



Pergamon

Progress in Oceanography 54 (2002) 33–58

Progress in
Oceanography

www.elsevier.com/locate/pocean

Plankton response to El Niño 1997–1998 and La Niña 1999 in the southern region of the California Current

B.E. Lavaniegos^{ab,*}, L.C. Jiménez-Pérez^a, G. Gaxiola-Castro^a

^a Departamento de Ecología. Centro de Investigación Científica y Educación Superior de Ensenada. km 107 Carr. Tijuana-Ensenada. Apdo. Postal 2732, 22800 Ensenada, Baja California, Mexico

^b Marine Life Research Group. Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA. 92093-0227, USA

Abstract

The IMECOCAL Program began in 1997, with the objective of sampling plankton systematically in the Mexican region of the California Current. We present results of chlorophyll *a* concentrations and zooplankton displacement volumes for the eight cruises from September 1997 to October 1999. The abundance of 22 zooplankton groups was also analyzed for the first four cruises. The response of plankton to the 1997–1998 El Niño was atypical. From September 1997 to January 1998, chlorophyll *a* and zooplankton volume were at typical values (median integrated chlorophyll was 27 mg/m² and zooplankton 100 ml/1000 m³ in 9801/02). After the peak of El Niño, the system shifted to cooler conditions. Integrated chlorophyll gradually increased to a median of 77 mg/m² in April 1999. In contrast, zooplankton volumes decreased from October 1998 onward, despite favorable phytoplankton availability in 1999. Zooplankton structure was dominated by copepods and chaetognaths through the ENSO cycle, but interannual changes were evident. In the fall of 1997 there was a higher proportion of copepods, chaetognaths, and other minor groups, while the fall of 1998 zooplankton was richer in salps and ostracods. Historical data from previous Baja California CalCOFI cruises indicated that zooplankton volumes measured during the IMECOCAL cruises were above the long-term mean for the period 1951–1984. This suggests a differential response of plankton to the El Niño of 1997–1998 compared to the El Niño of 1957–1959. Regional differences in zooplankton volumes were also found, with central Baja California having 41% higher biomass than northern Baja California. Volumes from both regions were larger than those recorded by CalCOFI off southern California during 1997–1998, but the situation was reversed in 1999. The higher biomasses in the 1997–1998 El Niño can be attributed to high abundance of salps, which showed an affinity with warm, saline water. © 2002 Elsevier Science Ltd. All rights reserved.

Contents

1. Introduction	34
2. Methods	35

* Corresponding author.

E-mail address: berlav@cicese.mx (B.E. Lavaniegos).

3. Results	37
3.1. Plankton biomass	37
3.1.1. Regional and long-term trends in plankton biomass	39
3.2. Zooplankton community structure	42
3.2.1. Regional differences	45
3.2.2. Interannual differences	46
3.2.3. Distribution of zooplankton groups	46
3.2.3.1. Crustacean herbivores	46
3.2.3.2. Gelatinous herbivores	46
3.2.3.3. Carnivores	46
3.2.4. Correlation among zooplankton groups	49
3.2.5. Correlation with environmental variables	51
4. Discussion	53

1. Introduction

The California Current System (CCS) is highly susceptible to climate changes. Interannual variability of the CCS is well documented in terms of the physical processes related to the El Niño/Southern Oscillation (ENSO) (Chelton, Bernal & McGowan, 1982; Simpson, 1983; Huyer & Smith, 1985; Reinecker & Mooers, 1986). The anomalous warming of the equatorial Pacific observed during the ENSO is propagated to eastern boundary currents as a Kelvin wave, deepening the thermocline and raising sea level (Huyer & Smith, 1985). The biological effects of ENSO are less well documented and are poorly understood, partly because of the inadequate description of what are ‘normal’ conditions. A deepening of the nutricline is expected during an ENSO, and consequently, a general decrease in primary productivity (Barber & Chavez, 1983; Chavez et al., 1999). A large decrease in macrozooplankton biomass has accompanied previous ENSOs (Chelton, Bernal & McGowan, 1982; Roesler & Chelton, 1987), however, the response of individual taxa has been variable. Smith (1985) showed that the biomass of copepods and euphausiids underwent only a minor decrease during the El Niño of 1958–1959, relative to the cold year of 1956, whereas the biomass of pelagic tunicates declined to <4% of its original biomass. The response of particular species to El Niño apparently depends on water mass affinities; species usually distributed at lower latitudes tend to replace some of the endemic species. This has been observed in the northern region of the CCS, where the subarctic euphausiid species *Thysanoessa spinifera* was partially replaced by the warm-temperate species *Nyctiphanes simplex* during the ENSO 1982–1983 (Brodeur, 1986). Shifts in the distribution patterns of fishes have also been observed (Miller, Batchelder, Brodeur, & Percy, 1985; Percy, Fisher, Brodeur, & Johnson, 1985; Fiedler, Methot, & Hewitt, 1986; Percy & Schoener, 1987).

The recent ENSO of 1997–1998 appears to have been comparable in magnitude and extent to the 1982–1983 ENSO (Wolter & Timlin, 1998), although other authors consider the earlier event as the strongest on record (Wang & Weisberg, 2000). Evidence of the most recent El Niño was first observed in the central Pacific in the spring 1997, through a weakening of the trade winds and an unprecedented warming of the surface of the ocean (McPhaden, 1999). Kelvin waves propagated eastward in about two months, depressing the thermocline in the eastern Pacific by more than 90 m in late 1997 (McPhaden, 1999). In the CCS, the first signs of the impending El Niño were noticed in July 1997 when the coastal countercurrent expanded and transported unusually warm and saline water northward at depths below 100 m (Lynn et al., 1998). The pelagic ecosystem was strongly influenced. Macrozooplankton biomass during spring 1998 in southern California was at its lowest in the 50-year time series of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) (Lynn et al., 1998). Harvests of market squid (*Loligo opalescens*) and sea urchins (*Strongylocentrotus franciscanus*) in southern California declined drastically, whereas catches of other spec-

ies increased, e.g. yellowtail (*Seriola lalandi*), barracuda (*Sphyraena argentea*), and albacore (*Thunnus albacares*) (California Department of Fish & Game, 1998). Enhanced activity of winter storms devastated the kelp forest communities (*Macrocystis pyrifera*), affecting the fisheries for associated benthic organisms (Tegner, 1998).

The ENSO 1997–1998 was strong but short. Positive sea level anomalies persisted from May 1997 to September 1998 in southern California, and then changed to negative anomalies from October 1998 to February 1999. There were similar changes in sea surface temperatures. The southward flow was strong and the salinity was low in the core of the California Current (Hayward et al., 1999). Phytoplankton biomass (as chlorophyll) increased in association with the transition to cool-water conditions, with the integrated chlorophyll in April 1999 the highest on record in southern California since 1984 (Hayward et al., 1999).

Study of the 1997–1998 El Niño in the region off Baja California started in late September 1997, when the temperatures in the CCS were at their highest. SST exceeded 26°C and salinity 34.8 in the surface layer near Punta Eugenia, and there was a strong near-surface poleward coastal jet along the peninsula south of Punta Eugenia (Lynn et al., 1998). Hurricane Nora, which struck the Baja California coast in September 1997, produced heavy rains and winds that destroyed kelp forests and abalone banks around Natividad Island (Keitt, 1998; Ladah, Zertuche-González, & Hernández-Carmona, 1999). The physical evolution of El Niño through 1998 and the transition to cool conditions is discussed elsewhere in this issue.

The Baja California region has been studied less than the northern region of the California Current System. The CalCOFI program produced excellent data for the Baja California region during the 1950s and 1960s, but subsequently the program was restricted to a station grid off southern California, so that there has been little recent sampling off Baja California until very recently. The IMECOCAL (Investigaciones Mexicanas de la Corriente de California) program was designed to re-establish the intensive monitoring at the abandoned CalCOFI stations by using the same sampling techniques. We present biological results from the first eight IMECOCAL cruises conducted between September 1997 and October 1999, to describe the planktonic response to the 1997–1998 El Niño and the 1998–1999 La Niña in the Baja California region of the CCS.

2. Methods

Oceanographic stations during IMECOCAL cruises off Baja California were occupied in September–October 1997, January–February, July, September–October 1998, January, April, August, and October 1999. These cruises are referred to as 9709/10, 9801/02, 9807, 9809/10, 9901, 9904, 9908, and 9910. The grid of stations is the same as that previously sampled by the CalCOFI between Ensenada (31.8°N) and Punta San Gregorio (26°N). It encompasses 11 sampling lines perpendicular to the coast (Fig. 1). Lines 100, 103, and 107 were not sampled during the first cruise. Line 127 was omitted in 9901, and line 130 in three cruises (9709/10, 9809/10, and 9901). Line 133 was occupied only in two cruises (9908 and 9910). The numbers of stations sampled per cruise were 39, 69, 65, 62, 54, 54, 79, and 83, respectively.

