Temporal Variation in Copepod Abundance and Composition in a
Strong, Persistent Coastal Upwelling Zone

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Abstract

Zooplankton abundance and species composition provide information on environmental variability in the ocean. While zooplankton time series span the west coast of North America, less data exist off north-central California. Here, we investigated a zooplankton time series, focusing specifically on copepods, collected within the Gulf of the Farallones-Cordell Bank area (37.5° to 38.5° N) from 2004 to 2009. Impacted by seasonally strong, persistent upwelling, this study area is located downstream of a major upwelling center (Point Arena). We found copepod abundance and species composition differed significantly, particularly between the first three years (2004 to 2006) and the latter three years (2007 to 2009) of the study. These changes were mainly observed as changes in abundance of boreal copepod species, *Pseudocalanus mimus* and *Acartia longiremis*. These taxa showed increasing abundances for the latter three years of the study (2007 to 2009). During the first three years of the time series, environmental measurements in the region showed lower alongshore wind stress, weaker upwelling, minimal surface alongshore flow, and warmer surface ocean temperatures. Temporal variations in copepod abundance and species composition correlated with several of these environmental measurements (e.g., surface cross-shore and alongshore flows, upwelling, and alongshore wind stress), indicating environmental forcing of primary consumers and ecosystem productivity in this strong, persistent upwelling zone.

Keywords: Zooplankton; Zooplankton Time Series; Copepods; Upwelling; USA, California, Cordell Bank; USA, California, Gulf of the Farallones

1. Introduction

The coastal upwelling region off north-central California is well known for its productivity throughout the food web (Yen et al., 2004; Santora et al., 2011). This region encompasses the Gulf of the Farallones, Farallon Islands, and Cordell Bank (37.5° to 38.5° N). The Gulf of the Farallones-Cordell Bank (GOF-CB) area exhibits high concentrations of phytoplankton (Garcia-Reyes and Largier, 2012) and provides rich feeding grounds for many upper trophic level species, including seabirds which breed on the Farallon Islands (Abraham and Sydeman, 2004; Abraham and Sydeman, 2006). Extensive research has been conducted on seabird reproductive success rates, diet, and general population dynamics on the Farallon Islands spanning several decades (Ainley and Boekelheide, 1990; Sydeman et al., 2001; Abraham and Sydeman, 2004). In addition, the association between ecosystem productivity and zooplankton abundance has been studied using comparisons of zooplankton and seabird breeding success on the Farallon Islands

(Jahncke et al., 2008). Drastic changes in both oceanographic conditions (Schwing et al., 2006; Kaplan et al., 2009) and breeding success of various seabirds on the Farallon Islands have been shown, including the unprecedented reproductive failures of 2005 and 2006 (Sydeman et al., 2006). In this north-central California region, only a few studies have specifically analyzed zooplankton variability (Papastephanou et al., 2006) or the possible links between this variability and changes in atmospheric and oceanographic conditions (Botsford et al., 2006; García-Reyes et al., 2014).

As documented elsewhere, atmospheric and oceanographic dynamics at multiple temporal and spatial scales can offer insight into variability of zooplankton abundance and community composition, along with providing information on the linkages between these dynamics and future ecosystem health: e.g., Peru (Aronés et al., 2009), Chile (Escribano et al., 2012), South Africa (Huggett et al., 2009), and Oregon (Peterson and Keister, 2003; Peterson, 2009). Specifically, studies that correlate abundance of lower trophic level zooplankton with atmospheric and oceanographic conditions provide important insight into ecosystem productivity (Mackas et al., 2001; Peterson et al., 2002; Aronés et al., 2009; Keister et al., 2011; Francis et al., 2012). In other coastal upwelling zones, zooplankton time series have been shown to be effective biological indicators and used as predictive markers of future year-to-year variation in upper-trophic level productivity (Hooff and Peterson, 2006; Ayón et al., 2008; Bi et al., 2011a; Peterson et al., 2014). Of particular interest and the focus of many time series are calanoid copepods; these zooplankton are abundant, relatively easy to sample, have short life spans (thus responding to seasonal and intra-seasonal variability), and are not fished by humans, which makes them ideal indicators of environmental changes in the ocean (Mackas and Tsuda, 1999; Mackas et al., 2001). In addition, copepods are primary consumers, providing the critical first step in the transfer of carbon from primary producers to zooplankton and fish (Mauchline, 1998). Within many coastal upwelling regions, variation of copepods has been shown to correlate with higher trophic level abundance and breeding success (Bertram et al., 2001; Hedd et al., 2002; Bi et al., 2011a; Peterson et al., 2014).

Zooplankton time series data on abundance and species composition are key to understanding ecosystem dynamics within, and differences among, productive coastal upwelling regions along the west coast of North America, which include: Vancouver Island, British Columbia (Mackas, 1992; Mackas et al., 2004; Mackas and Beaugrand, 2010); the Newport Line off Oregon (Peterson and Miller, 1975; Peterson et al., 2002; Hooff and Peterson, 2006; Bi et al., 2011b); the Trinidad Head Line off northern California (Leising et al., 2014); and the *California Cooperative Oceanic Fisheries Investigation* (CalCOFI) surveys in the Southern California Bight (Rebstock, 2001; Rebstock, 2002; Lavaniegos and Ohman, 2007). Regional differences in zooplankton species and biomass have been identified and correlated to regional

scale environmental differences (Mackas et al., 2006; Mackas and Beaugrand, 2010). Therefore, zooplankton time series are needed in multiple locations to understand the linkages and regional differences across a large marine ecosystem, such as the California Current System (CCS). Along the west coast of North America, however, there is a marked absence of zooplankton composition and abundance data for north-central California. The data gap is more pronounced when considering that this is the region where the most intense coastal upwelling occurs along the entire west coast of North America (Dorman and Winant, 1995; García-Reyes and Largier, 2010).

We investigated a time series of copepod species composition and abundance collected within the GOF-CB region, located off San Francisco Bay and Point Reyes, California (Figure 1). This region is known for stronger winds, more persistent seasonal upwelling, and colder surface waters during spring and summer than other locations along the U.S. west coast (Largier et al. 1993; Garcia-Reyes and Largier, 2012). Upwelling centers are found at most major headlands in California and Oregon, with coherent plumes of upwelled waters streaming southward and often separating from the shoreline (Rosenfeld et al., 1994; Barth et al., 2000; Halle and Largier, 2011). The GOF-CB region is located within a major upwelling plume south of the major upwelling center at Point Arena (Halle and Largier, 2011). This upwelling plume transports high abundances of phytoplankton into the region (Largier et al., 2006; Garcia-Reyes and Largier, 2012). Therefore, this study represents an analysis of copepod abundance and community composition in an important upwelling region, which differs from other sites further north and south where upwelling is less persistent, weaker, and/or not within an active upwelling plume.

