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Recent Ecosystem Disturbance in the Northern California Current

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Abstract

An extended marine heat wave occurred across the North Pacific during 2014–2016, including the formation of the warm “Blob” followed by a strong El Niño in 2016. Coincident with this marine heat wave, we documented unprecedented biological changes in plankton and nekton in the Northern California Current within pelagic surveys conducted over 20 years (1998–2017). The recent warm period was dominated by warm water gelatinous invertebrates and fishes, some of which were previously either extremely rare or absent. Mixing of organisms originating from more southern or western regions with those previously present in the Northern California Current may have resulted in novel and unpredictable trophic interactions that produced some of the changes in relative abundance we found. Continued long-term monitoring is needed to determine whether this is a temporary ecosystem disturbance or a fundamental change in the very productive Northern California Current upwelling region.

Introduction

The Northern California Current (NCC) Ecosystem (from the Canadian border to Cape Blanco, Oregon) has undergone a great deal of oceanic variability over the past 20 years, ranging from a strong El Niño in 1998, a strong La Niña in 1999, a Pacific Decadal Oscillation (PDO) regime shift during1998–2002 (Peterson and Schwing 2003), and a much delayed spring/summer upwelling period in 2005 (Lindley et al. 2009). These oscillations between warm and cool periods have resulted in shifts in abundance of many commercially important species, including squid, hake, rockfish, and juvenile salmonids.

In fall of 2014, an extreme warming of coastal waters occurred as a large parcel of anomalously warm water, the so called “Blob,” moved eastward and caused a sudden increase in coastal temperatures (Bond et al. 2015). The warm Blob formed in the Gulf of Alaska during the winter of 2013–2014 and generally persisted in the Northeast Pacific through 2016, although brief periods of cooling occurred during May–June 2015 following strong equatorward winds and upwelling (Peterson et al. 2015, 2017). The Blob was immediately followed by a strong El Niño event in 2015–2016 (Jacox et al. 2016). These oceanographic phenomena resulted in a prolonged marine heat wave throughout the NCC during 2014–2016 (Di Lorenzo and Mantua 2016; Gentemann et al. 2017). This heat wave resulted in shifts in occurrence and abundance of a broad range of taxa including copepods (Peterson et al. 2017), ichthyoplankton (Auth et al. 2017; Daly et al. 2017), squid (Sakuma et al. 2016), gelatinous invertebrates, krill and shrimp (Sakuma et al. 2016; Peterson et al. 2017; Brodeur et al., in revision), and fishes (Leising et al. 2015; Sakuma et al. 2016). Trophic shifts were also evident in juvenile salmon diets (Daly et al. 2017).

We have been collecting physical and biological data, including plankton and pelagic nekton, on the same coastal grid from central Oregon to the Washington–British Columbia border for the past 20 years (1998–2017). This has allowed us to develop an oceanographic and biological baseline for the pelagic ecosystem of the NCC. We documented unique abundance variations within our 20-year time series, with effects at all trophic levels. Unlike other recent publications, our data indicated continued biological disturbances through 2017, after cessation of surface manifestations of the Blob. This report describes effects of the recent marine heat wave on the NCC pelagic ecosystem and the status of the post-Blob NCC ecosystem. Because of impacts on larval and juvenile fishes, we expect marine heat wave effects to continue for several more years.

Methods

We obtained information from surveys conducted over the continental shelf, 1 to 30 nautical miles (1.9 to 56.0 km) offshore of Washington and Oregon, USA, in late June 1998–2017. During each survey, we sampled five to seven fixed stations along each of five to eight transect lines perpendicular to the shore between the northern tip of Washington (48°13.7'N) and Newport, Oregon (44°N40.0'; Figure 1). In this paper, we summarized sampling and analysis methods used for these surveys, but more detailed descriptions of these methods can be found in Brodeur et al. (2005), Morgan et al. (2005), and Peterson et al. (2010).

At each station we sampled temperature, chlorophyll-*a*, zooplankton, and nekton. Temperature was measured with a CTD (device that measures conductivity, temperature, and depth) to within 5 m of the bottom or a depth of 200 m, and chlorophyll *a* samples were collected at a depth of 3 m using a Niskin bottle. Temperatures for each station were averaged over the top 20 m of the water column that the trawl sampled. Zooplankton collections were made with either a ring net with a diameter of 1.0 m (1999–2000) or a bongo net with a diameter of 0.6 m (2001–2016), both of which were fitted with 335 µm mesh and a General Oceanics flowmeter to estimate water filtered. Plankton nets were fished by letting out 60 m of cable and immediately retrieved at 30 m/min. while being towed at 2 knots. The maximum depth fished was 20 to 30 m.

