# ANOMALOUS EPIPELAGIC MICRONEKTON ASSEMBLAGE PATTERNS IN THE NERITIC WATERS OF THE CALIFORNIA CURRENT IN SPRING 2015 DURING A PERIOD OF EXTREME OCEAN CONDITIONS

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## ABSTRACT

We report on the anomalous distribution, abundance, and community structure patterns of epipelagic micronekton from a midwater trawl survey in May–June 2015 that has a 26-year time series within a core region off central California (36°35'–38°10'N) and a 12-year time series with expanded spatial coverage (extending from 32°42.5'–39°50'N). The 2015 survey took place during an extended period of record-breaking warm surface temperatures in much of the northeast Pacific Ocean. In the neritic waters off central and northern California, this broad-scale extended marine heat wave was combined with more localized, above average coastal upwelling in spring 2015 that led to slightly cooler than normal surface temperatures over the continental shelf and shelf break. The unusual micronekton assemblages in our 2015 trawl survey featured anomalously high catches of warm water species such as pelagic red crabs (*Pleuroncodes planipes*), coincident with high catches of colder water species such as YOY rockfish (*Sebastes* spp.), and also large catches of pelagic tunicates such as *Pyrosoma atlanticum*. Principal component analysis (PCA) on a subset of the most frequently occurring species for both the shorter time series (expanded survey area) and the longer time series (core region) yielded similar results to previous studies off central California, with a suggested alternation between micronekton communities dominated by coastal pelagic species and those dominated by YOY groundfish (rockfish, Pacific hake [*Merluccius productus*], and sanddabs [*Citharichthys* spp.]), krill, and cephalopods. In addition, the leading principal components for the different regions of the expanded survey area were highly correlated, suggesting similar micronekton community responses to forcing mechanisms over a broad spatial scale. As the PCA analysis was limited to a relatively small subset of species and the time series for some frequently encountered species are not continuous throughout the history of the survey, we also report on species that reflect additional aspects of the unusual nature of the 2015 survey catches. Together, these results indicate that the micronekton community structure in the late spring of 2015 was highly anomalous in that species characteristic of what might generally be considered three different nominal states (YOY groundfish/market squid and krill, warm-water subtropical species, and pelagic tunicates) were all encountered in high abundance.

## INTRODUCTION

Oceanographic conditions within the California Current were highly variable from 2013–15. The region experienced extremely strong coastal upwelling and anomalously cold sea surface temperatures (SSTs) in 2013, near average coastal upwelling and record warm temperatures in 2014 (with mesoscale differences in upwelling patterns after June of 2014), and continued warm temperatures offshore with localized above average coastal upwelling in 2015 for areas north of 33°N (Wells et al. 2013; Leising et al. 2014, 2015). These conditions took place during an unprecedented marine heat wave for the broader northeast Pacific that developed in multiple stages, starting with rapid warming in the Gulf of Alaska in fall 2013 (Bond et al. 2015), warming in coastal Baja and southern California in spring 2014 (Zaba and Rudnick 2016), rapid warming of the neritic waters of central California in July 2014 (National Marine Fisheries Service 2014), and then a broad coast-wide warming from Alaska to Mexico in fall–winter 2014–15 (Di Lorenzo and Mantua 2016). In winter 2015, oceanographic conditions off California included anomalously low chlorophyll and an anomalously deep thermocline (Jacox et al. 2016), while in spring 2015 conditions included localized above average coastal upwelling and cooler than normal SSTs over the continental shelf and shelf break (fig. 1, Leising et al. 2015).

The anomalous oceanographic conditions over the 2013–15 period had dramatic impacts on the marine ecosystems of the northeast Pacific, including unprecedented toxic algal blooms and massive fisheries closures, and unusual mortality events for several populations of

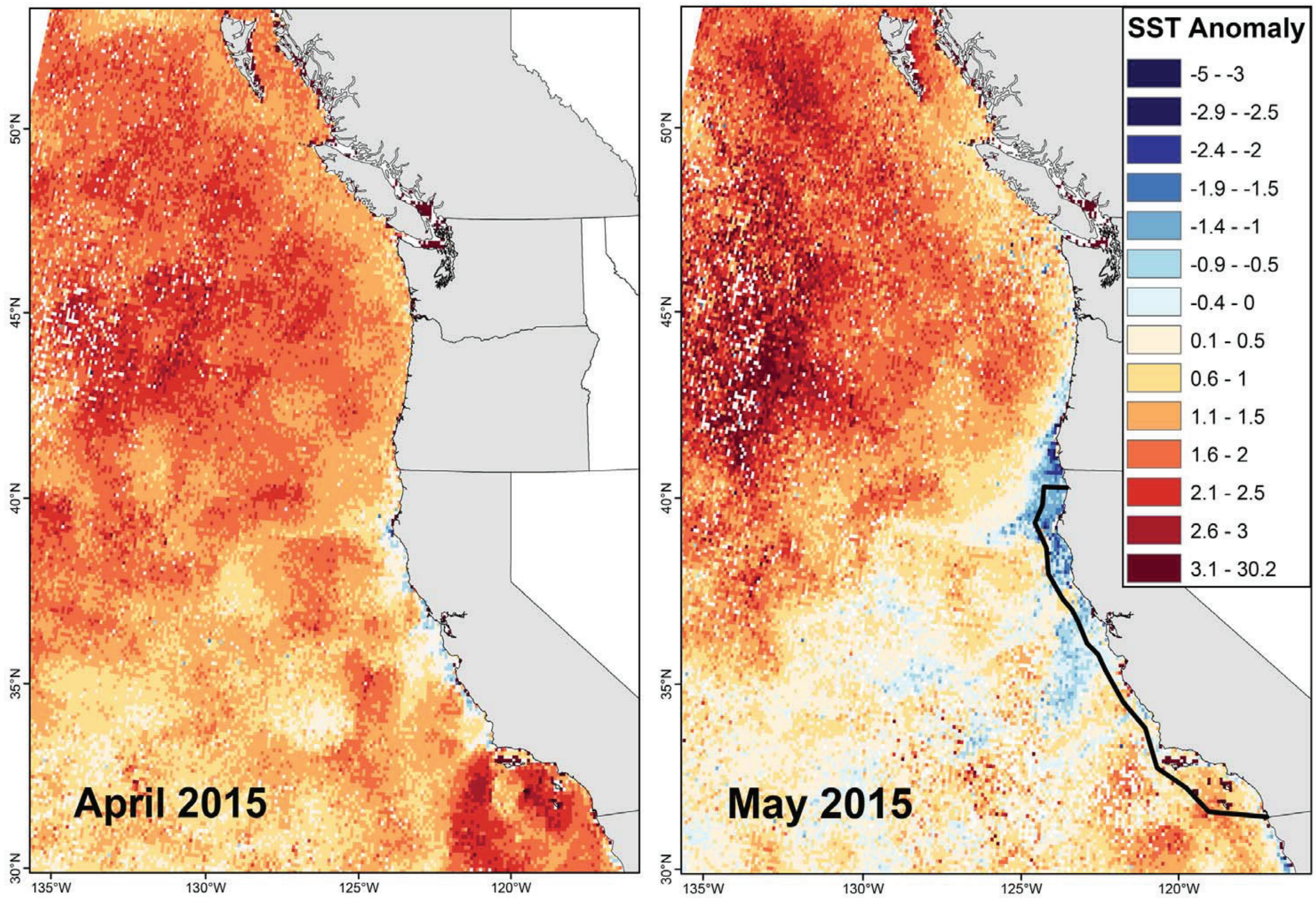


Figure 1. SST anomalies for months preceding and during the 2015 survey, with the spatial coverage of the survey overlaid (data from NOAA CoastWatch Program, 1985–95 climatology).

seabirds and marine mammals (reviewed in Di Lorenzo and Mantua 2016; Jacox et al. 2016). The cascading impacts to marine fisheries and coastal communities, particularly as a consequence of the toxic algal blooms, were also considered to be substantial (Peterson et al. 2015; Welch 2016).

Historically, during warm periods in the California Current, temperate upwelling associated species such as young-of-the-year (YOY) rockfish (*Sebastes* spp.), market squid (*Doryteuthis opalescens*), and krill (Euphausiacea) have been observed to be at low to very low abundance levels (Lenarz et al. 1995; Brodeur et al. 2006; Ralston et al. 2013, 2015). In such years, more southerly distributed warm water species such as the pelagic red crab (*Pleuroncodes planipes*) and California lizardfish (*Synodus lucioceps*) tend to increase in abundance and extend their distribution northward (Longhurst 1967; Aurioles-Gamboa et al. 1994). In order to examine the effects of the recent oceanographic conditions on the marine ecosystem, we analyzed data from a midwater trawl survey that has sampled the shelf and shelf-break waters off the central California coast for an extended period (1990–2015), with spatial coverage expanded to the majority of the California coast over a shorter time period (2004–15).

The Fisheries Ecology Division (FED) of the Southwest Fisheries Science Center (SWFSC) has conducted a midwater trawl survey off central California since 1983 with the primary goal of developing pre-recruit indices for YOY rockfish (Ralston et al. 2013). However, the survey also samples numerous other components of the epipelagic micronekton (free swimming organisms generally <200 mm), including many of the most frequently encountered forage species in a recently developed database of predator food habits in the California Current (Szoboszlai et al. 2015; see also Ainley et al. 2015). Ralston et al. (2015) analyzed these data to evaluate the species assemblage over a 23-year time span (1990–2012) and observed a contrast between the abundance of YOY groundfish (rockfish, Pacific hake and sanddabs, *Citharichthys* spp.), market squid, and krill with the abundance of adult clupeoids (Pacific sardine, *Sardinops sagax*, and northern anchovy, *Engraulis mordax*) and myctophids (Myctophidae). YOY groundfish, market squid, and krill were more abundant during years with depressed sea level anomalies (indicative of equatorward transport anomalies) and cooler conditions in the California Current, while clupeoids and myctophids were more abundant during years with elevated sea level anomalies (poleward transport anomalies) and warmer conditions. For our study, we expand upon the analysis of Ralston et al. (2015) using data from a shorter time series, but greater spatial coverage. In addition, we examined the observed impacts of the recent northeastern Pacific marine heat wave (Bond et al. 2015; Leising et al. 2015; Di Lorenzo and Mantua 2016) on the late spring micronekton and forage community over the shelf and shelf-break waters of the southern part of the California Current (Southern California Bight to Cape Mendocino).

## METHODS

### Midwater Trawl Survey

The FED SWFSC has conducted annual surveys in May through mid-June from 1983–2015 (and ongoing) using a modified Cobb midwater trawl with a 26 m headrope, 9.5 mm stretched mesh codend liner, and theoretical mouth opening of 12 m x 12 m (Wyllie Echeverria et al. 1990; Ralston et al. 2013). Trawl duration was 15 minutes at a target headrope depth of 30 m except for a few nearshore stations where bottom depths were shallower than 55 m, in which case the target headrope depth was adjustesd to 10 m to avoid contact with the bottom. Ship's speed through the water was ~3.7 km/hr (2.0 knots) and all trawls were conducted at night due to net avoidance during the day (FED SWFSC unpublished data). Trawls were conducted at fixed stations, although the number and location of these stations has changed over the years as new stations were added and others discontinued (fig. 2). For example, starting in 1997 select nearshore stations were discontinued due to reoccurring large catches of jellyfish (*Chrysaora fuscescens* and *Aurelia* spp.), which frequently damaged the gear, thus reducing sampling efficiency. A small percentage of trawls were also made of shorter duration (5 vs. 15 minutes) when jellyfish or pelagic tunicates were present in high abundance. Catches were then standardized to an expected 15 minute haul using a correction factor derived from comparing catch rates of 5 and 15 minute trawls conducted at the same time and place. Furthermore, some stations were dropped to add new stations in order to extend the spatial coverage farther offshore (e.g., two new stations were added off Monterey Bay in 2015; see inset of fig. 2). Despite these changes, most of the Central California core region stations have been sampled continuously since 1983. Additional survey details are provided in Ralston et al. (2013, 2015).

In 2004, in recognition of the need to sample a broader geographical range of a suite of YOY rockfish species, the survey area was expanded from San Diego to Point Delgada just south of Cape Mendocino (Sakuma et al. 2006) and in 2013 from Cape Mendocino north to survey the entire coast of California from the Mexican to Oregon borders. For the years with expanded spatial coverage (2004–15), the survey area can be separated into five regions: south, south central, core, north central, and north, which are shown in fig. 2. As the north region has only a limited amount of data (just three years), this region was excluded from the analyses in this study. No sampling was done in the south region in 2011 due to vessel and logistic constraints, nor in the north central region in 2012 due to inclement weather. From 1983–2008 the survey was conducted aboard the NOAA ship *David Starr Jordan*. After 2008, the survey was conducted aboard a mixture of charter vessels and NOAA ships including the NOAA ship *Miller Freeman* in 2009, the charter vessel *Frosti* in 2010, the charter vessel *Excalibur* in 2011, the NOAA ship *Bell M. Shimada* in 2012, and the charter vessel *Ocean Starr* (actually the repurposed *David Starr Jordan*) in 2013–15.

