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Influence of a multiyear event of low salinity on the zooplankton from Mexican eco-regions of the California Current

Bertha E. Lavaniegos *

Departamento de Oceanografía Biológica, CICESE, km 107 Carretera Tijuana-Ensenada, Apdo, Postal 360, 22860 Ensenada, Baja California, Mexico

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ABSTRACT

Data are presented from the southern part of the California Current System (CCS) for the period 1997–2007, derived from the IMECOCAL monitoring program. Apart from El Niño 1997 to 1998, and La Niña 1998–1999 the strongest perturbation occurred in 2002 due to an intrusion of subarctic water affecting all the CCS. The response of zooplankton biomass to the strong cooling and freshening of the upper layer was an immediate drop followed by a progressive recovery between 2003 and 2007. Though the low salinity influence ended in 2006, the increased zooplankton trend continued, reinforced by increased upwelling activity beginning 2005 off north Baja California region (30–32°N) and beginning 2006 off central Baja California (24–30°N). Multiple regression analysis was done between regional variables and Upwelling Index (UI) and two basin-scale proxies: the North Pacific Gyre Oscillation (NPGO), and Pacific Decadal Oscillation (PDO). The significant influence of the NPGO on surface salinity, salinity stratification, zooplankton volume and secondary consumers (zooplankton carnivores) suggests a basin scale control on these variables more than local mechanisms. The signature of the NPGO was also evident in the base of the trophic web, but more related to the group of crustacean herbivores in the north eco-region, and the tunicates in central Baja California. In this last region, the effect from NPGO on the zooplankton volume and tunicates was antagonist with UI indicative of similar importance of basin and local processes. However, when the time interval is limited to the post-subarctic intrusion (2003–2007) the significance of multiple regression models and physical variables was lost. Therefore, though data and bio-physical coupling analysis off Baja California suggest a better relation with NPGO compared to PDO, it is still not sufficient to explain the magnitude of the perturbation observed in 2002.

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1. Introduction

One third of the California Current System (CCS) is composed of Mexican waters, referred to as the Baja California sector, that are less inhabited by temperate biota and have the most subtropical characteristics. Though often the Baja California sector of the CCS has been considered one region (Hickey, 1998), this is more a geo-political than a natural separation. The northern portion off Baja California waters is part of the southern California Bight recirculation, and its limit of influence should be placed in Punta Baja (30°N). This region presents a marked stratification, minimum wind forcing and weak upwellings (USGLOBEC, 1994). South of Punta Baja, the bending of the coast-line toward the southeast (Fig. 1) combined with moderate winds produces moderate upwellings throughout the year (Huyer, 1983), Pacific equatorial water is more influential (Roden, 1971), and mesoscale activity is prominent (Soto-Mardones et al., 2004). These two eco-regions are named north and central in the present study. Subtropical species are dominant in both regions but the influence of temperate fauna is almost entirely limited to northern Baja California (Lavaniegos and Jiménez-Pérez, 2006).

Apart from the geographic regions, the CCS also presents different scales of temporal variability.

In the present study the focus is on inter-annual variability in the context of the period 1997–2007. Inter-annual variability related with the ENSO cycle 1997–1999 has been well documented in previous studies focused on Baja California (Durazo and Baumgaratner, 2002; Lavaniegos et al., 2002; Jiménez-Pérez and Lavaniegos, 2004; Hereu et al., 2006; Ambriz-Arreola, 2007). However, other inter-annual events are not well understood, such as the subarctic water intrusion that occurred along the CCS during 2002 (Huyer, 2003).

The subarctic intrusion brought cold and fresh water, rich in nutrients and high chlorophyll during summer 2002 off Vancouver Island, Oregon (Freeland et al., 2003; Freeland and Cummins, 2005), and southern California (Bograd and Lynn, 2003). In Baja California waters, negative anomalies were manifested in October

* Tel.: +52 646 1750500; fax: +52 646 1750587.
E-mail address: berlav@cicese.mx

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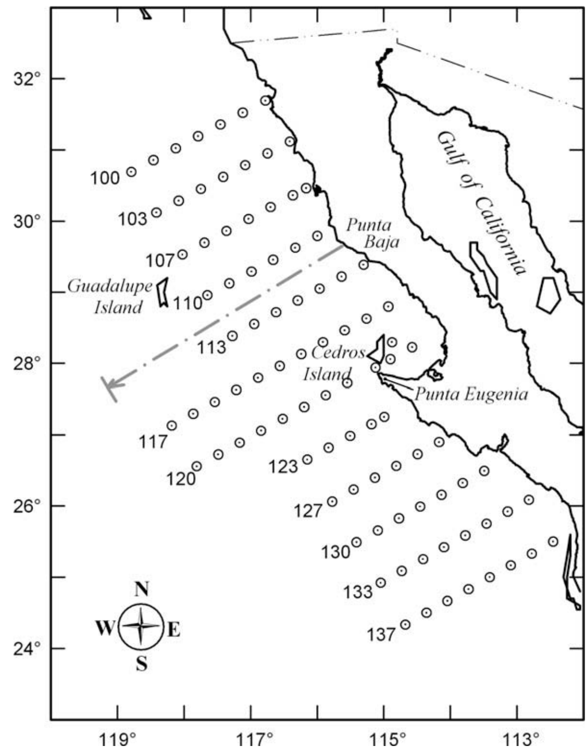

Fig. 1. Station grid in the California Current sector sampled during IMECOCAL cruises. Dashed line indicates demarcation of north and central regions off the Baja California peninsula. The numbers of transect lines are shown.