We did not include plankton samples from 1998 and 2017 in our results, since samples were taken at only a few stations in 1998 and are not yet analyzed for 2017.

Fish and invertebrate nekton were sampled using a Nordic 264 rope trawl (Nor'Eastern Trawl Systems, Bainbridge Island, Washington) towed to sample the upper 20 m of the water column for 15–30 min at approximately 6.5 km/hr. Only stations sampled during the day, over the continental shelf (≤ 200 m water depth), and in at least 10 of the study years, were included in our analyses. We did not include jellyfish data from 1998, since their occurrence was not reliably recorded. We report only on species that exhibited significant changes during the Blob period compared to previous years.

Our report consists of simple estimates of abundance for the biological organisms of interest. Our evaluation of inter-annual variation in abundance is also simple. We started by generating an overall mean abundance (grand mean [GM]) and variance (standard deviation [grand]), based on the average of 20 individual annual means (1998–2017, see below) Then, for each year of sampling, we determined the number of standard deviations (grand) between the annual mean (AM) and the GM. All calculations were done using Statgraphics Centurion 17.1. (StatPoint Technologies Inc., Warrenton, Virginia). We evaluate the abundance of organisms found in each year in reference to the number of standard deviations between the grand mean and the annual mean and designate these yearly abundance estimates as Typical (AM < 1 SD from GM), Notable (AM > 1 SD to 2 SD from GM), Exceptional (AM > 2 SD to 3 SD from GM), or Extreme (AM > 3 SD from GM).

Abundance was calculated differently for zooplankton and nekton. Total abundance of each zooplankton species caught in each haul was calculated using counts and water volume filtered, converting to biomass using length-to-mass regressions and literature values (Morgan et al. 2005), and then standardizing to units of mg C m^{-3}. Total abundance of each nekton species caught in each haul was either determined directly from a total count of individuals or estimated from the total weight caught, based on the number of individuals in a weighed subsample of that haul. Trawl catches of each species at each station were standardized to linear density by dividing station catch by the distance of the tow, as determined by a global positioning system receiver. After standardizing for distance, they were $\log_{10}$ transformed ($\mathrm{Log}_{10}(\mathrm{no.\ km}^{-1}+1)$) to make the data easier to visualize, interpret, and compare.

We used large-scale indices of ocean conditions, including the PDO and the Oceanic Niño Index (ONI), to place local-scale phenomena within a larger-scale mechanistic picture and to provide a framework in which to examine physical phenomena and lagged biological responses (Mantua et al. 1997; Fisher et al. 2015; Peterson et al. 2017). Positive PDO values were associated with relatively warm ocean conditions in our region. Similarly, positive ONI values, indicative of El Niño events on the equator, were also often associated with warming of the NCC. For our study, PDO was reported as an average of May and June values for each year (data available: http://jisao.washington.edu/pdo/PDO.latest.txt), and ONI was reported as an average of November–January and December–February values for each year (data available: origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php).

Results & Discussion

Physical Conditions in the Northern California Current

Temperatures in the NCC have been unusually warm since 2014 (Bond et al. 2015; Peterson et al. 2015). This was reflected by the strongly positive PDO during 2014–2016, which was the longest period of positive PDO in our time series (48 months; January 2014 to December 2017; Figure 2), and the highly positive 2016 ONI value, which reflected the extremely strong El Niño at the equator (http://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php). Despite overall warmer temperatures documented in the NCC due to the warm Blob (Bond et al. 2015; Peterson et al. 2015), the upper 20-m temperatures in June during our 2014–2016 surveys were not unusually high, due to short periods of upwelling prior to the surveys (https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html; Figure 2). However, the complete monthly time series in this region from 2014–2016 did show that temperatures in the upper water column were elevated. (Leising et al. 2015; McClatchie et al. 2016; Peterson et al. 2017). Finally, while physical oceanographic indicators suggested a return to neutral ocean conditions in the summer of 2017 (PDO; Peterson et al. 2017), temperatures in our survey area were still high.