All fish and select invertebrates were sorted and enumerated at sea with the YOY rockfish frozen and returned to the laboratory for further analysis. While YOY rockfish and other groundfish (e.g., Pacific hake) have been consistently enumerated at sea since 1983, subsampling of many other forage species, such as krill and mesopelagic fishes, was not standardized until 1990. In addition, in collaboration with University of California Santa Cruz (UCSC), krill were identified to species beginning in 2002. Note that for 2013–15 all krill numbers are preliminary (based on a small subsample of species assignments at sea) with the final numbers by species awaiting ongoing laboratory confirmation. Additionally, there was a hiatus in the identification of large jellyfish (*Chrysaora* spp. and *Aurelia* spp.) and gelatinous micronekton such as *Thetys vagina*, other salps (Salpidae), *Pyrosoma atlanticum*, and pelagic mollusks (Pterotracheoidea) that began in 2002, in response to time demands at sea. However, enumeration of large jellyfish resumed in 2005 in collaboration with UCSC, and enumeration of gelatinous micronekton was resumed in 2012 due to their prominence in the trawl catches that year.

### Hydrographic Data

Conductivity, temperature, and depth (CTD) casts were done at each nighttime trawl station starting in 1987. Additional CTD casts were made during the daytime in the area around the trawl stations, although the locations were not standardized until 1991. As the survey area expanded, new daytime CTD stations were added (fig. 2). CTD casts were typically conducted to the lesser

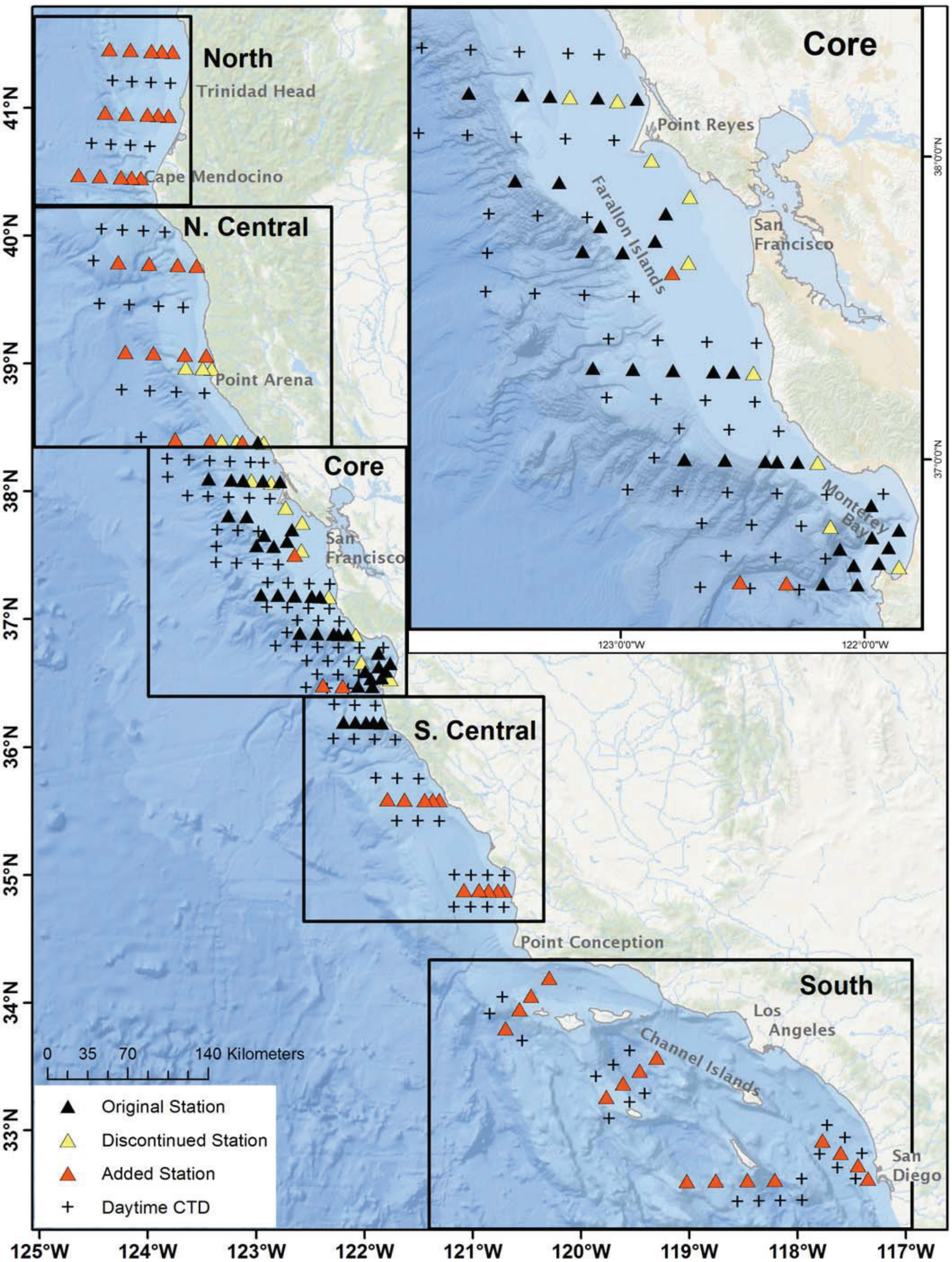


Figure 2. Midwater trawl and CTD station locations off California. Inset map shows the locations of the core region stations historically sampled since 1983. Stations that were added in later years and historic stations that are no longer currently sampled (discontinued) are also shown. In 2004, the survey area was expanded to include the south, south central, and north central regions. The north region was added in 2013.

TABLE 1
**Species/taxa occurring in 10% or more of trawls in the expanded survey area (All Areas) from 2004–15 listed in decreasing order of occurrence. The percent occurrence within each of the four survey regions is also shown. The region with the highest percent occurrence is in bold. For Ontogeny, Y = young-of-the-year, A = age 1+, and U = undetermined. With the exception of krill, all species/taxa were also enumerated in the core region since 1990 (data not shown). Species specific enumeration of krill began in 2002 with only total krill numbers available from 1990–2001 (data not shown).**

| Common Name | Scientific Name | Ontogeny | South | South Central | Core | North Central | All Areas |
|---|---|---|---|---|---|---|---|
| Krill | *Euphausia pacifica* | U | **89.3** | 79.7 | 81.4 | 86.5 | 83.2 |
| Sanddab | *Citharichthys* spp. | Y | **81.6** | 79.1 | 79.3 | 72.5 | 78.7 |
| Rockfish | *Sebastes* spp. | Y | **81.6** | 73.8 | 73.9 | 68.4 | 74.5 |
| Krill | *Thysanoessa spinifera* | U | 61.1 | 55.6 | **70.9** | 35.2 | 62.4 |
| Market Squid | *Doryteuthis opalescens* | U | **84.4** | 65.2 | 51.2 | 17.1 | 54.1 |
| Myctophid | Myctophidae | U | **82.8** | 52.9 | 40.0 | 63.7 | 52.2 |
| Pacific Hake | *Merluccius productus* | Y | 50.0 | 42.8 | 53.8 | **57.0** | 52.1 |
| Sergestid | Sergestidae | U | **57.0** | 38.0 | 32.3 | 54.4 | 40.3 |
| Octopus | Octopoda | U | 38.9 | **44.9** | 30.7 | 28.5 | 33.7 |
| Krill | *Nematoscelis difficilis* | U | **71.7** | 35.3 | 19.6 | 39.9 | 33.3 |
| Squid | Teuthoidea | U | **47.5** | 28.9 | 22.4 | 42.0 | 30.2 |
| California Headlightfish | *Diaphus theta* | U | 34.0 | 29.4 | 22.6 | **52.9** | 29.5 |
| California Smoothtongue | *Leuroglossus stilbius* | U | **50.0** | 31.0 | 24.5 | 15.5 | 28.5 |
| Blue Lanternfish | *Tarletonbeania crenularis* | U | 15.2 | 36.4 | 23.1 | **57.5** | 28.1 |
| Deep-Sea Smelt | Bathylagidae | U | 37.3 | 19.3 | 17.7 | **48.7** | 25.5 |
| Goby | Gobiidae | U | **55.3** | 30.5 | 15.5 | 4.7 | 22.8 |
| Rex Sole | *Glyptocephalus zachirus* | Y | 5.3 | 12.8 | 25.1 | **28.0** | 20.5 |
| Northern Anchovy | *Engraulis mordax* | A | 17.2 | **28.9** | 20.6 | 2.6 | 18.7 |
| Northern Anchovy | *Engraulis mordax* | Y | **50.4** | 29.4 | 7.9 | 6.2 | 17.8 |
| Pacific Sardine | *Sardinops sagax* | A | 9.4 | **17.7** | 16.7 | 16.1 | 15.5 |
| Slender Sole | *Lyopsetta exilis* | Y | 7.0 | 12.3 | **19.2** | 12.4 | 15.3 |
| Pacific Sanddab | *Citharichthys sordidus* | A | 1.2 | 12.8 | **20.4** | 8.8 | 14.5 |
| Barracudina | Paralepididae | U | 23.4 | 8.6 | 8.1 | **33.7** | 14.3 |
| Flatfish, Right Eye | Pleuronectidae | Y | 1.6 | 5.4 | 16.9 | **23.3** | 13.6 |
| King-Of-The-Salmon | *Trachipterus altivelis* | U | 16.0 | **22.5** | 11.0 | 6.2 | 12.7 |
| Pacific Hake | *Merluccius productus* | A | 4.1 | 5.4 | 14.6 | **15.0** | 11.7 |
| Lingcod | *Ophiodon elongatus* | Y | 2.5 | 4.8 | **16.9** | 8.3 | 11.7 |

of 10 m off the observed bottom depth or 500 m (some 1000 m casts have been conducted over time), with fluorometry data collection initiated in 1997 and oxygen data collection initiated in 2007. In 2011 no daytime CTD stations were sampled due to vessel and logistic constraints and no casts were done in the south region. In addition, in 2012 no CTDs were done in the north central region due to inclement weather. Similar to the trawl data, the north region CTDs are not included in our current study due to the limited temporal coverage.

## Analysis

The mean CTD temperature, salinity, and density at 30 m depth (between 25 and 35 m, i.e., the target depth sampled by the midwater trawl) for each year were estimated for the four regions (south = 2004–10 and 2012–15, south central = 2004–10 and 2012–15, core = 1991–2015, and north central = 2004–11 and 2013–15) as well as the mean depth of the 26.1 isopycnal. Only CTD stations that were consistently sampled every year within each region were used (see appendix 1 for the number of CTD casts by year and region).

Catch data from currently active trawl stations from the four survey regions (south, south central, and north central from 2004–15 and core from 1990–2015) were transformed by ln (trawl catch + 1) and the mean catch for each year was then plotted for select species/species groups (see appendix 1 for the number of trawls completed by year and region). The species or taxa that occurred in at least 10% of trawls conducted in the expanded survey area from 2004–15 are also provided, with the percent occurrence within each of the four survey regions during this time period (table 1). With the exception of krill (identified to species starting in 2002), the species/taxa listed in Table 1 were also consistently enumerated within the core region from 1990–2015. The species/taxa from this shorter time series (2004–15) in the expanded survey area are comparable to the longer time series (1990–2012) reported by Ralston et al. (2015) for the core region. A complete list of all the species collected from the expanded survey area, and their percent occurrence by region, is also provided (appendix 2), and the original catch data are available online.[1]

[1]Data are served by the ERDDAP, website https://coastwatch.pfeg.noaa.gov/erddap/index.html. Data set is entitled "Rockfish Recruitment and Ecosystem Assessment Survey," metadata are also provided.

Similar to the analyses of Ralston et al. (2015) we conducted a community analysis using principal components analysis (PCA), a frequently used method of examining patterns of covariance within time series data in order to concentrate the variance in the dataset into a smaller number of more easily interpretable indices (see also Hare and Mantua 2002; Koslow et al. 2011 for comparable analyses). As we expanded the spatial coverage to include the regions outside of the core region (i.e., south, south central, and north central), the shorter time series necessitated a reduction in the number of taxa that could be included (the number of variables must typically be smaller than the number of years in a PCA) relative to the analyses in Ralston et al. (2015). Nine taxa were chosen based on a combination of the relative frequency of occurrence (as in Ralston et al. 2015) and their relative importance in the food web. Specifically, we selected taxa that were present in at least 10% of trawls in three of the four regions (and overall), as well as were included in the 20 most frequently encountered forage taxa described in a meta-analysis of food habits studies in the California Current (Szoboszlai et al. 2015). As in Ralston et al. (2015) we pooled all YOY rockfish into one taxon due to the previously described strong temporal co-variability. However, unlike Ralston et al. (2015) we did the same with the two commonly observed species of YOY sanddab, Pacific and speckled (*Citharichthys sordidus* and *C. stigmaeus*) as well as all species of myctophids (including the California headlightfish, *Diaphus theta*, and the blue lanternfish, *Tarletonbeania crenularis*) as they too tended to co-vary over the longer time period in the core region (Ralston et al. 2015, although see Koslow et al. 2011). Although krill were identified to species from 2002–15, we pooled all adult stages of krill into a common group, as in Ralston et al. (2015). The remaining taxa in this analysis were also represented in the Ralston et al. (2015) analysis and include market squid, YOY Pacific hake, adult northern anchovy, adult Pacific sardine, and octopus (*Octopoda*). This level of taxonomic resolution is also consistent with that reported by Szoboszlai et al. (2015).