To the south of our study region, the CalCOFI time series on zooplankton species composition and biomass focuses on the Southern California Bight (30° to 34° N), south of Point Conception (Rebstock, 2001; Rebstock, 2002; Lavaniegos and Ohman, 2007). This region is characterized by weaker upwelling, resulting in warmer surface waters and lower nutrients in contrast to the strong, persistent upwelling north of 34°N that is characterized by cold, high-salinity, and nutrient-rich waters. North of our study region, time series on zooplankton communities are collected off Trinidad Head, California (41°N; Leising et al., 2014), central Oregon (44.5°N; Peterson and Miller, 1975; Peterson et al., 2002; Hooff and Peterson, 2006; Bi et al., 2011b), and Vancouver Island (48° to 49° N and 49.5° to 51.5° N; Mackas, 1992; Mackas et al., 2004; Mackas and Beaugrand, 2010). The Trinidad Head time series is closest to our study region, located about halfway between the central Oregon time series and the GOF-CB region. The Trinidad location is north of the most persistent upwelling region (which starts at Cape Mendocino); it is well downstream of the upwelling center at Cape Blanco and is not persistently in this upwelling plume. In comparison to the GOF-CB region, upwelling is more variable off Trinidad Head

1 and the influence of Cape Mendocino downstream results in warmer waters, which are ascribed to a
2 suppression of upwelling along the north shore of the Mendocino headland (Largier et al 1993). In
3 contrast, the GOF-CB region is within a persistent upwelling region, downstream of two major upwelling
4 centers (Cape Mendocino and Point Arena) and characterized by winds that are stronger and water that is
5 colder than elsewhere along the west coast during the upwelling season (Largier et al., 1993; Garcia-
6 Reyes and Largier, 2012). The Trinidad Head environment appears to be transitional between north-
7 central California and Oregon, which is characterized by a shorter summer upwelling season with
8 intermittent winds and a location poleward of any upwelling centers where the upwelling jet separates
9 from the shore (Barth et al., 2000; Bograd et al., 2009; Garcia-Reyes and Largier, 2012). The Vancouver
10 Island time series on zooplankton species composition and biomass is collected at the northern extent of
11 the CCS, in the transition from CCS influence to Alaska Current influence (Mackas, 1992; Mackas et al.,
12 2001). In summary, the GOF-CB study provides insight to copepod communities in the strong and
13 persistent upwelling region that separates the seasonally upwelling environments characteristic of Oregon
14 from the weak/sub-surface upwelling environments characteristic of southern California; our study region
15 is midway between the Oregon waters that are close to boreal copepod communities and the southern
16 California waters that are close to central and/or equatorial copepod communities.

17
18 We used a six-year zooplankton time series (2004 to 2009) comprised of 16 surveys collected within the
19 Gulf of the Farallones and Cordell Bank National Marine Sanctuaries. This time series spans variable
20 oceanographic conditions (Schwing et al., 2006; Kaplan et al., 2009) and changes in breeding success of
21 various seabirds on the Farallon Islands (Sydeman et al., 2006). Our objectives were to investigate
22 copepod variability and environmental indices across multiple temporal/spatial scales to show linkages
23 between oceanographic conditions and changes in copepod abundance and species composition.
24 Specifically, we identify indices for basin-scale (northeast Pacific) environmental variability, regional-
25 scale (north-central California) environmental variability, and local-scale (survey data) environmental
26 variability. Understanding the drivers of variability in copepod abundance and composition will provide
27 insight to future interannual predictions of ecosystem productivity.

2. Material and methods

2.1 Study Area

The in situ physical oceanographic and zooplankton data were collected by the Applied California
Current Ecosystem Studies (ACCESS) program (www.accessoceans.org), a partnership among Point Blue

Conservation Science, the Gulf of the Farallones National Marine Sanctuary and Cordell Bank National Marine Sanctuary. Research cruises were conducted on the R/V John H. Martin (Moss Landing Marine Laboratories, Moss Landing, California, USA), the R/V McArthur II (National Oceanic and Atmospheric Administration (NOAA)), and the R/V Fulmar (Monterey Bay National Marine Sanctuary, Monterey, California, USA). The ACCESS program has conducted upwelling season sampling since 2004; however, this study analyzed a subset of these data from July 2004 through September 2009. The study area, located within the GOF-CB region, consists of 10 east-west transect lines that extended from offshore stations in the west (near the 1000m isobath) to within several kilometers of the coast in the east (sampling 50-100m depths on the continental shelf). For the purposes of this paper, physical and biological data collected at stations only from lines 2, 4 and 6 were analyzed, as these lines were sampled in all years (Figure 1; Table 1). Five stations along each line were originally established in 2004, and a sixth station (the second-most inshore station) was added to each line in 2006 (Figure 1). Most stations were sampled along each line during each cruise. At times, stations were occasionally not sampled due to safety concerns in shipping lanes or cruise logistics. In addition, we collected more samples during cruises on the larger McArthur II vessel (i.e. May and June of 2007, April 2008); we were forced to break transect line 6 into different parts due to shallow bathymetry, leading to one station to be sampled on either side of the station.

2.2 Analysis of environmental variables

To understand how atmospheric and oceanographic conditions may affect the zooplankton community, environmental data/indices were obtained at three spatial scales: basin-wide, regional, and local (in situ). Basin-scale and regional indices tracked changes in ocean conditions across years (2004 to 2009), while regional and local conditions tracked changes within and across upwelling seasons (April to July).

2.2.1 Basin-scale indices

The basin-scale climate indices analyzed in this study included: the North Pacific Gyre Oscillation (NPGO), the Pacific Decadal Oscillation (PDO), and the multivariate ENSO Index (MEI). NPGO is defined as the second empirical orthogonal function of sea surface height in the Northeast Pacific ((Di Lorenzo et al., 2008; Di Lorenzo et al., 2009) <http://www.o3d.org/npgo/>). PDO is defined as the first principal component of detrended sea surface temperatures in the North Pacific, north of 20° N ((Mantua et al., 1997; Mantua and Hare, 2002) <http://jisao.washington.edu/pdo/PDO.latest>). MEI is calculated as the unrotated principal component of six atmospheric and oceanographic variables measured in the tropical Pacific ((Wolter and Timlin, 1998) <http://www.esrl.noaa.gov/psd/enso/mei>). Climate indices have influence at ocean basin-wide scales and are likely to show changes in ocean conditions more slowly

1 than local or regional indices (Hare and Mantua, 2000). Therefore, for basin-scale climate indices, a 4-
2 month average was calculated, which included the three months prior to and month of each cruise.

3 4 **2.2.2 Regional environmental variables**

5 At the regional scale, four variables were used to characterize the environment: (i) sea surface currents;
6 (ii) alongshore wind stress (AWS), (iii) sea surface temperature (SST); and (iv) Bakun Upwelling Index.
7 These regional environmental variables were analyzed for two different time periods. For each variable,
8 we calculated a 4-month winter average, which included data for December to March prior to each cruise
9 (referred to throughout this study as “winter average”). In addition, we calculated a 30-day pre-cruise
10 average (referred to throughout this study as “pre-cruise average”); we calculated weighted averages by
11 linearly interpolating between two monthly averages to obtain an average centered on the 30-day period
12 before the first day of each cruise.

13
14 High-frequency radar (HF-radar) data from the area off Point Reyes headland were collected from two
15 stations (BML 1: 38°19'02" N 123° 04'21" W; and PREY: 38°02'50" N 122° 59'21" W), and these data
16 were used to index changes in surface flow. These data were binned into a “nearshore region” and
17 “offshore region” (or shelf-edge region) located 0 to 15km and 30 to 45km off of the headland,
18 respectively (Figure 1). The offshore data represent the larger scale flow influenced by the mesoscale
19 eddy field, whereas the nearshore data represent more local wind-driven flow past the headland (Kaplan
20 et al., 2009; Halle and Largier, 2011). Monthly average alongshore and cross-shore current flow
21 components were calculated for each region, as in Bjorkstedt et al. (2010).

