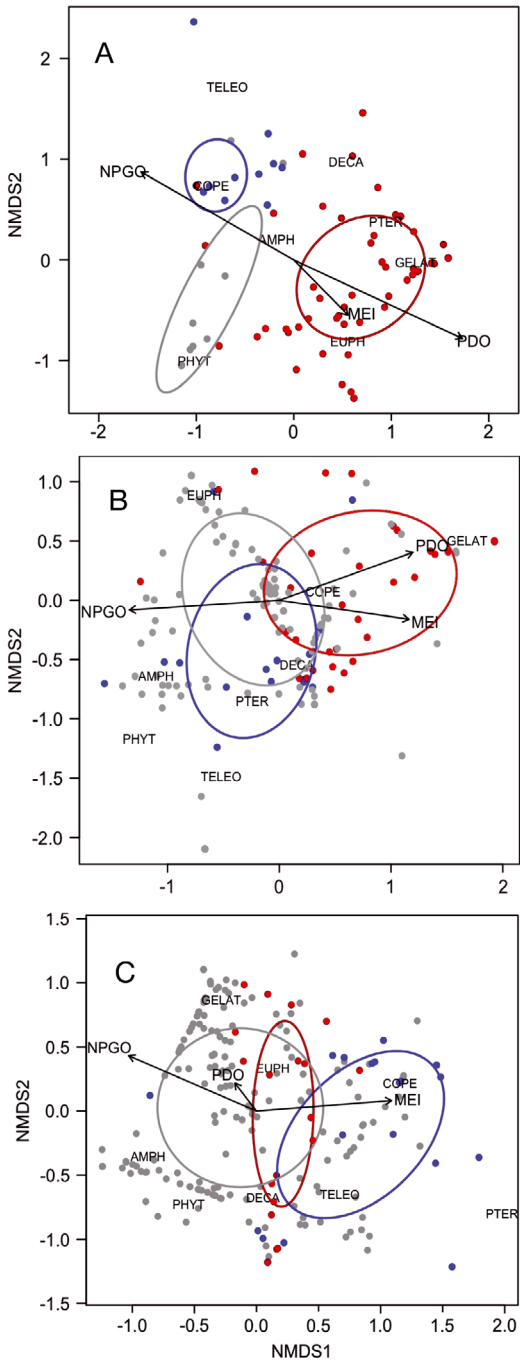
Fig. 8. Non-metric multidimensional scaling biplot of June diet composition of dominant forage fishes during the 3 regimes for the major taxonomic categories for (A) northern anchovy *Engraulis mordax*, (B) Pacific herring *Clupea pallasii* and (C) surf smelt *Hypomesus pretiosus*. The remaining species had insufficient sample size to plot for at least one of the regimes. The individual stomachs are indicated as points color-coded by regime (warm = red, average = grey, and cool = blue), and the ellipses indicate 1 standard deviation in the dominant 2 axes. The vectors represent the influence of the 3 major environmental variables on the prey taxa for the first 2 axes. Stress values for northern anchovy, Pacific herring and surf smelt are 0.09, 0.13 and 0.21, respectively

northern anchovy. Individuals were on average heavier during cool and average conditions in 4 of the 6 species, excluding jack mackerel and surf smelt. Weights of fishes in warm versus cool years were significantly different regardless of month (Mann-Whitney; $p < 0.001$); however, lengths were only significantly different in June analyses (Mann-Whitney; $p < 0.001$). Furthermore, the condition of the fish was better in cool years than in warm years for the 5 species that were examined in both cold and warm years (no jack mackerel diets were available during the cool regime), and significantly so for northern anchovy, Pacific herring and whitebait smelt (Mann-Whitney, $p < 0.001$; Fig. 9). For the species that were represented in the average years, the conditions were intermediate to the other conditions for northern anchovy and Pacific herring, whereas Pacific sardines and whitebait smelt were actually in better condition and surf smelt were in worse condition than in the cold and warm periods (Fig. 9).

DISCUSSION

The California Current is well-recognized for undergoing dramatic environmental shifts, particularly in the last few decades, driven primarily by fluctuations in the major large-scale environmental forcing mechanisms such as the PDO, MEI, and NPGO (Checkley & Barth 2009, Sydeman et al. 2013). However, the magnitude and duration of the anomalously warm oceanographic conditions in 2015 and 2016 resulting from the warm 'Blob' and a moderate El Niño were unprecedented in their effects, especially during the winter/spring periods preceding our sampling. Although the hydrographic properties of the water masses associated with the 2 events were similar, they had substantially different sources and led to anomalous fauna of different origins (offshore species during the 'Blob', southern species during the El Niño (Peterson et al. 2017)).