We developed year-specific abundance estimates based on an analysis of variance (ANOVA) model applied to haul-specific log-transformed catch data, where year and station were estimated as the main effects, and the year effects were calculated from parameter estimates by averaging over station effects using a least-squares means approach (the R package lsmeans [R Core Team 2012]). This model-based approach accommodates unbalanced sampling, but is less than ideal if abundance patterns are strongly influenced by interactions between years and stations. However, as in Ralston et al. (2015), the two factor ANOVA models performed well for virtually all taxa, and the resulting trends were consistent with those developed by using the mean of the log catch rate alone. The results of the ANOVA were subsequently converted into standardized anomalies based on the mean and standard deviation of the year effects for each taxa and region, and the matrix of standardized values over time was analyzed using PCA (the R package princomp [R Core Team 2012]). The PCA subsequently provides a set of scores (or, principal components) that reflect descending fractions of the temporal variability of the original data set. The analysis also produces loadings (or eigenvectors) that reflect the weightings of each of the scores on any given input component (e.g., the input taxa), such that positive loadings reflect a positive correlation with a given score (or PC) and negative loadings reflect a negative correlation, and eigenvalues, which indicate the amount of variance explained by each score.

## RESULTS

### Hydrographic Data

Data collected from CTD casts between 1991–2015 in the core region showed warm, low salinity, low density water with a deep 26.1 isopycnal layer in 1992 and 1998 and cold, saline, dense water with a shallow 26.1 isopycnal layer in 1991, 1999, 2008, and 2012 (fig. 3). Data from the other regions starting in 2004 generally follow the same trend observed in the core region. However, after 2012, there was a general warming trend with decreased salinity and density and a deeper 26.1 isopycnal layer, with the exception of the north central region, which saw cooler, higher salinity, higher density water and the shallowest 26.1 isopycnal layer in that region's time series in 2015. Our data for 2015 is consistent with the observation that despite anomalously warm surface waters offshore, the above average upwelling indices recorded in the spring of 2015 led to near average temperature, salinity, and density at 30 m in the south central and core survey regions during May–June (see Leising et al. 2015). An anomalously deep 26.1 isopycnal was observed in the south, south central, and core regions from May–June 2015.

### Species Catch Trends

In general, the annual mean catches of YOY groundfish and market squid showed similar patterns across years (fig. 4). YOY rockfish, YOY Pacific hake, YOY sanddabs, and market squid abundances were low in most regions in 1998 and 2005–07, while catches were very high in 2013 and 2015. In the core region both YOY rockfish and YOY sanddabs had the highest catches observed in the 26-year time series in 2013 and 2015. However, while YOY rockfish and YOY Pacific hake abundances were low in 1992, 1995, and 2012, market squid catches were relatively high in those years, with the highest

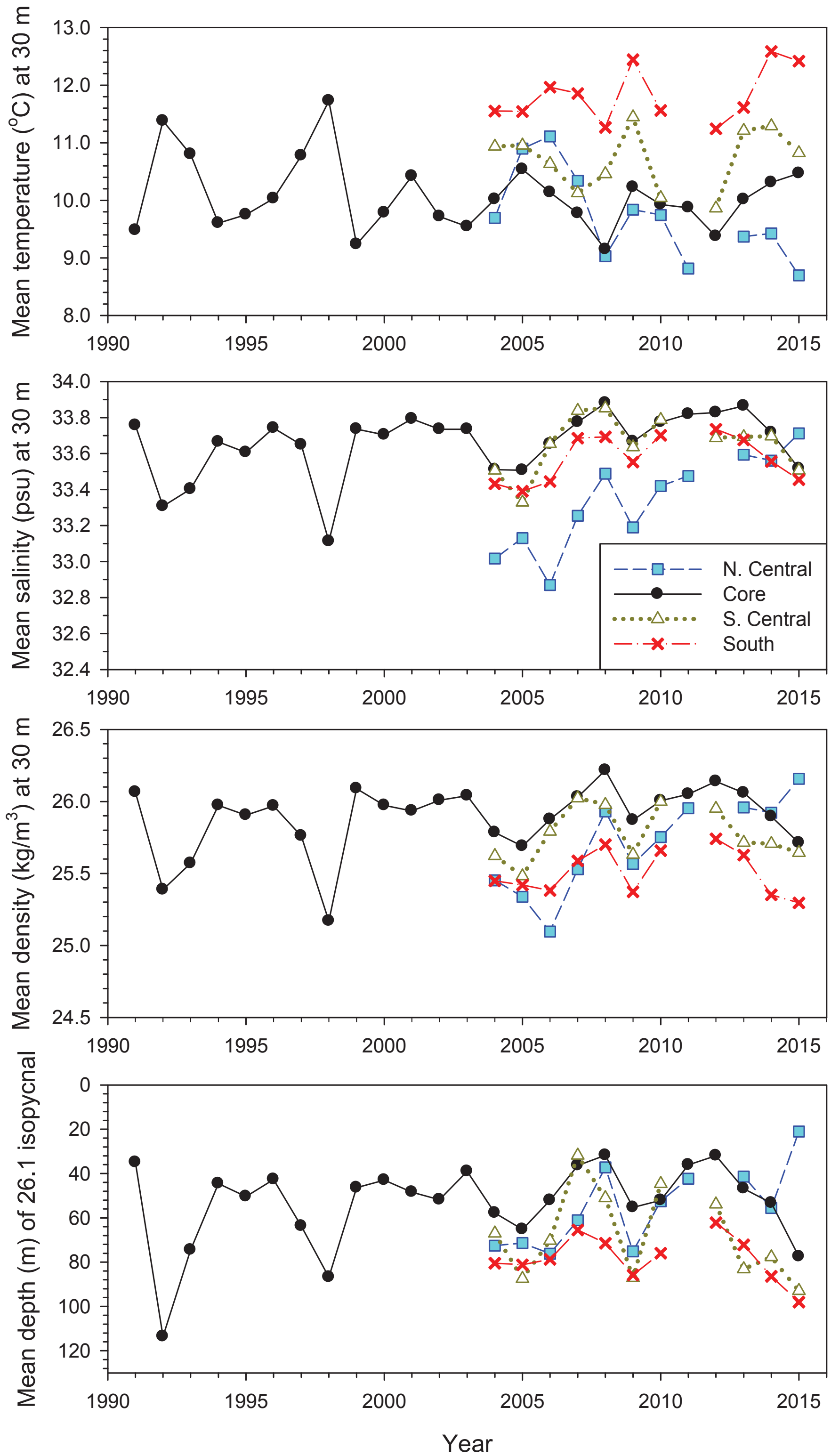


Figure 3. Annual mean temperature (°C), salinity (psu), and density (kg/m³) at 30 m depth and the mean depth of the 26.1 isopycnal from CTD data.

catch for market squid occurring in the south region in 2012. In addition, market squid were more abundant in 2014 than in 2013 and 2015 (although abundance was still relatively high in those years) and the highest catches of YOY sanddabs were observed in the south and south central regions in 2014. Patterns across regions generally showed similar trends although some region-specific differences were apparent for any given year. For

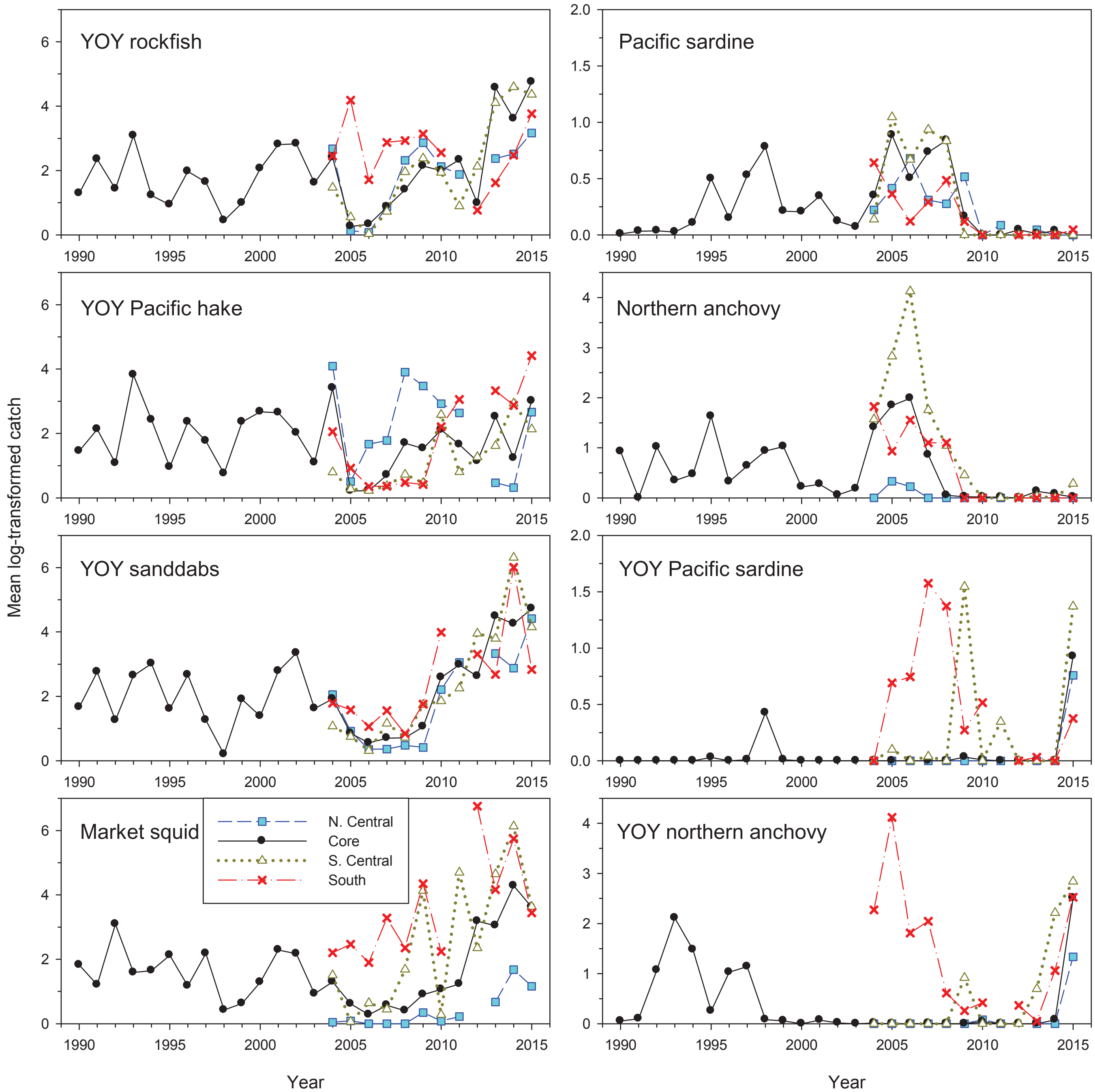


Figure 4. Annual means of log-transformed catches of YOY rockfish, YOY Pacific hake, YOY sanddabs, market squid, adult and YOY Pacific sardine, and adult and YOY northern anchovy from the south, south central, core, and north central regions.

example, YOY Pacific hake tended to have inverse catch trends between the southern (both south and south central) and north central regions in many years (with the core region catches typically falling between the two extremes), and YOY rockfish had very high catches in the core and south central regions in 2013, but relatively low catches in the south.

In contrast to the YOY groundfish, adult Pacific sardine and northern anchovy were abundant in 1995 and 2005–07, with catches declining dramatically beginning in 2010 and extending through 2015 (fig. 4). While the annual trends for YOY Pacific sardine and anchovy track those of the adults for most years, there was an increase in YOY northern anchovy in 2014 and record high catches of the YOY of both species in 2015 for the south central, core, and north central regions.