Biological Patterns of Change

In 2014, we observed biological changes coincident with development of the offshore Blob and a positive PDO (Figure 2). For example, in June 2014, chlorophyll-*a* concentrations were rated Exceptional and one of the three highest in the time series. Similarly, Peterson et al. (2017) also observed high chlorophyll-*a* concentrations in June 2014 during more frequent sampling off of Newport, Oregon. Among the animals sampled, both California market squid *Doryteuthis opalescens* and furcilia-stage larval krill *Euphausia pacifica* had notable deviations in abundance and were more numerous than in the previous 15 years (Figure 2).

In 2015, abundances of more species deviated markedly from their 20-year mean values (Figure 2; Table 1). The deviation in biomass abundance of krill furcilia-stage larvae was exceptional, and for Pacific sand crab *Emerita analoga* zoeal stage larvae it was notable. Both species were much more abundant than they had previously been in the time series. Abundances of all three common jellyfish species changed markedly, but differed in their direction of change. The deviation in abundance of the normally scarce water jellyfish *Aequorea sp.* was exceptional, and it became the most abundant jellyfish in our catches. In contrast, the generally most common jellyfish, sea nettle *Chrysaora fuscescens*, had notably lower abundances, and was nearly absent from our samples. The deviation in abundance of egg-yolk jellyfish *Phacellophora camtschatica* was notably high, and it became more abundant than in previous years. Finally, the abundance of three nektonic species increased. While only California market squid deviation in abundance was Notable, Pacific Pompano *Peprilus simillimus* and Jack Mackerel *Trachurus symmetricus* abundance was higher than any of the 8 previous years.

In 2016, 13 species had notable to extreme deviations in abundance (Figure 2; Table1), which occurred during the period spanning the Blob and following a winter with strongly positive sea surface height anomalies and strong poleward flow (Peterson et al. 2017). Two zooplankton species, Pacific sand crab zoea and krill furcilia, had exceptional deviations in abundance. Pacific sand crab zoeal biomass was higher than any previous year, while krill furcilia biomass was higher than all previous years except 2015. Two jellyfish species, water jellyfish and sea nettle, had 3xceptional deviations in abundance, while one, egg-yolk jellyfish, had an extreme deviation. Egg-yolk jellyfish numbers were higher than any previous year; water jellyfish numbers were higher than all previous years except 2015, while sea nettle numbers were lower than all but 2 previous years (2000 and 2014). Three nektonic species had notable deviations in abundance; California market squid, Pacific Chub Mackerel *Scomber japonicus* and yearling Coho Salmon *Oncorhynchus kisutch*; four species had extreme deviations, juvenile rockfish *Sebastes* spp., Pacific Pompano, young-of-the-year (YOY) Pacific Hake *Merluccius productus* and yearling Chinook Salmon *O. tshawytscha*; and one species—Jack Mackerel—had an exceptional deviation. California market squid, yearling Coho Salmon, and yearling Chinook Salmon declined in abundance, while the other five nektonic species were more abundant than any previous year.

In 2017, chlorophyll-*a* concentration had a notable deviation, and was the lowest value obtained during the 20-year time series, while five species had notable to extreme deviations in abundance. The most surprising extreme deviation was the first ever occurrence of the colonial gelatinous tunicate *Pyrosoma atlanticum*, which were extremely abundant throughout our entire survey area. Two other nektonic species, yearling Coho and Chinook Salmon, had notable deviations in abundance, and declined to the lowest numbers obtained during the 20-year time series. Two additional nektonic species, Pacific Pompano and Jack Mackerel, had exceptional deviations in abundance, with Pacific Pompano numbers being the second highest observed and Jack Mackerel being the highest observed during the 20-year time series.

Potential Mechanisms Leading to Changed Abundance

Multiple physical and ecological mechanisms are likely responsible for the variations in abundances we documented among many species (Table 2). Although the survey was not designed to determine which mechanisms caused these variations, we can make inferences based on three ecological and organismal traits: 1) Plankton drift passively and as such, when waters masses are transported from south to north or from west to east, the distribution of planktonic organisms changes; 2) Nekton can actively swim against currents and can thus change their distribution in response to local temperatures and seek out thermally preferred water masses; and 3) changes in abundance may be in response to changes in local processes that regulate population abundances (e.g., reproduction and predation). These mechanisms are not mutually exclusive and probably do not represent a complete list of possible processes. Moreover, in most cases, more than one mechanism likely is leading to the patterns of change we observed (see below).