At each station, a CTD/rosette cast was made to a depth of 2000 m or to within 10 m of the seabed. The mixed layer depth (MLD) was considered to be the depth at which the temperature was 0.5°C less than surface temperature. The Niskin bottles on the rosette were used to collect water at discrete depths of 0, 10, 20, 50, 100, and 150 m. One to two liters of each water sample was filtered (GF/F filters), and the filters frozen. During the first cruise, water samples were only collected from the surface. Chlorophyll *a* was later extracted from the filters with 90% acetone over 24 h at 4°C (Venrick & Hayward, 1984), then measured with a Turner Designs fluorometer (Holm Hansen, Lorenzen, Holmes, & Strickland, 1965). Chlorophyll data were depth-integrated to estimate total chlorophyll *a* per square meter.

Macrozooplankton was collected using a 61 cm diameter bongo net. The mesh size of the nets of both sizes was 500 µm. The tows were double obliques, generally towed from the surface to 210 m and back

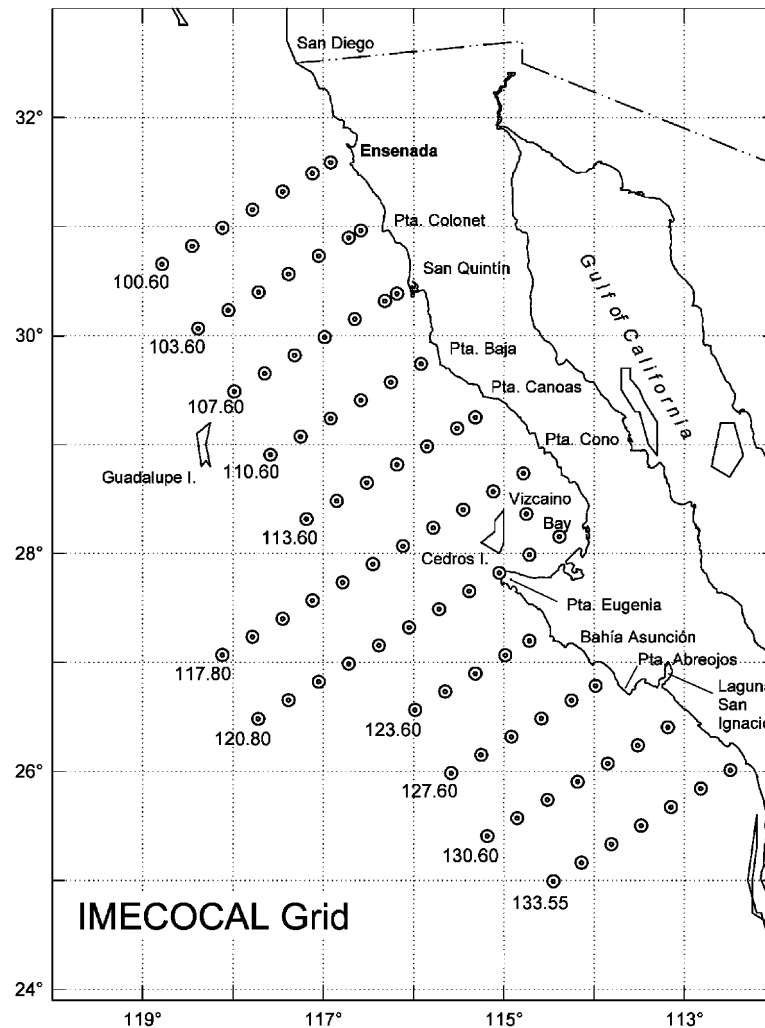


Fig. 1. Sampling stations during the IMECOCAL cruises.

again, but at stations shallower than 220 m the maximum depth of the tows was 10 m above the bottom. A flow-meter mounted in the mouth of the net measured the volume of water filtered (Smith & Richardson, 1977). Zooplankton volume was measured by displacement in a graduated cylinder (Smith & Richardson, 1977) one month after the end of each cruise. Zooplankton volumes and abundances were standardized to 1000 m³ filtered. Taxonomic analyses have been done for samples from the first four cruises (9709/10, 9801/02, 9807, and 9809/10). Samples were subdivided with a Folsom splitter into 1/8 or 1/16 and in some cases to 1/32 fractions. All specimens in the subsample were counted. Samples taken between 30 min after sunset to 30 min before sunrise were considered to be night time samples.

Data from previous Baja California cruises were used to estimate seasonal anomalies of zooplankton volumes and temperature at 10 m depth, using data from CalCOFI and CICIMAR (Centro Interdisciplinario de Ciencias Marinas) cruises. The CalCOFI data record is annual between 1951 and 1969, and was then more or less triennial until 1984 (see Hewitt, 1988, for detailed information of coverage and frequency of CalCOFI cruises). The CICIMAR cruises used were 8204, 8301, 8401, 8707, 8710, 8807, and 9109, which

mainly covered the area south to Punta Eugenia. Seasonal means of temperature at 10 m depth were estimated using CalCOFI data from 1951 to 1984. The long-term seasonal means were then removed from the seasonal means for every year to estimate anomalies. For zooplankton volume the same procedure was done but the data were log-transformed prior to calculation of the anomalies.

Statistical comparisons among cruises were done with the Kruskal–Wallis test, and when significant differences were found, the Mann–Whitney test was used to compare cruises by pairs. The area was divided into north (lines 100–110) and central (lines 113–130), to perform additional comparisons of zooplankton volume. In order to compare Baja California areas with the southern California region, integrated chlorophyll and zooplankton volume data were used from CalCOFI cruises 9709/10, 9801/02, 9804, 9807, 9810, 9901, 9904, 9908 and 9910 (SIO Data Report, 1999a,b,c; 2000a,b).

Spearman rank order correlation analysis was carried out between zooplankton abundance, biomass and environmental variables (10 and 200 m temperature, 10 and 200 m salinity, and mixed layer depth). The Bonferroni criterion for significance ($\alpha' = \alpha/k$) was used, where k is the number of correlations tested, to correct the α level for multiple testing.

3. Results

3.1. Plankton biomass

Near-surface chlorophyll *a* showed seasonal and interannual variability (Fig. 2). There was significant heterogeneity among cruises ($H=83.58$, $p<0.001$), with the lowest median in September–October 1997 and

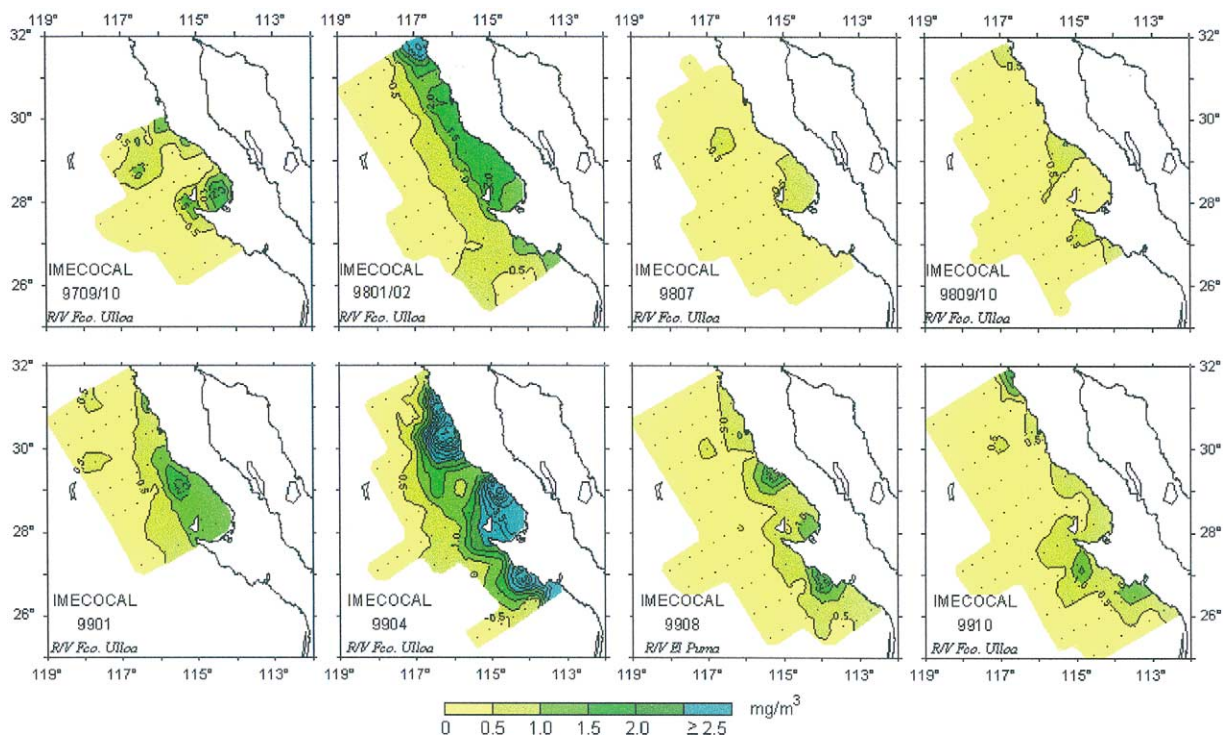


Fig. 2. Distribution of near-surface chlorophyll *a* (mg/m^3) from September 1997 to October 1999.

the highest in April 1999 (Table 1). During the 9709/10 cruise surface values were $<0.25 \text{ mg/m}^3$ in the southwest region of the study area (Fig. 2), while in the northeast, values were mainly in the range of $0.50\text{--}2.00 \text{ mg/m}^3$. In January–February 1998, despite El Niño, surface chlorophyll increased significantly ($z=-4.09$, $p<0.001$), and a strong gradient onshore–offshore had developed. Unfortunately we do not know if these high values persisted through the spring, 1998, but by summer, they had decreased again ($z=-6.46$, $p<0.001$), persisting at low levels through fall, 1998 (Fig. 2).