Myctophid catches in all regions were high in 2004–05 and 2009–10 (fig. 5). A dramatic drop in catches

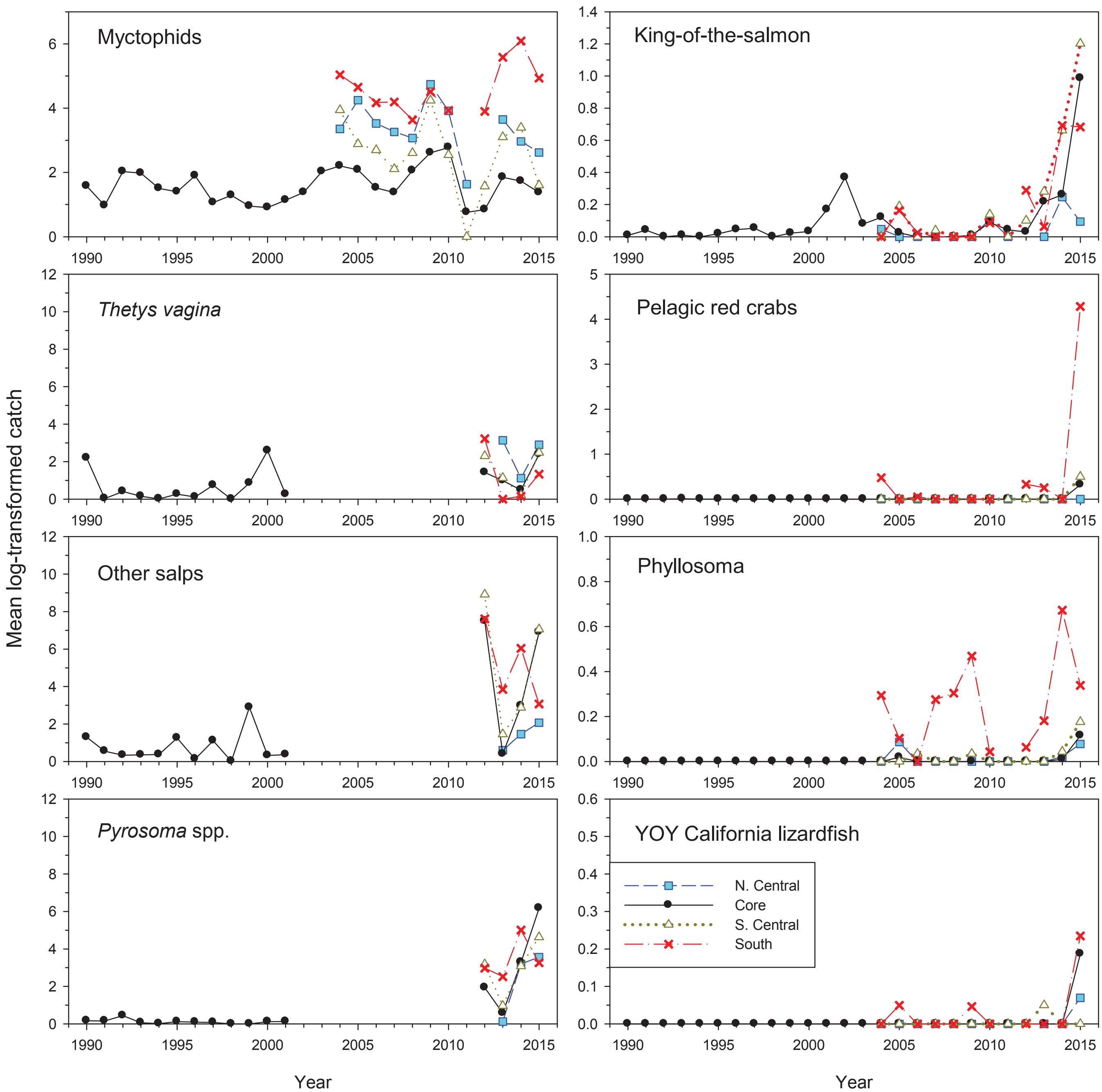


Figure 5. Annual means of log-transformed catches of myctophids, *Thetys vagina*, other salps, *Pyrosoma atlanticum*, king-of-the-salmon, pelagic red crabs, phyllosoma, and YOY California lizardfish from the south, south central, core, and north central regions.

occurred in 2011–12 with catches increasing somewhat in 2013. The highest catches were observed in the south region in 2014. Catches in all regions declined in 2015.

Catches of pelagic tunicates (salps and *Pyrosoma atlanticum*) were extraordinarily large in 2012 (which, as previously mentioned, led to damaged gear and the decision to resume counting them that year) (fig. 5, see also Wells et al. 2013). The unusually high salp biomass was also observed in both pelagic plankton samples and sediment trap collections in the offshore region of the Monterey Canyon (Smith et al. 2014). While in 2013 other salps and *Pyrosoma atlanticum* declined substantially from the 2012 levels, by 2015 their numbers were back up with the highest catches of *Pyrosoma* ever observed within the core region. Trends for the salp *Thetys vagina* were slightly different as large catches were observed in 1990 and 2000 within the core region. In addition, they were relatively abundant in the north central region in 2013 with decreased abundances in all regions in 2014. However, similar

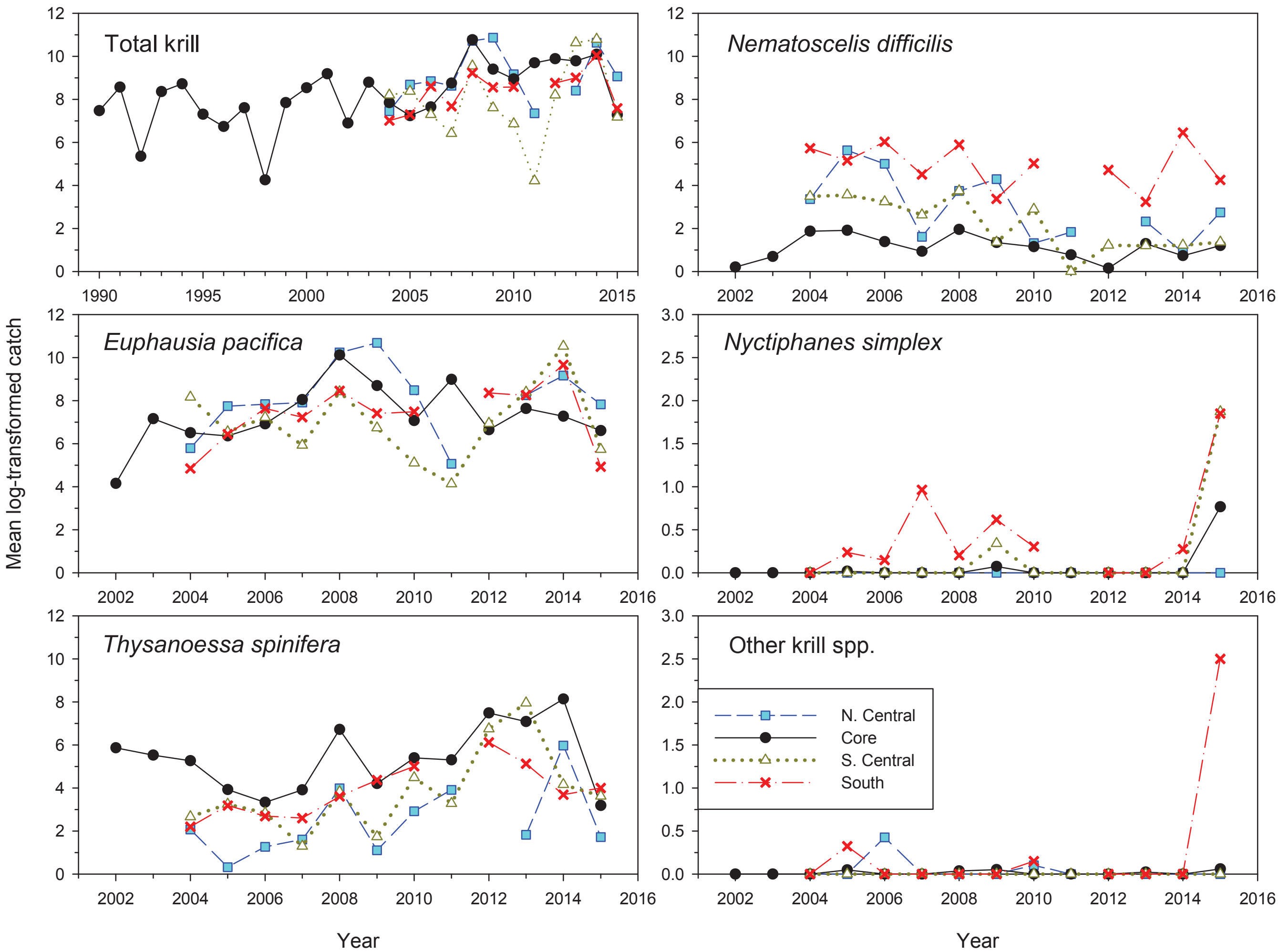


Figure 6. Annual means of log-transformed catches of total krill, *Euphausia pacifica*, *Thysanoessa spinifera*, *Nyctiphanes simplex*, *Nematoscelis difficilis*, and other krill species (species other than the previous four species) from the south, south central, core, and north central regions.

to the other gelatinous micronekton, catches of *Thetys vagina* increased in 2015.

Southerly distributed or offshore species with notable catches in 2015 in most (if not all) of the regions sampled in this survey included king-of-the-salmon (*Trachipterus altivelis*), pelagic red crabs, phyllosoma stage of California spiny lobster (*Panulirus interruptus*), and YOY California lizardfish (fig. 5). Also, the smalleye squaretail (*Tetragonurus cuvieri*) was collected for only the third time (prior occurrences were in 1985 and 1988) with raw catches in 2015 being 2.7 times greater than all prior years combined (2015 n = 19, while 1985 and 1988 combined n = 7). In addition, the following species were collected for the first time ever in the survey: the greater argonaut (*Argonauta argo*, n = 4), the pelagic stingray (*Dasyatis violacea*, n = 1), the slender snipefish (*Macroramphosus gracilis*, n = 6), and YOY Pacific bonito (*Sarda chiliensis*, n = 3). However, all of these latter species were encountered in the southern stations sampled only since 2004, so the presence of these and other southerly distributed species may not be hugely anomalous relative to past warm events in this region.

Total krill abundance in the core region was highest in 2008 while the lowest catches were observed in 1992 and 1998 (fig. 6). Catches were also quite low in the north central and south central regions in 2011. While catches in all regions increased in 2014 there was a dramatic decrease in abundance in all regions in 2015. This decrease in total krill catch in 2015 is due to the decrease in catches of the two numerically dominant species *Euphausia pacifica* and *Thysanoessa spinifera*. In contrast, there was an increase in catches of the more southern species *Nyctiphanes simplex* in 2015 with the highest catches ever observed in the south, south central, and core regions. There was also a large increase in other (typically rare) krill catches in the south region comprised mostly of the warm water species *Euphausia eximia*, which had not previously been collected by this survey, but are widely acknowledged to be a subtropical species based on historical plankton sampling (Brinton

TABLE 2
**Principal component scores and variance explained by region.**

| | South | | South Central | | Core | | North Central | |
|---|---|---|---|---|---|---|---|---|
| | PC1 | PC2 | PC1 | PC2 | PC1 | PC2 | PC1 | PC2 |
| 2004 | 3.06 | –0.19 | 1.13 | –0.37 | 0.38 | –1.98 | 0.26 | 1.91 |
| 2005 | 2.94 | –1.76 | 3.03 | –0.99 | 3.7 | –0.71 | 2.66 | –1.32 |
| 2006 | 1.96 | 1.77 | 3.01 | –0.74 | 3.28 | –0.5 | 2.88 | –1.08 |
| 2007 | 1.02 | 0.03 | 2.35 | –0.03 | 2.27 | 0.66 | 1.46 | 0.04 |
| 2008 | 0.97 | 1.37 | 0.41 | –0.83 | 1.08 | 1.29 | 0.53 | 0.83 |
| 2009 | –0.87 | 0.04 | –0.75 | –1.01 | 0 | –0.11 | 0.47 | –0.67 |
| 2010 | –0.71 | 0.14 | –0.02 | 1.1 | –0.86 | –0.56 | –0.57 | –0.1 |
| 2011 | n/a | n/a | 0.65 | 2.33 | –0.6 | 1.39 | –0.15 | 2.06 |
| 2012 | –1.79 | 1.5 | –0.46 | 1.26 | –0.59 | 1.79 | n/a | n/a |
| 2013 | –2.21 | 0.12 | –2.94 | –0.93 | –2.93 | –0.42 | –1.68 | –0.66 |
| 2014 | –3.65 | –0.69 | –4.27 | –1.02 | –2.75 | 0.52 | –3.42 | –2.69 |
| 2015 | –0.66 | –2.29 | –2.06 | 1.29 | –2.91 | –1.3 | –2.38 | 1.72 |
| Variance explained | 52% | 18% | 58% | 15% | 58% | 15% | 43% | 25% |