Planktonic water jellyfish, egg-yolk jellyfish, and Pacific sand crab larvae are normally associated with warmer waters to the south of our study area and/or offshore (Shenker 1984;

Suchman and Brodeur 2005). High abundances of these species in our catches from 2014 to 2016 suggest northward and/or eastward transport, corresponding with warmer southern or offshore waters moving onshore (Gentemann et al. 2017). Other planktonic species, such as copepods, have demonstrated similar patterns of unusual advection from southern and offshore waters into the waters off central Oregon during this same time period (Peterson et al. 2017). Northward shifts in distribution of these species have been also reported during other El Niño events (Pearcy and Schoener 1987; Pearcy 2002; Brodeur et al. 2005).

Thermal preferences, paired with spatial changes in water temperatures, may result in active migration by some species from south to north or west to east. For instance, California market squid, Pacific Pompano, Jack Mackerel, and Pacific Chub Mackerel are normally found in warmer southern waters and were observed in high abundances during the warm water years since 2014. Other studies have documented similar changes in distribution of these species during previous strong El Niño years (Pearcy and Schoener 1987; Pearcy 2002; Brodeur et al. 2005).

We sampled only the top 20 m of the water column during this survey with the trawl and plankton nets. Therefore, we cannot exclude the possibility that changes in abundance of some organisms captured by our gear were due to changes in their vertical distribution within our study area rather than horizontal transport or active migration into our study area from other locations. For example, some species of sea nettles are known to undergo diel vertical migration, although, this behavior has not been documented for species in our region (Suchman and Brodeur 2005; Suchman et al. 2012), and juvenile Chinook Salmon may move deeper in the water column in response to warmer surface water (Orsi and Wertheimer 1995). However, we currently lack the data to directly test for changes in depth distribution.

Information from other studies suggests that local processes rather than different migration patterns may have been responsible for the low abundance of juvenile Coho and Chinook Salmon in our catches in 2017. Juvenile Coho Salmon are not known to change depth preference in response to warm water (Orsi and Wertheimer 1995; Beamish et al. 2007; Beamish et al. 2018), yet abundance trends for this species were similar to those for juvenile Chinook Salmon in our study. In contrast to the low catches in our coastal samples, which mostly consist of Columbia River fish (Van Doornik et al. 2007; Teel et al. 2015), abundance of both juvenile Coho and Chinook Salmon in the Columbia River in 2017 was at least average, based on

Bonneville Dam smolt counts (the source of most of the juvenile salmon in our survey; Fish Passage Center 2017) as well as estuary purse seine smolt catches (L. Weitkamp, unpublished). We also conduct a separate survey in May, as smolts are entering the ocean, before any potential changes in northward migratory tendency could change their abundance. Our catches of juvenile salmon in May 2017 of both species were quite low relative to previous May survey catches (Morgan et al. 2017), which have been conducted since 1999 (Jacobson et al. 2012; Teel et al. 2015).

In contrast to Coho and Chinook Salmon, the notable and extreme abundance increases in Pacific sand crab larvae found in 2015 and 2016, respectively, were likely due to both local processes and northward transport. Adult sand crabs live in the wash zone of sandy beaches, spawn in summer and fall, and produce larvae that are planktonic for approximately 4 months (Johnson 1939; Efford 1970, 1976). Larval Pacific sand crab in our catches had a bi-modal age distribution caused by the presence of both early (zoeal stage I, ZI) and late (ZV) stage larvae, with both stages sometimes present in the same sample. We never found any intermediate stage (ZII–ZIV) larvae. We assume Z1 stage larvae represented local production of eggs, as these larvae were too young to have undergone long-range transport. The presence of older ZV stage larvae, coupled with the absence of ZII–ZIV larvae, suggest these larvae were transported from the south, as has been suggested to have occurred during other warm periods such as during the El Niños of 1997–1998 and during the warm period of 2004–2005 (Sorte et al. 2001; Figure 2).