22
23 In addition, SST and wind data measured at NDBC buoy 46013 (38°14'31" N 123°18'2" W; hereafter
24 referred to as NDBC-13) were analyzed. NDBC-13 collected SST and wind measurements were taken
25 from 5m above sea level. Wind speed and direction were then used to calculate AWS at 10m height
26 above sea level. SST and AWS data were smoothed on time scales of 6 and 12 hours, respectively, then
27 missing data points were interpolated up to a gap size of 5 hours. Gaps larger than 5 hours were filled
28 with nearby buoy data from NDBC buoy 46026 (37°45'18" N 122°50'21" W; hereafter referred to as
29 NDBC-26). Monthly averages were then calculated from December 2003 to December 2009, as
30 described in García-Reyes and Largier (2010) and García-Reyes and Largier (2012).

31
32 Lastly, the Upwelling Index (UI) was used as a bulk index of upwelling in this region, which is calculated
33 as monthly averages for every three degrees of latitude along the US west coast by the Pacific Fisheries

Environmental Laboratory (NOAA, www.pfel.noaa.gov). Due to the location of our study site, we averaged monthly UI values from 36° and 39° N latitude as a regional index.

2.2.3 Local in situ environmental variables

During ACCESS cruises, in situ hydrographic data were collected along lines 2, 4, and 6 (Figure 1) via a Seabird 19plus conductivity-temperature-depth (CTD) instrument with a WETStar fluorometer. Downcast data were processed with SBE Data Processing v7.2 and 1m-binned averages from 0 to 50m (or within 10m of the bottom for shallow depth stations) were used to represent the environment from which hoop net zooplankton samples were obtained. Average temperature and salinity were calculated for each cast at each station; these averaged values were then used to calculate an average for each cruise. The depth of the mixed layer was defined as the thermocline (while ignoring stratification often found in shallow waters). This was calculated at each station by first removing spurious variability in temperature using a 5m moving window average, then subtracting these smoothed temperature measurements from adjacent 1m cells. The mixed layer depth was defined as the shallowest depth at which the change in temperature between adjacent 1m cells was greater than 0.5°C. An average mixed layer depth value was calculated for each cruise.

2.3 Zooplankton sampling and processing

Concurrent with hydrographic data collection, zooplankton were sampled at six sampling stations per line during daytime hours using a 1m-diameter hoop net fitted with 333µm mesh (Figure 1). During daylight hours, oblique tows (50m to the surface) were collected at each station by lowering the net to the desired depth (while the ship was underway), then towed the net at 1 to 2 knots for about 10 minutes before retrieving it. Volume filtered was estimated from a mechanical flowmeter (General Oceanics model 2030RC) attached to the opening of the hoop net frame. The contents of each tow were preserved in a 10% formalin solution and stored in 1L plastic jars.

Preserved samples were identified and enumerated by Moira Galbraith at the Institute of Ocean Sciences, British Columbia, Canada. Zooplankton identification protocols were consistent with previous zooplankton analyses (Mackas and Galbraith, 2002). In brief, entire samples were scanned for large and/or rare taxa using a Wild M420 dissecting scope with 20x oculars and varying zoom objective (10-30x), depending on the contents of the sample. Using a Folsom splitter, the sample was quantitatively subsampled for counts of small abundant zooplankton taxa. Total counting effort was ≥ 400 -500 individuals per sample, sufficient to give an expected subsampling error of $\leq 20\%$ for the dominant species (Postel et al., 2000; Mackas and Galbraith, 2002; Mackas et al., 2005).

Copepod species were categorized into three main groups based on their common distribution along the west coast of North America using various literature sources (Fleminger, 1967; Mackas et al., 2001; Keister and Peterson, 2003; Razouls et al., 2005-2012; Lavaniegos and Jimenez-Perez, 2006), personal communications with other zooplankton biologists working in the CCS, and descriptions of Pacific water masses found in Brinton (1962). The three main copepod groupings were: cold water boreal species found at higher latitudes (roughly north of 40° N); transition zone species commonly found in temperate latitudes (about 20-40°N), including cosmopolitan species found throughout the CCS; and warm water central species found at lower latitudes (about 10-20° N; Table 2). All life stages of each species were summed per sample. We calculated abundances for each species (individuals m⁻³) and each copepod distribution group per sample, and these per-sample abundances were averaged for each cruise.

2.4 Data analysis and statistical methods

We analyzed both environmental and copepod data to evaluate variability among years (2004 to 2009) and between seasons (upwelling vs. non-upwelling). Throughout this study, upwelling season was defined as April to July and non-upwelling season was August to October (Garcia-Reyes and Largier, 2012).

To investigate the patterns observed in the environmental variables, as well as the relative influence of each variable, a Principal Components Analysis (PCA) was used to reduce the local, regional, and basin-scale indices into uncorrelated axes that explained the maximum variability in environmental variables across the samples. Environmental data associated with each zooplankton sample were examined for skewness and transformed if necessary; all variables were normalized.

Multivariate techniques were employed to examine whether the copepod community present during the upwelling season changed across years and identify the species contributing the most to temporal variability. All multivariate statistics were performed on PRIMER v6 software (Clarke and Warwick, 2001; Clarke and Gorley, 2006) . Prior to these analyses, all copepod species abundance data were square root transformed and Bray-Curtis similarities were calculated among samples. To examine patterns of similarity in copepod community composition across samples, we performed non-metric multidimensional scaling (NMDS) analyses. We then applied a two-way crossed analysis of similarities (ANOSIM) using year and month as factors to test for differences in copepod composition among years. To understand the copepod species that typify cruises within an upwelling season, as well as species that contributed to differences among years, a two-way crossed similarity percentages (SIMPER) test was used, using year and month as factors (Clarke, 1993). SIMPER results provide within year similarities,

1 which are measures of change in the copepod community across samples collected within each year.
2 When used to analyze among year differences, the two-way crossed SIMPER analysis analyzed
3 dissimilarities between two years of samples in which similar months of data were available. Therefore,
4 the SIMPER analysis was only performed on years with at least one month of sampling in common. The
5 abundance of the important species identified in the SIMPER analysis were averaged and plotted by each
6 sampling station on each line to examine for cross-shelf gradients in copepod abundances.

7
8 To determine how much of variance observed in the copepod species composition and abundance is
9 driven by the environmental factors, we performed a RELATE test, which examines whether a
10 relationship exists between the copepod and environmental matrices. This analysis was then followed up
11 with the BEST test, which links copepod species composition and abundance patterns to environmental
12 conditions (using a maximum of 10 environmental variables) by maximizing the rank correlation between
13 the two resemblance matrices (Clarke, 1993). For this analysis, the BIOENV algorithm was used, in
14 which all permutations of the environmental variables are tried. To further examine the possible
15 relationships between environmental and copepod data, linear regression analysis of environmental
16 variables to log transformed copepod species abundances were analyzed.

19 **3. Results**

21 **3.1 Environmental data analysis**

22 Environmental indices showed differences among years as well as within the upwelling season. Indices at
23 all spatial scales contributed to the primary four principal components as obtained through PCA. The top
24 four PCs had eigenvalues >1 and explained a combined total of 83.50% of the observed variance for the
25 24 environmental indices and measurements (Table 3; Figure 2). The first principal component (PC1)
26 explains 54.8% of total variance, along with PC 2, 3, and 4 explaining 11.6%, 9.1%, and 8% of the total
27 variance, respectively. PC1 was strongly associated with climate indices (NPGO and PDO), winter
28 conditions (reflected in winter averages of UI, SST, and AWS), and the pre-cruise average of SST (Table
29 3). In general, positive PC1 scores, observed for years 2004 to 2006, represent weaker upwelling with
30 negative NPGO values, positive PDO values, decreased winter upwelling, and warmer pre-cruise SST
31 (Figure 2). Negative PC1 scores represent stronger upwelling, as observed in 2007 to 2009 (Figure 2).
32 PC2 was primarily associated with indices for surface flow past Point Reyes, as well as in situ
33 temperature and mixed layer depth (Table 3).