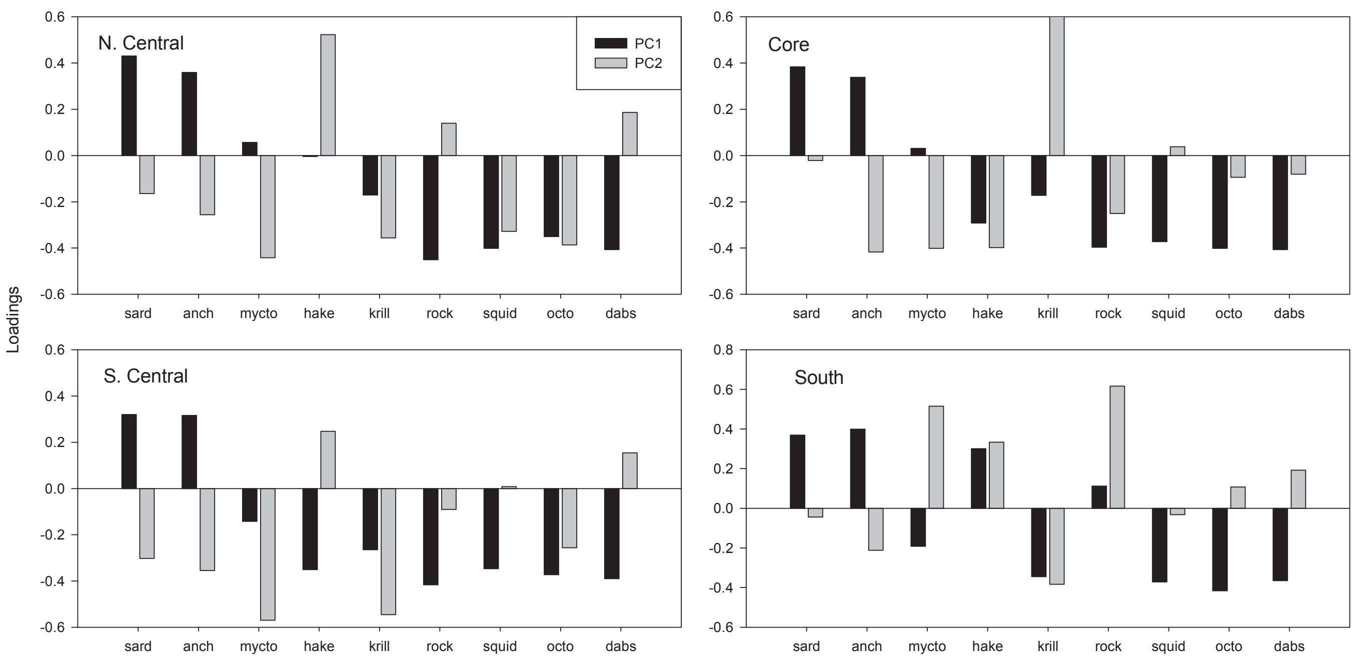


Figure 7. Loadings on PC1 and PC2 by taxa and region for the short (2004–15) time series. The order (from left to right) is determined by the average loading value across all four regions for each species or taxonomic group. Taxa abbreviations: Pacific sardine = sard, northern anchovy = anch, myctophid = mycto, YOY Pacific hake = hake, YOY rockfish = rock, market squid = squid, octopus = octo, and YOY sanddabs = dabs.

and Townsend 2003).

**Principal Components Analysis**

The results of the PCA were comparable to those originally reported by Ralston et al. (2015), with the first principal component (PC1) explaining between 43% and 58% of the variability for any given region, and the second principal component (PC2) explaining between 15% and 25% (table 2). The patterns in the loadings were generally comparable to the Ralston et al. (2015) analysis (where the species included overlapped), and these patterns are shown by region (fig. 7). In general, coastal pelagic species (Pacific sardine and northern anchovy) loaded on the opposite signs as YOY rockfish, YOY sanddabs, market squid, octopus, and krill. Myctophids and Pacific hake did not consistently load with either of these groups, often loading weakly with the first PC (e.g., Pacific hake in the north central region, myctophids in the north central and core region) or alternating between strong positive or negative loading. Interestingly, YOY rockfish and YOY Pacific hake in the southern region loaded with the coastal pelagic species, while myctophids loaded with krill, market squid, octopus, and sanddabs. In the core and south central regions all of the YOY groundfish loaded strongly with the cephalopods and krill.

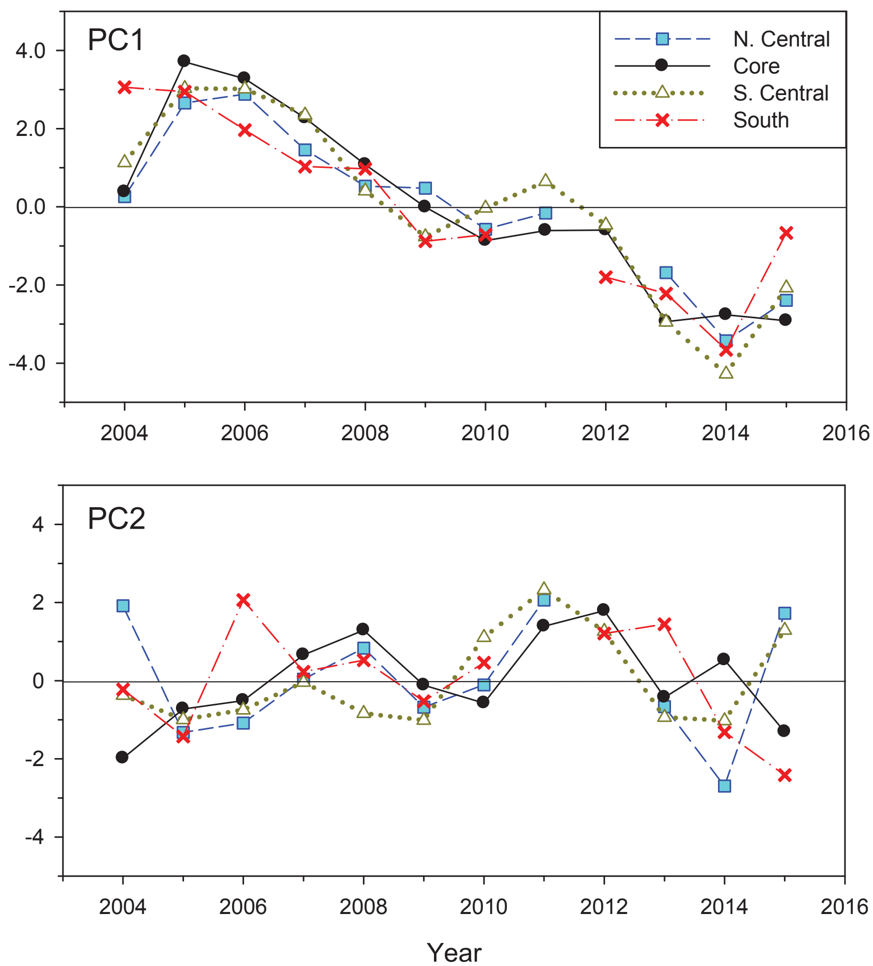


Figure 8. Time series of PCs 1 and 2 by region for the short (2004–15) time series.

This suggests little or no consistency in the relative abundance of YOY Pacific hake or myctophids across space, in contrast to the abundance of most of the other groups in this analysis. Unlike the loadings of PC1, loadings on PC2 did not follow a consistent pattern across space, and loadings tended to be greater for those species that did not load heavily on PC1, such as myctophids, YOY Pacific hake, and krill, and these tended to not show covariation in the loading patterns across space. For example, YOY Pacific hake did not load significantly on PC1 in the north central region, but had the highest loadings of all taxa on PC2 in that region, while similar patterns were seen for krill in the core region and myctophids in the south central region.

Despite some differences in the trends of various species across space, and some modest, but nontrivial differences in the loadings across space, PC1s in all four regions were highly correlated and followed a strongly consistent pattern (fig. 8). There was an increase in values between 2004 and 2005, a declining trend through 2014, and then a small uptick in most regions in 2015. The 2013–15 period varied substantially from the previous (2004–12) period for all regions in PC1, although these years all had mixed trends for PC2. Moreover, all four of the PC1s were strongly and significantly correlated with one another (correlation coefficients ranged from 0.81 to 0.96, table 3), indicating that the micronekton communities in all of these regions were generally responding to similar forcing mechanisms, although the effects may be realized in slightly different manifestations (e.g., different loadings, reflecting differences in regional abundances) depending on the region. PC2s

TABLE 3
**Correlation Coefficients for PCs 1 and 2 by region**

| PC1 | South | South Central | Core | North Central |
|---|---|---|---|---|
| South | 1 | | | |
| South Central | 0.889 | 1 | | |
| Core | 0.815 | 0.935 | 1 | |
| North Central | 0.831 | 0.950 | 0.965 | 1 |
| **PC2** | **South** | **South Central** | **Core** | **North Central** |
| South | 1 | | | |
| South Central | –0.079 | 1 | | |
| Core | 0.338 | 0.262 | 1 | |
| North Central | –0.106 | 0.668 | –0.100 | 1 |

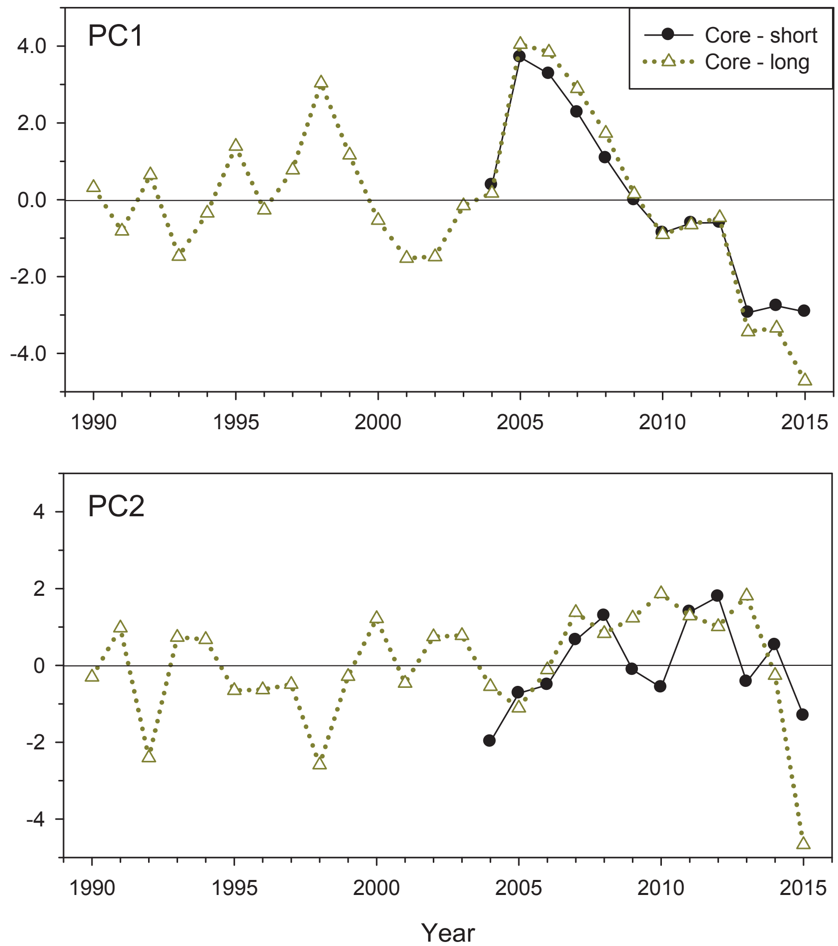


Figure 9. Comparison of short (2004–15) to long (1990–2015) time series in the consistently sampled core (central California) region.

for each region did not appear to track each other consistently over time, although the core and south central PC2s were well correlated, suggesting either that different processes are driving the patterns reflected in the south and north central time series, or that collectively the time series are too short to interpret the patterns in the second PCs in a comprehensive manner.

Extending the analysis for the core region over the entire duration of the time series (1990–2015), as an extension of the Ralston et al. (2015) analysis provided a result consistent with the shorter-term trend for this region. This indicates that the relationships among the different groups are coherent over longer time scales (fig. 9). More importantly, the extended time series in the core region reveals the extent to which 2015 is highly anomalous relative to the preceding 25 years. Specifically, the lowest score in the 26-year time series occurs in 2015 for both PC1 and PC2, demonstrating that even when considering only a small subset of the epipelagic micronekton community, the community structure in 2015 is highly anomalous.

Phase plots of the first and second PCs by region (fig. 10) illustrate that the trends in the second PCs are less consistent across space than those of the first PCs, and the unusual nature of the past three years as strongly separated from past "low productivity" periods (2005–06). Note that the core region plot includes the longer (1990–2015) time period, which emphasizes the unusual community structure observed in recent years. Due to autocorrelation in both these results and in most climate indices, a meaningful evaluation of the relationship to climate forcing is beyond the scope of this analysis.