The first observation of YOY Pacific Hake in our survey occurred in June 2016. During February 2016, Auth et al. (2017) found larval Pacific Hake at every station from 35 to 105 nautical mi off the coast of Newport, Oregon, which was 4 months prior to and well offshore of our sampling. This indicates YOY Pacific Hake were relatively abundant off the Oregon/Washington coast in 2016. Since this species usually spawns further south, off California (Ressler et al. 2007) the presence of YOY Pacific Hake suggested spawning may have shifted northward. Similarly, increased abundance of YOY Pacific Chub Mackerel in our June 2016 survey, may have been due to northward shift in adult distribution and spawning (Auth et al. 2017).

Comparisons with Other Studies

Since different ocean sampling studies may have dissimilar objectives and methods, using result from these studies to create a coherent picture of the California Current during the recent marine heat wave is much like the classic parable of blind people studying an elephant: each person touches a different part of the animal and thus describes a different creature. We suggest that common trends across studies may reflect large-scale patterns, whereas differences among studies may just be due to differences in local distribution, sampling design or methodology, or they may also reflect real differences.

Increased abundance of species such as California market squid, YOY Pacific Hake, YOY rockfish, and pyrosomes were observed off the California coast before similar changes occurred in our more northern survey region (Sakuma et al. 2016; Brodeur et al., in revision). Warm water anomalies first occurred in southern California coastal waters in spring of 2014 and were subsequently farther north later in that year (Gentemann et al. 2017). Similarly, northerly occurrences of more southern species were observed first in California and then later to the north in our survey area.

Several studies in the NCC have reported very low abundances of adult euphausiids during the past few years (Sakuma et al. 2016; Peterson et al. 2017; Brodeur et al., in revision). In strong contrast, we found anomalously high biomass of *E. pacifica* furcilia larvae during our study in 2014–2016. In addition, we counted, but did not report on several other larval stages of crustaceans in the same plankton samples. We found that abundances of an earlier larval stage (calyptopis) of *E. pacifica* were also the highest ever observed during this same time period, and larvae of another common euphausiid, *Thysanoessa spinifera* as well as shrimp (Caridae) larvae had similarly high abundance patterns during this time period (C. Morgan, unpublished). Given the short larval duration of *E. pacifica*, (20–35 days from hatching to early furcilia stages; Bi et al. 2011), adult euphausiids must have been present to release eggs in the NCC. Therefore, presence of larval and absence of adult euphausiids might have been the result of adults moving to cooler waters deeper or farther offshore.

The extraordinary increase in YOY rockfish (4 SD’s above the mean) in our 2016 catches was a coast wide event, documented from California (McClatchie et al. 2016) to Alaska (Strasburger et al. 2018) waters. This suggests that whatever factors caused this increase operated over an extremely large area. However, since the juveniles of the more than 70 northeast Pacific rockfish species are extremely difficult to distinguish (Love et al. 2002), we could not document which species were involved with, or attempt to identify mechanism(s) responsible for the increase. Continued assessment of older, easier to identify rockfish may provide more focus to our current observation.

Pyrosomes were extremely abundant in our 2017 catches, while other gelatinous species returned to more typical abundance levels (Figure 2). In 2014, other surveys encountered low numbers of pyrosomes further south of our study area as well as offshore (Wells et al. 2017; Brodeur et al. 2018; Brodeur et al., in revision). By 2015, these surveys captured pyrosomes at least as far north as Willapa Bay, Washington, but well off the continental shelf. Pyrosomes were also caught for the first time, and in high numbers, in Alaskan waters during the winter of 2016–2017 and through the summer of 2017 (NOAA Alaska Fisheries Science Center 2017; Brodeur et al. 2018). This dramatic range and abundance expansion clearly represents favorable conditions for pyrosomes, and suggests the exceptionally high and widespread abundance of pyrosomes was not solely due to changes in water transport.

Consequences of Species Abundance Changes

Understanding the consequences of extreme changes in species abundance in the NCC is challenging. Ruzicka et al. (2012) explored changes in abundances of different trophic groups in the NCC, and used modeling to predict how these changes would impact energy flows through the food web. Many of the taxonomic groups they identified as important nodes of energy flow (Figure 3 boxes) are ones we found to have undergone large increases (e.g., water jellyfish, euphausiids, California market squid, Pacific Chub and Jack Mackerel, and Pacific Hake) or decreases (e.g., sea nettles, juvenile Chinook and Coho Salmon) in abundance. However, our survey focused on the upper water column during the day, and did not sample all the species included in the food web analysis.