During the cold year 1999, surface chlorophyll was high, particularly near the coast, associated year-round with active upwelling. During cruise 9904, the phytoplankton biomass at Punta Baja and Vizcaino Bay reached values of 7.87 and 4.15 mg/m^3 respectively. After spring, the oceanic area returned to low biomass, but along the coast concentrations remained between $0.50\text{--}2.00 \text{ mg/m}^3$ (Fig. 2).

Considering integrated chlorophyll for the upper 150 m through 1998 and 1999, a difference in distributional pattern was evident, showing generally a richer oceanic region in 1999 (Fig. 3). Only cruise 9801/02 revealed very similar patterns for both surface and integrated chlorophyll, indicating that the maximum values were occurring at the surface, whereas during other periods the chlorophyll maximum was subsurface. Despite the high values observed near the coast, in January–February 1998 median integrated chlorophyll was 27 mg/m^2 , which was significantly lower than during the later periods ($p<0.001$). Therefore, El Niño apparently produced decreased phytoplankton biomass only in the oceanic area.

Surface chlorophyll was correlated with zooplankton displacement volume (Table 2). Surface chlorophyll and zooplankton biomass generally decrease in the oceanic region (Figs. 2 and 4). However, the progressive increase in median integrated chlorophyll observed from 9801/02 to 9904 was not followed by median zooplankton biomass, which decreased with the change to cool conditions (Table 1). Zooplankton biomass was the highest during fall–winter 1997–1998. Fall 1997 and fall 1998 were significantly different ($Z=-2.3$, $p=0.023$), median values were $103 \text{ ml}/1000 \text{ m}^3$ and $65 \text{ ml}/1000 \text{ m}^3$, respectively. Both winters were also differed significantly ($Z=-4.8$, $p<0.001$), with median values declining by 50% from 9801/02 to 9901 (Table 1). There were also differences between both summers ($Z=-2.7$, $p<0.007$) and between fall 1998 and fall 1999 ($Z=-2.4$, $p<0.014$), with respective reductions in the median values of 32 and 25%.

After the winter of 1997–1998, not only was there a decrease in zooplankton volumes, but remarkable changes in distribution also occurred. Through 1998 a strong latitudinal gradient was observed in the oceanic area, with the southern regions being the richer, whereas in 1999 there was a contrast between coast and offshore regions (Fig. 4). The richest area during the sampling period was Vizcaino Bay, except in fall 1998, when the highest volumes were observed in the offshore area.

Higher concentrations of integrated chlorophyll were associated with surface waters of lower temperatures and salinities, and a shallower mixed layer (Table 2). In contrast, higher zooplankton volumes were

Table 1

Median surface and vertically integrated chlorophyll, and zooplankton displacement volume during IMECOCAL cruises

	Surface Chlorophyll (mg/m^3)	Integrated Chlorophyll (mg/m^2)	Zooplankton Volume ($\text{ml}/1000 \text{ m}^3$)
September–October 1997	0.13	–	103
January–February 1998	0.49	27	100
July 1998	0.19	38	77
September–October 1998	0.30	44	65
January 1999	0.42	59	46
April 1999	0.62	77	60
August 1999	0.34	63	52
October 1999	0.30	51	49

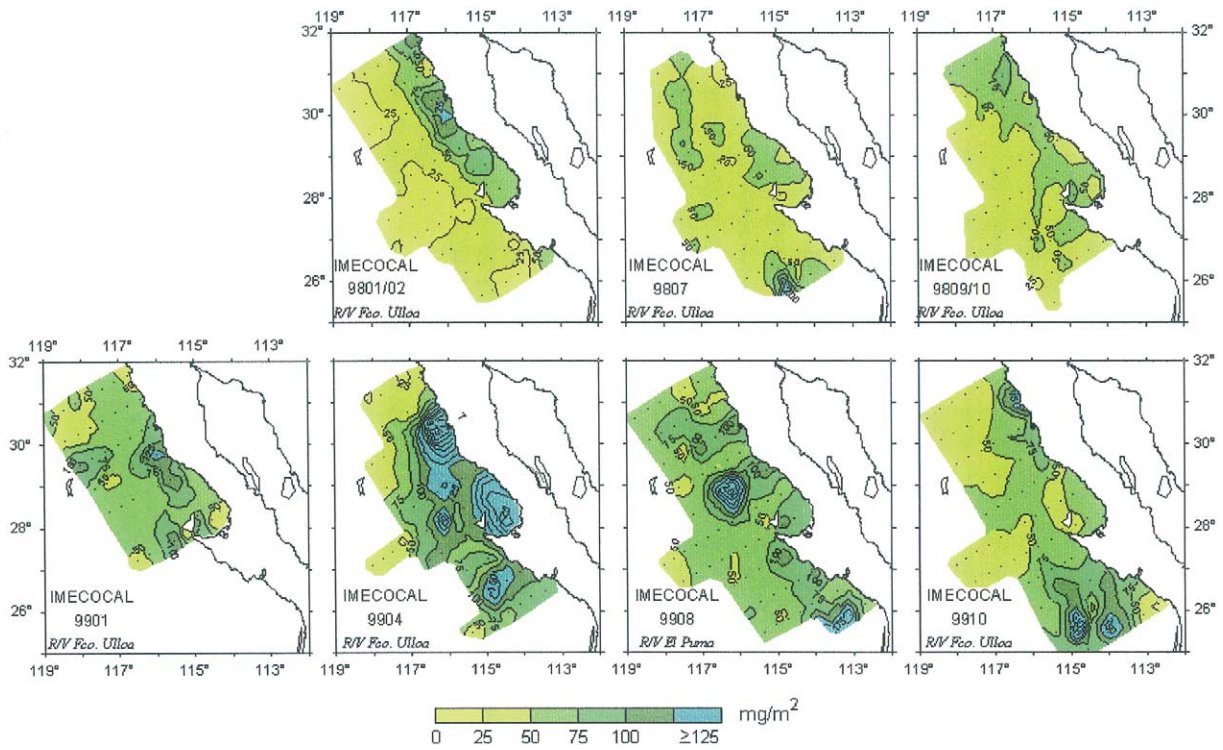


Fig. 3. Distribution of integrated chlorophyll *a* (mg/m^2) from January 1998 to October 1999.

associated with higher salinity surface waters. Contrary to expectations, there was no correlation between zooplankton biomass and the temperature at 10 m. Temperature at 200 m was positively related to zooplankton volume, but inversely related to integrated chlorophyll. Higher salinities at 200 m were associated with higher biomass of both zooplankton and integrated chlorophyll. Not surprisingly, mixed layer depth showed a significant correlation with both temperature and salinity at 10 m (Table 2), but was unrelated to zooplankton.

3.1.1. Regional and long-term trends in plankton biomass

Punta Baja (30°N) has been considered the boundary between two oceanographic regions (US GLOBEC, 1994). However, comparison of the chlorophyll data for the north and central Baja California regions (lines 100–110 and 113–130) showed no consistent differences between the areas. The median for surface chlorophyll over the whole study period was $0.34 \text{ mg}/\text{m}^3$ and for integrated chlorophyll was $51 \text{ mg}/\text{m}^2$. Comparing El Niño integrated chlorophyll medians from IMECOCAL and CalCOFI (lines 80–93) regions showed them to be similar (Fig. 5). During La Niña, beginning in January 1999, they became different, the highest value was in central Baja California ($65 \text{ mg}/\text{m}^2$), followed by north Baja California ($52 \text{ mg}/\text{m}^2$) and the lowest in southern California ($36 \text{ mg}/\text{m}^2$).

In contrast, the zooplankton biomass data showed differences between the north and central Baja California regions ($Z=-5.2$, $p<0.001$): the median for the northern Baja region was 35% lower than for the central Baja region (50 and $77 \text{ ml}/1000 \text{ m}^3$ respectively). In northern Baja California, zooplankton volumes declined from fall 1997 to fall 1999, decreasing from 113 to $36 \text{ ml}/1000 \text{ m}^3$. In central Baja California zooplankton biomass also decreased, but during some cruises values were slightly higher than in the northern region (Fig. 5). In southern California (lines 80–93), extreme changes in zooplankton also occurred.