The period of 2004 to 2009 is known to have large basin-wide changes in climate, which were also observed at regional scales in our data set. During 2004 to 2006, PDO was weakly positive and NPGO weakly negative. A marked switch to positive NPGO and negative PDO occurred in 2007 that lasted to 2009 (Figure 3). Reflecting these basin-wide changes, average winter conditions prior to each upwelling season varied. Minimal winter AWS (equatorward stress $<0.03 \text{ N/m}^2$) was measured prior to the 2004 to 2006 upwelling seasons, in contrast to strong winter AWS for 2007 to 2009 (equatorward stress $>0.06 \text{ N/m}^2$; Figure 4). Other winter averages of regional environmental indices showed similar patterns, with low UI and warmer SST for 2004 to 2006 (<25 and $>11.5^\circ\text{C}$) and higher UI and cooler SST for 2007 to 2009 (>40 and $<11.5^\circ\text{C}$; Figure 4). Also, surface current flow past Point Reyes exhibited concurrent patterns. Stronger alongshore flow was measured nearshore (0 to 15 km) and offshore (30 to 45 km) during the upwelling seasons of 2004, 2007, 2008, and 2009, in contrast to 2005 and 2006 (Figure 5a; Figure 6c). In general, strong alongshore surface flow was observed ($>45 \text{ cm/s}$) in April and May. However, the pre-cruise surface flow in 2005 and 2006 was markedly lower ($<35 \text{ cm/s}$; Figure 6c). Cross-shore flow was minimal in comparison to alongshore flow; however, cross-shore flow patterns also explained variance attributed to PC2 and PC3 loadings (Figure 5b; Table 3).

Environmental conditions measured at basin-wide and regional scales were also reflected in atmospheric and oceanographic measurements acquired at local and shorter temporal scales. Pre-cruise average SST and AWS showed similar patterns to other variables (Figure 6). The colder surface SST and stronger AWS observed prior to cruises in 2007 and 2008 were also observed in the in situ data collected during each cruise (Figure 6a; Figure 6b; Figure 7). Cruises in 2007 and 2008 tended to have colder, saltier, denser water in the top 50m in contrast to 2005 and 2006, which had warmer, less dense water (Figure 7). Intra-seasonal changes were also observed in regional and local scale indices. For example, the three cruises in 2009 were conducted during different pre-cruise environmental conditions and the in situ salinity and temperature data collected reflected these regional changes (Figure 6; Figure 7).

3.2 Copepod analysis

3.2.1 Copepod abundance

Boreal copepod species common to coastal/shelf waters were most abundant, but transition zone species common to oceanic waters occurred in more samples during our study (Table 2). Summarizing copepods by distribution region (boreal, central, transition) showed a substantial change in boreal and central species abundance among years and between seasons (Figure 8).

3.2.2 Copepod composition

1 Along with abundance, NMDS analysis showed copepod species composition varied significantly within
2 upwelling seasons and among years. The NMDS ordination plot showed variation in copepod species
3 composition among years (Figure 9), and significant differences of copepod species composition were
4 found among all years (ANOSIM $global R = 0.565$, $p < 0.001$). The first three years of the study (2004
5 to 2006) and the latter three years (2007 to 2009) grouped together, respectively (Figure 9). The NMDS
6 characterizations showed similar patterns to the grouping of cruises on the PCA bi-plot (Figure 2).

7
8 Within year and during the upwelling season, species composition differed across months (SIMPER
9 analysis; Table 4). Copepod communities were the least variable across samples collected in 2008 and
10 2004, showing 53.54% and 51.64% within year similarities, respectively (Table 4). The boreal species
11 *Pseudocalanus mimus* was recognized as the most important species contributing to within-year similarity
12 in 2007-2009, explaining at least 40% of the similarity of copepod composition for these years.
13 Additionally, the transition copepod species, *Calanus pacificus*, was the most important contributor to
14 within-year similarity in 2004-2006. *C. pacificus* explained at least 57% of the similarity of copepod
15 composition among cruises for these years.

16
17 Patterns of copepod species composition and abundance observed among years were similar to within-
18 year patterns (Table 4; Table 5). The largest dissimilarity in copepod composition among years were
19 observed between 2006 or 2005 and the latter three years of the study (2007, 2008, or 2009; >75%
20 dissimilarity; Table 5). The dissimilarity in copepod composition for the remaining year groupings drops
21 below 70% and the smallest dissimilarities were observed between 2008 and 2009 (49.74% dissimilarity)
22 and between 2005 and 2006 (54.54% dissimilarity; Table 5). Copepod composition in 2004 had mixed
23 results when compared to other years, showing the highest dissimilarity with 2009 (71.08% dissimilarity),
24 then 2006 (69.40% dissimilarity), followed by 2005 (62.57% dissimilarity; Table 5). The top four species
25 contributing to dissimilarity among years were two boreal species (*P. mimus* and *A. longiremis*) and two
26 transition/cosmopolitan species (*C. pacificus* and *Metridia pacifica* (small form)). For years with the
27 largest dissimilarities (>75%), the average abundance of *P. mimus* increased from 2005 or 2006 to 2007,
28 2008, or 2009 (Table 5). *C. pacificus* exhibited the opposite pattern where its average abundance
29 decreased from 2006 or 2005 to 2007, 2008, or 2009 (Table 5). *A. longiremis* did not become abundant in
30 this region until 2008, thereby becoming a major contributor to between-year differences in copepod
31 composition for comparisons among early years (e.g. 2005 and 2006) and the last two years in our time
32 series (Table 5).

3.2.3 Cross-shelf Patterns in Copepod Abundance

When considering the top four copepod species responsible for within-year similarities and between-year differences, there was some evidence for cross-shelf variation in abundances. In general, species abundances did not vary greatly and it was not consistent at each line (Figure 10a). The species showing the largest variation in abundance was *P. mimus* on line 6, with a higher average abundance (81.3 m^{-3}) at the eastern-most station (E) compared to the western-most station (W; 25.5 m^{-3}). The copepod abundances at each station were also averaged over the two year groups (2004-2006 and 2007-2009). *C. pacificus* and *M. pacifica* (short form) abundances across lines showed the greatest variation in the warm water years (Figure 10b), but no clear east-west gradient across all lines was detected. For all years, *M. pacifica* (short form) showed the highest abundance (8.3 m^{-3}) towards the middle of line 2 at station M (east of the shelf break), while *C. pacificus* showed peaks in abundance at E (15.3 m^{-3}) and ME (15.1 m^{-3}) on line 6. Similar to the results for all years, *P. mimus* had the highest cross-shelf variation in abundance of the four species during the cold water years (Figure 10c). This cross-shelf variation for *P. mimus* was most noticeable on line 6.