2002 affecting the upper 200 m, rich in chlorophyll but low in zooplankton biomass (Durazo et al., 2005; Gaxiola-Castro et al., 2008). The freshening was observed from July 2002 to July 2006, but below the upper stratum (~200 m), a tendency completely opposite to the increasing salinity that was reported off Baja California (Peterson et al., 2006).

Further confusion to understanding the phenomenon comes from the incidence of a strong La Niña in 1999 (Schwing and Moore, 2000), and some authors consider 1999–2002 a cool period influenced by the negative phase of the Pacific decadal oscillation (PDO) (Hooff and Peterson, 2006). Chhak and Di Lorenzo (2007) identified a relation between the depths of the upwelled water near the coast and the PDO, with a deeper upwelling cell during the 'cool' phase, and shallower during the 'warm' phase, with more horizontal entrainment of surface waters from the north. These authors also show that the changes in the coastal upwelling cell did not exhibit a latitudinal uniformity.

However, there does not appear to be a linear correspondence between PDO and regional ecosystems. Other 'modes' of variability have been proposed to explain the departures from PDO, such as the Victoria mode in the Gulf of Alaska (Bond et al., 2003) and the North Pacific Gyre Oscillation (NPGO) in the California Current (Di Lorenzo et al., 2008). The NPGO index is driven by regional and basin-scale variations in wind-driven upwelling and horizontal advection. Those are the fundamental processes controlling salinity and nutrient concentrations and explain the observed tendencies in chlorophyll (Di Lorenzo et al., 2008).

In the present study is addressed the relation of North Pacific basin-scale indices with inter-annual variability of zooplankton during the period 1997–2007 for the Baja California regions of the CCS. It is shown that periods occurred with high coherence between different sectors of the CCS followed by others with higher influence of local features.

2. Methods

2.1. Sampling

The study area has an extension of 185,000 km^2 off Baja California, sampled by the IMECOCAL (*Mexican Research of the California Current*) program since September 1997. Quarterly cruises representing the seasons of the year were conducted on the RV *Francisco de Ulloa*, through a station grid of 12 transects approximately perpendicular to the coast (Fig. 1). In the 10 year period of IMECOCAL sampling, the only missing cruises were April 1998, October 2006 and October 2007. Two other cruises were very short (September 1997 was limited to lines 110–127 and April 2001 to lines 100–113). At each station, conductivity, temperature and pressure casts were done using a Seabird CTD.

Zooplankton was collected with a bongo net of 505 μm meshwidth doing double oblique hauls in the upper 210 m or from 10 m above the bottom to the surface at shallow stations. The diameter of the net was 61 cm before October 2001, and then it was replaced by one of 71 cm. The data through the time-series may be considered comparable based on a previous study evaluating zooplankton volumes collected with bongo nets of 61 and 71 cm diameter (Ohman and Smith, 1995). The volume of water strained was measured with a flowmeter in the mouth of the net. Samples were preserved with 4% formalin and sodium borate. A total of 2773 zooplankton samples were collected through 38 cruises.

2.2. Laboratory analysis

All the zooplankton samples were processed for biomass one month after the end of each cruise following the method of displacement volume with a graduated cylinder. Only nighttime samples (1342) were selected for taxonomic analyses of major taxa: copepods, euphausiids, appendicularians, doliolids, salps, pyrosomes, chaetognaths, siphonophores, medusae, ctenophores and heteropods. A fraction of the sample was counted (1/8, 1/16 or 1/32) using a stereomicroscope. Smaller subsamples were used only in cases with exceptionally abundant plankton.

2.3. Data analysis

Zooplankton biomass was standardized to m^3 of filtered water and transformed to logarithms. Abundance of zooplankton taxa was standardized also to m^3 and aggregated by trophic levels: (1) crustacean herbivores (copepods + euphausiids), (2) tunicates herbivores (appendicularians, doliolids, salps, pyrosomes) and (3) carnivores (chaetognaths, siphonophores, medusae, ctenophores, and heteropods). Levels 2 and 3 have a clear trophic identity, while the many copepods and euphausiids of level 1 are omnivores. In this study they were considered herbivores, as a first approximation to the trophic zooplankton structure, bearing in mind the strong increase of their populations linked to primary productivity in eastern boundary upwelling ecosystems. Further, abundances of each trophic level were log-transformed ($\log x + 1$). Anomalies of zooplankton volume, taxa abundance and physical variables were calculated removing the long-term seasonal mean for the period 1997–2007 in two separate regions (Fig. 1) following the regional classification from US GLOBEC (1994).

Upwelling Indices (UI) from two locations (30°N 119°W and 27°N 116°W) were taken from the PFEL web site (ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon). Two environmental proxies of the North Pacific basin were used: PDO and NPGO. Monthly values of these proxies are available in the web sites http://jisao.washington.edu/pdo/PDO. latest, and http://ero-

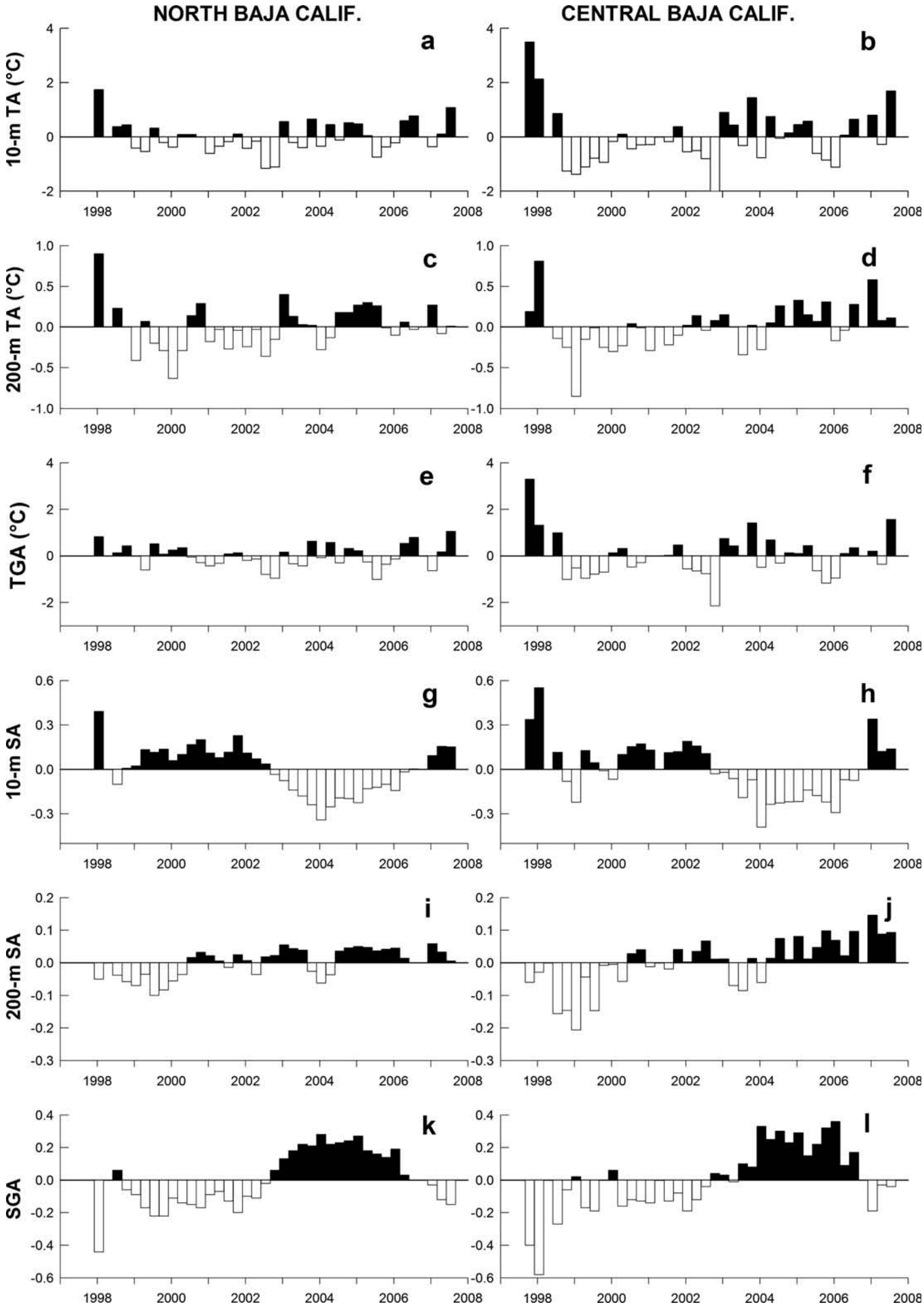

Fig. 2. Temperature and salinity in eco-regions off Baja California: (a, b) temperature anomaly (TA) at 10 m, (c, d) 200 m depths, and (e, f) temperature gradient anomaly (TGA); (g, h) salinity anomaly (SA) at 10 m, (i, j) 200 m depths, and (k, l) salinity gradient anomaly (SGA). Gradient means the absolute difference between values of both depths. Anomalies were estimated removing seasonal means for the period 1997–2007.

s.eas.gatech.edu/npgo/data/NPGO.txt. Caution must be taken with the NPGO values of 2004–2007 which are preliminary estimations of the index.

Monthly values of PDO, NPGO and UI were correlated with Spearman rank order test. Multiple linear regression analysis of physical and biological variables was performed to investigate their relation with environmental proxies. Previously, monthly values of the PDO, NPGO, and UI were converted to quarterly means: winter (Dec–Jan–Feb), spring (Mar–Apr–May), summer (Jun–Jul–Aug), and fall (Sep–Oct–Nov). Upwelling indices were further log-transformed to normalize data, and anomalies were estimated for the period 1997–2007. Similar low frequency anomalies were calculated for all dependent variables: temperature and salinity at two depths (10 and 200 m), thermal and saline stratification (the difference between 10 and 200 m depths), zooplankton biomass, and abundance by trophic levels.