## DISCUSSION

A number of analyses have reported on the unusual atmospheric and oceanographic conditions within the northeast Pacific and the California Current in the 2013–15 time period (Bond et al. 2015; Leising et al. 2015; Zaba and Rudnick 2016; Di Lorenzo and Mantua 2016; Jacox et al. 2016). Our results are consistent in documenting the unusual nature of this event from the perspective of the epipelagic micronekton community off of California, for which the survey catches were unusual, even in the context of past warm periods. As described

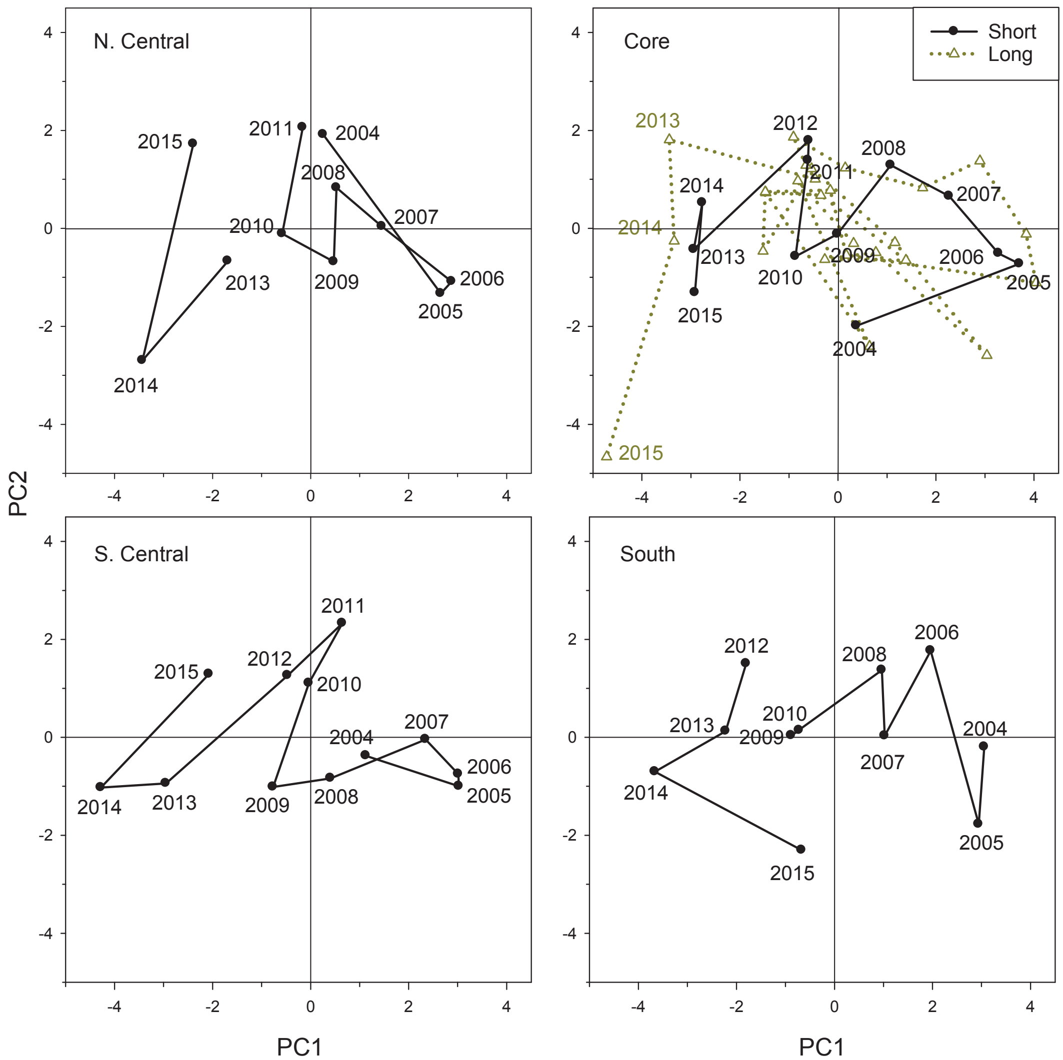


Figure 10. Phase plots of PC1 (horizontal axis) against PC2 (vertical axis) by region of the short (2004–15) time series. For the core region, the long (1990–2015) time series is also shown.

in the introduction, offshore SSTs in the northeastern Pacific were considerably warmer than average during the spring and summer of 2015, despite the fact that above average upwelling winds kept coastal SSTs closer to long-term mean levels above 33˚N during the time period of our survey (fig. 1). Our concurrent CTD sampling showed cool temperatures and a shallow 26.1 isopycnal in the north central region indicative of ongoing coastal upwelling (fig. 3). In contrast, in the other regions of the survey, temperatures were fairly warm with a deep 26.1 isopycnal. These time series from the expanded survey area are relatively short (12 years) and other evaluations of long-term subsurface conditions could be better made with longer term oceanographic data sets (such as CalCOFI). Of particular interest to this analysis is that the abundance of many forage species (YOY groundfish, krill, market squid, and mesopelagic fishes) ranged from average to record high levels during this warm event, unusual relative to the response from past warm events (figs. 4–6). In contrast, adult coastal pelagic species (Pacific sardine and northern anchovy) remained at very low levels (similar to those observed over the past 5–6 years), although high catches of the YOY of both species were widely observed throughout the survey area (fig. 4). These trends are consistent with those observed in the stock assessment for Pacific sardine (Hill et al. 2015) as well as analyses of relative abundance trends of northern anchovy based on CalCOFI data (Fissel et al. 2011; MacCall et al. 2016).

The PCA results showed that trends in relative abundance of the most frequently encountered micronekton species were very consistent over the spatial scale of this survey, indicating that the ocean forcing was acting over a fairly broad scale of 500–1000 km. However, north of Cape Mendocino, catches of YOY rockfish and other groundfish were at very low levels in both 2014 and 2015 (Leising et al. 2015), suggesting that the biological impacts of these anomalous conditions are heterogeneous over still broader spatial scales. This is likely a function of the major promontories that represent different oceanographic and biogeographic regions, such as Point Conception and Cape Mendocino (Checkley and Barth 2009; Gottscho 2016). While all of the PCAs indicated that the 2013–15 period was anomalous relative to the years that preceded, the PCA for the core region for the longer time series (1990–2015) clearly demonstrated just how unusual the community structure was in 2015 relative to historical patterns. For both PCs the scores were essentially unprecedented in the history of the survey, even before considering the multitude of taxa that were not included in this relatively narrow representation of the epipelagic micronekton community.

The abundance of numerous southern, warm water species is typically considered to be an indicator of strong El Niño-driven warm events off the West Coast of the United States. In 2015, we observed record high numbers of pelagic red crabs, California spiny lobster phyllosoma, California lizardfish, and the largely subtropical krill *Nyctiphanes simplex* (figs. 5–6). Pelagic red crabs are widely recognized to be a classic El Niño signature species, typically confined to upwelling regions and coastal areas off Baja California (Longhurst 1967). Similarly, California spiny lobster phyllosoma have been described as associated with all varieties of warm events, from El Niño to positive phases of the Pacific Decadal Oscillation (PDO) (Koslow et al. 2012). California lizardfish are considered relatively common throughout the Southern California Bight and rare north of Point Conception, but were found throughout the West Coast during the 1982–83 El Niño (Pearcy et al. 1985; Lea and Rosenblatt 2000), and in 2015 they were observed at very high abundances (relative to this time series) throughout the survey area. *Nyctiphanes simplex* also normally occur south of Point Conception, but its distribution can extend much further northward with increased abundances observed during El Niño years (Marinovic et al. 2002; Brinton and Townsend 2003). Additionally, subtropical and tropical species such as the greater argonaut, slender snipefish, YOY Pacific bonito, and the krill *Euphausia eximia* were recorded for the first time in the survey in 2015, although all of these were encountered only in the southern survey region.

The particularly unusual aspect about 2015 is that these warm, El Niño indicator species have historically been present when most other micronekton species (YOY groundfish, market squid, the coastal krill *Thysanoessa spinifera*) are at low abundance levels. For example 1983, 1992, 1998, and 2005–06 were anomalously warm, low productivity years throughout the northern California Current associated with low numbers of YOY groundfish, market squid, and krill (Lenarz et al. 1995; Brodeur et al. 2006; Ralston et al. 2013, 2015). By contrast, YOY rockfish numbers in 2015 were the highest ever observed in the 33-year history of this time series (fig. 4), and numbers of other forage species typically associated with high-transport, high productivity conditions (such as YOY sanddabs, YOY Pacific hake, and market squid) were also at above average to very high levels. Simultaneously, the abundance of gelatinous zooplankton (primarily pelagic tunicates, such as salps and *Pyromosa atlanticum*, but also including pelagic mollusks) (fig. 5) continued to be sustained at high numbers (albeit from an interrupted time series). This gelatinous zooplankton assemblage is widely acknowledged to have the potential for substantial impacts on the productivity and energy flow of pelagic ecosystems by virtue of their extraordinarily high growth potential (Silver 1975) and the intense grazing pressure exhibited during periods of high abundance (Lavaniegos and Ohman 2007). The high abundance of pelagic tunicates could have also been a contributing factor to the ongoing record numbers of king-of-the-salmon (fig. 5), which are known to prey on the salp-associated hyperiid amphipod *Phronima* (Shenker 1983) that was also observed at high abundance in 2015. Although *Phronima* abundance data only exist from an interrupted time series (1990–2001 and 2015), the 2015 abundance was nearly an order of magnitude greater than in any previous year. The smalleye squaretail is also considered to be a salp-associated species (Janssen and Harbison 1981) and in 2015 we observed the highest catches in the 33-year history of the survey. While there were indications in 2012 that the high abundance of salps in the California Current were in part seeded from northern regions (Wells et al. 2013), the species composition and sources of the high abundances of salps in the California Current in 2015 is unclear.

The micronekton community structure in the late spring of 2015 was highly unusual in that species characteristic of all three of what might very generally be considered nominal states (YOY groundfish/market squid and krill dominated catches, subtropical species dominated catches, and pelagic tunicate dominated catches) were encountered in high abundance throughout the survey area. Ongoing efforts to develop diversity indices (such as species richness and evenness) are consistent with the observations that 2015 included extraordinarily high levels of taxonomic diversity.[2] The extent to which this event is truly unprecedented with respect to long-term variability is unclear. The relative "normality" of ocean conditions during the time of the survey was clearly indicative of only localized conditions (strong upwelling during a period of otherwise warm ocean

[2]Biodiversity of pelagic fish reflects unprecedented climate variability in the California Current. Unpublished manuscript (in preparation). J. A. Santora, E. L. Hazen, I. D. Schroeder, S. J. Bograd, K. Sakuma, and J. C. Field.

conditions) during a year in which large scale climate and ocean conditions were highly anomalous (Bond et al. 2015; Leising et al. 2015; Di Lorenzo and Mantua 2016; Jacox et al. 2016). The future of upwelling under climate change scenarios has been extensively evaluated, but most projections are considered to be highly uncertain due to a number of factors, which includes the expectation of high spatial heterogeneity in mesoscale physical characteristics and processes (Bakun et al. 2015; Garcia-Reyes et al. 2015). Given this consideration, the observation that the micronekton community seems to be responding to a highly consistent signal over the scale of approximately eight degrees of latitude (albeit over a relatively short time frame) is also of some interest. One global climate model prediction that may be somewhat more robust is the expectation for a northward shift in the distribution of upwelling centers (Rykaczewski et al. 2015), and in this scenario, the unusual abundance patterns observed in 2015 could be indicative of the expected types of response in the micronekton community, in which unusual transport patterns and mixing of water masses lead to a more heterogeneous mix in the micronekton assemblage.

Although it is too early to fully assess the potential impacts on a broad suite of higher trophic level predators, levels of seabird productivity (breeding success) at the Southeast Farallon Islands (shown in Santora et al. 2014 and references therein) link closely to the pelagic forage assemblage sampled by our survey and indicate average to above average levels of productivity for most seabird species in spring 2015 (Leising et al. 2015). However, this observation is limited to fledging chicks rather than the longer-term productivity of the populations. Given that the summer and fall of 2015 continued to demonstrate considerably warm and unusual ocean conditions, the longer term impacts may take considerable time to fully understand.

We recognize that our data and analysis on the expanded survey area off California are not necessarily representative of the entire extent of the California Current. Comparable surveys to ours (initially focused on sampling YOY Pacific hake) have also been conducted off Oregon and Washington by a collaborative effort between the Northwest Fisheries Science Center (NWFSC) and the Pacific Whiting Conservation Cooperative (PWCC) from 2001–09 (described in Sakuma et al. 2006), and in 2011, 2013–15 by the NWFSC (R. Brodeur, pers. com.). While differences in time period and taxonomic resolution of catches exist, incorporating the data of all of these surveys (likely on a limited set of species) could better resolve mesoscale abundance, distribution, and species assemblage patterns and how these communities respond to both local and large-scale forcing within the California Current off the entire West Coast.