3.3 Copepod-environment relationships

Overall, the RELATE analysis showed a significant relationship between environmental indices and copepod species composition ($\rho = 0.557$, $p = 0.1\%$). The BEST analysis determined two equally likely combinations of environmental variables that correlated best with variation in copepod composition (0.630 and 0.626 correlation coefficients; Table 6). All correlation combinations used eight or fewer of the maximum ten environmental indices possible for this test. The correlation between copepod composition and environmental variables was highest with winter averages of AWS and UI, cross-shore flow past Point Reyes in the nearshore environment, and the pre-cruise averages of offshore/shelf-edge alongshore flow. The PDO also correlated with copepod composition in four of the top five results.

The most significant environmental variables identified in the BEST analysis were further analyzed with the average abundance of the four important species (*P. mimus*, *C. pacificus*, *A. longiremis*, and *M. pacifica* (short form)) identified as important contributors between-year and within-year patterns. Increased AWS and UI in winter were observed in the latter three years of the study (Figure 4), when we also observed an increase from extremely low May-June average abundances of *P. mimus* ($<0.05 \text{ m}^{-3}$) in 2005 and 2006 to high average abundances ($>85 \text{ m}^{-3}$) in 2008 and 2009 (Figure 11). *P. mimus* and *A. longiremis* abundances were higher in years where the previous winter had stronger AWS, stronger upwelling, and minimal westward cross-shore flow. In comparison, *C. pacificus* showed higher average abundances for years where the previous winters had decreased AWS, weaker upwelling, and westward cross-shore flow (2005 and 2006; Figure 11). *M. pacifica* (short form) did not respond in a consistent way

1 to the winter variables; this species appeared to increase in weaker AWS, stronger upwelling, and
2 eastward cross-shore flow, with the exception of 2009 (Figure 11).

3
4 Basin-scale and pre-cruise regional environmental variables showed relationships with copepod species
5 that were similar to those exhibited with the winter values of AWS, UI, and cross-shore nearshore flow.
6 Linear regression showed a significant relationship of increasing abundance of *P. mimus* and decreasing
7 abundance of *C. pacificus* with lower PDO indices and stronger negative (southward) offshore/shelf-edge
8 flow past Point Reyes (Figure 12). Alongshore wind stress during the pre-cruise period did not show a
9 significant relationship with these two species, nor the other two important species (*A. longiremis* and *M.*
10 *pacifica* (short form)) identified in the SIMPER analysis.

11 12 13 **4. Discussion**

14
15 This study provides an in-depth analysis of copepod time series data from a strong, persistent upwelling
16 region off the west coast of North America. Two phases of environmental structure were evident in this
17 time series: weak upwelling from 2004 to 2006 and strong upwelling from 2007 through 2009. The
18 changes in atmospheric and oceanographic conditions were closely followed by a response in the copepod
19 community and changes in copepod abundance.

20
21 Atmospheric and oceanographic changes for the GOF-CB region were evident on multiple scales (basin-
22 wide, regional, and local). Within one year, from 2006 to 2007, several significant environmental changes
23 were observed: climate indices (NPGO and PDO) indicated a basin-scale change to cold water and
24 productive ocean conditions (Figure 3); winter conditions showed colder SST and higher AWS in the
25 region throughout the year (Figure 4); pre-cruise measurements showed stronger, earlier upwelling
26 conditions (Figure 6); and in situ oceanographic data reflected colder, more saline waters were present in
27 the region where copepods were sampled (Figure 7). During this same one-year period, from May 2006 to
28 May 2007, the average abundances of boreal copepod taxa increased by a factor of 100 (Figure 11).
29 Interannual variations in copepod community structure were best explained by a set of regional variables
30 (winter measures of cross-shore flow nearshore, UI, AWS; and pre-cruise measures of offshore
31 alongshore flow and AWS) and one basin-scale variable (PDO; Table 6). In other regions along the west
32 coast of North America, this relationship among multiple environmental scales of measurement was not
33 strong (Hooff & Peterson, 2006), and this may be due to the high alongshore wind stress and intense

seasonal upwelling characterized by the north-central California region (Largier et al., 1993; Garcia-Reyes and Largier, 2012).

While correlations between the environment and copepods are evident from our data, determining the mechanism of increased boreal copepod abundance is challenging. We expect that interannual differences in the copepod community may occur as a result of changes in pelagic habitat, changes in spatial distribution, and/or alongshore advection. The existence of appropriate cold-water habitat for enhanced local production of the boreal species may be a factor, as observed with increased abundances of *P. mimus* and *A. longiremis* during cold-water years. Regional conditions of stronger alongshore winds and upwelling conditions during the winter may influence the spatial distribution of the boreal species, leading to conditions which transport these species further offshore during the upwelling season. However, we did not find elevated abundances at offshore stations, although this did occur at times in the southern portion of our study region (line 6) where the upwelling jet separates from the shore (Vander Woude et al., 2006). In addition, increased boreal copepod abundances were observed in years with minimal westward cross-shore flow in the winter, suggesting the importance of local wind-driven processes to copepod abundance and distribution. The presence of energy-rich boreal copepods may be related to transport from higher latitudes through alongshore advection; the strong, non-linear, step-like functional relationships with the large scale (PDO) and regional (offshore alongshore flow) variables prior to the upwelling season highlight the influence of alongshore advection on the boreal copepod population, as has been shown in other regions (Peterson et al., 2002; Hooff and Peterson, 2006; Keister et al., 2011). Other research has shown the significance of large-scale and local-scale processes in the CCS, with remote forcing explaining most of the physical variability in nearshore CCS waters, while local processes drive variations in the ecological state, particularly in the central CCS (Frischknecht et al., 2015). The higher copepod abundances observed in years where environmental conditions were consistent throughout an upwelling season suggests that advection from higher latitudes and population growth may both play a role in sustaining these high abundances, both processes that require persistence (the former to cover long distances, and the latter to allow for population growth). For example, ocean conditions remained consistent throughout the 2008 upwelling season, and we observed high abundances of boreal copepods. In direct contrast was 2009, when strong upwelling and cold conditions in winter and early spring gave way to minimal upwelling later in the spring and early summer, marking the transition to the 2009-10 “warm pool” El Niño (Kim et al., 2011). These environmental changes in 2009 were reflected in the copepod community with high abundances observed in May and June and decreased abundance measured in July.

Beyond environmental correlations, the variability in lower-trophic-level productivity observed in this time series exhibits patterns similar to those observed in other west coast regions. For example, the low productivity in 2005 and 2006 in the GOF-CB region was also observed in other areas of the CCS. Mackas et al. (2006) reported a decrease in total biomass, total copepods, and euphausiids for the central California region (36°N), similar to the decreases in copepod abundance we observed off north-central California (37° to 38.5° N). We observed significant differences in the abundance of boreal copepod species, which contributed strongly to interannual changes in species composition in this study region (Figure 8; Table 5). Fluctuations in boreal copepod species were similar to those observed to the north, off central Oregon during this time period (Mackas et al., 2006). We find that the north-central California region bridges two distinct geographic and oceanographic regions and provides an important link to understanding zooplankton variability throughout the CCS, including southern California and Oregon.