Table 2
Spearman's rank correlation matrix among zooplankton volume (ml/1000 m³), surface chlorophyll (mg/m³), integrated chlorophyll (mg/m³), temperature (°C), salinity, and mixed layer depth (m). Number of data pairs in parentheses

Variable	Zooplankton Volume	Surface Chlorophyll	Integrated Chlorophyll	Temperature °C at 10 m	Temperature °C 200m	Salinity at 10 m	Salinity at 200 m	MLD
Zooplankton	–							
Surface chlorophyll	(445)	0.28 ^a	0.05	0.08	0.22 ^a	0.33 ^a	0.22 ^a	–0.09
Integrated chlorophyll	(421)	–	0.43 ^a	–0.41 ^a	0.03	0.05	0.31 ^a	0.07
Temperature at 10 m	(498)	(416)	–	–0.26 ^a	–0.17 ^a	–0.18 ^a	0.17 ^a	–0.16 ^a
Temperature at 200 m	(426)	(451)	(428)	–	0.45 ^a	0.48 ^a	0.01	–0.31 ^a
Salinity at 10 m	(490)	(382)	(364)	(434)	–	0.61 ^a	0.47 ^a	0.11
Salinity at 200 m	(427)	(442)	(421)	(500)	(431)	–	0.24 ^a	0.22 ^a
Mixed layer depth	(483)	(382)	(364)	(435)	(434)	(433)	–	–0.12
		(436)	(417)	(494)	(433)	(492)	(435)	–

^a Significant correlation at 0.05 level, corrected for multiple testing

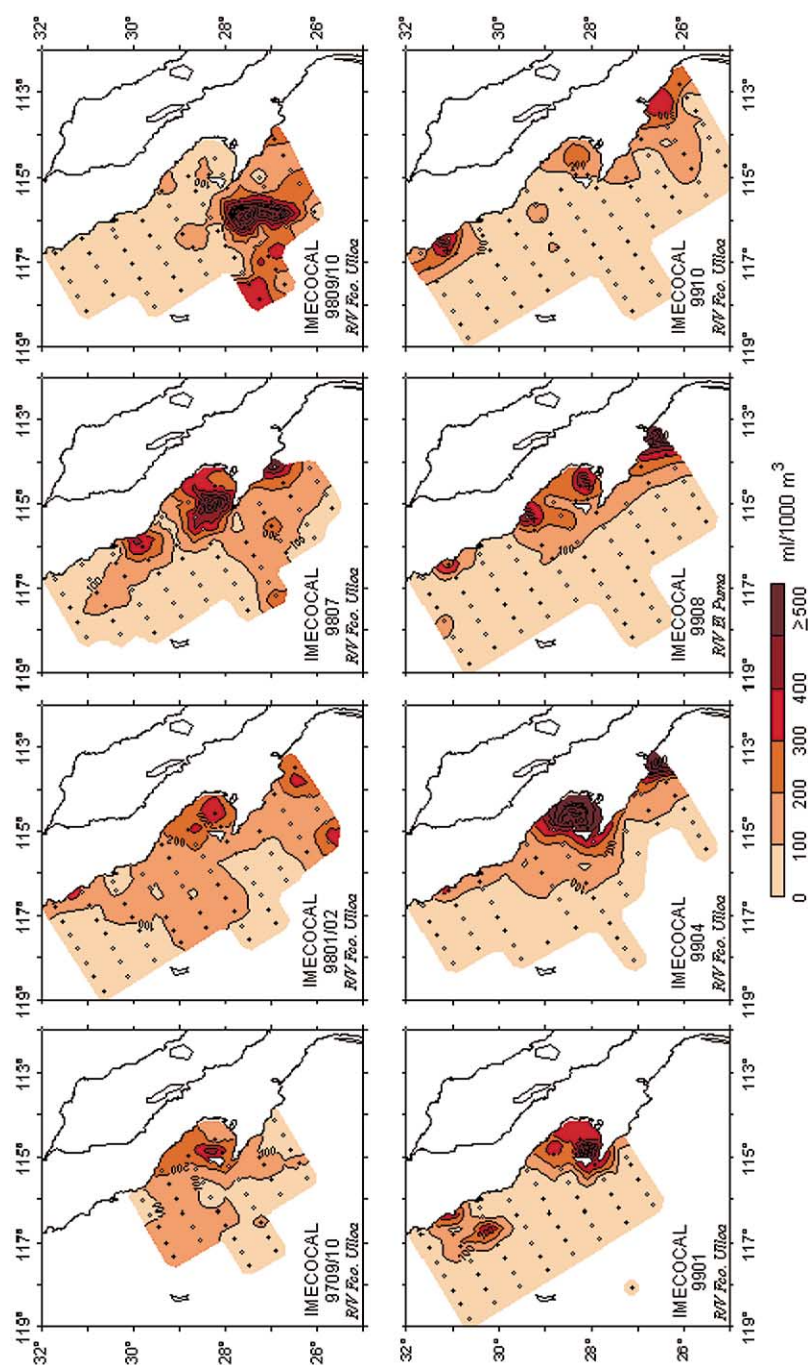


Fig. 4. Distribution of zooplankton displacement volumes ($\text{ml}/1000 \text{ m}^3$) from September 1997 to October 1999. Samples collected during daylight and dark hours are indicated with open and closed circles, respectively.

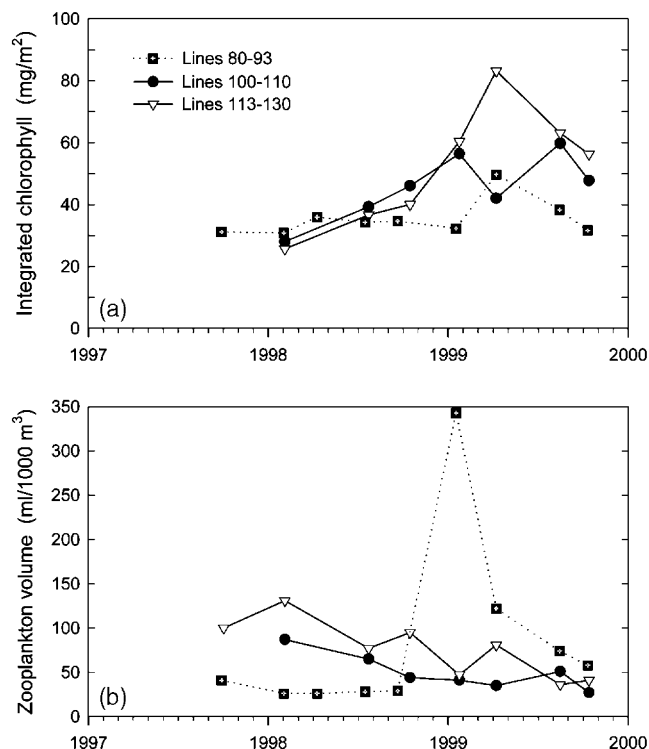


Fig. 5. Median of integrated chlorophyll *a* and zooplankton volumes in northern and central Baja California by cruise. Medians for the southern California region are also shown, obtained from data in the SIO Data Reports (1999a,b,c; 2000a,b).

During 1998, medians from southern California were lower than in Baja California. With the arrival of La Niña, the zooplankton biomass showed a pronounced increase in southern California, while in Baja California it continued to decrease.

Zooplankton biomass within the Baja California region also appears to have changed in response to previous ENSO events. The prolonged ENSO of 1957–1959 had a striking effect on zooplankton (Fig. 6), with negative anomalies remaining in northern and central Baja California for as many as five consecutive years, particularly during the summers. There are few data for the ENSO 1982–1983 for Baja California, but the 1984 CalCOFI cruises (the last in Mexican waters) recorded an ENSO-type response in the northern area. In contrast, in the central area, the CICIMAR cruise (winter 1984) showed an increase in zooplankton volume (Fig. 6), despite the high positive temperature anomalies at 10 m depth. A similar atypical response was again observed during the ENSO 1997–1998, with zooplankton anomalies positive or close to zero, particularly in the central area.