Decreased sea nettle abundance during 2015–2017 coincided with increased abundance of zooplankton prey species. Sea nettles are known to feed on early stage euphausiids (Suchman et al. 2008), so the decline in sea nettles may have resulted in the high abundance of larval euphausiids in 2015 and 2016. The high abundance of juvenile rockfish abundance in 2016 may have been partly influenced by the very low numbers of sea nettles in 2015 due to both decreased predation on larval rockfish in 2015 as well as decreased competition for food by sea nettles with larval rockfish.

The sudden presence and extremely high abundance of pyrosomes may be the best example of an ecosystem consequence. Pyrosomes were not a component of the Ruzicka et al. (2012) ecosystem analysis as this organism had never been observed in the NCC (Welch 2017; Brodeur et al. 2018). *P. atlanticum* has been found to be an extremely effective grazer, with clearance rates among the highest recorded for any pelagic grazer (Perissinotto et al. 2007). The high abundance of pyrosomes could explain the extremely low chlorophyll-*a* concentrations we observed in 2017, and could have reduced energy flow to higher trophic levels. If this organism remains abundant in subsequent years, it could produce lasting effects upon the NCC ecosystem by outcompeting other filter feeders, which in turn might reduce the food supply to organisms higher in the food web.

Finally, changes in abundance of various juvenile fish species, including Pacific Hake, rockfish, and Coho and Chinook Salmon, will affect top predators such as sharks, pinnipeds, toothed whales, and humans. We think that increased abundance in YOY Pacific Hake and Pacific Chub Mackerel in our 2016 samples was probably due to shifts in adult spawning distribution (Auth et al. 2017), and thus may not be indicative of increased abundance on a broad, regional scale. If this is true, we do not expect the abundance of adults of these species to greatly increase in the future. In contrast, we think that very high abundance of juvenile rockfish in our 2016 samples and very low abundance of yearling Coho and Chinook Salmon in our 2017 samples represent real changes in abundance that will likely affect adult recruitment. Low catches of juvenile salmon in our June surveys have already been associated with poor adult returns (Burke et al. 2013; Peterson et al. 2014), so we anticipate poor returns of Coho Salmon to the Columbia River in 2018 and poor returns of Chinook Salmon in 2019. The high abundance of juvenile rockfish in 2016 was an extraordinary event, spanning at least 2500 km of coastline along the West Coast of North America. While Ralston et al. (2013) suggested that pelagic abundance of juvenile rockfish is a good indicator of adult recruitment in Central California, the actual consequences of high juvenile rockfish abundance in 2016 remains to be seen in future years.

Conclusion

We have documented recent dramatic changes in abundance of fish and invertebrates in the surface waters of the NCC since 2014. These changes likely reflect changes in physical processes and ecological mechanisms (Table 2). Some of what we observed was due to a shift of organisms from south to north and from west to east, while other changes may be the result of alterations in biological processes for organisms that have not changed their distributions. It is notable that we have not seen a complete changeover of species within the NCC ecosystem. Rather, we have seen the novel occurrence of some organisms mixed with other species that are normally present (Table 2). Mixing of organisms from different regions may result in novel trophic interactions with unpredictable results (Naiman et al. 2012). We are particularly interested in potential continued ecological effects of the occurrence and abundance of pyrosomes in the NCC in 2017 and beyond.

We think the value of this paper lies not only in specific results we described, but also as a reminder of the importance of obtaining and maintaining long-term baselines to measure biological change (McClatchie et al. 2014). We have already described clear ecosystem-scale change in response to large-scale climatic changes (the Blob and El Niño). The current National Marine Fisheries Service emphasis on ecosystem management will only be successful if robust field surveys of those ecosystems continue (Levin et al. 2009).

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Figure Captions

Figure 1. Locations of stations included in this analysis for plankton (white) and pelagic nekton (white and yellow).