The assemblage of epipelagic micronekton in our study represents some of the most important prey species for a broad suite of higher trophic level predators in the California Current ecosystem (Ainley and Boekelheide 1990; Wells et al. 2012; Thayer et al. 2014; Fleming et al. 2015; McClatchie et al. 2016; Szoboszlai et al. 2015; Ainley et al. 2015). Consequently, tracking the relative abundance, distribution, and forcing factors related to the productivity of this assemblage represents a key step towards quantifying prey availability and predator responses in a manner that would improve both resource management decisions and our understanding of the longer term impacts of climate variability and climate change on the California Current ecosystem.

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APPENDIX 1

**Number of standard station trawls and CTDs by year and region used in the current study. Note that additional nonstandard trawls and CTDs were conducted in most years, but these were not used in the analyses and therefore not listed. No trawls or CTDs were conducted in the south region in 2011 due to vessel/logistic constraints and none were conducted in the north central region in 2012 due to inclement weather. In addition, due to vessel/logistic constraints, no daytime CTD stations were sampled in 2011 thereby reducing the number of CTD stations consistently sampled across years to only those conducted at nighttime trawls stations.**

| | Trawls | | | | CTDs | | | |
|---|---|---|---|---|---|---|---|---|
| Year | South | South Central | Core | North Central | South | South Central | Core | North Central |
| 1990 | | | 80 | | | | | |
| 1991 | | | 93 | | | | 66 | |
| 1992 | | | 73 | | | | 56 | |
| 1993 | | | 75 | | | | 51 | |
| 1994 | | | 75 | | | | 45 | |
| 1995 | | | 74 | | | | 47 | |
| 1996 | | | 76 | | | | 48 | |
| 1997 | | | 74 | | | | 47 | |
| 1998 | | | 79 | | | | 50 | |
| 1999 | | | 77 | | | | 53 | |
| 2000 | | | 84 | | | | 54 | |
| 2001 | | | 78 | | | | 52 | |
| 2002 | | | 65 | | | | 41 | |
| 2003 | | | 86 | | | | 48 | |
| 2004 | 19 | 5 | 76 | 15 | 13 | 2 | 47 | 2 |
| 2005 | 28 | 11 | 73 | 16 | 17 | 4 | 46 | 2 |
| 2006 | 28 | 20 | 63 | 27 | 16 | 4 | 36 | 3 |
| 2007 | 26 | 18 | 82 | 24 | 15 | 4 | 44 | 3 |
| 2008 | 30 | 22 | 31 | 10 | 15 | 6 | 30 | 2 |
| 2009 | 15 | 20 | 72 | 12 | 9 | 4 | 48 | 2 |
| 2010 | 16 | 5 | 74 | 23 | 10 | 2 | 46 | 4 |
| 2011 | | 2 | 48 | 8 | | | 33 | 2 |
| 2012 | 11 | 11 | 58 | | 11 | 2 | 50 | |
| 2013 | 22 | 22 | 60 | 16 | 14 | 4 | 37 | 3 |
| 2014 | 14 | 25 | 66 | 22 | 9 | 6 | 41 | 4 |
| 2015 | 35 | 26 | 64 | 20 | 20 | 5 | 36 | 3 |

APPENDIX 2

**Species/taxa occurring in the expanded survey area (All Areas) from 2004–15 listed in decreasing order of occurrence. The percent occurrence within each of the four survey regions is also shown. For Ontogeny, Y = young-of-the-year, A = age 1 +, and U = undetermined. With the exception of krill, Years = ALL, denotes species/taxa that were also consistently enumerated in the core region since 1990 (data not shown). Krill have an * as species specific enumeration began in 2002 with only total krill numbers (i.e., no species specific counts) available from 1990–2001 (data not shown). For species/taxa not consistently enumerated from 2004–15, the years in which they were enumerated are listed in the Years column. Species/taxa with a ** were also enumerated from 1990–2001 (data not shown).**

| Common Name | Scientific Name | Ontogeny | Years | South | South Central | Core | North Central | All Areas |
|---|---|---|---|---|---|---|---|---|
| Krill | *Euphausia pacifica* | U | ALL* | 89.3 | 79.7 | 81.4 | 86.5 | 83.2 |
| Sanddab | *Citharichthys* spp. | Y | ALL | 81.6 | 79.1 | 79.3 | 72.5 | 78.7 |
| Rockfish | *Sebastes* spp. | Y | ALL | 81.6 | 73.8 | 73.9 | 68.4 | 74.5 |
| Pyrosoma | *Pyrosoma* spp. | U | 2012–15** | 87.8 | 79.8 | 65.4 | 60.3 | 71.1 |
| Salp | Salpidae | U | 2012–15** | 82.9 | 77.4 | 61.1 | 46.6 | 65.9 |
| Krill | *Thysanoessa spinifera* | U | ALL* | 61.1 | 55.6 | 70.9 | 35.2 | 62.4 |
| Phronima | *Phronima* spp. | U | 2015** | 45.7 | 96.2 | 57.6 | 55.0 | 61.2 |
| Market Squid | *Doryteuthis opalescens* | U | ALL | 84.4 | 65.2 | 51.2 | 17.1 | 54.1 |
| Myctophid | Myctophidae | U | ALL | 82.8 | 52.9 | 40.0 | 63.7 | 52.2 |
| Pacific Hake | *Merluccius productus* | Y | ALL | 50.0 | 42.8 | 53.8 | 57.0 | 52.1 |
| Thetys Salp | *Thetys vagina* | U | 2012–15** | 36.6 | 41.7 | 38.9 | 67.2 | 42.4 |
| Armhook Squid | *Gonatus* spp. | U | 2006–15 | 39.1 | 47.4 | 35.8 | 56.2 | 40.8 |
| Sergestid | Sergestidae | U | ALL | 57.0 | 38.0 | 32.3 | 54.4 | 40.3 |
| Octopus | Octopoda | U | ALL | 38.9 | 44.9 | 30.7 | 28.5 | 33.7 |
| Krill | *Nematoscelis difficilis* | U | ALL* | 71.7 | 35.3 | 19.6 | 39.9 | 33.3 |
| Squid | Teuthoidea | U | ALL | 47.5 | 28.9 | 22.4 | 42.0 | 30.2 |
| Blacktip Squid | *Abraliopsis felis* | U | 2006–15 | 57.4 | 25.7 | 16.7 | 52.5 | 29.8 |
| California Headlightfish | *Diaphus theta* | U | ALL | 34.0 | 29.4 | 22.6 | 52.9 | 29.5 |
| California Smoothtongue | *Leuroglossus stilbius* | U | ALL | 50.0 | 31.0 | 24.5 | 15.5 | 28.5 |
| Blue Lanternfish | *Tarletonbeania crenularis* | U | ALL | 15.2 | 36.4 | 23.1 | 57.5 | 28.1 |
| Deep-Sea Smelt | Bathylagidae | U | ALL | 37.3 | 19.3 | 17.7 | 48.7 | 25.5 |
| Goby | Gobiidae | U | ALL | 55.3 | 30.5 | 15.5 | 4.7 | 22.8 |
| Rex Sole | *Glyptocephalus zachirus* | Y | ALL | 5.3 | 12.8 | 25.1 | 28.0 | 20.5 |
| Northern Anchovy | *Engraulis mordax* | A | ALL | 17.2 | 28.9 | 20.6 | 2.6 | 18.7 |
| Northern Anchovy | *Engraulis mordax* | Y | ALL | 50.4 | 29.4 | 7.9 | 6.2 | 17.8 |
| Sword-Tail Squid | *Chiroteuthis calyx* | U | 2006–15 | 13.7 | 19.9 | 13.6 | 30.3 | 16.8 |
| Heteropod | Pterotracheoidea | U | 2012–15** | 43.9 | 17.9 | 8.2 | 12.1 | 16.4 |
| Pacific Sardine | *Sardinops sagax* | A | ALL | 9.4 | 17.7 | 16.7 | 16.1 | 15.5 |
| Slender Sole | *Lyopsetta exilis* | Y | ALL | 7.0 | 12.3 | 19.2 | 12.4 | 15.3 |
| Pacific Sanddab | *Citharichthys sordidus* | A | ALL | 1.2 | 12.8 | 20.4 | 8.8 | 14.5 |
| Barracudina | Paralepididae | U | ALL | 23.4 | 8.6 | 8.1 | 33.7 | 14.3 |
| Flatfish, Right Eye | Pleuronectidae | Y | ALL | 1.6 | 5.4 | 16.9 | 23.3 | 13.6 |
| King-Of-The-Salmon | *Trachipterus altivelis* | U | ALL | 16.0 | 22.5 | 11.0 | 6.2 | 12.7 |
| Boreal Clubhook Squid | *Onychoteuthis borealijaponica* | U | 2013–15 | 8.5 | 12.3 | 12.2 | 19.0 | 12.6 |
| Sea Nettle | *Chrysaora fuscescens* | U | 2005–15** | 0.0 | 0.8 | 21.5 | 2.7 | 12.5 |
| Octopoteuthis | *Octopoteuthis deletron* | U | 2015 | 0.0 | 15.4 | 19.7 | 5.0 | 12.2 |
| California Lanternfish | *Symbolophorus californiensis* | U | 2005–15 | 24.5 | 14.3 | 6.7 | 18.0 | 12.2 |
| Pacific Hake | *Merluccius productus* | A | ALL | 4.1 | 5.4 | 14.6 | 15.0 | 11.7 |
| Lingcod | *Ophiodon elongatus* | Y | ALL | 2.5 | 4.8 | 16.9 | 8.3 | 11.7 |
| Dover Sole | *Microstomus pacificus* | Y | ALL | 5.3 | 10.2 | 10.9 | 11.4 | 9.9 |
| Pacific Sardine | *Sardinops sagax* | Y | ALL | 26.2 | 17.1 | 4.4 | 3.6 | 9.7 |
| Pacific Pompano | *Peprilus simillimus* | U | ALL | 13.5 | 15.0 | 9.1 | 0.5 | 9.5 |
| Turbot | *Pleuronichthys* spp. | Y | ALL | 2.9 | 18.7 | 7.9 | 10.9 | 8.8 |
| Moon Jelly | *Aurelia* spp. | U | 2005–15** | 2.1 | 10.5 | 10.6 | 2.7 | 8.2 |
| Medusafish | *Icichthys lockingtoni* | U | ALL | 6.2 | 13.9 | 6.1 | 11.4 | 7.9 |
| Combfish | Zaniolepididae | U | ALL | 6.6 | 8.0 | 9.7 | 1.0 | 7.8 |
| Blackdragon | Idiacanthidae | U | ALL | 15.6 | 7.5 | 4.0 | 6.7 | 6.8 |
| Sand Sole | *Psettichthys melanostictus* | Y | ALL | 0.0 | 3.2 | 8.7 | 8.3 | 6.5 |
| Plainfin Midshipman | *Porichthys notatus* | U | ALL | 0.4 | 13.9 | 6.5 | 1.6 | 5.8 |
| Jack Mackerel | *Trachurus symmetricus* | Y | ALL | 30.3 | 3.7 | 0.0 | 0.0 | 5.7 |
| Fried Egg Jellyfish | *Phacellophora camtschatica* | U | 2009–15 | 1.8 | 8.1 | 6.3 | 3.0 | 5.5 |
| Glass Shrimp | *Pasiphaea pacifica* | U | ALL | 8.2 | 8.0 | 4.9 | 1.0 | 5.3 |
| Longfin Dragonfish | *Tactostoma macropus* | U | ALL | 1.2 | 5.4 | 5.0 | 11.9 | 5.3 |
| Painted Greenling | *Oxylebius pictus* | Y | ALL | 8.2 | 10.7 | 3.8 | 0.5 | 5.0 |
| Spiny Lobster Larvae | Palinuridae | U | ALL | 20.1 | 3.7 | 1.1 | 2.6 | 4.9 |
| Cabezon | *Scorpaenichthys marmoratus* | Y | ALL | 3.3 | 8.0 | 4.6 | 4.7 | 4.8 |
| Pacific Argentine | *Argentina sialis* | U | ALL | 4.9 | 4.8 | 5.6 | 0.0 | 4.6 |
| Blackbelly Dragonfish | *Stomias atriventer* | U | ALL | 23.8 | 1.1 | 0.3 | 0.0 | 4.4 |
| Fish | Pisces | Y | ALL | 8.2 | 4.8 | 2.8 | 4.7 | 4.2 |

(*continued*)