3.2. Zooplankton community structure

Zooplankton groups from the period 1997–1998 showed the expected importance of copepods (31–45%) in the community, followed by chaetognaths (Table 3). Both taxa combined comprised over half of the community. Gelatinous herbivores (i.e. appendicularians, salps, doliolids, pteropods), though less abundant than crustaceans, showed important contributions. Amongst the gelatinous herbivores, salps generally ranked first, although appendicularians displaced them in fall 1997. Carnivorous taxa (i.e. chaetognaths, siphonophores, medusae, ctenophores, heteropods) comprised about 30% of the community, except in sum-

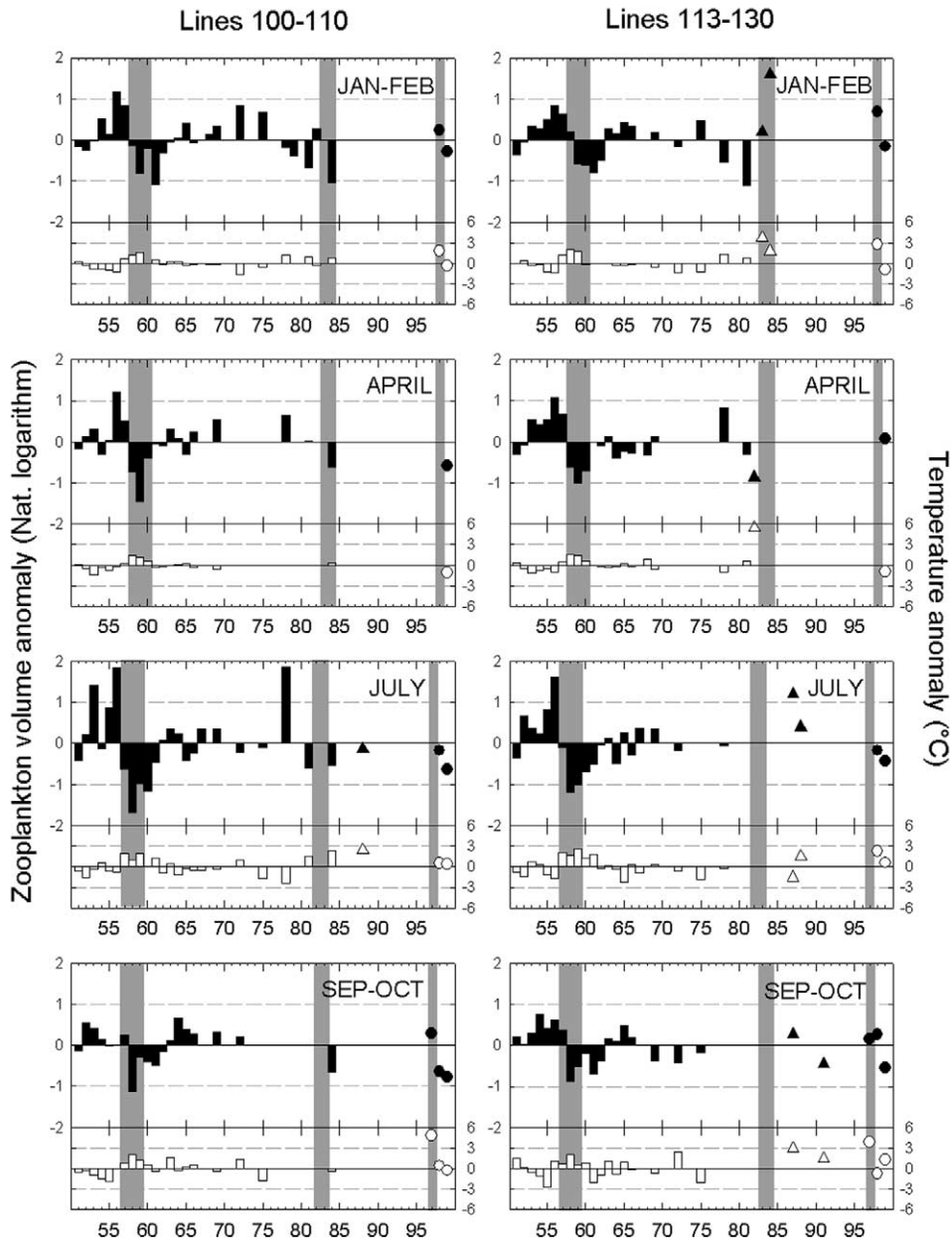


Fig. 6. Annual anomalies of zooplankton displacement volume (dark symbols) and temperature at 10-m depth (open symbols) by season in northern (left panels) and central (right panels) Baja California. Anomalies were estimated for CalCOFI (bars), CICIMAR (triangles) and IMECOCAL cruises (circles), after removing the long-term mean for the period 1951–1984. (Only CalCOFI cruises were used to calculate long-term mean.) Shaded areas indicate strong ENSOs.

Table 3
Zooplankton taxa median relative abundance (%) during the ENSO cycle 1997–1998

TAXA	September–October 97 (n=37)	January–February 98 (n=69)	July 98 (n=65)	September–October 98 (n=61)
Copepods	38.13	41.12	45.02	31.33
Cladocerans	0.00	0.00	0.06	0.20
Ostracods	1.50	1.63	1.58	2.76
Amphipods	0.61	0.53	0.70	1.12
Euphausiids	4.18	4.88	5.62	5.59
Decapods	0.87	0.21	0.44	0.55
Polychaetes	0.17	0.11	0.10	0.15
Pteropods	2.60	1.30	0.83	1.72
Heteropods	1.19	0.35	0.21	0.42
Medusae	0.85	0.69	1.16	1.55
Siphonophores	5.31	4.45	5.00	7.17
Chaetognaths	20.86	23.15	6.27	15.42
Appendicularians	4.27	2.25	1.41	2.43
Doliolids	0.10	0.00	0.00	0.00
Salps	1.96	2.88	2.92	4.29
Stomatopod larvae	0.23	0.13	0.00	0.00
Fish larvae	0.62	0.31	1.15	0.64
Fish eggs	0.14	0.40	0.39	0.10
Other larvae	0.49	0.28	0.48	0.95

mer 1998, when they fell to only 15%. Interestingly, during this period, copepods reached their highest relative abundance. With the exception of chaetognaths, most of the carnivores were present in low proportions. Nevertheless, because of their large sizes and predatory activity, they may have had a strong influence on the community.

3.2.1. Regional differences

Community structure showed important differences between regions. The most remarkable was the small proportion of salps observed through 1998 in the northern region compared to the increase in the central region (Fig. 7). The chaetognaths showed low percentages during July 1998 in both areas, but the shift from the previous cruise was more extreme in the northern region (from 26 to 3%) than in central Baja California (from 21 to 8%). This change together with the scarcity of salps, resulted in the contribution by copepods rising to >60% in the northern region during July 1998.

Other abundant groups were euphausiids, siphonophores, and appendicularians. These taxa together contributed about 15% by numbers in both regions. Their proportions were more or less conservative, although an increase of euphausiids was apparent in the northern area during September–October 1998, representing 9% of the total abundance, compared to 4% in the southern area. Other groups, that were infrequently observed in the samples included ctenophores, mysids, cumaceans and cephalopod larvae. The abundance

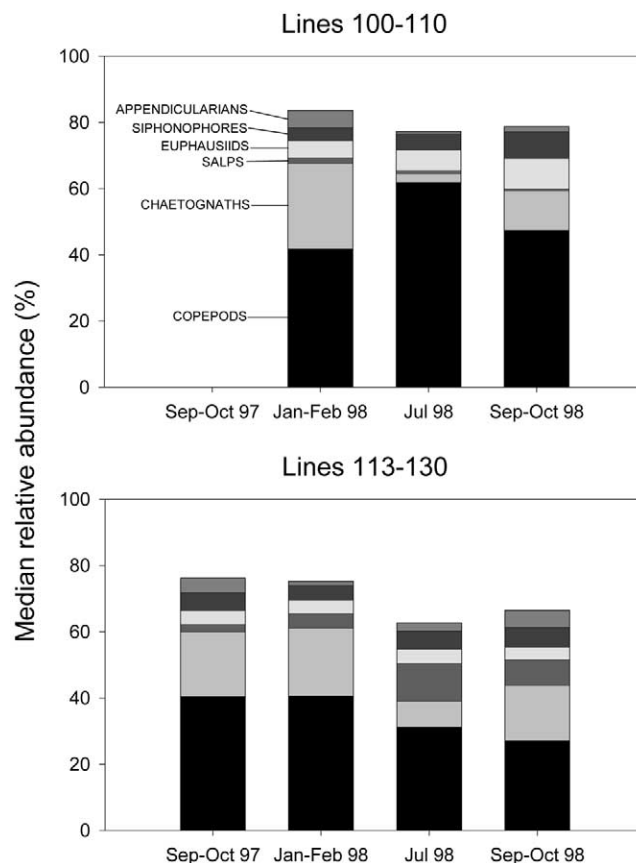


Fig. 7. Mean relative abundance of the main zooplankton groups by cruise in northern and central Baja California.

of ctenophores is likely to have been underestimated because they rapidly disintegrate in formalin. Mysids and cumaceans are taxa associated with the bottom, and so they mainly occurred at the coastal stations.

3.2.2. Interannual differences

It is not possible to test for statistical differences in relative abundance during the ENSO in relation to non-ENSO conditions because time series for abundance by taxon do not exist in the CalCOFI records. However, two of the IMECOCAL cruises were conducted in fall. We can compare fall 1997 when El Niño conditions were prevailing, with fall 1998 when the system was returning to 'normal' conditions. Within the area sampled during both cruises (lines 110–127), significant differences were found for seven taxa (Mann–Whitney test, Table 4). In fall 1998 the zooplankton community sampled contained fewer copepods than in fall 1997. The opposite occurred with salps, whose relative abundance was higher in fall 1998 than in fall 1997. Other minor groups differed, but their proportional contribution to the community (in terms of abundance) was low.

3.2.3. Distribution of zooplankton groups

Zooplankton organisms occurred across a broad trophic spectrum. Omnivory is widely observed in the zooplankton. Except for some groups of obligate carnivores (chaetognaths, siphonophores, medusae, ctenophores and heteropods), most of the groups include both omnivorous and carnivorous species. However, many omnivores graze actively when phytoplankton is available. In the light of these considerations, we defined the following functional groups to describe the distribution of the most important taxa found in this study.

3.2.3.1. Crustacean herbivores During the ENSO cycle, captures of copepods were generally one order of magnitude higher than those of euphausiids, and two orders higher than of ostracods and amphipods. Through fall 1997 to summer 1998, abundances of copepods at 25–50% of the stations were 25–50 ind/m³ (Fig. 8), but later, in fall 1998, they were <25 ind/m³ in 97% of the samples. During all the cruises, the major aggregations of copepods occurred at Vizcaino Bay where they reached up to 1853 ind/m³ in 9807.

Euphausiid distributions showed a strong onshore–offshore pattern (Fig. 9). Abundances were >10 ind/m³ near the coast and lower offshore. Vizcaino Bay was also very rich in euphausiids, except in fall 1998. In contrast to euphausiids, ostracods had a more oceanic pattern, with relatively low abundance in the Vizcaino Bay area. Captures were between 0.5 and 5 ind/m³ in most of the oceanic stations, except summer 1998 when abundances were <0.5 ind/m³ (data not shown) at many stations.

Amphipod abundances were mainly in the range of 0.1–0.5 ind/m³, and only infrequently were >0.5 ind/m³. However, in January–February 1998, amphipods were abundant in Vizcaino Bay. Other groups of crustaceans (decapods, stomatopods, and cladocerans) were found in low abundances in most of the samples. Whereas mysids and cumaceans were found in <50% of the samples.

3.2.3.2. Gelatinous herbivores Salps and appendicularians were the most abundant gelatinous herbivores in the plankton. Salp abundance was <5 ind/m³ in all but one station during fall 1997 (Fig. 10). Their abundance increased through 1998 in the offshore region of central Baja California, rising to 240 ind/m³ in 9801/02. In contrast, appendicularians occurred in higher numbers in the northern area during January–February 1998 (Fig. 11), and later in 1998 their abundance was extremely low. Doliolids were relatively important during fall 1997, being observed in 60% of the samples, but occurred in 30% or less of the samples the rest of the time (data not shown).

3.2.3.3. Carnivores The main carnivores were chaetognaths, siphonophores, and medusae. Chaetognaths were one order of magnitude more abundant than siphonophores and two orders more than medusae. Chaetognaths were very abundant during El Niño, with captures mostly in the range of 5–15 ind/m³ (Fig.

Table 4
Zooplankton taxa median relative abundance (%) during fall 1997 and fall 1998 for the area comprised from line 110 to 127. The probability of fall medians being equal (Mann–Whitney test) is also shown, and the percentage of change (NS=not significant at $p<0.05$)

TAXA	September–October 97 ($n=37$)	September–October 98 ($n=45$)	p	% Change
Copepods	38.13	27.15	<0.001	–10.98
Pteropods	2.60	1.39	0.025	–1.21
Heteropods	1.19	0.38	<0.001	–0.81
Decapods	0.87	0.47	0.004	–0.40
Salps	1.96	5.91	<0.001	+3.95
Other larvae	0.49	0.76	<0.001	+0.27
Cladocerans	0.00	0.20	0.002	+0.20
Chaetognaths	20.86	16.39	0.108	NS
Siphonophores	5.31	7.32	0.074	NS
Appendicularians	4.27	3.52	0.967	NS
Euphausiids	4.18	3.79	0.254	NS
Ostracods	1.50	2.60	0.057	NS
Medusae	0.85	1.09	0.321	NS
Fish larvae	0.62	0.71	0.412	NS
Amphipods	0.61	1.01	0.220	NS
Stomatopod larvae	0.23	0.00	0.109	NS
Polychaetes	0.17	0.16	0.944	NS
Fish eggs	0.14	0.11	0.464	NS
Doliolids	0.10	0.00	0.402	NS

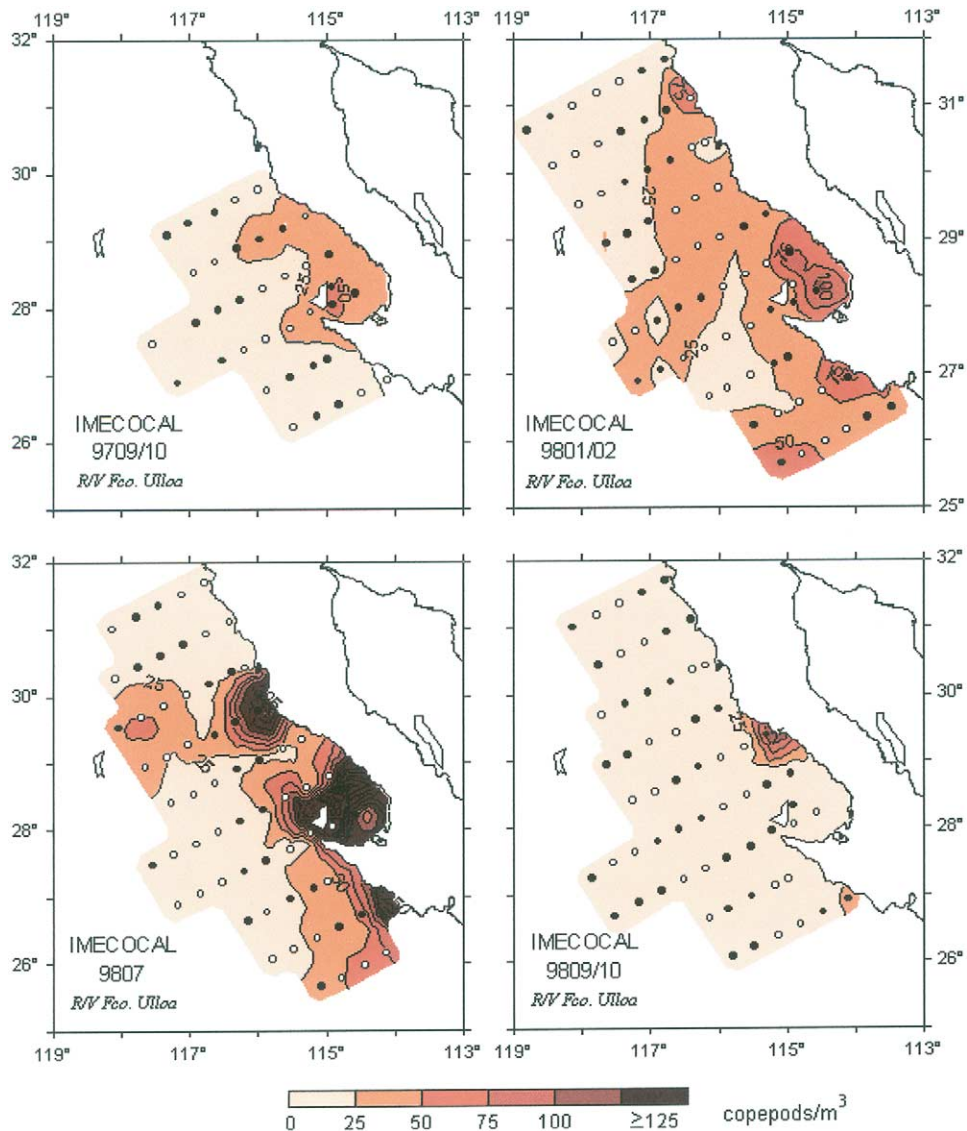


Fig. 8. Distribution of copepods during the ENSO cycle 1997–1998.

12). The lowest captures were in summer 1998, particularly in the northern stations, where abundance was <0.5 ind/ m^3 at most of the stations. During fall 1998 chaetognath abundance increased but were consistently lower in the northern area relative to the central area.