3. Results

3.1. Hydrographic conditions

The California Current core water has the lowest temperature and salinity in the CCS. When the current is weak, there is a tendency to increased sea surface temperature (SST) and salinity (SSS) and positive anomalies occur, as observed during the 1997–1998 El Niño (Fig. 2a,b,g,h). In contrast, the cool phase of ENSO (La Niña 1998–1999) was marked by a decrease in SST and SSS. The only exception to decrease in salinity during La Niña is near the coast where saline deep water was upwelled to the surface. After a short period of 'normal' conditions (2000–2001) water properties dramatically changed in 2002 with an intrusion of subarctic water with low SST and SSS. These conditions persisted until 2006 (Fig. 2g and h). Even though the freshening event lasted 4 years, the negative SSS anomalies were not accompanied by negative SST anomalies after 2002. Thus, while SST anomalies suggested the end of the subarctic intrusion in 2003, SSS anomalies appears to indicate a continuation of that event.

It is also possible there was an accumulation of low salinity water in the upper stratum due to higher stratification of the water column. A phase of increased stratification was evident (Fig. 2k and l) in the contrast between the freshening in the surface stratum and the saltier water detected in subsurface waters (Fig. 2i and j; Suppl. Table S1). However, the temperature gradient did not show a stratification increase (Fig. 2e and f). Gradient temperature anomalies of high magnitude were linked to events of the 1997–1998 El Niño and the subarctic intrusion in 2002 and were observable only in the central region (Fig. 2f).

3.2. Total zooplankton biomass and abundance of trophic groups

The zooplankton biomass showed changes through the period 1997–2007 (Fig. 3a and b). Negative biomass anomalies occurred from La Niña (1999) to the subarctic water invasion (2002). The negative anomalies had higher magnitude in the north Baja California region. Since 2003, the zooplankton has progressively increased through the phase of low salinity influence in both regions. This tendency continued through 2007 although the salinity apparently had returned to normal values.

Considering the north eco-region, all trophic assemblages presented a significant increase based on linear regressions (Fig. 3c,e,g; Suppl. Table S1). In contrast, the central eco-region

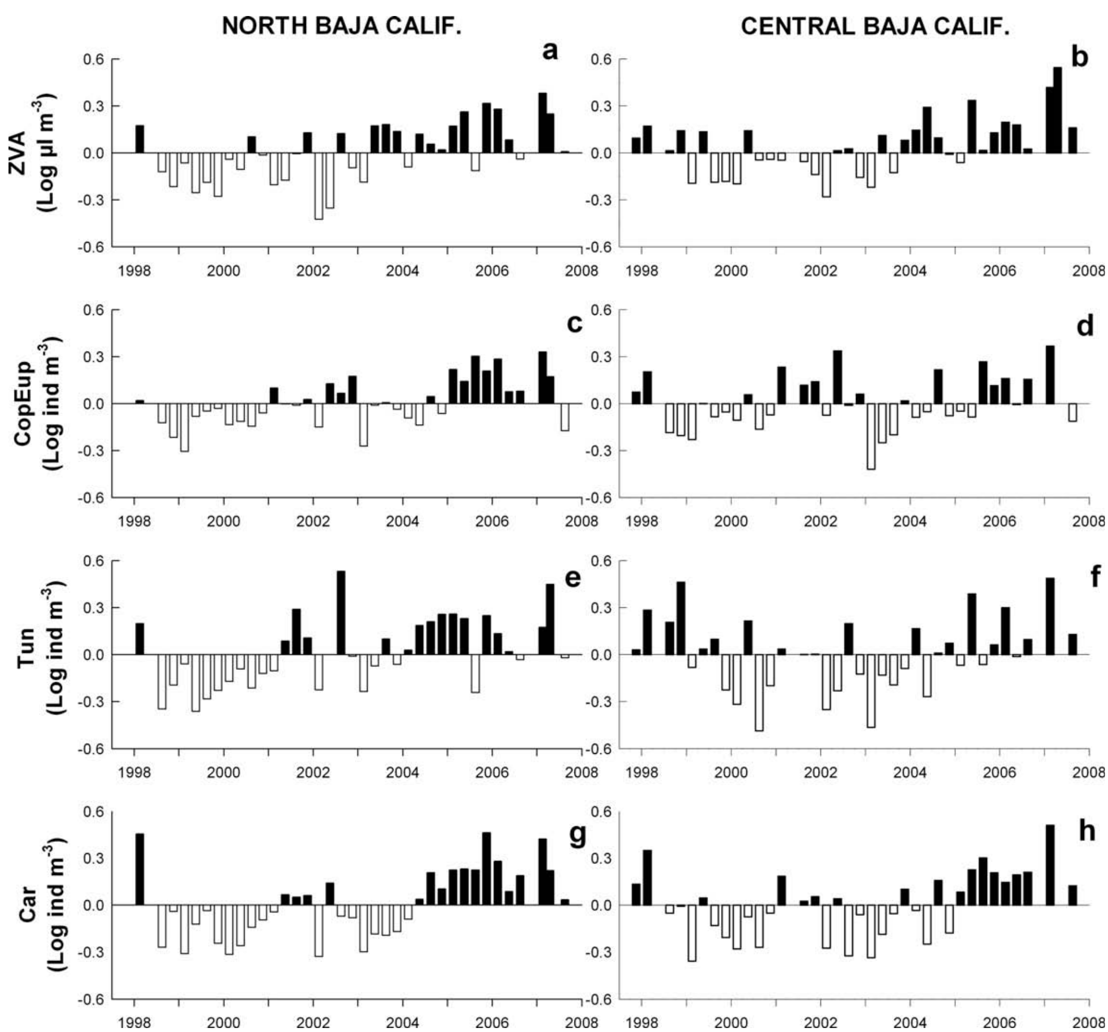

Fig. 3. Zooplankton biomass and abundance in eco-regions off Baja California: (a, b) zooplankton volume anomaly (ZVA), and abundance anomaly of (c, d) copepods + euphausiid (CopEup), (e, f) tunicates (Tun) and (g, h) carnivores (Car). Anomalies were estimated removing seasonal means for the period 1997–2007 on data previously log-transformed.

did not present a defined long-term tendency for crustacean (copepods + euphausiids) and gelatinous (tunicates) herbivores. Only the invertebrate carnivores showed a significant increase (Fig. 3d,f,h; Suppl. Table S1).

3.3. Bio-physical coupling with supra-regional indices

The PDO index presented 4 years of negative anomalies from July 1998 to July 2002, followed by another 4 years of positive anomalies between August 2002 and July 2006 (see Suppl. Fig. S1a). The only obvious exception within this positive phase was the autumn 2005 recording of high negative anomalies. The NPGO index during the study period was usually in the positive phase with two short periods of negative anomalies: one before November 1997 and another from November 2004 to February 2006 (Suppl. Fig. S1b). Monthly values of the PDO and NPGO indices were negatively correlated ($r = -0.34$, $p < 0.001$). However, no correlation existed for any of those proxies with the upwelling index.

Multiple regression analysis between basin-scale proxies and local variables was significant in most of the variables from the north region (Table 1). Exceptions were the thermal gradient, SST, and tunicates abundance. The highest r^2 were observed for saline gradient and SSS, with the NPGO coefficient highly significant in both cases, but with opposite signs (Table 1). Thus a strong Pacific gyre promoted increased SSS but reduced salinity stratification. The saline gradient appeared to also have an antagonist influence from the PDO (Table 1). Interestingly, the subsurface properties were more related to the PDO. Multiple regressions with biological variables in the north were significantly related to only the NPGO. UI did not have a significant influence in any regression from this eco-region.

On the other hand, the central eco-region presented low r^2 in several multiple regressions (Table 2). In this region the thermal as well as the saline gradients were related to proxies, the first positively with the PDO and the second negatively with the NPGO. The results for the surface and subsurface properties were remarkably opposite to those observed in the north region (compare Tables 1 and 2). The absence of significance for simple variables (200 m temperature, 200 m salinity, SSS), which determine the gradients, denote major changes in the stratification of the water column. The zooplankton volume in the central region had a high r^2 and significant coefficients for NPGO and UI. The same relation was shown by the tunicates in the central region (Table 2), contrasting with the results for the north region (Table 1). The central eco-region also presented differences for crustaceans, but the significance for multiple regressions with carnivores was shared in both regions.

Table 1
Multiple regression analysis on physical and biological variables in the north region off Baja California and proxies: PDO, NPGO, Upwelling index (UI). Monthly values of NPGO, PDO, and UI were converted to quarterly values averaging each three months. UI was from site 30°N 119°W. Dependent variables were anomalies of thermal stratification (ΔT), saline stratification (ΔS), 10 m temperature (10 mT), 10 m salinity (10 mS), 200 m temperature (200 mT), 200 m salinity (200 mS), zooplankton volume (ZV), and abundances of copepods + euphausiids (CopEup), tunicates (Tun), and main carnivores (Car). The significance of each coefficient is labeled (*) when $p < 0.05$, (**) $p < 0.01$, and (***) $p < 0.001$; $N = 37$.

	Model				R^2	F	P
	Intercept	PDO	NPGO	UI			
ΔT	0.060	−0.053	−0.059	−0.261	0.02	0.2	0.886
ΔS	0.093**	+0.071**	−0.083***	−0.301	0.52	12.1	<0.001
10 mT	0.126	+0.071	−0.113	−0.441	0.08	0.9	0.446
10 mS	−0.084**	−0.052	+0.076***	+0.244	0.44	8.7	<0.001
200 mT	0.066	+0.130*	−0.060	−0.180	0.28	4.4	0.011
200 mS	0.009	+0.019*	−0.008	−0.057	0.25	3.8	0.020
ZV	0.082	+0.036	−0.074*	+0.212	0.27	4.0	0.016
CopEup	0.076*	+0.003	−0.068**	−0.037	0.23	3.2	0.035
Tun	0.076	+0.015	−0.068	−0.073	0.13	1.6	0.209
Car	0.131**	+0.003	−0.117***	+0.220	0.36	6.1	0.002

Table 2
Multiple regression analysis on physical and biological variables in the central region off Baja California and proxies: PDO, NPGO, UI (site 27°N 116°W). Codes for dependent variables are explained in Table 1 ($N = 36$).

	Model				R^2	F	P
	Intercept	PDO	NPGO	UI			
ΔT	0.005	+0.430*	−0.037	−1.339	0.22	3.0	0.045
ΔS	0.107*	−0.022	−0.102***	−0.248	0.29	4.4	0.010
10 mT	0.080	+0.507*	−0.112	−1.318	0.26	3.8	0.019
10 mS	−0.089	+0.028	+0.085**	+0.236	0.20	2.6	0.070
200 mT	0.075	+0.078	−0.075	+0.021	0.19	2.4	0.082
200 mS	0.019	−0.002	−0.019	−0.081	0.08	0.9	0.472
ZV	0.074**	+0.033	−0.069***	+0.539**	0.48	9.8	<0.001
CopEup	0.027	−0.011	−0.023	+0.270	0.05	0.5	0.654
Tun	0.088	+0.019	−0.078*	+0.919*	0.30	4.6	0.008
Car	0.085	+0.035	−0.079*	+0.496	0.28	4.1	0.015

The oscillation type of the NPGO appears to be more gradual compared to the shifts of the PDO. The period sampled by IMECOCAL comprised a complete crest of the NPGO (Suppl. Fig. S1b) between 1999 and 2004. The recent period of zooplankton increase started in 2003, coincident with the decreasing trend of the NPGO. Clearly a point of change exists in the middle of the complete time-series under study, at 2002. To explore more closely the relation of supra-regional indices and local variables after the subarctic intrusion, the multiple regression analysis was repeated for the interval 2003–2007. When this was done, the significance of regression equations was lost for physical variables in both regions (Suppl. Table S2). This suggests another kind of perturbation was causing the freshening of the upper layer that is not well captured by any of the indices used as proxies of the Pacific basin.

Biological variables within the period 2003–2007 continued to be significant in most cases but the balance among coefficients gave more weight to UI in detriment to the NPGO (Suppl. Table S2). Zooplankton volume retained significance only in the central region, but the influential coefficient was from UI. Northern crustaceans showed similar results independently of the period considered. Central crustaceans appeared to be more related to the proxies during 2003–2007 due to a high r^2, but no coefficient had a significant weight in the model (Suppl. Table S2). Tunicates showed similar results with extended or reduced periods. In the case of carnivores, UI had a higher specific weight in equations from both regions when the time interval was reduced to 2003–2007 (Suppl. Table S2).

4. Discussion

The NPGO index, derived from analyses of Northeast Pacific sea surface anomalies of temperature and pressure height in the north Pacific basin, has been related to fluctuations of salinity, nutrients and chlorophyll in southern California waters (Di Lorenzo et al., 2008). The Mexican sector of the California Current is located even further south, and some similarities were found in the present study in the relationship between NPGO and salinity off Baja California. Di Lorenzo et al. (2008) proposed the NPGO to make clear the changes in salinity and nutrients that are not well explained by the PDO. Both indices are related with the large scale circulation in the north Pacific, which is dominated by the North Pacific Current (NPC), flowing eastward and bifurcating in two branches: the Alaska Current and the California Current. It has been proposed that an alternation in the strength of those currents is indicated by the PDO, while the force of both currents varies simultaneously in the case of the NPGO. Therefore, a negative phase of the PDO would have induced the cooling observed in the CCS during 1999–2002 (Schwing et al., 2002) when simultaneously the NPGO was strong, reinforcing the California Current.

However, the NPGO appears to have a gradual type of oscillation and consequently it is not clear why the decrease in salinity was so strong and sudden in 2002. Only the PDO changed in 2002 but it entered a positive phase, and the expectations were for a warming of the SST and a weakening of the California Current. Furthermore, the occurrence of a simultaneous El Niño developing in the Central Pacific during 2002–2003 (Lagerloef et al., 2003; McPhaden, 2004) also projected a weakening of the California Current.

Therefore, the invasion of low salinity water appeared to be related with another event producing an opposite effect: enhancing the California Current. This enhancement was the anomalous northward shift of the NPC bifurcation during 2002, reported by Freeland and Cummins (2005). They showed a migration of the bifurcation up to nine latitudinal degrees northward (from 42° to 51°N) at 150°W during 2002. Though the position of the NPC apparently returned to climatological position by the middle of 2003, the low salinity water continued affecting the CCS until winter 2006 as has been described in the present study. The near-surface stratification caused by the "excess" of subarctic water, served as an obstacle to deep mixing (Freeland and Cummins, 2005). This would explain the strong density stratification in Station Papa (50°N) during 2002–2004, also observed off Baja California.

The temperature and salinity in CCS showed a different process through the water column. Whereas the cool temperature associated with subarctic intrusion disappeared after 2002, the freshening remained for 4 years. Positive SST anomalies in 2003–2007 (except 2005) pointed more to a process of global warming. Furthermore, the termohaline conditions at 200 m depth showed a similar tendency to positive anomalies (Fig. 2c,d,i,j) indicating an expansion of the California Undercurrent. Thus, the weakening of the North Pacific gyre between 2004 and 2006 could have contributed to the California Undercurrent enhancement.

Though primary productivity experienced a dramatic increase with the subarctic intrusion during 2002, it was not followed by an immediate increase of zooplankton (Wheeler et al., 2003; Gaxiola-Castro et al., 2008). In the bottom of the Oregon shelf a decrease in oxygen was reported during 2002 (Grantham et al., 2004) with "natural eutrophication" due to decay of phytoplankton which was "respired rather than passed onto higher trophic levels" (Wheeler et al., 2003). In this region, low copepod richness was associated with the anomalous subarctic intrusion (Hooff and Peterson, 2006). The same perturbation due to the rapid cooling and freshening probably caused a mismatch between phyto and zooplankton in Baja California waters (Gaxiola-Castro et al., 2008). After the mismatch between phyto and zooplankton, this last progressively increased. The simultaneous increase in different trophic levels suggests a general augmentation in secondary production particularly off north Baja California. The ecosystem of the central region did not reflect this behavior so precisely, and the increase of zooplankton appeared to start later than in the north. The time-lag in the central region could be related with a slow recovery from the subarctic perturbation in a community inhabited by species associated with warmer water (tropical and subtropical), in addition to oceanic equatorial species coming with El Niño 2002–2003.

The increasing tendency of zooplankton during the period of low salinity influence continued through 2007 when the salinity apparently returned to normal values (Fig. 3). In contrast, a drop in chlorophyll concentration was reported between 2003 and 2004 off Baja California (Peterson, et al., 2006), and this tendency continued during 2005 and 2006 in the north Baja California region (Gaxiola-Castro et al., 2008). Therefore, an intensive grazing could have occurred during most of the freshening event, explaining the contrast between phyto and zooplankton biomass. The primary productivity could be high despite stratification of the water column, thanks to advection of nutrients from the north. These explanations are reinforced by the significant increase in different types of herbivores (copepods, euphausiids, and tunicates) and carnivores. A dramatic increase of carnivores in the north eco-region during 2003–2007 suggests a possible reduction of herbivores by direct predation from secondary consumers. Unpublished data of euphausiids from July 2002 indicated abundance higher than during La Niña 1999 (Ambriz-Arreola, 2007). Particularly dense swarms of *Euphausia pacifica* were observed also in 2005 (Lavaniegos and Ambriz-Arreola, 2007). Though long-time-series of species are required, these preliminary data point to advection as a predominant factor in the 4 years freshening influence.

The mechanisms responsible for the two mode oscillations (PDO and NPGO) are still not clear. Fluctuations in the NPGO have been explained as regional and basin-scale variations in wind-driven upwelling and horizontal advection (Di Lorenzo et al., 2008). The data from Baja California waters analyzed in the present study better support the advection mechanism. The absence of correlation between UI and the NPGO also point in this direction. The UI has been criticized, particularly the index used here to represent the north Baja California region (30°N 119°W) due the large distance from the coast (Pérez-Brunius et al., 2006). However, UI from 27°N 116°W used for the central region is located near the coast and presented consistent correlations with coastal shelf zooplankton, suggesting increased upwelling. The small influence of UI denoted by crustacean herbivores combined with a positive relation between UI for tunicates and carnivores suggest a possible competition between crustaceans and tunicates and direct predation of crustaceans by carnivores.

A previous study by Chhak and Di Lorenzo (2007) had proposed a strong relation between upwelling cells and PDO. They found deepest water being pumped to the surface in the negative or cool phase of the PDO. The present study appears to agree with these model-derived conclusions, because although no correlation was observed between PDO and SSS, the lack of a high salinity signal near the coast could indicate a pumping from a relatively shallow stratum. However the subarctic invasion itself remains unexplained by the PDO.

Thus, the strongest perturbation in the IMECOCAL time-series 1997–2007 was the subarctic intrusion. The time-series presented here have shown the coherence of the perturbation along the CCS. Mesoscale structures also require attention as possible sources masking the relations between basin scale index and regional variables.

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Appendix A. Supplementary material

This section contains results of simple linear regression analysis for anomalies of physical and biological variables in function of time (Suppl. Table S1). It also contains a table of multiple regressions with proxies (PDO, NPGO, UI) showing only those equations that remained significant for a shortened period 2003–2007. (Suppl. Table S2). The basin-scale indices used in correlation analysis with physical and biological variables are shown in Suppl. Fig. S1. Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocean.2009.07.037.

References

Ambriz-Arreola I., 2007. Multivariate study of the euphausiid communities from the southern sector of the California Current during the 1997–1999 ENSO cycle. M.S. Thesis, Department of Biological Oceanography, CICESE, Ensenada, Baja California, Mexico, unpublished.

Bograd, S.J., Lynn, R.J., 2003. Anomalous subarctic influence in the southern California Current during. Geophysical Research Letters 30 (15), 8020. doi:10.1029/2003GL017446.

Bond, N.A., Overland, J.E., Spillane, M., Stabeno, P., 2003. Recent shifts in the state of the North Pacific. Geophysical Research Letters 30 (23), 2183. doi:10.1029/2003GL018597.

Chhak, K., Di Lorenzo, E., 2007. Decadal variations in the California Current upwelling cells. Geophysical Research Letters 314, L14604. doi:10.1029/2007GL030203.

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

Durazo, R., Baumgaratner, T.R., 2002. Evolution of oceanographic conditions off Baja California: 1997–1999. Progress in Oceanography 54, 7–31.

Durazo, R., Gaxiola-Castro, G., Lavaniegos, B.E., Castro-Valdez, R., Gómez-Valdés, J., Mascarenhas Jr., A.S., 2005. Oceanographic conditions west of the Baja California coast, 2002–2003: a weak El Niño and subarctic water enhancement. Ciencias Marinas 31 (3), 537–552.

Freeland, H.J., Cummins, P.F., 2005. Argo: a new tool for environmental monitoring and assessment of the world's oceans, an example from the N.E. Pacific. Progress in Oceanography 64, 31–44.

Freeland, H.J., Gatien, G., Huyer, A., Smith, R.L., 2003. Cold halocline in the northern California Current: an invasion of subarctic water. Geophysical Research Letters 30 (3), 1141. doi:10.1029/2002GL016663.

Gaxiola-Castro, G., Durazo, R., Lavaniegos, B.E., De-la-Cruz, M.E., Millan-Nuñez, E., Soto-Mardones, L., Cepeda-Morales, J., 2008. Pelagic ecosystem response to interannual variability off Baja California. Ciencias Marinas 34 (2), 263–270.

Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenco, J., Menge, B.A., 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature 429, 749–754.

Hereu, C.M., Lavaniegos, B.E., Gaxiola-Castro, G., Ohman, M.D., 2006. Composition and potential grazing impact of salp assemblages off Baja California during the 1997–1999 El Niño and La Niña. Marine Ecology Progress Series 318, 123–140.

Hickey, B.M., 1998. Coastal oceanography of western North America from the tip of Baja California to Vancouver Island: coastal segment. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea, vol. 11. J. Wiley and Sons, New York. pp. 345–393.

Hooff, R.C., Peterson, W.T., 2006. Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California Current ecosystem. Limnology and Oceaonography 51 (6), 2607–2620.

Huyer, A., 1983. Coastal upwelling in the California Current system. Progress in Oceanography 12, 259–284.

Huyer, A., 2003. Preface to special section on enhanced subarctic influence in the California Current, 2002. Geophysical Research Letters 30 (15), 8019. doi:10.1029/2003GL017724.

Jiménez-Pérez, L.C., Lavaniegos, B.E., 2004. Changes in dominance of copepods off Baja California during the 1997–1999 El Niño and La Niña. Marine Ecology Progress Series 277, 147–165.

Lagerloef, G.S.E., Lukas, R., Bonjean, F., Gunn, J.T., Mitchum, G.T., Bourassa, M., Busalacchi, A.J., 2003. El Niño Tropical Pacific Ocean surface current and temperature evolution in 2002 and outlook for early 2003. Geophysical Research Letters 30 (10), 1514. doi:10.1029/2003GL017096.

Lavaniegos, B.E., Ambriz-Arreola, I., 2007. Significant presence of subarctic euphausiids off Baja California during the summers of 2002 and 2005. In: Fourth International Zooplankton Production Symposium, Book of Abstracts, Hiroshima, Japan, 28 May–1 June 2007, p. 232.

Lavaniegos, B.E., Jiménez-Pérez, L.C., 2006. Biogeographic inferences of shifting copepod distribution during 1997–1999 El Niño and La Niña in the California Current. In: Hendrickx, M.E. (Ed.), Contributions to the Study of East Pacific Crustaceans, vol. 4. Instituto de Ciencias del Mar y Limnología, UNAM, Mexico, DF. pp. 113–158.

Lavaniegos, B.E., Jiménez-Pérez, L.C., Gaxiola-Castro, G., 2002. Plankton response to El Niño 97–98 and La Niña 99 in the southern region of the California Current. Progress in Oceanography 54, 33–58.

McPhaden, M.J., 2004. Evolution of the 2002–03 El Niño. Bulletin of the American Meteorological Society 85, 677–695.

Ohman, M.D., Smith, P.E., 1995. A comparison of zooplankton sampling methods in the CalCOFI time series. California Cooperative Fisheries Investigations Report 36, 153–158.

Pérez-Brunius, P., López, M., Pineda, J., 2006. Hydrographic conditions near the coast of northwestern Baja California: 1997–2004. Continental Shelf Research 26, 885–901.

Peterson, W.T., Emmett, R., Goericke, R., Venrick, E., Mantyla, A., Bograd, S.J., Schwing, F.B., Hewitt, R., Lo, N., Watson, W., Barlow, J., Lowry, M., Ralston, S., Forney, K.A., Lavaniegos, B.E., Sydeman, W.J., Hyrenbach, D., Bradley, R.W., Warzybok, P., Chavez, F., Hunter, K., Benson, S., Weise, M., Harvey, J., Gaxiola-Castro, G., Durazo, R. 2006. The State of the California Current, 2005–2006: warm in the North, cold in the South. California Cooperative Fisheries Investigations Report 47, 30–74.

Roden, G.I., 1971. Aspects of the transition zone in the Northeastern Pacific. Journal of Geophysical Research 76, 3462–3475.

Schwing, F.B., Bograd, S.J., Collins C.A., Gaxiola-Castro, G., García, J., Goericke, R., Gómez-Valdés, J., Huyer, A., Hyrenbach, D., Kosro, P.M., Lavaniegos, B.E., Lynn, R.J., Mantyla, A., Ohman, M.D., Peterson, W.T., Smith, R.L., Sydeman, W.J., Venrick, E., Wheeler, P.A. 2002. The State of the California Current, 2001–2002: will the CCS keep its cooling, or is El Niño looming? California Cooperative Fisheries Investigations Report 43, 31–68.

Schwing, F.B., Moore, C.S., 2000. A year without summer for California or a harbinger of a climate shift? Eos Transactions. American Geophysical Union 81, 301–305.

Soto-Mardones, L., Parés-Sierra, A., García, J., Durazo, R., Hormazabal, S., 2004. Analysis of the mesoscale structure in the IMECOCAL region (off Baja California) from hydrographic, ADCP and altimetry data. Deep-Sea Research II 51, 785–798.

US GLOBEC, 1994. A science plan for the California Current. United States GLOBEC Ocean Ecosystem Dynamics, Report 11, Department of Integrative Biology, University of California, Berkeley, California, 124 p.

Wheeler, P.A., Huyer, A., Fleischbein, J., 2003. Cold halocline, increased nutrients and higher productivity off Oregon in 2002. Geophysical Research Letters 30 (15), 8021. doi:10.1029/2003GL017395.