Figure 2. Variables included in this analysis: large scale physical indices (teal), average temperature (°C) in the top 20 m (red), chlorophyll-*a* (µg L^{-1}) (green), biomass of two plankton

species (mg Carbon m^{-3}) (purple), and surface trawl catches (Log$_{10}$ (no. km^{-1}+ 1)) of jellyfish (cyan), pyrosomes (pink), squid (orange), and fish (blue). Circles indicate the June average for each year and bars are ± 1 standard error. The right y-axis and the corresponding horizontal lines indicate the number of standard deviations from the grand mean (dark red short dash = ± 1 SD, dark red long dash = ± 2 SD, and light gray long dash = 3-6 SD). The three warm periods, 1998, 2005, and 2014-2016 (described in this paper) are shaded in light gray. The plots of Pacific Chub Mackerel and Pacific Hake are total catch, with the smaller insets showing only young-of-the-year (YOY) catches for those species. YOY insets follow the same format as other plots, but year shading, and SD labels are not shown.

Figure 3. Energy flow pathways between major functional groups in the Northern California Current food web (modified by J. Ruzicka from Figure 6a in Ruzicka et al. 2012). Box size is proportional to group production rates. Red shading indicates species identified in this paper that have greatly increased or decreased during the recent marine heat wave.

Table 1. Number of standard deviations (SD) above or below the grand mean for each variable or species examined, 2014- 2017. A SD > 1 is Notable, > 2 SD is Exceptional, and > 3 SD is an Extreme. Red indicates positive standard deviations and blue negative. NA indicates that the variable was not available in that year.

	2014	2015	2016	2017
Oceanic Niño Index			**+2**	
Pacific Decadal Oscillation	**+1**	**+1**	**+2**	
Top 20 m Temperature				
Chlorophyll *a*	**+2**			**-1**
Euphausia pacifica		**+2**	**+2**	NA
Pacific sand crab		**+1**	**+2**	NA
Water jellyfish		**+2**	**+2**	
Sea nettle		**-1**	**-1**	
Egg-yolk jellyfish		**+1**	**+3**	
Pyrosoma atlanticum				**+4**
CA market squid	**+1**	**+1**		
Juvenile rockfish			**+4**	
Pacific Pompano			**+3**	**+2**
Yearling Coho Salmon				**-1**
Yearling Chinook Salmon				**-1**
Jack Mackerel			**+2**	**+3**
Pacific Chub Mackerel (YOY)			**+4**	
Pacific Chub Mackerel			**+1**	
Pacific Hake (YOY)			**+4**	

Table 2. A description of the persistence of a given species within our 20 year survey (continuous, sporadic, or novel during the marine heat wave [2014-2017]), and change in abundance during the marine heat wave (increase or decrease). Also provided is a description of whether the organism drifts with or can swim against currents (plankton or nekton), inferred changes in spatial distribution during the marine heat wave, and whether changes in abundance during the marine heat wave might be attributed to local ecological processes. A question mark indicates that changes in abundance might be due to a change in depth distribution, but we have no data to test that possibility.

				Inferred distribution change			
	Presence	Recent abundance (heat wave)	Plankton or Nekton	South to North	West to East	Shallow to deep	Local processes
Euphausia pacifica (larvae)	continuous	increase	plankton				✓
Pacific sand crab (larvae)	sporadic	increase	plankton	✓			✓
Water jellyfish	continuous	increase	plankton	✓	✓		
Sea nettle	continuous	decrease	plankton			?	✓
Egg-yolk jellyfish	continuous	increase	plankton	✓	✓		
Pyrosoma atlanticum	novel	increase	plankton	✓	✓		✓
CA market squid	continuous	increase	nekton	✓			
Juvenile rockfish	continuous	increase	nekton				✓
Pacific Pompano	sporadic	increase	nekton	✓			
Yearling Coho salmon	continuous	decrease	nekton			?	✓
Yearling Chinook salmon	continuous	decrease	nekton			?	✓

Jack Mackerel	continuous	increase	nekton	✓	✓
Pacific Chub Mackerel (YOY)	sporadic	increase	nekton		✓
Pacific Chub Mackerel	sporadic	increase	nekton	✓	✓
Pacific Hake (YOY)	novel	increase	nekton	✓	✓