Copepod abundance and composition can be used to reflect environmental conditions that are associated with higher overall ecosystem productivity, including production of upper trophic levels. In this study, we show that boreal copepod species exhibit large interannual variation off north-central California. These boreal copepod species are known for their regional distribution above 40°N (Hooff and Peterson, 2006; Mackas et al., 2006; Leising et al., 2014), but minimal research on these species has occurred in waters further south (Hopcroft et al., 2002; Papastephanou et al., 2006). In longer time series off central Oregon, similar variation in boreal species has been well documented and used to indicate productive ocean conditions (Peterson and Keister, 2003; Hooff and Peterson, 2006; Peterson, 2009; Bi et al., 2011a; Keister et al., 2011; Peterson et al., 2014). Off the Washington and Oregon coasts, a positive correlation was observed between the abundance of some boreal copepod species and abundance of juvenile coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon (Bi et al., 2011a). The boreal (cold, neritic) species *P. mimus* is known as a lipid-rich copepod, with greater bioenergetic content than copepods with lower lipid reserves and presumed to provide a greater energy transfer throughout the food web (Hooff and Peterson, 2006; Peterson et al., 2014). Within the GOF-CB region, *P. mimus* and a second boreal copepod, *A. longiremis*, contributed significantly to within-year similarity and between-year dissimilarity (SIMPER test; Table 5). The abundance of *P. mimus* and *A. longiremis* increased from negligible numbers in 2006 to $>18 \text{ m}^{-3}$ in 2008. This abundance tracked changes in climate indices, regional measures of stronger alongshore equatorward flow, colder SST, and stronger AWS, along with higher salinity and colder in situ temperatures.

Coho and Chinook salmon are important sport and recreational fisheries along the west coast of North America. Population dynamics of these salmon within California waters have previously been correlated

1 with environmental measurements, including sea surface temperature and the upwelling index (Botsford
2 and Lawrence, 2002; Wells et al., 2007) that showed significant correlation with zooplankton variability
3 in this study. Changes in environmental conditions that correlate with variability in boreal copepod
4 species appear to be an effective indicator of upper-trophic-level productivity. Further support for boreal
5 copepods (and correlated environmental indices) as indicators of ecosystem health in this region can be
6 seen via the collapse of the Central Valley salmon stocks and subsequent closure of the salmon fishery in
7 Oregon and California occurred during 2008 and 2009 (Lindley et al., 2009). This drastic decline in
8 salmon fish stocks corroborates poor ocean conditions (i.e., lack of lipid-rich boreal copepods) in this
9 region three years prior to the collapse (2005 and 2006), when salmon smolts entering the ocean
10 encounter a dearth of high-quality copepod food. Additionally, the Cassin's auklet experienced
11 unprecedented reproductive failure on Southeast Farallon Island in 2005 and 2006 (Sydeman et al., 2006),
12 which we have shown to be years of low copepod abundance in the upper water column. While we have
13 not established relationships between copepods and upper trophic level organisms in this study, we expect
14 that the abundance of these cold, boreal copepod species, specifically *P. mimus*, may correlate positively
15 with important salmon fisheries within the GOF-CB region, as both copepods and salmon may be
16 responding similarly to environmental variability.

17
18 We have not identified all the factors contributing to environmental variability in this region. Our simple
19 examination of the spatial distribution of copepods did not reveal strong cross-shelf gradients across all
20 transect lines, although a latitudinal gradient is evident and deserves further study. Because the mesh size
21 was too coarse to capture smaller copepod species or earlier life stages of certain species, we could not
22 directly explore local production. While our sampling occurred in the daytime (when many species may
23 be at depth) and our results may be biased towards zooplankton with limited vertical migration behaviors,
24 the daytime copepod composition in the upper waters is likely to be important to upper trophic levels as
25 these copepods are available to important visual predators such as salmon and seabirds.

26
27 The strong correlations that we have observed between environment indices and copepod diversity and
28 abundance, on both intra-seasonal and inter-annual time scales, point to specific mechanisms in
29 explaining the links between upwelling variability and ecosystem productivity. The importance of winter
30 conditions is likely related to the length of the upwelling season, which will enhance advective import of
31 boreal copepods and also provide a stable environment in which specific copepod populations can bloom.
32 During years of strong upwelling, the boreal-dominated copepod community extends south to this latitude
33 from Oregon and further north, while in weaker upwelling years or when the upwelling season is
34 disrupted there is an absence of boreal copepods and a low-abundance of transitional and neritic

copepods. In the GOF-CB region, as in other CCS regions, environmental measurements and copepod species composition analyzed during the upwelling season may provide predictive measurements for upper-trophic-level abundances and breeding success (Bi et al., 2011a; Rupp et al., 2012; Peterson et al., 2014). With the expectation that the timing and intensity of upwelling in the CCS will change with global climate change (Bakun, 1990; Snyder et al., 2003; García-Reyes and Largier, 2010; Sydeman et al., 2014), it is essential for management of our future marine resources to understand the connections between environmental variability and the copepod community.

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Table 1. Zooplankton sampling in the Gulf of the Farallones-Cordell Bank region from 2004 to 2009. Research cruises are listed with dates, transect lines completed, and total number of zooplankton samples collected along transect lines 2, 4, and/or 6. For zooplankton abundance graphs and analyses all cruises were analyzed. For zooplankton composition and comparisons to oceanographic measurements, only cruise data for spring and summer months (April to July) were used.

Year	Month	Date	Transect Lines Completed			# of Hoop Net Samples Analyzed
2004	July	26-28	2	4	6	12
	September	21-23	2	4	6	14
	October	21-23	2	4	6	14
2005	April	23-25	2	4	6	15
	May	26-28	2	4	6	15
	June	23-25	2	4	6	14
	July	26-28	2	4	6	14
	October	20-22	2	4	6	14
2006	May	23-24		4	6	12
	June	23-25	2	4	6	18
	July	15-17	2	4	6	18
	October	11-13	2	4	6	18
2007	May	27-29	2	4	6	19
	June	19-20	2	4	6	19
	September	25-27	2	4	6	18
2008	April	8-10	2	4	6	19
	May	25-27	2	4	6	18
	June	27-29	2	4	6	17
	September	23-25	2	4	6	17
2009	May	11 & 14			6	7
	June	15-17	2	4	6	18
	July	17-18 & 20	2	4	6	13
	September	14-15 & 18	2	4	6	14

Table 2. Copepod species enumerated in study samples listed by their common latitudinal distribution (boreal, transition/cosmopolitan, and central) and whether they occur on or off the continental shelf along the west coast of North America. Average abundance (individuals m⁻³) and the number of samples present for all upwelling season cruises in our study period (Apr-Jul, 2004-2009) are shown.

	Average abundance	# samples present
BOREAL, COLD WATER SPECIES		
coastal / shelf		
<i>Acartia hudsonica</i>	0.19798	10
<i>Acartia longiremis</i>	4.87492	106
<i>Aetideus divergens</i>	0.01537	18
<i>Calanus marshallae</i>	0.20752	12
<i>Centropages abdominalis</i>	0.01711	15
<i>Pseudocalanus mimus</i>	26.40769	152
<i>Pseudocalanus moultoni</i>	0.02335	4
<i>Pseudocalanus newmani</i>	0.00404	2
<i>Tortanus discaudatus</i>	0.62463	105
oceanic		
<i>Metridia pacifica</i>	0.00253	2
<i>Neocalanus cristatus</i>	0.01166	40
<i>Neocalanus plumchrus</i>	0.04068	21
<i>Pseudocalanus minutus</i>	0.00340	6
<i>Scolecithricella minor</i>	0.05262	50
TRANSITION ZONE		
coastal / shelf		
<i>Acartia tonsa</i>	2.58096	115
<i>Aetideus bradyi</i>	0.00547	22
<i>Aetideus acutus</i>	0.00025	1
<i>Calocalanus tenuis</i>	0.00059	3
<i>Candacia columbiae</i>	0.00033	3
<i>Centropages bradyi</i>	0.00012	1
<i>Corycaeus anglicus</i>	0.00028	3
<i>Ctenocalanus vanus</i>	0.08776	31
<i>Epilabidocera longipedata</i>	0.02827	9
<i>Euchirella pseudopulchra</i>	0.01704	18
<i>Metridia pacifica</i> (small form)	2.85678	138
<i>Paracalanus parvus</i>	0.00003	1
oceanic		
<i>Calanus pacificus</i>	4.77572	212
<i>Candacia bipinnata</i>	0.00064	3
<i>Clausocalanus arcuicornis</i>	0.17305	47

<i>Clausocalanus furcatus</i>	0.00001	1
<i>Clausocalanus lividus</i>	0.00539	5
<i>Clausocalanus mastigophorus</i>	0.00067	1
<i>Clausocalanus parapergens</i>	0.00119	5
<i>Eucalanus californicus</i>	1.11887	228
<i>Euchirella bitumida</i>	0.00002	1
<i>Heterorhabdus spinifrons</i>	0.00182	1
<i>Heterorhabdus tanneri</i>	0.00011	1
<i>Mesocalanus tenuicornis</i>	0.26159	118
<i>Oithona atlantica</i>	0.41253	95
<i>Oithona similis</i>	1.64671	32
<i>Pareucalanus parki</i>	0.00014	5
<i>Pleuromamma abdominalis</i>	0.00077	3
<i>Pleuromamma borealis</i>	0.00158	7
<i>Rhincalanus nasutus</i>	0.00747	32
<i>Scaphocalanus echinatus</i>	0.00051	1
<i>Scolecithricella ovata</i>	0.00074	1
<i>Undeuchaeta plumosa</i>	0.00006	2

CENTRAL

oceanic

<i>Acartia danae</i>	0.05991	33
<i>Eucalanus hyalinus</i>	0.00926	19
<i>Euchaeta media</i>	0.00093	7
<i>Euchirella galeata</i>	0.00001	1
<i>Euchirella rostrata</i>	0.00956	49
<i>Heterorhabdus papilliger</i>	0.00142	8
<i>Lucicutia flavicornis</i>	0.00524	7
<i>Pleuromamma xiphias</i>	0.00012	1
<i>Scolecithrix bradyi</i>	0.00038	3
<i>Scolecithrix danae</i>	0.00021	2

OTHER

<i>Caligus clemensi</i>	0.00033	8
<i>Caligus macarovi</i>	0.00125	18
<i>Oncaea conifera</i>	0.00063	1
<i>Paraeuchaeta elongata</i>	0.00069	6
<i>Sapphirina angusta</i>	0.00006	1
<i>Undeuchaeta intermedia</i>	0.00175	15
<i>Pleuromamma spp</i>	0.00018	1
<i>Candacia spp</i>	0.00004	2
<i>Corycaeus spp</i>	0.00001	1
<i>Epilabidocera spp</i>	0.00037	2

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<i>Eucalanus</i> spp	0.00290	1
<i>Euchaeta</i> spp	0.00067	4
<i>Euchirella</i> spp	0.03695	29
<i>Haloptilus</i> spp	0.00074	1
Harpacticoid	0.00002	1
<i>Labidocera</i> spp	0.00003	1
<i>Sapphirina</i> spp	0.00009	1
<i>Undeuchaeta</i> spp	0.00015	3

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Table 3. Principal Components Analysis shows loadings of environmental indices.

Variable	PC1	PC2	PC3	PC4
NPGO	-0.281	-0.104	-0.185	-0.009
PDO	0.262	0.186	0.222	0.178
MEI/ENSO	0.231	-0.114	0.399	-0.083
Alongshore Offshore Flow_winter**	0.190	0.257	-0.391	-0.080
Cross-shore Offshore Flow_winter**	0.207	0.080	0.485	0.108
Alongshore Nearshore Flow_winter	0.225	0.295	-0.055	-0.123
Cross-shore Nearshore Flow_winter	-0.191	-0.388	0.165	-0.299
Upwelling Index_winter	-0.281	-0.024	0.171	0.002
SST_winter	0.281	0.187	0.094	0.131
AWS_winter	0.267	0.139	-0.240	0.136
Alongshore Offshore Flow_pre cruise	0.215	-0.268	-0.175	0.225
Cross-shore Offshore Flow_pre cruise	0.081	-0.120	0.138	-0.319
Alongshore Nearshore Flow_pre cruise	0.137	-0.472	-0.070	0.309
Cross-shore Nearshore Flow_pre cruise**	-0.140	0.163	0.314	-0.003
Upwelling Index_pre cruise	-0.179	0.079	0.157	0.557
AWS_pre cruise	0.228	-0.130	0.173	-0.242
SST_pre cruise	0.283	0.049	0.041	-0.165
Temperature_during cruise	0.226	-0.339	-0.123	0.118
Salinity_during cruise	-0.216	0.123	0.125	0.332
Depth of Mixed Layer_during cruise	0.227	-0.291	0.057	0.187
Eigenvalues (PCA)	11.00	2.32	1.81	1.60
Cumulative Variance Explained	54.8%	66.4%	75.5%	83.5%

** transformed prior to PCA analysis

Table 4. Two-way crossed SIMPER analysis showing percent similarity in zooplankton composition within years for samples obtained during the upwelling season (April to July). The average abundances of copepod species (individuals m⁻³) explaining the top 60% of the cumulative similarity per year are listed.

	Avg abundance	Avg contribution of species	Similarity/ standard deviation	Contribution (%)	Cumulative (%)
Group "2008" (avg similarity: 53.54)					
<i>Pseudocalanus mimus</i>	6.28	29.43	2.63	54.97	54.97
Group "2004" (avg similarity: 51.64)					
<i>Calanus pacificus</i>	4.38	29.64	2.36	57.4	57.4
Group "2005" (avg similarity: 51.52)					
<i>Calanus pacificus</i>	2.27	30.47	2.06	59.14	59.14
Group "2006" (avg similarity: 50.68)					
<i>Calanus pacificus</i>	1.64	29.26	1.88	57.74	57.74
Group "2009" (avg similarity: 48.64)					
<i>Pseudocalanus mimus</i>	6.21	19.59	1.27	40.27	40.27
Group "2007" (avg similarity: 37.14)					
<i>Pseudocalanus mimus</i>	3.2	16.76	1.48	45.12	45.12
<i>Metridia pacifica</i> (short form)	1.6	5.31	0.68	14.29	59.41

Table 5. a) Two-way crossed SIMPER analysis showing the dissimilarity in copepod species composition among years for samples obtained during the upwelling season (April to July). The average abundances of zooplankton species (individuals m⁻³) explaining the top 60% of the cumulative dissimilarity are listed. b) The between-year average dissimilarity values for the upwelling season.

	Average abundance	Average abundance	Average Dissimilarity	Dissimilarly / standard deviation	Contribution (%)	Cumulative (%)
Groups '2006 & 2008'	2006	2008				
<i>Pseudocalanus mimus</i>	0.09	6.28	36.04	3.16	41.89	41.89
<i>Acartia longiremis</i>	0.08	2.05	14.38	1.23	16.72	58.61
Groups '2005 & 2008'	2005	2008				
<i>Pseudocalanus mimus</i>	0.07	6.28	31.09	2.48	37.95	37.95
<i>Calanus pacificus</i>	2.27	0.85	11.26	1.16	13.74	51.69
<i>Acartia longiremis</i>	0	2.05	8.84	0.89	10.79	62.48
Groups '2006 & 2007'	2006	2007				
<i>Pseudocalanus mimus</i>	0.09	3.2	21.45	1.53	26.45	26.45
<i>Calanus pacificus</i>	1.64	0.65	13.65	0.97	16.84	43.29
<i>Metridia pacifica</i> (short form)	0.45	1.6	10.14	1.15	12.51	55.8
Groups '2006 & 2009'	2006	2009				
<i>Pseudocalanus mimus</i>	0.09	6.21	24.82	1.43	31.21	31.21
<i>Acartia longiremis</i>	0.08	2.92	15.06	1.34	18.94	50.15
<i>Calanus pacificus</i>	1.64	1.53	7.45	1.34	9.37	59.52
Groups '2005 & 2007'	2005	2007				
<i>Pseudocalanus mimus</i>	0.07	3.2	19.94	1.42	25.08	25.08
<i>Calanus pacificus</i>	2.27	0.65	13.13	1.22	16.51	41.6
<i>Metridia pacifica</i> (short form)	0.69	1.6	10.69	1.17	13.44	55.04
Groups '2005 & 2009'	2005	2009				
<i>Pseudocalanus mimus</i>	0.07	6.21	25.55	1.45	32.58	32.58
<i>Acartia longiremis</i>	0	2.92	14.08	1.28	17.96	50.54
<i>Calanus pacificus</i>	2.27	1.53	7.35	1.24	9.37	59.91

	2004	2005	2006	2007	2008	2009
2004	-	-	-	-	-	-
2005	62.57	-	-	-	-	-
2006	69.4	54.54	-	-	-	-
2007	*	79.5	81.07	-	-	-
2008	*	81.93	86.03	64.17	-	-
2009	71.08	78.42	79.51	69.01	49.27	-

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1 ** no data, as only pairs of year with at least one common month sampled were used in this SIMPER*
2 *analysis*
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Table 6. BEST BIOENV results shows the environmental variables, which best correlate with the copepod composition data. The top five results are shown here.

Variable	Result 1	Result 2	Result 3	Result 4	Result 5
PDO	x	x		x	x
NPGO					
MEI/ENSO					
Alongshore Offshore Flow_winter					
Cross-shore Offshore Flow_winter		x	x		x
Alongshore Nearshore Flow_winter					
Cross-shore Nearshore Flow_winter	x	x	x	x	x
Upwelling Index_winter	x	x	x	x	x
SST_winter					
AWS_winter	x	x	x	x	x
Alongshore Offshore Flow_pre-cruise	x	x	x	x	x
Cross-shore Offshore Flow_pre-cruise					
Alongshore Nearshore Flow_pre-cruise					
Cross-shore Nearshore Flow_pre-cruise					
Upwelling Index_pre-cruise					
AWS_pre-cruise	x	x	x	x	x
SST_pre-cruise					x
Temperature_during cruise					
Salinity_during cruise		x		x	
Depth of Mixed Layer_during cruise					
Total Number of Variables	6	8	6	7	8
ρ (Spearman Rank Correlation)	0.630	0.626	0.626	0.626	0.626

Figure Captions

Figure 1. Map of Gulf of the Farallones-Cordell Bank study region, showing boundaries of the National Marine Sanctuaries (NMS) as of June 2015. The Gulf of the Farallones (GOF) NMS referred to in this paper is now known as the Greater Farallones NMS. Transect lines, 2, and 6 are shown in black, sampling stations for CTD and hoop net tows are marked with white circles, and blue squares denote HF-radar surface current averaging regions nearshore (0 to 15 km) and offshore (30 to 45 km) from Point Reyes. Bodega buoy (NDBC-13) and San Francisco buoy (NDBC-26) locations are also shown in dark gray boxes.

Figure 2. Principal Components Analysis (PCA) biplot for environmental indices per cruise. Each cruise is labeled by year-month, with colors representing the year and month written above data points on graph.

Figure 3. Monthly averages of climate indices plotted from December 2003 to December 2009 for North Pacific Decadal Oscillation (NPGO), Pacific Decadal Oscillation (PDO), and Multivariate El Niño Southern Oscillation Index (MEI/ENSO).

Figure 4. 4-month winter averages (December to March) prior to the upwelling seasons of 2004 to 2009 for: a) alongshore wind stress (N/m^2), b) 36 & 39°N averaged Upwelling Index ($\text{m}^3/\text{second}/100\text{m}$ of coastline), and c) sea surface temperature ($^{\circ}\text{C}$). SST and wind velocity measured at NDBC-13.

Figure 5. Monthly averages of surface currents (cm/s) past Point Reyes in the offshore (30 to 45 km) and nearshore (0 to 15 km) environment from December 2003 to December 2009 for a) alongshore flow and b) cross-shore flow. Negative values refer to flow to the south and to the west for alongshore and cross-shore flow, respectively.

Figure 6. Pre-cruise conditions for 30-day weighted average using averages of the month prior to and month of the cruise and plotted per cruise for: a) alongshore wind stress (N/m^2) measured at NDBC-13, b) c) sea surface temperature ($^{\circ}\text{C}$) measured at NDBC-13, and c) offshore (30 to 45 km) and nearshore (0 to 15 km) alongshore flow (cm/s) past Point Reyes. Negative wind stress and alongshore flow refer to winds from the north and flow to the south, respectively. Environmental measurements are plotted per cruise and identified by month and year of data collection (x-axes).

Figure 7. T-S diagram of CTD data obtained at each sampling station along Lines 2, 4, and 6 from 2004 to 2009. CTD data was averaged from near surface to a depth of 50m. The year of each CTD cast is indicated by color.

Figure 8. Average copepod abundance (individuals m^{-3}) per distribution region plotted per cruise. Cruises are identified on the x-axis by the year and month of data collection.

Figure 9. NMDS ordination plots of zooplankton composition from upwelling season samples (April to July) from 2004 to 2009 with year indicated by color. a) NMDS ordination plot for zooplankton species found in >10 samples. b) NMDS ordination plot for all copepod species found in all samples.

Figure 10. Cross-shelf gradients in the four important copepod species, with each vertical panel summarizing results from a different time period: a) all years; b) the first three years (2004-2006); and c) the last three years (2007-2009). In each panel, each figure displays the average abundance of each species (y-axis) at each station (x-axis). Figures are ordered north (top) to south (bottom), and stations are ordered east (right) to west (left).

Figure 11. The average of May-June log abundance for *P. mimus*, *A. longiremis*, *M. pacifica* (short form), *C. pacificus* (bar graph, y-axis on left) compared to 4-month averages of previous winter (December to March) conditions for: a) alongshore wind stress (N/m^2) and Upwelling Index averaged for 36 and 39 deg N and b) nearshore (0 to 15 km) cross-shore surface currents past Point Reyes (cm/s).

Figure 12. Linear regressions of log-abundance values of *P. mimus* (left graphs) and *C. pacificus* (right graphs) on the y-axis and environmental variables (as identified in the BEST test) on the x-axis. Environmental variables are the 4-month average of previous winter (December to March) of the Pacific Decadal Oscillation (PDO; top graphs) and averages for the month and the month prior of the poleward surface flow offshore (30 to 45 km; cm/s) past Point Reyes (bottom graphs). Significance of regression listed next to species name: * $p < 0.05$, ** $p < 0.01$.

Figure

Figure 1

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Figure 3

Figure 4

Figure 5

a) Alongshore Flow

b) Cross-shore Flow

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

Figure 12