Siphonophore abundance did not fluctuate strongly during the ENSO cycle. Their distribution stayed relatively uniform, although Vizcaino Bay was usually richer than the other areas. Medusae occurred in low abundances in the northern offshore area during the peak of ENSO, but later, more stations in the central offshore area contained low abundances. Heteropods were (after ctenophores) the least abundant carnivores in the study area. However, during fall 1997, they were relatively important. Pteropods were a major zooplankton group, but it is difficult to consign them to a single functional category. In most of the stations during the peak of El Niño, they were in the range of 0.5–5 ind/ m^3 and in later cruises were less

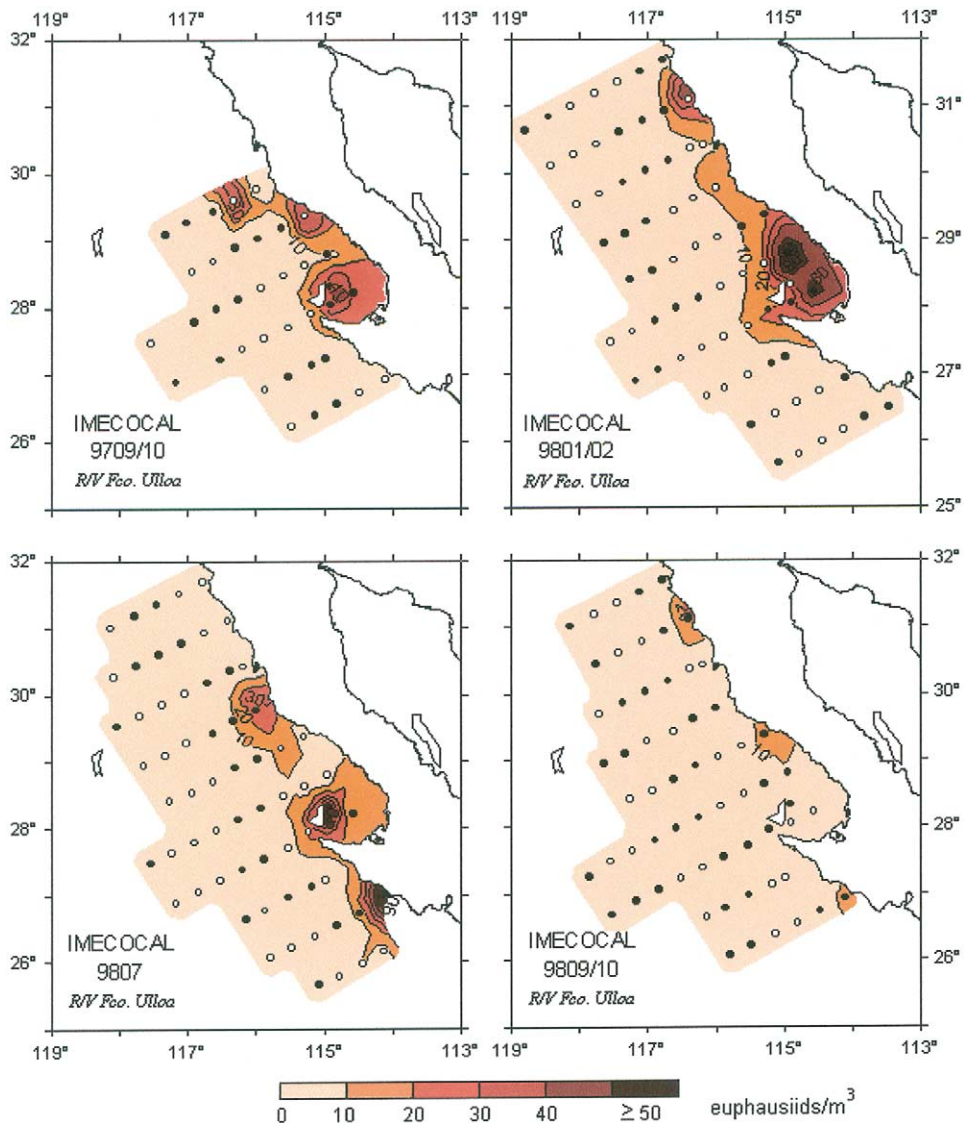


Fig. 9. Distribution of euphausiids during the ENSO cycle 1997–1998.

abundant ($0.01\text{--}0.5$ ind/m³). Although many are carnivorous, pelagic polychaetes can also display omnivory. They (as well as many meroplanktonic forms), were regularly present in samples but in low numbers.

3.2.4. Correlation among zooplankton groups

Spearman rank order correlation for pairs of zooplankton groups was significant in 41% of the cases ($N=231$). The four more abundant groups (copepods, chaetognaths, siphonophores, and euphausiids) showed correlations with 12 or more groups ($0.24 < r < 0.65$, $p < 0.05$), generally excluding those less abundant. However, ostracods, which were relatively abundant, appeared to have a pattern of variability that differed from that of the dominant crustaceans (copepods and euphausiids), since no correlation was found between

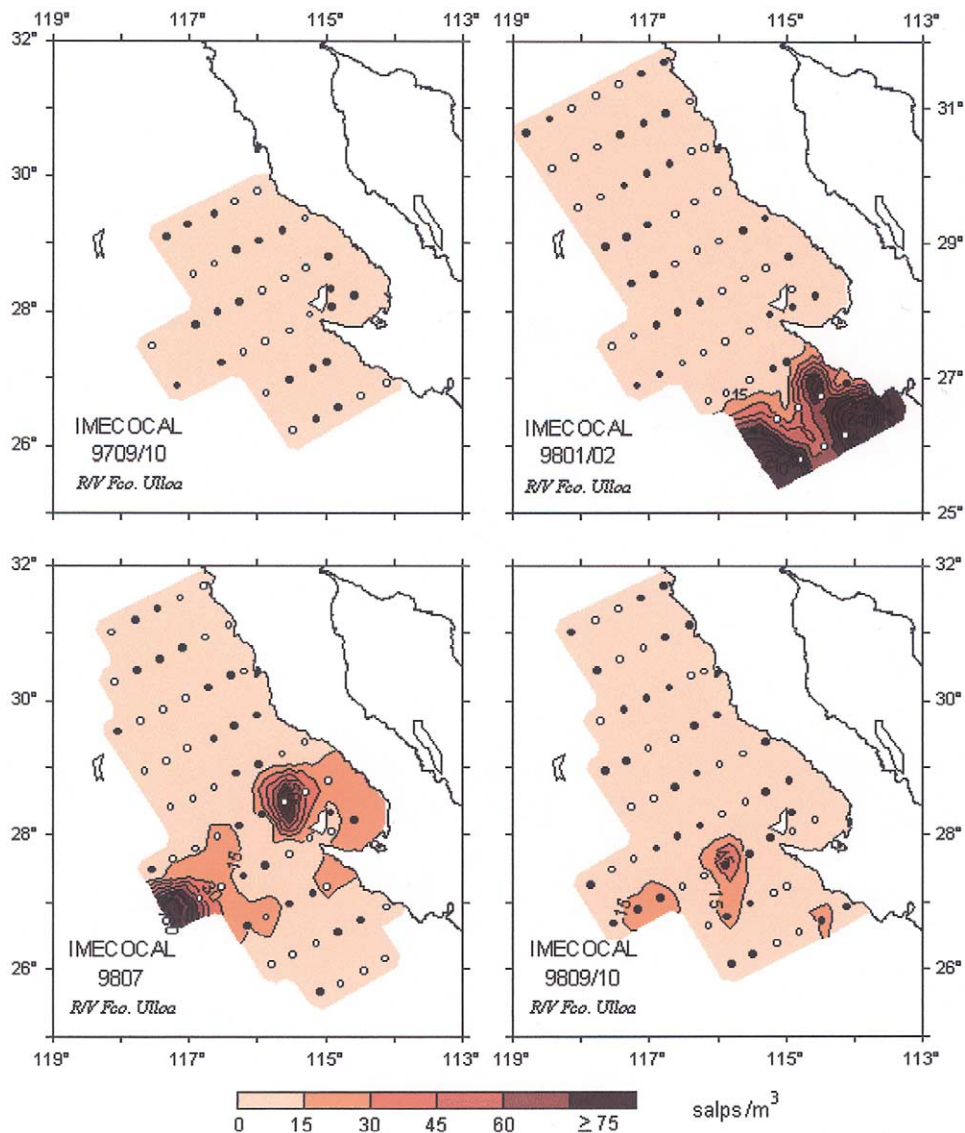


Fig. 10. Distribution of salps during the ENSO cycle 1997–1998.

ostracods and those taxa. The only negative coefficient observed in crustaceans was between copepods and cladocerans ($r=-0.26$, $p=0.018$).

Salps and appendicularians, which have a similar herbivorous role, showed interesting differences. Appendicularians covary with euphausiids, since they were positively correlated ($r=0.34$, $p<0.001$). However salps were not correlated with euphausiids.

All carnivores (except ctenophores) showed significant correlations with each other ($0.34<r<0.44$, $p<0.001$). Interestingly ctenophores were negatively correlated with chaetognaths, suggesting a possible competitive exclusion between them ($r=-0.31$, $p<0.001$).