APPENDIX 2, continued

**Species/taxa occurring in the expanded survey area (All Areas) from 2004–15 listed in decreasing order of occurrence. The percent occurrence within each of the four survey regions is also shown. For Ontogeny, Y = young-of-the-year, A = age 1 +, and U = undetermined. With the exception of krill, Years = ALL, denotes species/taxa that were also consistently enumerated in the core region since 1990 (data not shown). Krill have an * as species specific enumeration began in 2002 with only total krill numbers (i.e., no species specific counts) available from 1990–2001 (data not shown). For species/taxa not consistently enumerated from 2004–15, the years in which they were enumerated are listed in the Years column. Species/taxa with a ** were also enumerated from 1990–2001 (data not shown).**

| Common Name | Scientific Name | Ontogeny | Years | South | South Central | Core | North Central | All Areas |
|---|---|---|---|---|---|---|---|---|
| Pelagic Red Crab | *Pleuroncodes planipes* | U | ALL | 17.2 | 3.2 | 1.5 | 0.0 | 4.2 |
| Sculpin | Cottidae | Y | ALL | 0.4 | 2.7 | 5.4 | 5.2 | 4.1 |
| Loosejaw | Malacosteidae | U | ALL | 9.4 | 5.4 | 1.8 | 6.2 | 4.1 |
| Pacific Electric Ray | *Torpedo californica* | U | ALL | 1.2 | 2.7 | 6.0 | 0.5 | 4.0 |
| Pipefish | Syngnathidae | U | ALL | 8.6 | 10.7 | 1.9 | 0.0 | 3.9 |
| Crangon Shrimp | *Crangon* spp. | U | ALL | 0.0 | 0.5 | 5.0 | 7.3 | 3.9 |
| Ronquil | Bathymasteridae | U | ALL | 5.7 | 5.0 | 0.5 | 0.8 | 3.8 |
| Krill | *Nyctiphanes simplex* | U | ALL* | 11.1 | 6.4 | 1.8 | 0.0 | 3.7 |
| Slender Sole | *Lyopsetta exilis* | A | ALL | 1.6 | 1.6 | 4.5 | 3.1 | 3.4 |
| Pandalid Shrimp | *Pandalus jordani* | U | ALL | 0.8 | 0.0 | 3.8 | 7.8 | 3.3 |
| Snailfish | Liparidae | U | ALL | 0.4 | 0.0 | 3.3 | 9.8 | 3.2 |
| Pacific Tomcod | *Microgadus proximus* | Y | ALL | 0.0 | 0.0 | 3.9 | 3.1 | 2.6 |
| Smelt | Osmeridae | A | ALL | 0.0 | 0.0 | 2.9 | 6.2 | 2.5 |
| North Pacific Spiny Dogfish | *Squalus suckleyi* | U | ALL | 0.0 | 2.7 | 3.5 | 1.0 | 2.5 |
| Wolf-Eel | *Anarrhichthys ocellatus* | Y | ALL | 2.5 | 3.2 | 2.4 | 1.0 | 2.3 |
| Highfin Dragonfish | *Bathophilus flemingi* | U | ALL | 1.6 | 2.1 | 1.1 | 8.3 | 2.3 |
| Baseball Squid | *Cranchia scabra* | U | 2005–15 | 5.8 | 4.4 | 0.7 | 2.3 | 2.3 |
| Lightfish | Phosichthyidae | U | ALL | 9.0 | 2.1 | 0.5 | 0.5 | 2.2 |
| Fire Squid | Pyroteuthidae | U | 2008–15 | 11.9 | 0.8 | 0.2 | 0.0 | 2.2 |
| Blob Octopus | Alloposidae | U | 2006–15 | 9.6 | 1.2 | 0.6 | 0.0 | 2.1 |
| Pallid Eelpout | *Lycodapus mandibularis* | U | ALL | 1.6 | 0.5 | 3.1 | 0.0 | 2.1 |
| Mantis Shrimp | Stomatopoda | U | 2009–15 | 14.2 | 0.0 | 0.0 | 0.0 | 2.0 |
| Poacher | Agonidae | U | ALL | 0.4 | 2.7 | 2.5 | 1.0 | 2.0 |
| Shrimp | Natantia | U | ALL | 2.1 | 6.4 | 1.1 | 0.0 | 1.8 |
| Leptocephalus | Elopomorpha | Y | ALL | 5.7 | 0.5 | 0.5 | 3.1 | 1.8 |
| Purple-Striped Jelly | *Chrysaora colorata* | U | 2005–15** | 0.7 | 3.0 | 2.0 | 0.0 | 1.7 |
| Greenling | Hexagrammidae | Y | ALL | 4.1 | 0.5 | 1.3 | 1.0 | 1.6 |
| Humboldt Squid | *Dosidicus gigas* | U | 2005–15 | 0.0 | 1.7 | 1.3 | 4.5 | 1.5 |
| Pacific Mackerel | *Scomber japonicus* | A | ALL | 0.4 | 1.1 | 1.8 | 2.1 | 1.5 |
| Irish Lord | *Hemilepidotus* spp. | Y | ALL | 0.0 | 0.0 | 1.8 | 2.6 | 1.3 |
| Krill | *Euphausia eximia* | U | ALL* | 7.0 | 0.0 | 0.1 | 0.0 | 1.3 |
| King Salmon | *Oncorhynchus tshawytscha* | Y | ALL | 0.0 | 0.0 | 2.1 | 0.0 | 1.2 |
| California Lizardfish | *Synodus lucioceps* | U | ALL | 2.5 | 0.5 | 1.1 | 0.5 | 1.2 |
| Jack Mackerel | *Trachurus symmetricus* | A | ALL | 0.8 | 3.2 | 0.9 | 0.5 | 1.1 |
| Arrowtooth Flounder | *Atheresthes stomias* | Y | ALL | 0.0 | 0.0 | 0.8 | 3.6 | 0.9 |
| Pacific Herring | *Clupea pallasii* | A | ALL | 0.0 | 0.0 | 1.0 | 2.6 | 0.9 |
| Lamprey | Petromyzontidae | U | ALL | 0.0 | 0.0 | 1.3 | 1.6 | 0.9 |
| Fish | Pisces | U | ALL | 2.5 | 0.5 | 0.8 | 0.0 | 0.9 |
| Pacific Sandlance | *Ammodytes hexapterus* | U | ALL | 0.0 | 0.0 | 1.1 | 1.6 | 0.8 |
| Jacksmelt | *Atherinopsis californiensis* | U | ALL | 0.0 | 0.0 | 1.5 | 0.0 | 0.8 |
| Red Shrimp | *Bentheogennema burkenroadi* | U | ALL | 2.5 | 1.1 | 0.4 | 0.5 | 0.8 |
| Sablefish | *Anoplopoma fimbria* | Y | ALL | 0.8 | 1.6 | 0.8 | 0.0 | 0.8 |
| King Salmon | *Oncorhynchus tshawytscha* | A | ALL | 0.0 | 0.0 | 1.4 | 0.0 | 0.8 |
| Smelt | Osmeridae | Y | ALL | 0.0 | 0.0 | 0.5 | 3.6 | 0.8 |
| English Sole | *Parophrys vetulus* | A | ALL | 0.0 | 0.0 | 1.1 | 0.5 | 0.7 |
| Pacific Mackerel | *Scomber japonicus* | Y | ALL | 3.7 | 0.0 | 0.0 | 0.0 | 0.6 |
| Smalleye Squaretail | *Tetragonurus cuvieri* | U | ALL | 2.1 | 1.1 | 0.3 | 0.0 | 0.6 |
| Eelpout | Zoarcidae | U | ALL | 0.8 | 1.1 | 0.4 | 1.0 | 0.6 |
| Ragfish | *Icosteus aenigmaticus* | U | ALL | 0.4 | 0.5 | 0.4 | 1.6 | 0.6 |
| Ronquil | Bathymasteridae | U | ALL | 0.4 | 0.0 | 0.4 | 1.6 | 0.5 |
| Krill | Euphausiacea | U | ALL | 0.8 | 1.1 | 0.3 | 0.5 | 0.5 |
| Robust Clubhook Squid | *Onykia robusta* | U | 2006–15 | 1.0 | 0.6 | 0.2 | 0.6 | 0.4 |
| Krill | *Euphausia gibboides* | U | ALL* | 2.1 | 0.0 | 0.0 | 0.5 | 0.4 |
| Mysid | Mysidacea | U | ALL | 0.0 | 0.0 | 0.8 | 0.0 | 0.4 |
| Ghost Shrimp | *Callianassa californiensis* | U | ALL | 0.0 | 0.0 | 0.5 | 0.5 | 0.4 |
| Bigscale | Melamphaidae | U | ALL | 1.2 | 0.5 | 0.0 | 0.5 | 0.4 |
| Common Mola | *Mola mola* | U | ALL | 0.0 | 1.6 | 0.3 | 0.0 | 0.4 |
| Spookfish | Opisthoproctidae | U | ALL | 0.0 | 0.5 | 0.3 | 1.0 | 0.4 |
| Starry Flounder | *Platichthys stellatus* | Y | ALL | 0.4 | 0.0 | 0.5 | 0.0 | 0.4 |

(*continued*)

APPENDIX 2, continued

**Species/taxa occurring in the expanded survey area (All Areas) from 2004–15 listed in decreasing order of occurrence. The percent occurrence within each of the four survey regions is also shown. For Ontogeny, Y = young-of-the-year, A = age 1 +, and U = undetermined. With the exception of krill, Years = ALL, denotes species/taxa that were also consistently enumerated in the core region since 1990 (data not shown). Krill have an * as species specific enumeration began in 2002 with only total krill numbers (i.e., no species specific counts) available from 1990–2001 (data not shown). For species/taxa not consistently enumerated from 2004–15, the years in which they were enumerated are listed in the Years column. Species/taxa with a ** were also enumerated from 1990–2001 (data not shown).**

| Common Name | Scientific Name | Ontogeny | Years | South | South Central | Core | North Central | All Areas |
|---|---|---|---|---|---|---|---|---|
| Starry Flounder | *Platichthys stellatus* | A | ALL | 0.0 | 0.0 | 0.1 | 2.1 | 0.4 |
| Topsmelt | *Atherinops affinis* | U | ALL | 0.0 | 0.0 | 0.5 | 0.0 | 0.3 |
| Krill | *Euphausia mutica* | U | ALL* | 1.2 | 0.0 | 0.1 | 0.0 | 0.3 |
| Krill | *Euphausia recurva* | U | ALL* | 0.0 | 0.0 | 0.3 | 1.0 | 0.3 |
| Curlfin Sole | *Pleuronichthys decurrens* | A | ALL | 0.0 | 1.6 | 0.1 | 0.0 | 0.3 |
| Krill | *Thysanoessa gregaria* | U | ALL* | 0.8 | 0.0 | 0.3 | 0.0 | 0.3 |
| Slender Snipefish | *Macroramphosus gracilis* | U | ALL | 1.2 | 0.0 | 0.0 | 0.0 | 0.2 |
| Grunt Sculpin | *Rhamphocottus richardsonii* | Y | ALL | 0.0 | 0.0 | 0.1 | 1.0 | 0.2 |
| Argonaut | *Argonauta argo* | U | ALL | 0.8 | 0.0 | 0.0 | 0.0 | 0.1 |
| Clupeiform | Clupeiformes | Y | ALL | 0.4 | 0.0 | 0.1 | 0.0 | 0.1 |
| Threespine Stickleback | *Gasterosteus aculeatus* | U | ALL | 0.0 | 0.0 | 0.3 | 0.0 | 0.1 |
| Sunbeam Lampfish | *Lampadena urophaos* | U | ALL | 0.8 | 0.0 | 0.0 | 0.0 | 0.1 |
| Snipe Eel | Nemichthyidae | U | ALL | 0.4 | 0.0 | 0.1 | 0.0 | 0.1 |
| Armhook Squid | *Berryteuthis* spp. | U | 2009–15 | 0.0 | 0.0 | 0.2 | 0.0 | 0.1 |
| Wolf-Eel | *Anarrhichthys ocellatus* | A | ALL | 0.0 | 0.5 | 0.0 | 0.0 | 0.1 |
| Arrowtooth Flounder | *Atheresthes stomias* | A | ALL | 0.0 | 0.0 | 0.0 | 0.5 | 0.1 |
| Pacific Saury | *Cololabis saira* | U | ALL | 0.0 | 0.0 | 0.0 | 0.5 | 0.1 |
| Pelagic Stingray | *Dasyatis violacea* | U | ALL | 0.4 | 0.0 | 0.0 | 0.0 | 0.1 |
| Rex Sole | *Glyptocephalus zachirus* | A | ALL | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |
| Dover Sole | *Microstomus pacificus* | A | ALL | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |
| Silver Salmon | *Oncorhynchus kisutch* | Y | ALL | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |
| Salmon | *Oncorhynchus* spp. | U | ALL | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |
| Lingcod | *Ophiodon elongatus* | A | ALL | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |
| Sand Sole | *Psettichthys melanostictus* | A | ALL | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |
| Big Skate | *Raja binoculata* | U | ALL | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |
| Pacific Bonito | *Sarda chiliensis* | Y | ALL | 0.4 | 0.0 | 0.0 | 0.0 | 0.1 |
| Scombrid | Scombridae | Y | ALL | 0.4 | 0.0 | 0.0 | 0.0 | 0.1 |
| Hatchetfish | Sternoptychidae | U | ALL | 0.4 | 0.0 | 0.0 | 0.0 | 0.1 |
| California Tonguefish | *Symphurus atricauda* | A | ALL | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |