CICIMAR Oceánides 30(1): 45-62 (2015)

ZOOPLANKTON FUNCTIONAL GROUPS FROM THE CALIFORNIA CURRENT AND CLIMATE VARIABILITY DURING 1997-2013

Lavaniegos, B. E.[1], O. Molina-González[1] & M. Murcia-Riaño[1,2]

[1]Centro de Investigación Científica y Educación Superior de Ensenada. Carretera Ensenada-Tijuana No. 3918, Zona Playitas, 22860. Ensenada, Baja California, México. [2]Instituto de Investigaciones Marinas y Costeras, Calle 25 No. 2-55, Playa Salguero, Santa Marta, Colombia. email: berlav@cicese.mx; magnolia.murcia@invemar.org.co

ABSTRACT. Zooplankton plays an important role in recycling matter and energy trough the pelagic ecosystem. The California Current is one of the large marine ecosystems with high productivity and bio-physical variability at multiple time scales. An interannual scale or longer periods requires data series sufficiently long to ensure reliable averages of zooplankton abundance in order to estimate their low frequency variability. Here, tendencies in physical and biological variables are presented for the period 1997-2013 with data obtained from IMECOCAL cruises in the Mexican sector of the California Current. The area was divided into four regions, two oceanic (off North and Central Baja California) and two neritic (Vizcaino bay and Gulf of Ulloa). Sea surface temperature (SST) and El Niño Oceanic Index (ONI) showed correlation in all areas, while extratropical indices (PDO and NPGO) exhibited different tendencies among the regions. The PDO had significant correlation with SST only in the central and Vizcaino bay regions. The NPGO was not correlated with temperature but presented significantly strong correlation with sea surface salinity in all regions, which has been attributed to changes in large-scale circulation of the north Pacific subtropical gyre. In spite of a significant influence of the El Niño Southern Oscillation (ENSO) in SST, the correlation between ONI and zooplankton abundance was limited to gelatinous herbivorous (tunicates) from the North region. Local influence was remarkable in Vizcaino bay where the tunicates showed a period of negative abundance anomalies (2000-2004) followed by increasing positive anomalies between 2005 and 2013 associated with positive upwelling index anomalies. Geometric mean abundance of salps (per oceanographic cruise) averaged in Vizcaino bay 33.3 ind m^{-3} during 2005-2013 compared to 1.4 ind m^{-3} in 2000-2004. Salps partially displaced crustacean herbivores since they compete for feeding particles; copepods decreased from 88.2 ind m^{-3} during 2000-2004 to 59.7 ind m^{-3} in 2005-2013; and euphausiids from 16.1 ind m^{-3} to 10.4 ind m^{-3}. In the oceanic domain a period of saline stratification during 2002-2006 was associated with positive anomalies of all trophic groups (crustaceans, tunicates and carnivores). Alternation of particular taxa of tunicates and carnivores is discussed. The increase of gelatinous organisms associated to higher stratification in the oceanic region and enhanced upwellng in the coastal shelf appears to be in detriment of crustaceans, though the time-series are short to outline a more defined trend. That tendency is particularly disturbing in Vizcaino bay affecting the availability of food for fishes and other predators.

Keywords: Baja California, ENSO, salps, copepods, euphausiids

Grupos funcionales de zooplancton de la corriente de California y variabilidad climática durante 1997-2013

RESUMEN. El zooplancton juega un papel fundamental en el flujo de materia y energía en el ecosistema pelágico. La Corriente de California es uno de los grandes ecosistemas marinos con elevada productividad y amplia variabilidad físico-biológica a múltiples escalas temporales. A escala interanual y de mayor periodo es necesario contar con series de datos lo suficientemente extensas temporalmente que permitan calcular promedios robustos de la abundancia del zooplancton y poder estimar la variabilidad de baja frecuencia. En el presente estudio se muestran las tendencias en variables físicas y biológicas del periodo 1997-2013 de los datos obtenidos por los cruceros IMECOCAL en el sector mexicano de la Corriente de California. El área fue dividida en cuatro regiones, dos oceánicas (frente a Baja California, Norte y Central) y dos neríticas (Bahía Vizcaíno y Golfo de Ulloa). En todas las regiones la temperatura superficial del mar (TSM) estuvo correlacionada con El Niño Oceanic Index (ONI). Los índices extratropicales (PDO y NPGO) mostraron diferentes tendencias entre regiones. El PDO tuvo fuerte correlación con la TSM solo en la región central y en Bahía Vizcaíno. El NPGO no se correlacionó con la temperatura pero presentó correlación significativa con la salinidad superficial del mar en todas las regiones, lo cual ha sido atribuido a cambios en la circulación a gran escala del giro subtropical del Pacífico norte. A pesar de una influencia significativa del ENSO en la TSM, la correlación entre el ONI y la abundancia del zooplancton estuvo limitada a los herbívoros gelatinosos (tunicados) de la región Norte. La influencia local fue notable en Bahía Vizcaíno donde los tunicados mostraron un periodo de anomalías negativas (2000-2004) seguido por un periodo con anomalías positivas de creciente amplitud entre 2005 y 2013 asociadas con anomalías positivas del índice de surgencias. La abundancia expresada mediante medias geométricas de salpas (por crucero) mostró en Bahía Vizcaíno 33.3 ind m^{-3} durante 2005-2013 comparada con 1.4 ind m^{-3} en 2000-2004. Las salpas desplazaron parcialmente a los crustáceos herbívoros puesto que ambos compiten por las partículas de alimento; los copépodos disminuyeron de 88.2 ind m^{-3} durante 2000-2004 a 59.7 ind m^{-3} en 2005-2013; los eufáusidos disminuyeron de 16.1 ind m^{-3} a 10.4 ind m^{-3}. En el dominio oceánico un periodo de estratificación salina durante 2002-2006 estuvo asociado con anomalías positivas de todos los grupos tróficos (crustáceos, tunicados y carnívoros). Se discute la alternancia de taxa particulares de tunicados y carnívoros. El incremento de organismos gelatinosos asociado a una mayor estratificación en la región oceánica y a la intensificación de las surgencias en la plataforma costera parece ir en detrimento de los crustáceos, aunque las series de tiempo son cortas para establecer una tendencia definida. Dicha tendencia es particularmente perturbadora en Bahía Vizcaíno al afectar la disponibilidad de alimento para peces y otros depredadores.

Palabras clave: Baja California, ENSO, salpas, copépodos, eufáusidos

Lavaniegos, B. E., O. Molina-González & M. Murcia-Riaño. 2015. Zooplankton functional groups from the California current and climate variability during 1997-2013. *CICIMAR Oceánides*, 30(1): 45-62.

Fecha de recepción: 26 de marzo de 2015 Fecha de aceptación: 23 de abril de 2015

INTRODUCTION

Zooplankton abundance is highly variable in space and time and in greater extent in advective marine ecosystems as the California Current (CC). The Mexican region off Baja California has received increasing attention thanks to the intensive plankton monitoring by the California Current Mexican Investigations program (IMECOCAL, Spanish acronym) (Fig. 1). The better studied zooplankton at species level in the IMECOCAL region are copepods (Jiménez-Pérez & Lavaniegos, 2004; Lavaniegos & Jiménez-Pérez, 2006), euphausiids (Lavaniegos & Ambriz-Arreola, 2012), amphipods (Lavaniegos, 2014; Lavaniegos & Hereu, 2009), salps (Hereu *et al.*, 2006), and fish larvae (Funes-Rodríguez *et al.*, 2006; Jiménez-Rosenberg *et al.*, 2007, 2010). However, communities as a whole remain elusive due to the arduous and time consuming work required to identify species from multiple taxonomic groups in subtropical regions; which are particularly diverse as has been shown for amphipods (Lavaniegos & Hereu, 2009). An alternative way to address community structural changes is through functional diversity, namely the abundances of organisms with different morphology and trophic function in the ecosystem (Walker, 1992). Functional groups are relatively easy to identify and may be counted from one fraction of the sample (Ohman & Lavaniegos, 2002).

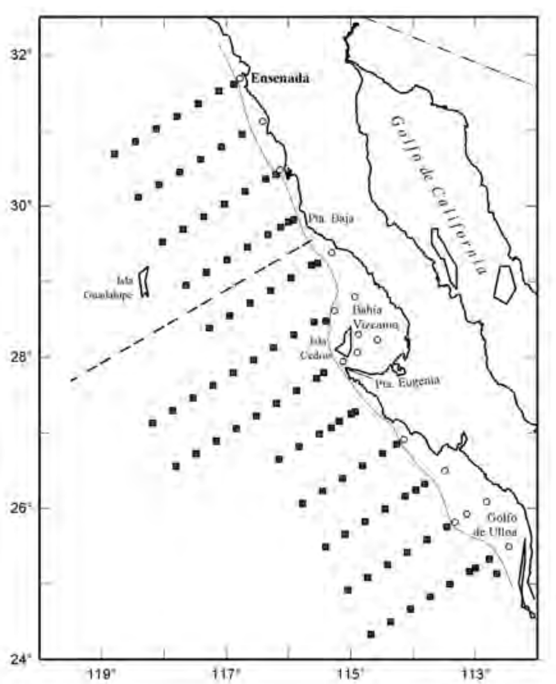

Figure 1. Sampling area showing oceanographic stations and the 200 m isobath. Oceanic and coastal stations are indicated with black squares and white circles, respectively. Dashed line is the boundary of north and central regions used in this study.

Species are better valuable indicators of climate variability, particularly those adapted to narrow temperature ranges. Functional groups are considered relatively less sensitive but they may also respond to different types of environmental perturbations (Lavaniegos & Ohman, 2007; Lavaniegos, 2009; Lavaniegos *et al.*, 2010). One example of this ecological sensitivity is the increase in chaetognaths abundance during the strong El Niño 1997-1998, while salps increased during the transition to La Niña conditions with swarms of these organisms covering a large area off Baja California (Lavaniegos *et al.*, 2002; Hereu *et al.*, 2006). Long-term changes are also reflected by functional groups as it has occurred with the biomass declination of salps during the warm regime of 1977-1998 off southern California (Lavaniegos & Ohman, 2003).

Lavaniegos (2009) analyzed the interannual variability of zooplankton groups by trophic levels in the Mexican sector off the California Current during the period 1997-2007, and detailed time-series for zooplankton major taxa were offered in Lavaniegos *et al.* (2010). The most remarkable events were El Niño 1997-1998, followed by La Niña 1998-2000, and the subarctic water intrusion in 2002-2003. This last atmospheric and oceanographic event produced sequential events in the pelagic ecosystem causing high chlorophyll-*a* concentrations (Gaxiola-Castro *et al.*, 2010), apparently not consumed due to a drop in zooplankton biomass at the end of 2002. Furtherly, the zooplankton biomass followed a progressive recovery between 2003 and 2007 (Lavaniegos, 2009). The increasing abundance trend was observed in herbivores (crustaceans and tunicates) and carnivores (chaetognaths, siphonophores, medusae, ctenophores, and heteropods) suggesting a general increase in secondary production. A significant correlation of zooplankton biomass and North Pacific Gyre Oscillation prompted to think in a basin scale forcing more than regional mechanisms (Lavaniegos, 2009). However, the influence of two weak El Niño events (2004-2005 and 2006-2007) and La Niña 2005-2006 were not specifically discussed by Lavaniegos (2009).

El Niño events have been weak since the beginning of the 21st century presenting moderate sea surface temperature (SST) anomalies complicating their forecast (Fedorov *et al.*, 2003; Lee & McPhaden, 2010). These weak El Niño events are currently considered a new type of El Niño, with high warm anomalies limited to the central equatorial Pacific flanked by anomalously cooler SST to its east and west, what is named El Niño Modoki or Central Pacific (CP) El Niño (Ashok *et al.*, 2007; Kug *et al.*, 2009). This anomalous SST pattern is different from that observed during typical El Niño events or Eastern Tropical Pacific (EP) El Niño with propagation of warm SST anomalies from central to eastern equatorial Pacific. Atmospheric differences are also observed with a western displacement of the main rainfall center during CP El Niño (Yeh *et al*., 2009). Yeh *et al*. (2009) confirmed a higher incidence of CP El Niño since 1990 which could be associated to global warming. In the present study we re-analyse of the biophysical coupling between zooplankton and climatic indices including ENSO with updated time series (1997-2013) to infer if the weak El Niño events produced detectable changes in the abundances of zooplankton identified into major taxa or these were only caused by the strong events (1997-1998).

MATERIAL AND METHODS

The study area is located in the Mexican sector of the California Current, downstream along the Baja California peninsula (Fig. 1). This region was sampled between September 1997 and May 2013 by quarterly cruises on the R/V Francisco de Ulloa. The total number of cruises performed was 55 with only 8 missing cruises (see Appendix Table 1 for dates of cruises). At each station hydrographic casts were done using a Seabird CTD. Zooplankton was collected with a bongo net of 0.5 mm mesh-width by performing oblique tows in the upper 210 m to the surface (from 10 m above the bottom at shallow stations). The diameter of the net was 61 cm before October 2001, and later it was replaced by one of 71 cm. The volume of water strained was measured with a digital flow-meter fixed in the mouth of the net. Samples were preserved with 4% formalin and sodium borate.

In the laboratory, the zooplankton was counted from a fraction of the original sample, between 1/8 and 1/32, depending on the amount of plankton. Major taxa were counted under a stereoscopic microscope. Taxa considered in this study were crustaceans herbivores/omnivores (copepods and euphausiids), herviborous tunicades (appendicularians, doliolids, salps, and pyrosomes), and carnivores (chaetognaths, siphonophores, medusae, ctenophores, and heteropods). Other taxonomic groups usually had low abundances and were neglected. The zooplankton was counted only from samples collected during night in the oceanic regions (bottom depth >200 m) in order to reduce the well known day-night variability due to zooplankton vertical migration and daytime visual zooplankton net avoidance. In the coastal shelf all samples were analyzed regardless of the hour of sampling given the low number of coastal stations (Fig. 1, Appendix Table 1).

Zooplankton taxa abundances were standardized to ind m^{-3}. In order to normalize the data these were transformed to logarithms (log x + 1). Subsequently, anomalies of zooplankton abundances were calculated removing the long-term seasonal means for the period 1997–2013 in four separate ecoregions (Fig. 1): two oceanic (north and central) and two coastal (Vizcaino bay and Gulf of Ulloa). Several cruises did not cover all four sampling regions or had few data in some region, and therefore were discarded in the calculation of abundance anomalies.

Anomalies of environmental variables were estimated in the same form described for zooplankton data. Cruises with only one datum of physical variables for any particular region, as in biological variables, were discarded for anomalies calculation. Several oceanographic cruises had a time lag compared to usual sampling months, introducing uncertainty in calculations of sea surface temperature anomalies. This is particularly critical in summer and autumn when surface temperature typically changes 1-2°C from one month to the next (or even larger changes in the coastal shelf, see Appendix Figure). For example, cruises 9908 and 0708 had 20 and 38 days of delay respectively in relation to the average performance of the rest of summer cruises. Due to the climatological mean is more representative of July would result in overestimation of anomalies in cruises done in August. The bias introduced by time lags was corrected adding (or subtracting) the monthly increment of temperature based in information from CALCOFI data from the period 1951-1966. This correction to mean temperature in such cruises out of date was applied only when the time lag was >15 days and if the monthly increment represented >0.5°C (see Appendix Tables 1 for date cruises and Table 2 for temperature values).

Spearman correlations were done between zooplankton taxa abundances and environmental variables (Table 1). Regional environmental variables were sea surface temperature (SST), sea surface salinity (SSS), and upwelling Index (UI). The measurement at 10 m was used to represent SST and SSS to avoid diurnal variations and ensuring the stabilization of CTD sensor. In oceanic stations thermal and saline stratification (dT and dS respectively) were also included as the difference between values at 10 and 200 m depths. Large-scale climatic indices were also correlated with local variables: El Niño Oceanic Index (ONI), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO). Source for each environmental variable is shown in Table 1. Monthly values of the PDO, NPGO, and UI anomalies were converted to quarterly means in correspondence with the zooplankton data frequency for further Spearman correlation analysis. This was done averaging values for winter (December to February), spring (March to May), summer (June to August), and autumn (September to November).

RESULTS

Large scale Pacific indices

El Niño index for the oceanic region 3.4 (ONI) is based on surface temperature and during the study period the highest positive values (>2) were associated with El Niño 1997-1998 (Fig. 2a). The rest of El

Table 1. Environmental variables used in correlation analyses.

Variables	Code	Source
Local		
10 m temperature anomalies	SST	IMECOCAL
10 m salinity anomalies	SSS	IMECOCAL
Thermal stratification anomalies (10-200 m)	dT	IMECOCAL
Saline stratification anomalies (10-200 m)	dS	IMECOCAL
Upwelling Index station 30°N, 119°W (used for north and Vizcaino bay regions) station 27°N, 116°W (used for central and Ulloa regions)	UI	NOAA Pacific Fisheries Environmental Laboratory (http://www.pfel.noaa.gov/products/PFEL/modeled/indices/PFELindices.html) Indicate water transport due to wind stress with units of $m^3 s^{-1}$ per 100 m of coastline. Monthly means were calculated from daily values. Negative index indicate downwelling and positive for upwelling (from –270 to +442 and –241 to +607 in the selected locations).
Large-scale		
El Niño Oceanic Index 3.4 (region 5°N-5°S, 120°-170°W)	ONI	NOAA Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml). Index based on sea surface temperature anomalies and is defined as the three-month running-mean SST departures NOAA ERSST data. El Niño is characterized by ONI ≥ +0.5 C, and La Nina ≤ -0.5 C in 5 consecutive 3-months running mean.
Pacific Decadal Oscillation Index	PDO	(http://jisao.washington.edu/pdo/PDO.latest) Derived as the leading principal component of monthly SST anomalies in the north Pacific Ocean, poleward to 20°N. Value ranged from –3.6 to +3.5 during 1900-2013
North Pacific Gyre Oscilllation	NPGO	(http://eros.eas.gatech.edu/npgo/data/NPGO.txt) Second dominant mode of sea surface height variability (2nd EOF SSH) in the Northeast Pacific. Assuming that anomalies of SSH reflect changes in geostrophic flow, positive values indicate strengthening of the North Pacific Current and in consequence in the California Current. Value range is -3 to +3.

Niño events presented lower values with short peaks just over +1 anomaly only in three events (2002-2003, 2006-2007, and 2009-2010). In contrast, the cool phase of ENSO showed a persistence of two years in three La Niña events (1998-2000, 2007-2009, and 2010-2012), and only La Niña 2005-2006 was less than two years.

The North Pacific decadal oscillation showed a pattern relatively similar with the ONI (Fig. 2b). Major shifts of PDO occurred at the end of the years 1998, 2002, and 2007. Further, between 2007 and 2013 values remained negative excepting one short period in 2009-2010. The North Pacific Gyre Oscillation changed from negative to positive in the winter of 1998 remaining positive until the end of 2004 (Fig. 2c). After a short period of two years with negative values, the NPGO changed again observing a long period of positive values (2007-2013). The PDO and NPGO varied inversely for long periods though there was an interval in 2002-2004 in which both indices (and also the ONI) were positive.

Environmental variables

Anomalies of temperature, salinity, and upwelling index off Baja California presented different long-term tendencies (Figs. 3-5). In consequence, the correlations with large scale indices were also variable and not always coherent among sampling regions (Table 2). The ONI showed significant positive correlations with SST anomalies from all regions (Figs. 3a, 4a, 5a, c) suggesting that the ENSO influence reached the study region. However, the low correlation coefficients between ONI and SST (Table 2) are also indicative of local factors influence. SST positive anomalies followed well the positive anomalies of the ONI except during 2002 when negative anomalies occurred off Baja California and were particularly strong in October 2002 for the central region (Fig. 3a). These negative anomalies corresponded with a subarctic water intrusion (Durazo *et al*., 2005), apparently causing a delay in the warming due to El Niño 2002-2003; that effect was finally observed as a shift from negative to positive anomalies in local temperature in the beginning of 2003.

Another difference between ONI and regional temperatures was the magnitude of La Niña events. Following the ONI, three cool events of similar magnitude may be traceable (1999-2000, 2007-2008, and 2010-2012; see Fig. 2a). In contrast, oceanic regions off Baja California recorded lower intensity for the first two events compared to La Niña 2010-2012 (Figs. 3a, 4a). Similar observations were found from Vizcaino bay (Fig. 5a). In the Gulf of Ulloa SST anomalies (Fig. 5c) had more negative values during 1999 (-1 to -2°C) compared to Vizcaino bay, and could be even more negative but there were gaps in the first part of the time-series when the warm phase of the ENSO took place. La Niña 2007-2008 showed weak and fleeting anomalies, coherent in the coastal shelf as in oceanic regions compared to the strength and endurance depicted by the ONI.

Thermal stratification (dT) anomalies in the oceanic regions (Figs. 3b, 4b) were similar to SST indicating that the interannual warming (cooling) is less intense at 200 m during El Niño (La Niña) and therefore the difference with the SST produced a higher (lower) gradient. However dT anomalies were significantly correlated with ONI only in the Central region (Table 2).

The upwelling index was inversely correlated with ONI (Table 2) showing negative UI anomalies roughly coincident with El Niño events (Figs. 3e, 4e). However, differences between ONI and UI were also evident as the predominance of negative anomalies in 2000-2004, followed by a period of positive anomalies only interrupted by a short interval of strongly negative anomalies between October 2009 and April 2010. This period of relaxed UI is consistent with a shift from El Niño 2009-2010 to La Niña 2010-2012. Therefore, the UI pattern appears to be opposite to that observed during the 1997-2000 ENSO cycle which presented light positive anomalies during the warm phase and close to zero in the cool phase.

Positive significant correlations were found between the PDO and local temperature, similar to those observed with ONI, as the variability pattern of PDO and ONI were quite similar (Fig. 2a,b). Negative PDO values were roughly consistent with La Niña while positive values with El Niño. A different pattern was obtained for the sea surface salinity (SSS) without correlation with the ONI. Instead, the SSS anomalies in the four regions (Figs 3c, 4c, 5b, d) were significantly correlated with the NPGO (Table 2). According to Di Lorenzo *et al*. (2008) NPGO index captures changes in the strength of the North Pacific Current implying that positive values observed most of the time during 1997-2013 could lead to reinforce the CC. Sign anomaly reversions

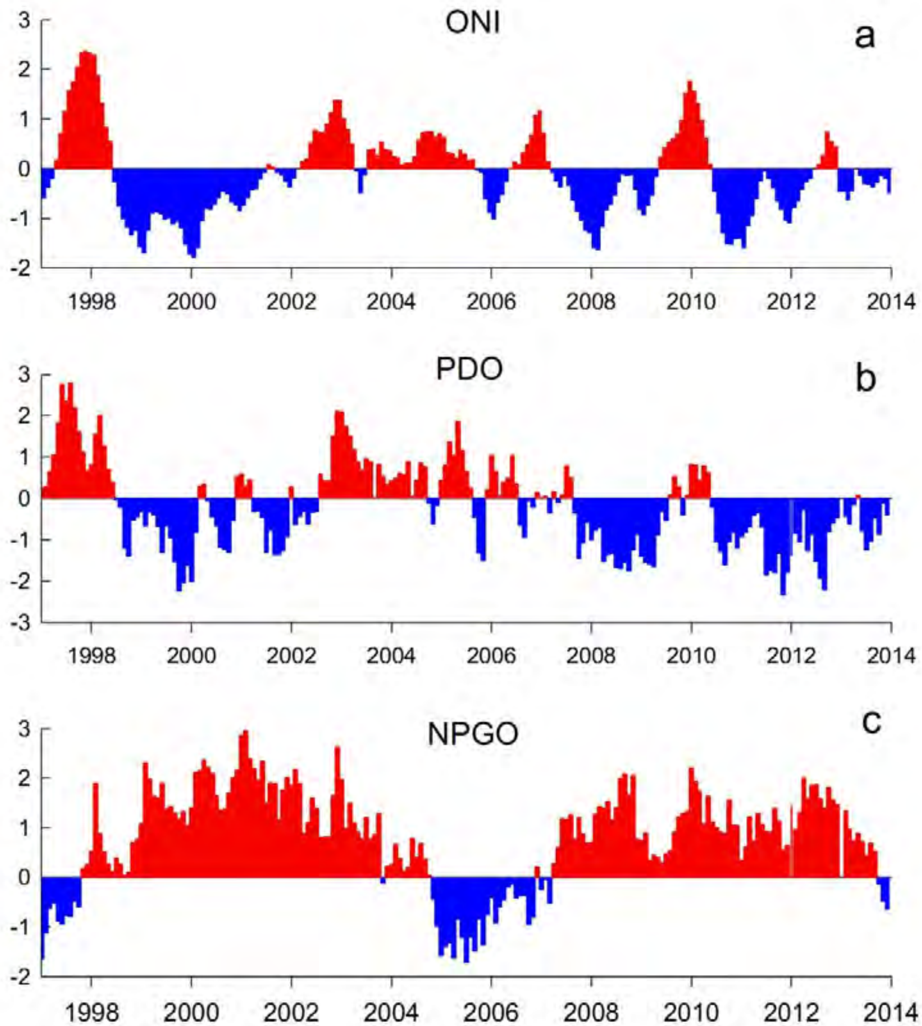

Figure 2. Climatic indices: (a) El Niño Oceanic Index from region 3.4 (5°N-5°S, 120°-170°W), (b) Pacific Decadal Oscillation, and (c) North Pacific Gyre Oscillation.

Table 2. Spearman correlation matrix between environmental variables (anomalies) and climatic indices in four regions off Baja California: oceanic (North and Central) and coastal (Vizcaino bay and Gulf of Ulloa). Significant coefficients are highlighted: p<0.001 (***), p<0.01 (**), and p<0.05 (*). For complete name of variables see Table 1.

Variable	n	ONI	PDO	NPGO
North Region				
SST	54	0.343 **	0.159	−0.145
dT	54	0.154	0.039	−0.046
SSS	54	−0.184	−0294 *	0.619 ***
dS	54	0.247	0.307 *	−0.598 ***
UI	63	−0.265 *	−0.250 *	−0.099
Central Region				
SST	53	0.560 ***	0.447 ***	−0.144
dT	53	0.448 ***	0.475 ***	−0.091
SSS	53	0.136	−0.094	0.511 ***
dS	53	−0.048	−0.015	−0.518 ***
UI	63	−0.409 ***	−0.443 ***	−0.046
Vizcaino bay				
SST	52	0.505 ***	0.400 **	−0.036
SSS	52	0.067	−0.136	0.458 ***
Gulf of Ulloa				
SST	45	0.527 ***	0.020	0.039
SSS	45	0.294	−0.065	0.528 ***

appear to be gradual excepting the winter of 2004-2005 which means drastic weakening of the North Pacific Current (Fig. 2c). In coincidence, local SSS anomalies during 2002-2003 experienced a gradual decrease in magnitude changing from positive to negative and reaching the most negative value in February 2004, more clearly observed in the North oceanic region (Fig. 3c). Shortly after, the inverse process took place reaching positive SSS anomalies in 2007. The oscillation in SSS anomalies was not entirely gradual during the second period of positive NPGO (2007-2013), showing a decreasing pulse in 2010-2011.

In the oceanic domain, inverse correlations were found between saline stratification anomalies (dS) and NPGO. The inverse pattern of dS anomalies (Figs. 3d, 4d) and SSS anomalies (Figs. 3c, 4c), reversing signs in the water column, could be attributable to a more saline subsurface water mass y a strengthening of the California Undercurrent at 200 m. Therefore, the period of positive dS anomalies recorded in 2004-2007 indicate a strong saline stratification coincident with the negative NPGO (Fig. 2c).

Correlations between PDO and salinity anomalies were found only in the north region, positive for SSS and inverse to dS (Table 2). Correlation coefficients were lower to those observed for the NPGO and with reverse signs due the PDO is inversely correlated with NPGO (r = -0.29, p = 0.022).

Trophic zooplankton groups

Abundances of the trophic zooplankton groups presented high seasonal and interannual variability (Figs. 6-7). Crustaceans (herbivore/omnivores) were the most abundant taxonomic group in the oceanic regions followed by carnivores, and tunicates in third place (Fig. 6a, b). In the north region, all trophic groups presented similar patterns of abundance anomalies (Fig. 6c-e) with a predominance of negative anomalies between 1998 and 2004 and positive anomalies between 2004 and 2010. However, some differences in magnitude may be observed as a higher positive anomaly of carnivores compared to herbivore groups in the winter of 1998, highest positive anomalies of tunicates in the summers of 2001 and 2002, as well as slight time offsets in the shift from positive to negative anomalies at the end of the time-series.

All the northern trophic groups were inversely correlated with the NPGO while positive correlations with ONI were restricted to tunicates and carnivores, and none correlation was observed with the PDO (Table 3). The lack of correlation with local variables is noteworthy, except for tunicates and ds that indicate increasing abundances with saline stratification. The proportion of doliolids was higher in most of the 1999-2002 cruises while during the years of strongest dS anomalies (2003-2006) the

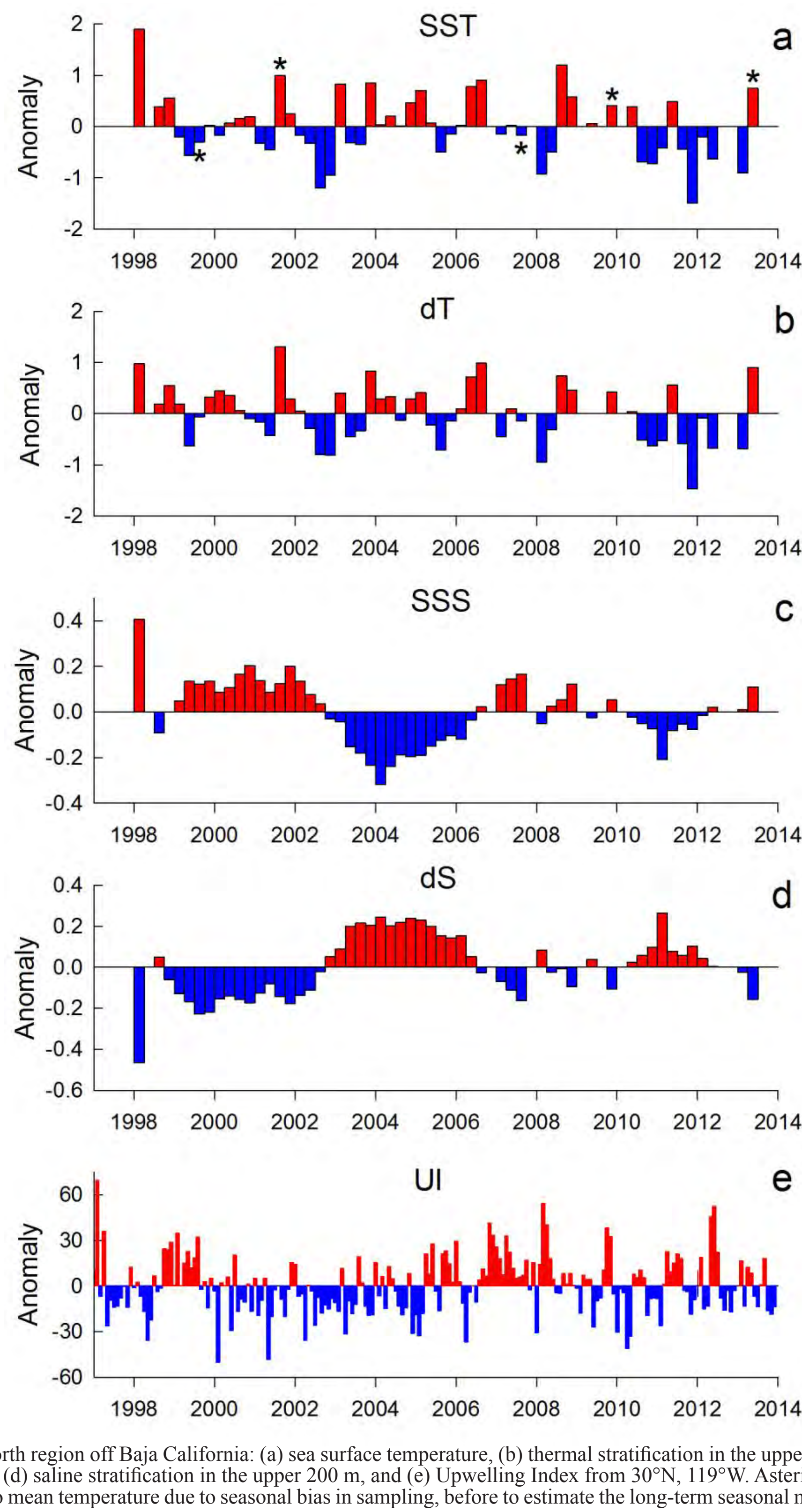

Figure 3. North region off Baja California: (a) sea surface temperature, (b) thermal stratification in the upper 200 m, (c) sea surface salinity, (d) saline stratification in the upper 200 m, and (e) Upwelling Index from 30°N, 119°W. Asterisks indicate corrections made to mean temperature due to seasonal bias in sampling, before to estimate the long-term seasonal mean and anomalies.

Table 3. Spearman correlation between zooplankton abundance anomalies with environmental variables (anomalies) and climatic indices in four regions off Baja California: oceanic (North and Central) and coastal (Vizcaino bay and Gulf of Ulloa). Significant coefficients are highlighted: p<0.001 (***), p<0.01 (**), and p<0.05 (*). For complete name of variables see Table 1.

Variable	n	Crustaceans	Tunicates	Carnivores
North Region				
ONI	54	0.163	0.448 ***	0.282 *
PDO	54	0.089	0.214	0.061
NPGO	54	−0.366 **	−0.391 **	−0.511 ***
SST	54	−0.154	0.120	0.003
dT	54	−0.249	0.067	−0.140
SSS	54	−0.130	−0.203	−0.176
dS	54	0.239	0.281 *	0.267
UI	54	−0.051	−0.014	0.157
Central Region				
ONI	53	0.153	0.131	0.297 *
PDO	53	−0.026	0.225	0.302 *
NPGO	53	−0.074	−0.254	−0.305 *
SST	53	−0.048	0.122	0.374 **
dT	53	−0.118	0.091	0.288 *
SSS	53	0.140	0.028	0.116
dS	53	0.048	−0.090	−0.027
UI]	53	0.385 **	0.193	0.095
Vizcaino bay				
ONI	52	0.130	−0.176	−0.078
PDO	52	0.341 *	−0.215	0.194
NPGO	52	−0.109	−0.188	−0.402 **
SST	52	−0.026	0.146	0.066
SSS	52	−0.036	0.043	−0.056
UI	52	−0.005	0.286 *	0.194
Gulf of Ulloa				
ONI	43	0.169	0.115	0.072
PDO	43	0.134	0.184	0.238
NPGO	43	−0.124	−0.313 *	−0.310 *
SST	43	−0.076	0.000	−0.240
SSS	43	−0.070	−0.087	−0.112
UI	43	0.072	0.019	0.234

community was characterized by predominance of appendicularians and salps (Fig. 8b).

Anomaly patterns of the trophic groups maintained a relative temporal coherence in the central region (Fig. 6f-h), albeit less harmonized compared to the northern zooplankton. The group of tunicates from central region showed strong anomalies during 1998 and 2010 probably associated to El Niño events but no significant correlation was observed with ONI (Table 3). In contrast the carnivores from the central region were correlated with the three Pacific indices (ONI, PDO, and NPGO), and also with local variables (SST and dT), suggesting that thermal stratification was favorable for the proliferation of these organisms. Chaetognaths were the main proportion of carnivores during El Niño 1997-1998 with a mean of 65% (Fig. 8f). Furtherly, chaetognaths continued as the most abundant carnivores but during the stratified period of 2003-2006 represented a lower proportion (55%), gained by siphonophores (38%). Crustaceans showed correlation only with UI anomalies without evident changes in the proportion of copepods and euphausiids through the time-series (Fig. 8d). Tunicates were not correlated with any environmental variable (Table 3).

Trophic groups from the coastal shelf presented stronger seasonal and interannual variability (Fig. 7a, b) compared to oceanic zooplankton. Crustaceans were the most abundant group while abundances of tunicates and carnivores were relatively similar. In Vizcaino bay, contrasting long-term trends were observed in abundance anomalies of crustaceans and gelatinous herbivores, with the first decreasing while the second increased (Fig. 7c, d). Patterns of abundance anomalies were of the same sign in carnivores (Fig. 7e) and tunicates (Fig. 7d) but only the latter presented amplified anomalies toward the end of the time-series. None of the trophic groups in coastal habitat were correlated with ONI (Table 3). Instead, correlations with other indices were observed, crustaceans with PDO and carnivores with NPGO. Dominance of negative anomalies for crustaceans during 2007-2013 coincided with negative values of the PDO and euphausiids appeared to be more affected after 2010 (Fig. 8g). However, absolute abundances of both copepods and euphausiids showed a strong decrease in Vizcaino bay between 2007-2013, with abundances of 40 and 7 ind m^{-3} respectively, implying a decrease of 48 and 43% in comparison with 1998-2006 period.

Carnivores were inversely correlated with NPGO in Vizcaino bay (Table 3). During the stratified period (2003-2006) the highest proportion of carnivores were siphonophores (66%) while chae-

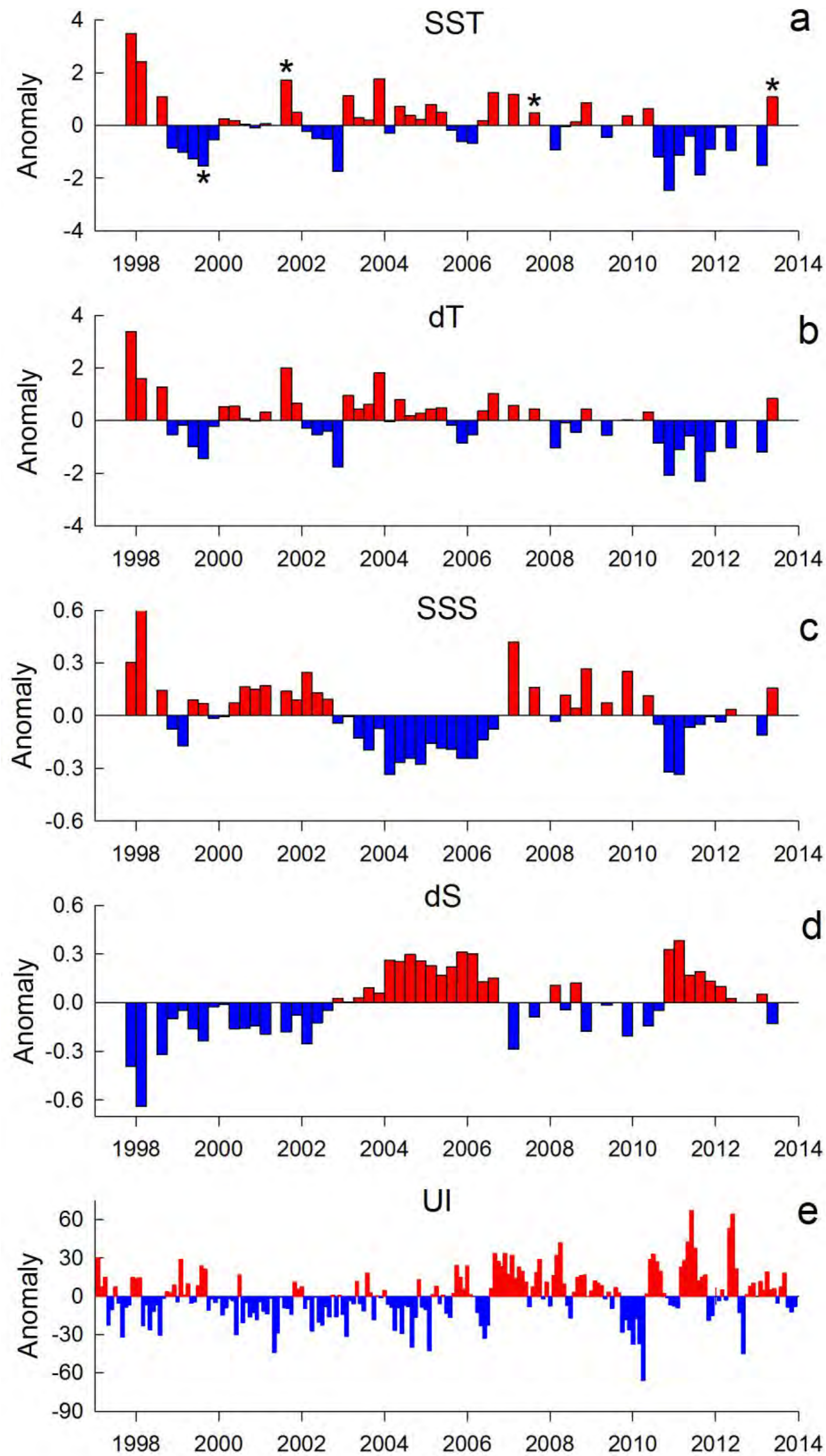

Figure 4. Central region off Baja California: (a) sea surface temperature, (b) thermal stratification in the upper 200 m, (c) sea surface salinity, (d) saline stratification in the upper 200 m, and (e) Upwelling Index from 27°N, 116°W. Asterisks indicate corrections made to mean temperature due to seasonal bias in sampling, before to estimate the long-term seasonal mean and anomalies..

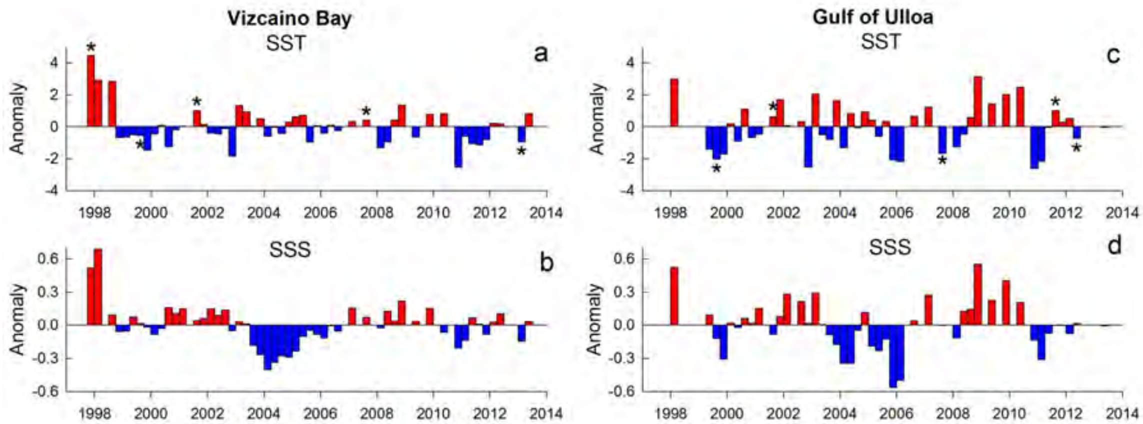

Figure 5. Coastal shelf properties at Vizcaino bay (a-b) and the Gulf of Ulloa (c-d). Anomalies of sea surface temperature (a, c) and sea surface salinity (b, d) are shown. Asterisks indicate corrections made to mean temperature due to seasonal bias in sampling, before to estimate the long-term seasonal mean and anomalies. Anomalies from the Gulf of Ulloa must be taken with caution due to a deficient sampling coverage.

tognaths averaged only 25% (Fig. 8i). The tunicates were correlated with UI anomalies (Table 3). Appendicularians reaching a mean of 72% of the tunicates numerically predominated during the period with mostly negative UI anomalies (2000-2004) (Fig. 8h). In contrast during 2005-2013, when UI anomalies were mostly positive, appendicularians represented only 31% of the tunicates. As appendicularians decreased their abundances, salps increased from 24 to 60 % during 2005-2013.

Slightly different patterns were found in the Gulf of Ulloa for all the trophic groups (Fig. f-h). Contrary to observations in Vizcaino bay, crustaceans from the Gulf of Ulloa showed several positive anomalies during 2010-2013 (Fig. 7f), tunicates had mainly moderate positive anomalies between 2005 and 2010 shifting further to negative (Fig. g), and carnivores shifted to moderated negative anomalies since 2008 (Fig. 7h). The only significant correlations were with NPGO for the groups of tunicates and carnivores (Table 3). A low number of data available for the Gulf of Ulloa probably precluded significant correlations for carnivores with environmental variables. The proportion of appendicularians was higher during 2000-2004 (Fig. 8k) as it occurred in Vizcaino bay (Fig. 8h). However, the relative abundance of doliolids was higher in the Gulf of Ulloa, particularly during 2005 (Fig. 8k). The incidence of salps increased mainly after 2008. However, mean absolute abundances for salps in the Gulf of Ulloa during 2008-2013 were considerably lower (8 ind m^{-3}) than abundances from Vizcaino bay (44 ind m^{-3}).

DISCUSSION

The period covered in the present study (1997-2013) was complicated by the simultaneous occurrence of diverse atmospheric and oceanographic processes. Among these were: 1) the ENSO with two different flavors (Canonical and Modoki) forcing the ecosystem from the equatorial Pacific; 2) extra-tropical oscillations related to geo-position of atmospheric pressure cells (PDO), and the strength of the North Pacific gyre (NPGO); 3) local upwelling intensity fueled forced by global warming.

ENSO effects

Following the ENSO signal in the study region was particularly difficult due to problems with SST anomalies. These are the basis for identifying the propagation of the thermal signal from the tropics but require robust seasonal means not only in the number of years involved but also in the month of sampling schedule. This problem was evident with several IMECOCAL cruises mainly for the summer. Fortunately, monthly temperatures for Baja California waters are available from the historic CALCOFI cruises (1951-1966) performed on a monthly basis that represent a strong baseline to understand seasonal variability of temperature in this region. These were useful to adjust *in situ* temperatures with time-lags during the study period (1997-2013). After temporal correction, a correlation was found between ONI and SST, which was particularly strong in the oceanic central region (r = 0.560). The same result was found by Herrera-Cervantes *et al*. (2014) using satellite derived sea surface temperature off Punta Eugenia.

While it is true that El Niño influence was detected, differences in magnitude between ONI and local SST anomalies are intriguing, as well as differences in SST within regions. For the event of 2002-2003 Lavaniegos (2014) suggested a blocking of the poleward propagation of El Niño during summer 2002 due to a large eddy of subarctic water located offshore to Punta Eugenia. Mesoscale eddies that are recurrent in the vicinity of Punta Eugenia (Soto-Mardones *et al*., 2004) could be enhanced

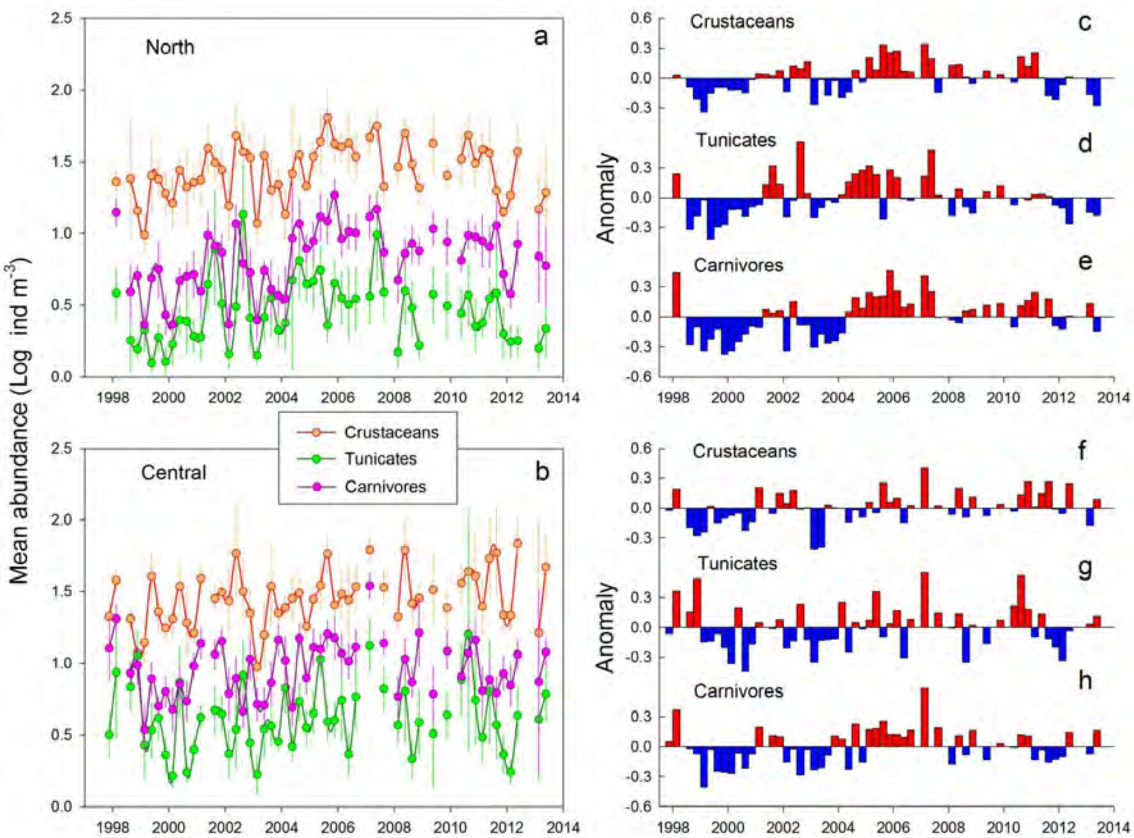

Figure 6. Trophic zooplankton groups mean abundances (± 95% confidence interval) from north (a) and central (b) oceanic regions. Anomalies are also shown for the north (c-e) and central (f-h) regions in separated insets for crustaceans (c, f) tunicates (d, g), and carnivores (e, h).

during other weak El Niño events, avoiding the spread northward to Punta Baja of SST anomalies, inasmuch a significant correlation between SST and ONI was not found in the north region during 2002. The advection of water and the propagation of SST anomalies has become an issue in El Niño theoretical discussions (Yeh *et al*., 2009; Lee & McPhaden, 2010). However, the period of 2002-2007 with frequent weak El Niño events (mostly Modoki type) presented other influential perturbations in the water column as was higher thermohaline stratification in 2003-2006. Stronger thermal and saline gradients could affect to vertical migrating organisms as was observed in copepods by Lougee *et al*. (2002); but in contrast it could be favorable for gelatinous zooplankton which efficiently maintains an osmotic balance with seawater (Sanders & Childress, 1995).

Decadal Variability

Peterson and Schwing (2003) considered the occurrence of a climate shift in 2002-2003 as the PDO reversed sign, and a higher numerical dominance of cold water copepods was observed. In the present study, isolated significant correlations were observed for PDO, crustaceans from Vizcaino bay and carnivores from the central region. A strong decrease of abundance of crustacean (copepods and euphausiids) is consistent with negative values of PDO in 2002-2003 and again during the 2007-2013 period (Figs. 2b and 7c). This could indicate that subtropical dominant species such as *Calanus pacificus* and *Nyctiphanes simplex* could be affected by cold water. The response of the euphausiid *N. simplex* as a function of the PDO was documented with an increased abundance during warm regime for southern California (Brinton & Townsend, 2003).

However, changes observed in the zooplankton community in the present study joint with salinity were better correlated with the NPGO. The shift in 2002-2003 was marked with a northward movement of the North Pacific Current from 42° to 51°N (Freeland & Cummins, 2005) increasing the volume of subarctic water in the California Current (Bograd & Lynn, 2003; Huyer, 2003; Durazo *et al*., 2005). The subarctic water intrusion promoted high productivity at first, but after 2002 a strong decrease in chlorophyll-*a* concentration followed and remained low until 2006 (Gaxiola *et al*., 2010), which could be related with stratification of the water column as

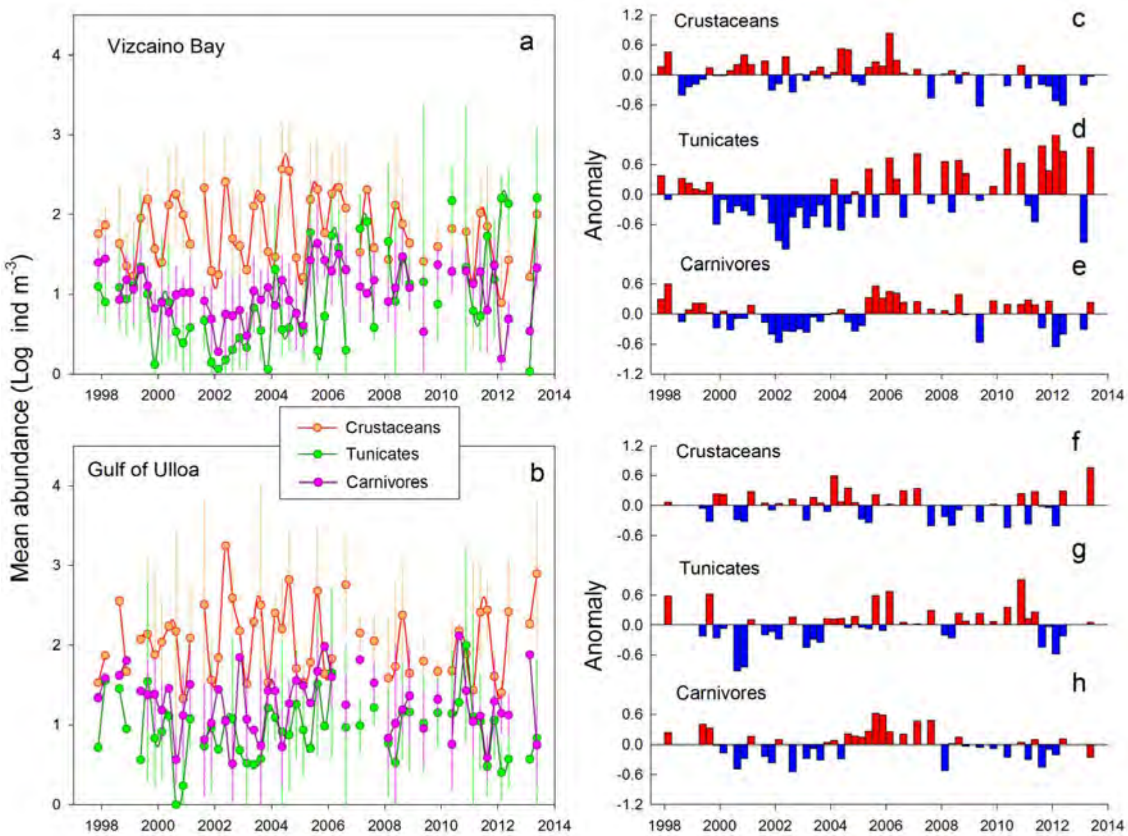

Figure 7. Trophic zooplankton groups mean abundances (± 95% confidence interval) from Vizcaino bay (a) and the Gulf of Ulloa (b). Anomalies are also shown for Vizcaino bay (c-e) and and the Gulf of Ulloa (f-h) in separated insets for crustaceans (c, f) tunicates (d, g), and carnivores (e, h).

the pattern was similar to SSS and dS anomalies reported in the present study (Figs. 3-4). Therefore, the variability of chlorophyll-*a* concentration and salinity appears to be more related to NPGO than to El Niño events. Satellite derived surface chlorophyll-*a* off Punta Eugenia did not show correlation with the multivariate El Niño index (Herrera-Cervantes *et al*., 2014). Tunicates showed a significant correlation with dS in the north region (Table 3), meaning that low chlorophyll-*a* concentrations during high stratification in 2003-2006 (Gaxiola *et al*., 2010) were favorable for these gelatinous herbivores. These observations are consistent with the incidence of salps and doliolid blooms reported in mesotrophic conditions which are more suitable to their fine mucous filters (Deibel *et al.,* 2009). The size of phytoplankton particles could also play a part in the formation of large aggregations of tunicates. This last statement is suggested by the remarkable high proportion of appendicularians (Fig. 8b), which are known to feed on nanophytoplankton (Acuña *et al*., 1996).

Upwelling effects

The correlation between SST anomalies and ONI was significant but coefficients were relatively low (r < 0.6). Other influences are affecting the pelagic ecosystem as it is reflected in the SST anomalies; for example the low magnitude for negative anomalies during La Niña 2007-2008 (Figs. 3a, 4a, 5a, c). Climate change could be behind the inconsistencies in magnitude of temperature anomalies since has been documented a persistent warming of the word ocean since 2006 (Roemmich *et al*., 2015). This also could explain the intensification of coastal upwelling since 2005, induced by enhanced alongshore winds by differential land-ocean heating due to greenhouse effect (Bakun *et al*., 2015; Wang *et al*., 2015). While strong upwelling may lead to enhanced nutrient enrichment, hypoxic events will be prone to occur and ocean acidity will rise. Hypoxic events are already underway in Vizcaino bay where fishermen from Isla Natividad reported unusual high mortality of abalone, sea urchins, and other benthic organisms during the spring 2009 and summer 2010, associated with shoaling of hypoxic waters (Micheli *et al*., 2012) similar to other events reported in northern coastal areas of the California Current

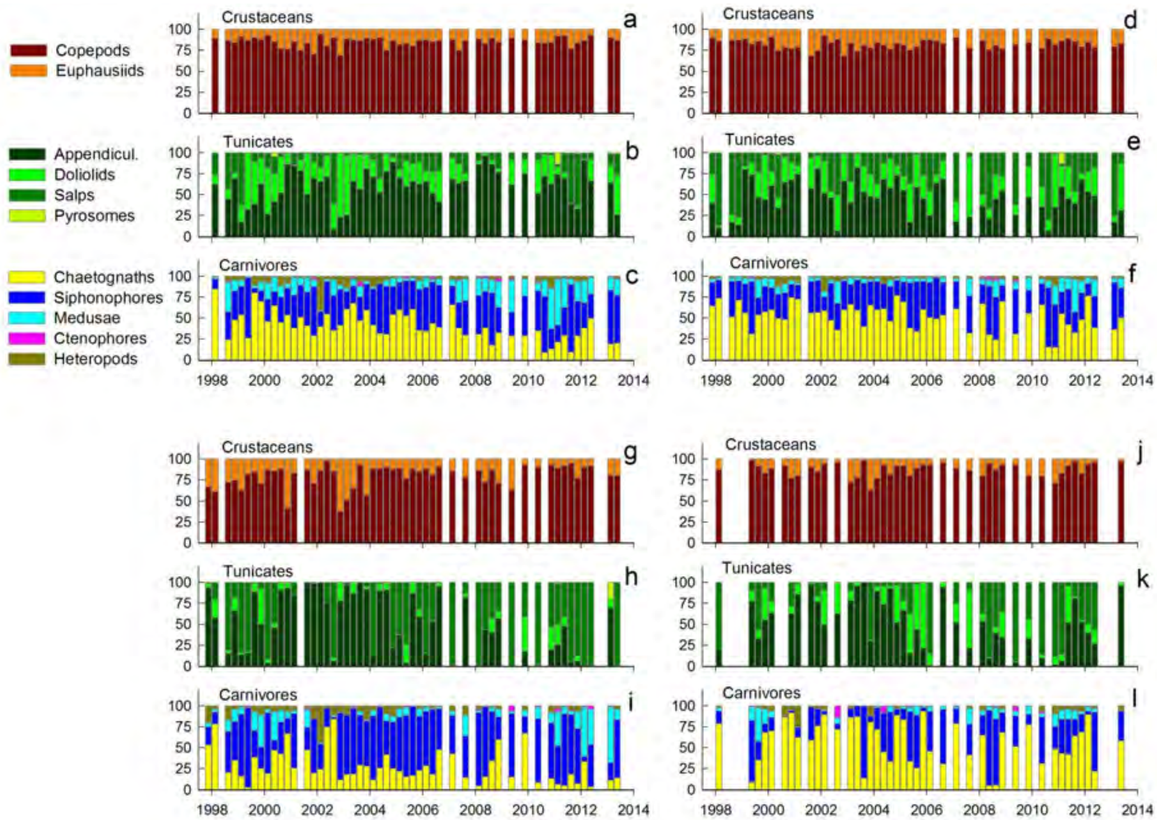

Figure 8. Percentage structure of the trophic groups based in geometric means of the zooplankton taxa (staked bars) from the four regions: North (a-c), Central (d-f), Vizcaino bay (g-i) and the Gulf of Ulloa (j-l). Trophic groups are crustaceans (a, d, g, j), tunicates (b, e, h, k), and carnivores (c, f, i, l).

(Connolly *et al*., 2010). Low oxygen concentration is also contributed by turbulence as the subsurface eddy recorded off north Baja California during July 2004 (Jeronimo & Gómez-Valdés, 2007).

El Niño has also changed in the global warming scenario, with higher incidence and intensity of CP El Niño in the last 30 years (Lee & McPhaden, 2010). Based in models, Yeh *et al*. (2009) concluded that the ratio of EP-El Niño/CP-El Niño could increase fivefold at the end of 21th century.

In conclusion, to the question whether weak El Niño events that occurred during the study period produced any detectable changes in the abundances of zooplankton major taxa, the response would be negative, despite the temperature signal indicating a link with ENSO. In the present study, the main factor influencing structural changes in zooplankton community were associated to stratification in oceanic regions and upwelling enhancement in the coastal shelf. Stratification of the water column appears to be linked to geostrophic circulation (NPGO) mainly in the oceanic region. The notable increase of gelatinous organisms associated to these processes appears to be in detriment of crustacean plankton though the time-series are still short to outline a more defined trend. That tendency is particularly disturbing in Vizcaino bay with a drastic decrease of grazing crustaceans which in turn nourish fish larvae and adults of sardines and anchovies and, in turn, are being foraged by large predators. It appears that global warming may be behind the enhancement of coastal upwelling but the link between NPGO and global warming or with ENSO requires future investigation.

AKNOWLEDGEMENTS

José Luis Cadena assisted in zooplankton counting. Thanks are given to all the people involved in the performance of the IMECOCAL cruises. We are especially grateful for the critical insights of Jaime Gómez Gutiérrez to the manuscript. Financial support was from CONACYT (G0041T, G35326T, 42569, 23947, 99252) and SEMARNAT-CONACYT (23804). There were additional funds for curing the zooplankton collection from CONACYT (47044, 129611) and UCMEXUS (CN07-125).

REFERENCES

Acuña, J. L., D. Deibel & C. C. Morris. 1996. Particle capture mechanism of the pelagic tunicate *Oikopleura vanhoeffleni*. *Limnol. Oceanogr.*, 41: 1800-1814.

Ashok, K., S. K. Behera, S. A. Rao, H. Weng & T. Yamagata. 2007. El Niño Modoki and its possible teleconnection, *J. Geophys. Res.*, 112, C11007, doi:10.1029/2006JC003798.

Bakun, A., B. A. Black, S. J. Bograd, M. García-Reyes, A. J. Miller, R. R. Rykaczewski & W. J. Sydeman. 2015. Anticipated effects of climate change on coastal upwelling ecosystems. *Curr. Clim. Change Rep.*, doi: 10.1007/s40641-015-0008-4.

Bograd, S. J. & R. J. Lynn. 2003. Anomalous subarctic influence in the southern California Current during 2002. *Geophy. Res. Lett.*, 30(15), 8020, doi:10.1029/2003GL017446.

Brinton, E. & A. Townsend. 2003. Decadal variability in abundances of the dominant euphausiid species in the southern sectors of the California Current. *Deep Sea Res. II*, 50: 2449-2472.

Connolly, T. P., B. M. Hickey, S. L. Geier & W. P. Cochlan. 2010. Processes influencing seasonal hypoxia in the northern California Current System, *J. Geophys. Res.*, 115, C03021, doi:10.1029/2009JC005283.

Deibel, D. & G. A. Paffenhöfer. 2009. Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea). *J. Plankton Res.*, 31: 1571-1579.

Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell & P. Riviere. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophy. Res. Lett.*, 35, L08607, doi:10.1029/2007GL032838

Durazo, R., G. Gaxiola-Castro, B. E. Lavaniegos, R. Castro-Valdez, J. Gómez-Valdés & A. S. Mascarenhas Jr. 2005. Oceanographic conditions west of the Baja California coast, 2002–2003: a weak El Niño and subarctic water enhancement. *Cienc. Mar.*, 31: 537–552.

Fedorov, A.V., S. L. Harper, S. G. Philander, B. Winter & A. Wittenberg. 2003. How predictable is El Nino? *B. Am. Meteorol. Soc.*, 84(7): 911-919.

Freeland, H. J. & P. F. Cummins. 2005. Argo: a new tool for environmental monitoring and assessment of the world's oceans, an example from the NE Pacific. *Prog. Oceanogr.*, 64:31-44.

Funes-Rodríguez, R., A. Hinojosa-Medina, G. Aceves-Medina, S. P. A. Jiménez-Rosenberg & J. Bautista-Romero. 2006. Influences of El Niño on assemblages of mesopelagic fish larvae along the Pacific coast of Baja California Sur. *Fish. Oceanogr.*, 15: 244–255.

Gaxiola-Castro, G., J. Cepeda-Morales, S. Nájera-Martínez, T. L. Espinosa-Carreón, M.E. De la Cruz-Orozco, R. Sosa-Avalos, E. Aguirre-Hernández & J. P. Cantú-Ontiveros. 2010. Biomasa y producción del fitoplancton. 59-85, In: G. Gaxiola-Castro & R. Durazo (Eds.), *Dinámica del ecosistema pelágico frente a Baja California, 1997-2007*. CICESE/UABC/INE, México, D. F., 503 p.

Hereu, C.M., B. E. Lavaniegos, G. Gaxiola-Castro & M. D. Ohman. 2006. Composition and potential grazing impact of salp assemblages off Baja California during the 1997-1999 El Niño and La Niña. *Mar. Ecol. Prog. Ser.*, 318: 123-140.

Herrera-Cervantes, H., S. E. Lluch-Cota, D. B. Lluch-Cota & G. Gutiérrez-de-Velasco. 2014. Interannual correlations between sea surface temperature and concentration of chlorophyll pigment off Punta Eugenia, Baja California during different remote forcing conditions. *Ocean Sci.*, 10: 345-355.

Huyer, A. 2003. Preface to special section on enhanced subarctic influence in the California Current, 2002. *Geophy. Res. Lett.*, 30, doi:10.1029/2003GL017724.

Jerónimo, G. & J. Gómez-Valdés. 2007. A subsurface warm-eddy off northern Baja California in July 2004. *Geophy. Res. Lett.*, 34, L06610, doi:10.1029/2006GL028851, 2007

Jiménez-Pérez, L. C. & B. E. Lavaniegos. 2004. Changes in dominance of copepods off Baja California during the 1997-1999 El Niño and La Niña. *Mar. Ecol. Prog. Ser.*, 277: 147-165.

Jiménez-Rosenberg, S. P. A., R. J. Saldierna-Martínez, G. Aceves-Medina & V. M. Cota-Gómez. 2007. Fish larvae in Bahía Sebastián Vizcaíno and the adjacent oceanic region, Baja California, México. *Check List*, 3(3): 204-223.

Jiménez-Rosenberg, S. P. A., R. J. Saldierna-Martínez, G. Aceves-Medina, A. Hinojosa-Medina, R. Funes-Rodríguez, M. Hernández-Rivas & R. Avendaño-Ibarra. 2010. Fish larvae off the northwestern coast of the Baja California Peninsula, Mexico. *Check List*, 6(2): 334-349.

Kug, J. S., F. F. Jin & S. I. An. 2009. Two types of El Niño events: cold tongue El Niño and warm pool El Niño. *J. Climate*, 22: 1499-1515.

Lavaniegos, B. E. 2009. Influence of a multiyear event of low salinity on the zooplankton from Mexican eco-regions of the California Current. *Prog. Oceanogr.*, 83: 369-375.

Lavaniegos, B. E. 2014. Pelagic amphipod assemblages associated with subarctic water off the west coast of the Baja California peninsula. *J. Marine Syst.*, 132: 1-12.

Lavaniegos, B. E. & I. Ambriz-Arreola. 2012. Interannual variability in krill off Baja California in the period 1997-2005. *Prog. Oceanogr.*, 97-100: 164-173.

Lavaniegos, B. E., I. Ambriz-Arreola, C. M. Hereu, L. C. Jiménez-Pérez, J. L. Cadena-Ramírez, & P. García-García. 2010. Variabilidad estacional e interanual del zooplancton en la sección mexicana de la Corriente de California. 87-126, In: Gaxiola-Castro G. & R. Durazo (Eds.), *Dinámica del ecosistema pelágico frente a Baja California, 1997-2007*. CICESE/UABC/INE, México, D.F., 501 p.

Lavaniegos, B. E. & C. M. Hereu. 2009. Seasonal variation in hyperiid amphipods and influence of mesoscale structures off Baja California. *Mar. Ecol. Prog. Ser.*, 394: 137-152.

Lavaniegos, B. E. & L. C. Jiménez-Pérez. 2006. Biogeographic inferences of shifting copepod distribution during 1997-1999 El Niño and La Niña in the California Current. 113-158, In: Hendrickx, M. E. (Ed.), *Contributions to the study of east Pacific crustaceans, Vol. 4*, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, 158 p.

Lavaniegos, B. E., L. C. Jiménez-Pérez & G. Gaxiola-Castro. 2002. Plankton response to El Niño 1997-1998 and La Niña 1999 in the southern region of the California Current. *Prog. Oceanogr.*, 54(1-4): 33-58.

Lavaniegos, B. E. & M. D. Ohman. 2003. Long-term changes in pelagic tunicates of the California Current. *Deep Sea Res. II*, 50: 2473-2498.

Lavaniegos, B. E. & M. D. Ohman. 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. *Prog. Oceanogr.*, 75(1): 42-69.

Lee, T. & M. J. McPhaden. 2010. Increasing intensity of El Nino in the central-equatorial Pacific. *Geophy. Res. Lett.*, 37, doi:10.1029/2010gl044007.

Lougee, L. A., S. M. Bollens & S. R. Avent. 2002. The effects of haloclines on the vertical distribution and migration of zooplankton. *J. Exp. Mar. Biol. Ecol.*, 278: 111–134.

Micheli, F., A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. Espinoza-Montes, M. Rossetto & G. A. De Leo. 2012. Evidence that marine reserves enhance resilience to climatic impacts. *PlosOne*, 7(7): e40832, doi:10.1371/journal.pone.0040832

Ohman, M. D. & B. E. Lavaniegos. 2002. Comparative zooplankton sampling efficiency of the ring net and bongo net with comments on pooling of subsamples. *Cal. Coop. Ocean. Fish. Invest. Rep*, 43: 162-173.

Peterson W. T. & F. B. Schwing. 2003. A new climate regime in northeast pacific ecosystems. *Geophys. Res. Lett.*, 30, doi:10.1029/2003GL017528.

Roemmich, D., J. Church, J. Gilson, D. Monselesan, P.Sutton & S. Wijffels. 2015. Unabated planetary warming and its ocean structure since 2006. *Nat. Clim. Change*, 5: 240-245.

Sanders N. & J. Childress. 1995. Nitrogen and buoyancy in marine organisms. 51-62, In: Walsh P.J. & P. Wright (Eds.), *Nitrogen metabolism and excretion*, CRC Press, Inc., Boca Ratón, Florida, 341 p.

Soto-Mardones, L., A. Parés-Sierra, J. Garcia, R, Durazo & S. Hormazaba. 2004. Analysis of the mesoscale structure in the IMECOCAL region (off Baja California) from hydrographic, ADCP and altimetry data. *Deep Sea Res II*, 51: 785-798.

Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conserv. Biol.*, 6(1): 18-23.

Wang, D., T. C. Gouhier, B. A. Menge & A. R. Ganguly. 2015. Intensification and spatial homogenization of coastal upwelling under climate change. *Nature*, 518: 390-394.

Yeh, S. W., J. S. Kug, B. Dewitte, M. H. Kwon, B. P. Kirtman & F. F. Jin. 2009. El Niño in a changing climate. *Nature*, 46: 511-515.

APPENDIX

Table 1. Cruise dates and number of zooplankton samples used in taxonomic identification. All nighttime samples were used with additional daytime samples from coastal stations. (*) Cruises with >15 days of time-lag from the mean sampling day.

Cruise Name	Start date	End date	Nighttime samples	Daytime samples
9710	28 Sep 1997	6 Oct 1997	18	4
9801	25 Jan 1998	11 Feb 1998	33	2
9807	15 Jul 1998	30 Jul 1998	17	5
9810	28 Sep 1998	1 Nov 1998	32	3
9901	14 Jan 1999	31 Jan 1999	26	4
9904	30 Mar 1999	16 Apr 1999	22	7
9908 *	8 Aug 1999	22 Aug 1999	35	5
9910	10 Oct 1999	22 Oct 1999	41	2
0001	14 Jan 2000	1 Feb 2000	46	4
0004	4 Apr 2000	21 Apr 2000	31	3
0007	10 Jul 2000	30 Jul 2000	36	8
0010	10 Oct 2000	29 Oct 2000	38	3
0101	16 Jan 2001	3 Feb 2001	37	4
0104	5 Apr 2001	12 Apr 2001	8	1
0107 *	26 Jun 2001	16 Jul 2001	29	6
0110	3 Oct 2001	23 Oct 2001	43	8
0201	19 Jan 2002	6 Feb 2002	35	3
0204	19 Apr 2002	7 May 2002	27	3
0207	12 Jul 2002	01 Aug 2002	40	6
0210	23 Oct 2002	9 Nov 2002	41	0
0302	30 Jan 2003	19 Feb 2003	48	4
0304	4 Apr 2003	22 Apr 2003	31	3
0307	07 Jul 2003	27 Jul 2003	35	7
0310	10 Oct 2003	29 Oct 2003	47	4
0402	30 Jan 2004	18 Feb 2004	36	7
0404	18 Apr 2004	6 May 2004	32	6
0407	09 Jul 2004	29 Jul 2004	36	6
0410	9 Oct 2004	27 Oct 2004	45	5
0501	21 Jan 2005	10 Feb 2005	51	8
0504	14 Apr 2005	5 May 2005	39	7
0507	14 Jul 2005	04 Aug 2005	41	8
0510	13 Oct 2005	27 Oct 2005	41	3
0602	5 Feb 2006	25 Feb 2006	39	6
0604	19 Apr 2006	1 May 2006	19	1
0607	7 Jul 2006	25 Jul 2006	33	4
0701	23 Jan 2007	10 Feb 2007	51	3
0704	26 Apr 2007	6 May 2007	10	0
0708 *	25 Aug 2007	13 Sep 2007	42	9
0801	23 Jan 2008	11 Feb 2008	35	5
0804	16 Apr 2008	1 May 2008	21	7
0807	14 Jul 2008	02 Aug 2008	41	8
0810	14 Oct 2008	26 Oct 2008	29	4
0904	9 Apr 2009	23 Apr 2009	31	4
0911 *	30 Oct 2009	13 Nov 2009	38	5
1004	29 Mar 2010	17 Apr 2010	38	5
1008	29 Jul 2010	7 Aug 2010	16	1
1010	4 Oct 2010	18 Oct 2010	28	1
1101	20 Jan 2011	6 Feb 2011	39	3

Table 1. Continued.

Cruise Name	Start date	End date	Nighttime samples	Daytime samples
1104 *	19 Apr 2011	9 May 2011	32	6
1107	10 Jul 2011	27 Jul 2011	34	6
1110	4 Oct 2011	25 Oct 2011	42	5
1202	25 Jan 2012	11 feb 2012	49	5
1203 *	8 Mar 2012	24 Mar 2012	41	7
1302 *	8 Feb 2013	27 Feb 2013	14	0
1305 *	23 May 2013	7 Jun 2013	26	8

Table 2. Temperature corrections in cruises out of phase performed previously to estimation of climatologic means and anomalies. The correction was done with AMT = MT • TL • DTC; where (MT) is the mean temperature, (AMT) adjusted mean temperature, (TL) are days before (negative) or after (positive) the mean seasonal sampling date, and (DTC) is daily temperature change which was based in monthly means from the period 1951-1966 (see Appendix Figure 1). Only AMT with differences higher than 0.5°C were considered in the estimation of climatologic means and anomalies (highlighted in bold).

Region	Mean seasonal sampling date	Out-of-phase Cruise	TL (d)	Temperature difference (1951-1966)	DTC (°C d-1)	MT (°C)	AMT (°C)
NORTH	Winter (Jan 27)	1302	19	Jan–Feb –0.23	–0.008	14.73	14.88
	Spring (Apr 16)	9904	–15	Mar–Apr 0.37	0.012	14.89	15.08
		1104	18	Apr–May 0.54	0.018	15.94	15.62
		1203	–36	Feb–Apr 0.24	0.004	14.82	14.96
		1305	39	Apr–Jun 1.10	0.018	16.93	**16.22**
	Summer (Jul 21)	9908	20	Jul–Aug 1.05	0.035	18.60	**17.90**
		0107	–22	Jun–Jul 1.15	0.038	18.35	**19.19**
		0708	38	Jul–Sep 2.07	0.035	19.34	**18.03**
	Autumn (Oct 13)	0911	19	Oct–Nov –0.84	–0.028	18.72	**19.25**
CENTRAL	Winter (Feb 6)	1302	19	Feb–Mar –0.56	–0.019	15.55	15.90
	Spring (Apr 23)	1203	–34	Mar–Apr –0.04	–0.001	15.65	15.60
		1305	44	Apr–Jun 0.73	0.012	18.22	**17.68**
	Summer (Jul 29)	9908	19	Jul–Aug 1.55	0.052	19.46	**18.48**
		0107	-20	Jun–Jul 2.04	0.068	20.36	**21.72**
		0708	40	Jul–Sep 2.27	0.038	22.00	**20.49**
	Autumn (Oct 21)	9710	–20	Sep–Oct –0.35	–0.012	24.40	24.17
		0911	19	Oct–Nov –0.27	–0.009	21.29	21.46
VIZCAINO BAY	Winter (Feb 3)	1302	21	Feb–Mar –0.84	–0.028	14.34	**14.93**
	Spring (Apr 21)	1203	–33	Mar–Apr 0.21	0.007	14.81	15.04
		1305	38	Apr–Jun 0.45	0.008	15.47	15.19
	Summer (Jul 26)	9908	20	Jul–Aug 1.10	0.037	17.61	**16.88**
		0107	–21	Jun–Jul 1.86	0.062	17.14	**18.44**
		0708	38	Jul–Sep 3.00	0.050	19.75	**17.85**
	Autumn (Oct 19)	9710	–17	Sep–Oct –1.23	–0.041	24.62	**23.92**
		0911	18	Oct–Nov –0.31	–0.010	20.25	20.44

Table 2. Continued.

Region	Mean seasonal sampling date	Out-of-phase Cruise	TL (d)	Temperature difference (1951-1966)	DTC (°C d-1)	MT (°C)	AMT (°C)
GULF OF	Spring (Apr 23)	1203	–31	Mar–Apr –0.96	–0.032	15.54	**14.55**
ULLOA		1305	43	Apr–Jun –0.20	–0.003	15.22	15.36
	Summer (Aug 1)	9908	19	Jul–Aug 4.66	0.155	20.17	**17.22**
		0107	–19	Jun–Jul 2.44	0.081	18.32	**19.87**
		0708	39	Jul–Sep 6.64	0.111	21.90	**17.58**
		1107	–18	Jul–Aug 4.66	0.155	17.45	**20.25**
	Autumn (Oct 25)	0911	17	Oct–Nov –0.79	–0.026	24.27	24.72

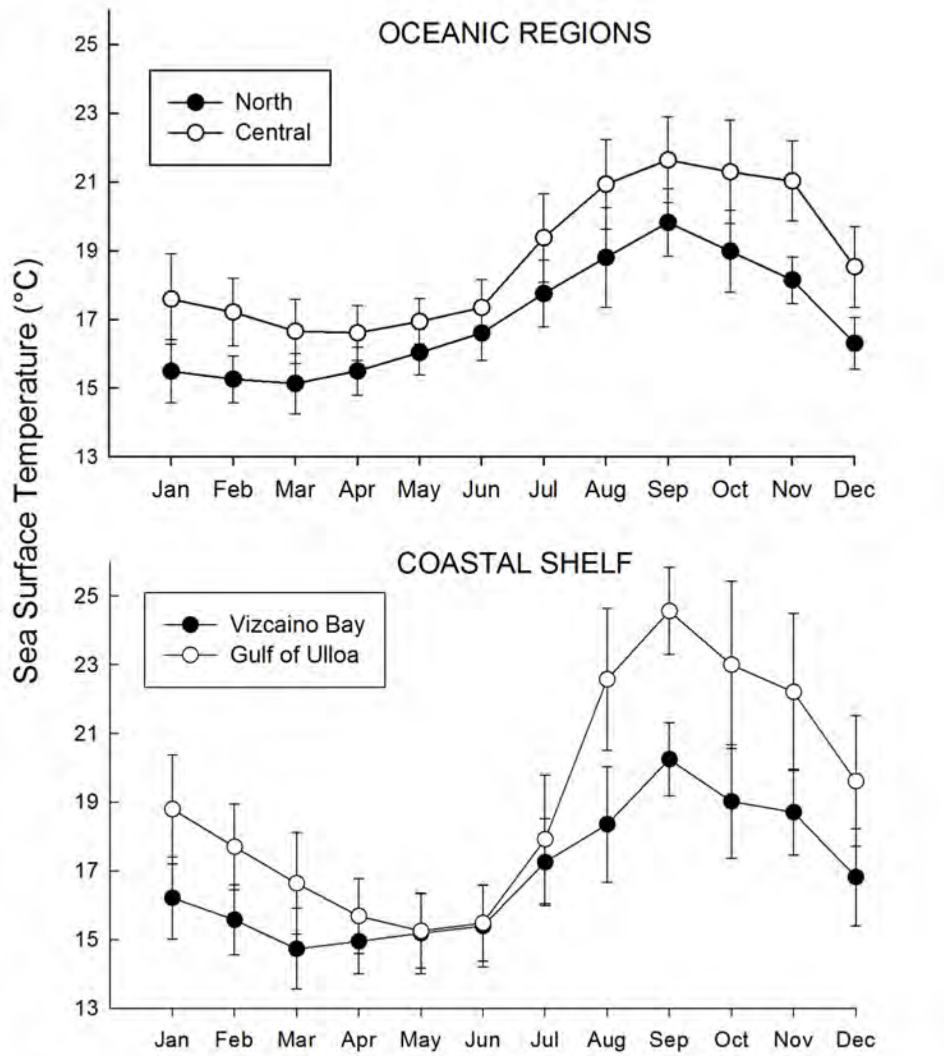

Figure 1. Seasonal mean temperature at 10 m depth for the period 1951-1966 in oceanic and coastal shelf regions (mean ± standard deviation). Data generated by the California Cooperative Oceanic Fisheries Investigations program (http://www.calcofi.org/new.data/index.php/publications/calcofi-data-reports/archived-data-reports).