The atmospheric and oceanographic patterns associated with the warm 'Blob' have not been documented previously in the North Pacific; however, the NCC is subjected to regular incursions of subtropical water due to the periodic occurrence of El Niño events, frequently followed by the opposing condition, i.e. La Niña (Fisher et al. 2015). The past major El Niño events have had marked negative effects on mesozooplankton abundance levels, with a shift towards smaller size composition, often leading to a depauperate prey community (Miller et al. 1985, Peterson et al. 2002, Francis et al. 2012, Fisher et al.
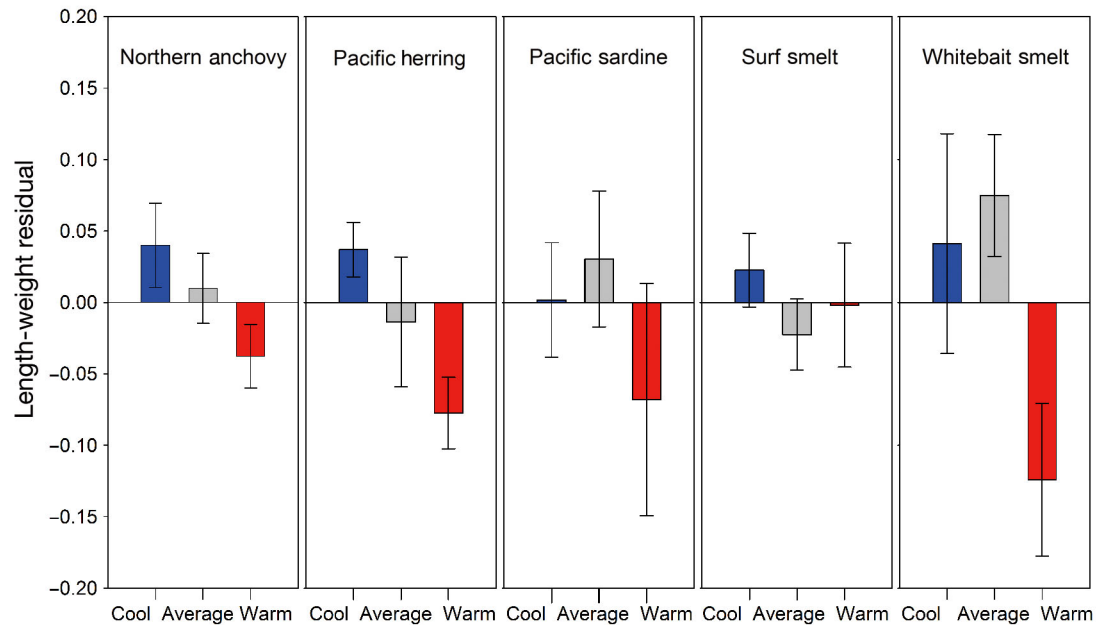
Fig. 9. Condition factor of forage fishes for each environmental regime expressed as the residuals from the overall length-weight regression. Data shown are the means and 95% confidence intervals for each regime. There were no jack mackerel *Trachurus symmetricus* collected during the cool environmental regime

2015). Brodeur & Pearcy (1992) examined diet variability in higher trophic level fishes and elasmobranchs during 4 contrasting years of ocean conditions off Oregon and Washington, including the 1983/84 El Niño. This study found dramatic shifts in ecosystem structure including novel prey (e.g. the southern California Current euphausiid *Nyctiphanes simplex*) and longer food chains during the warm El Niño period compared to the more normal 1982 summer, when the typical resident euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*) and upwelling-adapted fish prey dominated the diet (Brodeur & Pearcy 1992). In a later study off the coast of Oregon and Washington, Lee & Sampson (2009) found anomalous prey in the diets of 3 rockfish species (*Sebastes* spp.) during the extreme 1998 El Niño, including the presence of *N. simplex* and gelatinous material, which also was not identified to species, but was thought to be salps or ctenophores, in contrast to the more typical euphausiid and fish prey found in normal years.

Similarly, in 2015 and 2016, we found more warm-water and oceanic taxa such as salps and juvenile rockfishes (in jack mackerel *Trachurus symmetricus* stomachs) in the diets of several species compared to *Cancer* crab larvae and *T. spinifera* adults in normal years. The few euphausiids consumed were all small individuals of the offshore euphausiid species, *E. pacifica*, and no nearshore *T. spinifera* were observed. These changes correspond to what is known about

the availability of prey from plankton and small-mesh trawl sampling conducted during 2015 and 2016. Peterson et al. (2017) reported that relatively low abundances of *E. pacifica* and *T. spinifera* were collected from sampling on the Newport Hydrographic line in the summer of 2015, but instead, record numbers of salps were caught compared to the previous 14 yr. The abundances of both euphausiids and salps in 2016 were less anomalous but still different from the long-term mean in this study. NCC juvenile fish surveys conducted since 2011 also showed several order-of-magnitude decreases in euphausiid abundances but marked increases in salps, pyrosomes, and other gelatinous taxa in both 2015 and 2016, suggesting a shift to a more gelatinous food web associated with the recent marine heatwave (McClatchie et al. 2016, Brodeur et al. unpubl. data). Parallel extreme anomalies were seen in pelagic trawl sampling off California in 2015, compared to the previous 25 yr period (Sakuma et al. 2016). Similarly, off the west coast of British Columbia north of our study area, Galbraith & Young (2017) found a shift from chitinous crustacean taxa to gelatinous taxa in 2015 and 2016 compared to the previous 25 yr of sampling.

A limitation in our study was the inability to identify the gelatinous material to species or even higher-level classifications. We did find tentacles likely from cnidarians, muscle bands from salps, and comb rows

from ctenophores in several instances. We also found fragments of the oceanic pyrosome *Pyrosoma atlanticum*, which is generally distributed in offshore tropical waters but has been increasingly common off Oregon since the onset of the recent warming conditions (Brodeur et al. 2018). Gelatinous taxa lack hard parts and are more easily digested and evacuated from fish stomachs than other prey (Arai et al. 2003), which would lead to an underestimate of their importance compared to fish or crustacean prey. Therefore, unless the gelatinous prey was relatively recently consumed, it is less likely to be identified to species if present, and may be voided from the stomach completely by the time the fish was captured. We are presently using stable isotopes to examine the contribution of gelatinous zooplankton to the diets of these species in 2015 and 2016 relative to more normal conditions (M. Hunsicker unpubl. data).

Significant differences in sizes of most fish species were observed between cool, warm, and average years, and some proportion of this difference may have contributed to differences in their diets. However, studies have shown an increase in feeding on gelatinous material with increasing fish size (e.g. Yamamura et al. 2002, Alegre et al. 2015), which is in contrast with our observation of smaller fish from the warm period feeding proportionally higher on gelatinous prey. Moreover, this trend was observed across species and irrespective of size, suggesting that the main driver of gelatinous zooplankton contributions to diet were attributed to their availability in the prey field. Our observation of lower condition factor in fish from warm years with higher contributions of gelatinous material to diets would further suggest that the lower nutritional condition of these fish may have been due to the lower abundance and availability of more energy-rich prey. Gelatinous zooplankton have a substantially lower energy content relative to crustacean and other prey (Davis et al. 1998, Cardona et al. 2012), the higher consumption of which would be reflected in the condition factor of the predator.

Until recently, jellyfish had been thought of as a trophic dead end, and when they occurred in high biomass, were thought to be underutilized by higher trophic level predators. However, many fish species are now recognized as feeding at least partially on gelatinous zooplankton (Mianzan et al. 1996, Purcell & Arai 2001, Link & Ford 2006, Cardona et al. 2012, Milisenda et al. 2014). Although these studies suggest a broad range of fish types feed on gelatinous prey, some to the exclusion of most other prey, the fishes documented to do so are not considered small pelagic forage species. There have been extensive studies conducted of the diets of forage fishes in this system and other upwelling (Brodeur et al. 1987, van der Lingen 2002, Espinoza et al. 2009, Garrido et al. 2015) and non-upwelling regions of the world (Bachiller & Irigoien 2015, Brosset et al. 2016). These studies document that most small pelagic species consumed primarily phytoplankton and small crustacean prey such as copepods and euphausiids, and occasionally small gelatinous taxa such as larvaceans (see also reviews by van der Lingen et al. 2009, Garrido & van der Lingen 2014). Even jack mackerel, the largest and most piscivorous of the species we examined, consumed mainly crustacean zooplankton prey such as euphausiids prior to 2015. This species consumed a higher proportion of fish prey in 2016 yet still consumed gelatinous prey in both years.