.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html

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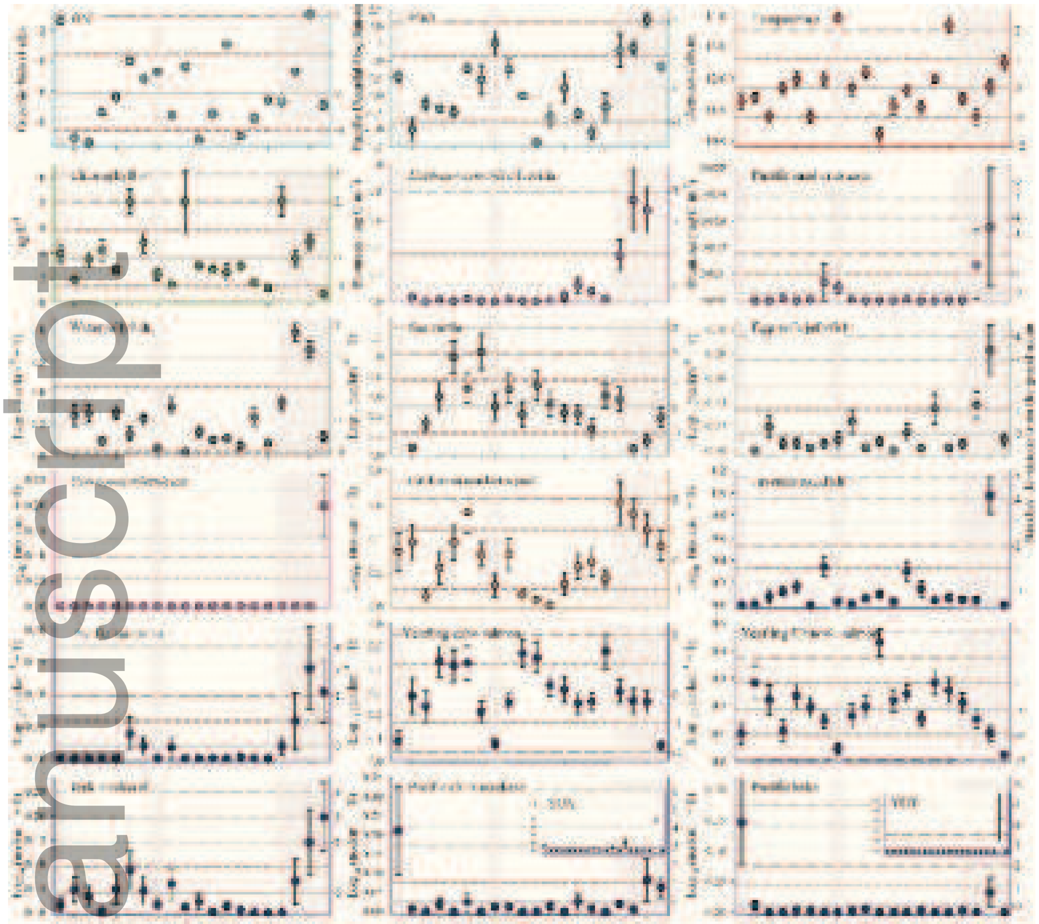

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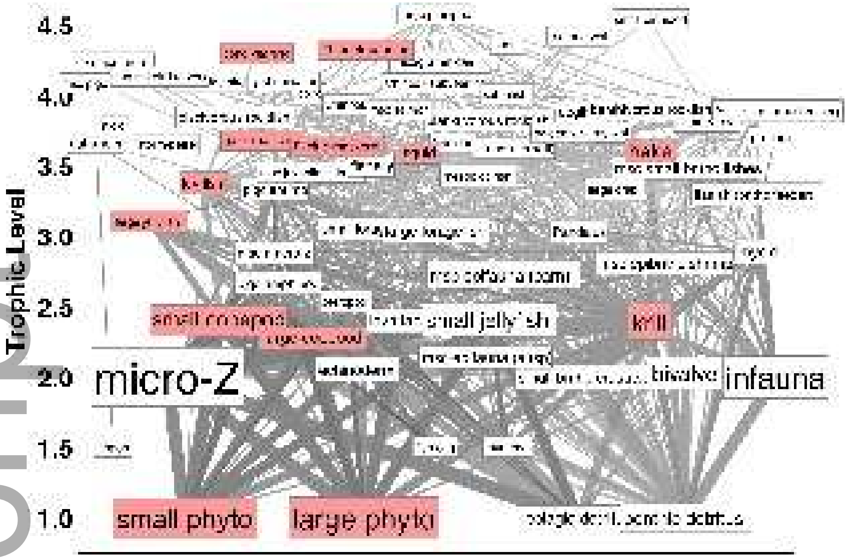

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