An exception to this has been shown for anchovies *Engraulis anchoita* feeding on dense aggregations of a salp species along a frontal region off Argentina (Mianzan et al. 2001). This anomaly was attributed to the lack of the normal microcrustacean prey in this system, relegating the anchovy to feed on salps, the only prey available. It may be possible that pelagic fishes in the California Current may become more gelativorous during certain periods of the year, such as winter, when the productivity of crustacean or fish prey may be greatly reduced. We presently lack data on the diets of these species during the non-upwelling season, but it could be that forage fishes may subsist on sub-optimal prey such as gelatinous zooplankton to a much great extent during the less productive times of the year (Mianzan et al. 1996).

Our somewhat limited analyses suggest that several forage species (Pacific herring *Clupea pallasii*, northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and whitebait smelt *Allosmerus elongatus*) had lower body condition in the warm years compared to cooler or even average years. The forage taxa showed some overlap in their diet composition during the warm years that may contribute to a limitation in the amount of food available for these species. A more direct measure of food limitation would be to examine the relative feeding intensities (average stomach fullness expressed as a percentage of body weight) in the different time periods. Unfortunately, differences in the collection times among the regimes are likely to affect feeding intensity. However, the fact that we found poorer body condition, a much less sensitive indicator than stomach fullness, in warm years suggests that the feeding conditions were suboptimal during the recent period. Most of the gelatinous taxa consumed are likely to be much larger than the typical prey that these species

normally consume, such as copepods and phytoplankton, and could have led to the observation of a higher average prey weight per fish. We are uncertain what effect these diet shifts may have on the growth and survival of these fish populations in the long-term.

Gelatinous zooplankton are generally of poorer nutritional quality than other likely prey (Doyle et al. 2007), where a reliance on these prey may lead to reduced growth and reproductive output. However, laboratory studies have indicated that pelagic species such as Atlantic mackerel *Scomber scombrus* will feed on small medusae even when offered copepods, and can capture these very efficiently (close to 100% within the swimming path) due to their reduced avoidance capability (Runge et al. 1987). Moreover, these authors found that a single medusa has the same energy content as 10 small copepods due to their substantially larger size. A more direct measure of their condition would be to examine the energy density and lipid dynamics of these forage species among the different environmental conditions (Rosa et al. 2010, Heintz et al. 2013, Albo-Puigserver et al. 2017). Previous analyses in the NCC demonstrated that northern anchovy, Pacific sardine and Pacific herring all had higher lipid levels in the early summer of a normal upwelling year (2006) compared to 2005, a year of delayed upwelling and reduced productivity (Litz et al. 2010).

Overall, we observed major dietary shifts in a suite of planktivorous forage fishes in the northern California Current related to anomalously warm ocean conditions occurring during 2 recent years. In particular, these forage fishes shifted from having an interannually variable diet consisting mostly of crustacean prey to a more consistent diet with important contributions from gelatinous prey sources, with potentially important ecological and energetic implications. We suggest that it is imperative to continue monitoring the trophic ecology of these species, given the potential for increasing jellyfish blooms in the world's oceans (Richardson et al. 2009, Condon et al. 2013). With projections of increased extreme warming events and changes in productivity due to climate change forecast for the northeast Pacific Ocean (Timmermann et al. 2009, Cai et al. 2015), we may expect future range shifts of prey taxa including gelatinous zooplankton and alterations to food web components that depend upon them (Ruzicka et al. 2012, Albouy et al. 2014).

It is uncertain to what degree the Northern California Current and other eastern boundary upwelling ecosystems will be affected by increasing ocean temperatures, but the expectation is that conditions will be substantially altered and probably less favorable for pelagic fish production in the coming decades (Doney et al. 2012, Bakun et al. 2015, García-Reyes et al. 2015). A better understanding of how environmental conditions affect prey availability, prey quality and the bioenergetics of forage fishes will help provide a clearer picture of the potential impacts of rising ocean temperatures on marine food web dynamics in the Northern California Current ecosystem and elsewhere.

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