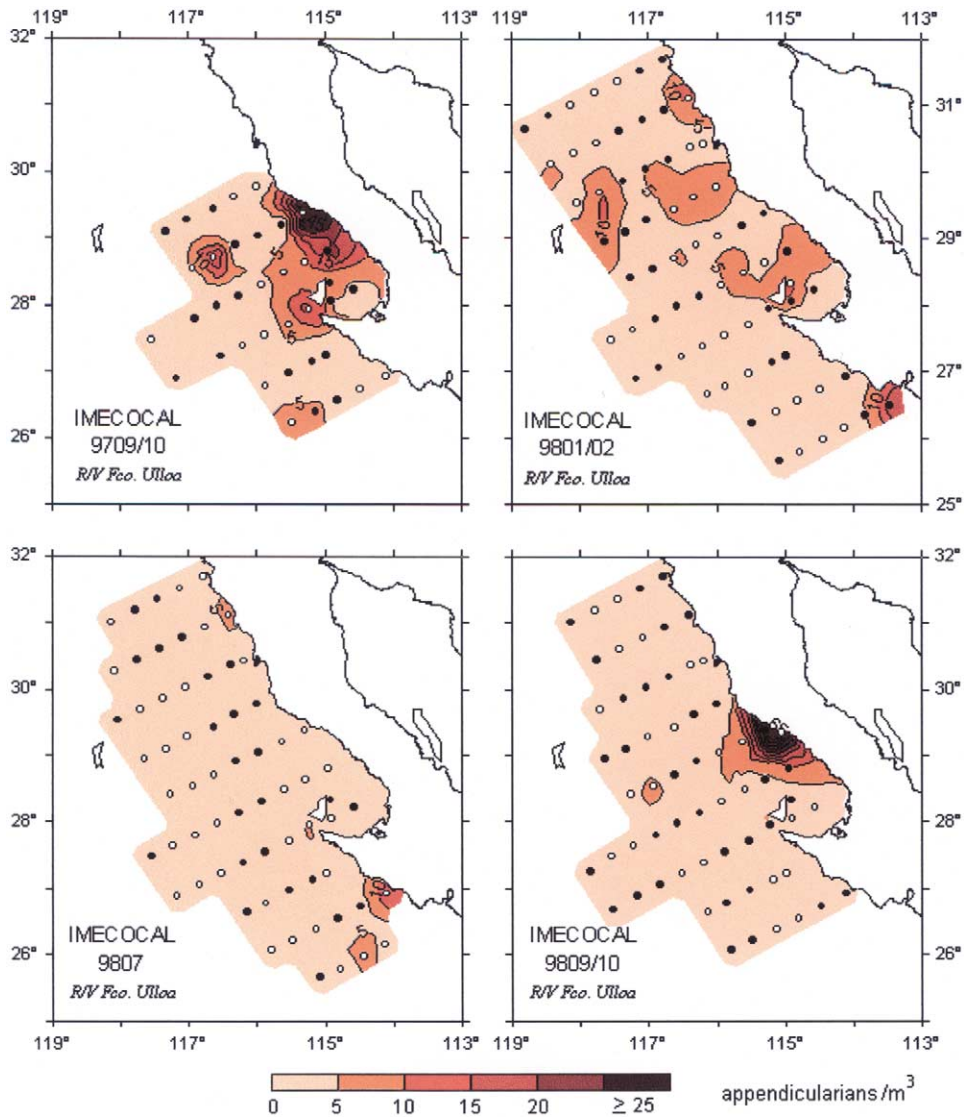


Fig. 11. Distribution of appendicularians during the ENSO cycle 1997–1998.

3.2.5. Correlation with environmental variables

Positive correlation was found between zooplankton displacement volume and 13 taxa ($0.23 < r < 0.56$, $p < 0.05$). Among them were the two most abundant groups of crustaceans and large gelatinous organisms (chaetognaths, siphonophores, salps, medusae, and heteropods). However, r^2 values were lower than 0.31 in all cases.

Surface chlorophyll concentration, instead of integral chlorophyll data, was analyzed in relation to abundances of zooplanktonic groups, since only surface chlorophyll data were available from the first cruise. Linear correlations were found between surface chlorophyll concentrations and the main group of zooplanktonic crustacean herbivores [copepods ($r = 0.29$, $p = 0.003$), euphausiids ($r = 0.37$, $p < 0.001$)], but not with gelatinous herbivores. Positive correlations were found between chlorophyll and two predatory groups

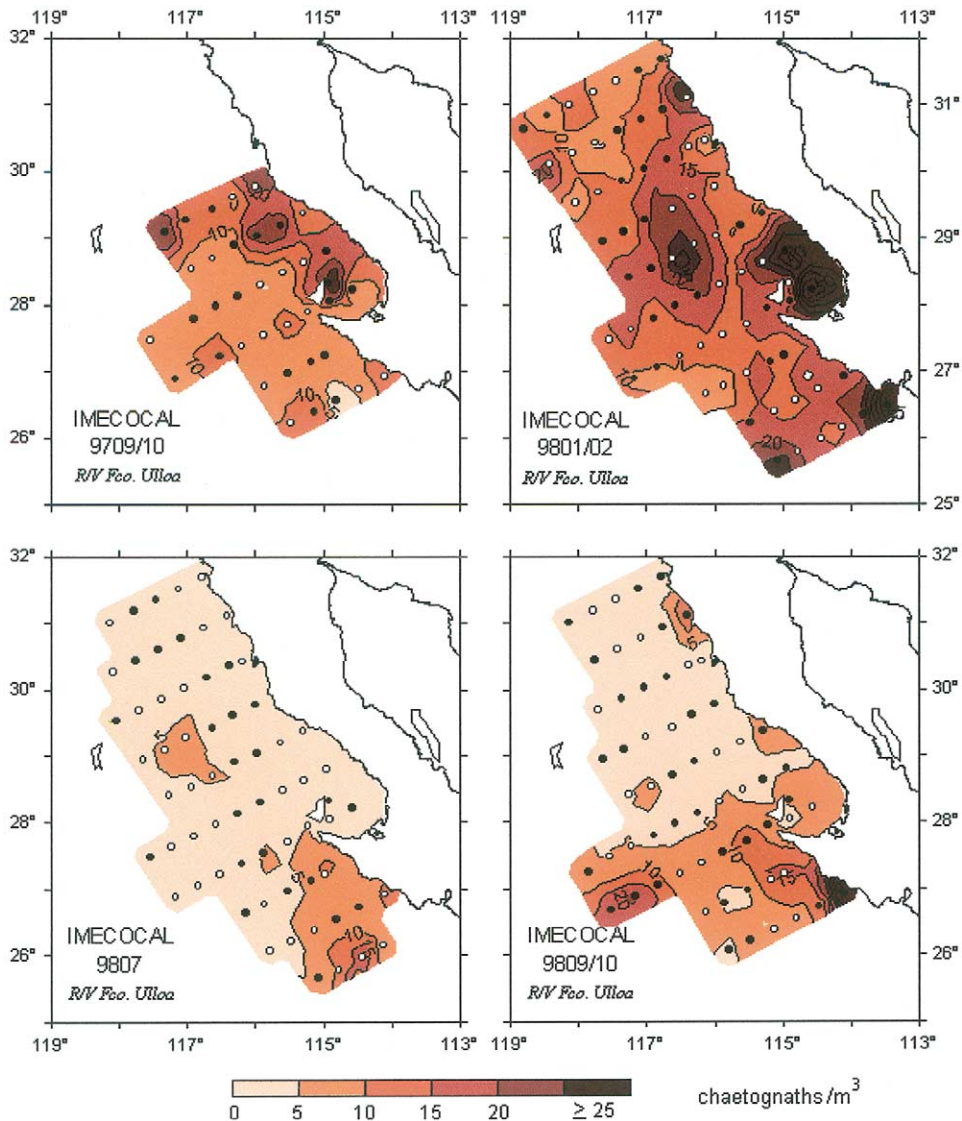


Fig. 12. Distribution of chaetognaths during the ENSO cycle 1997–1998.

($p < 0.001$), stomatopods ($r = 0.41$, $p < 0.001$), and other invertebrate larvae ($r = 0.27$, $p = 0.017$). The only significant negative correlation was between chlorophyll and cladocerans ($r = -0.30$, $p = 0.002$).

Negative correlation between some zooplankton groups with 10 m temperature and salinity could indicate an affinity of those groups to subarctic water. This could be the case for cladocerans and ctenophores, whose coefficients (-0.30 and -0.25) were negatively related ($p < 0.01$) with 10 m salinity. Other groups (siphonophores and salps) were positively correlated ($0.26 < r < 0.42$, $p < 0.05$) with both temperature and salinity at 10 m, suggesting an affinity of these groups to surface water from the central Pacific gyre, which is the warmest and the most saline in the region. Eight more groups were correlated with salinity, but not with temperature at 10 m, which could make it difficult to associate them with upwelling or subtropical water masses.

Salps, some of which are active vertical migrators, were correlated with both temperature ($r=0.38$, $p<0.001$) and salinity ($r=0.28$, $p=0.015$) at 200 m, the depth of the countercurrent. Other taxa showed positive coefficients only with temperature at 200 m, making it difficult to associate them with equatorial deep water.

The mixed layer had only four significant correlation coefficients ($p<0.01$), one positive with chaetognaths ($r=0.54$, $p<0.001$) and three negative, with cladocerans ($r=-0.27$, $p=0.11$), ctenophores ($r=-0.36$, $p<0.001$), and fish larvae ($r=-0.28$, $p=0.005$). Therefore, thicker mixed layers are associated with more chaetognaths, while the thinner mixed layers contain more cladocerans, ctenophores, and fish larvae. These last groups are more abundant near the coast, while chaetognaths are more abundant in oceanic waters (Mackas & Yelland, 1999).

4. Discussion

The El Niño of 1997–1998 was one of the strongest ENSO events of the last 50 years. It was comparable in magnitude and extent to the event of 1982–1983 (Wolter & Timlin, 1998). It began in the central equatorial Pacific in March 1997 (McPhaden, 1999), and it moved eastward, reaching the CCS in late summer. Its oceanographic signals in the CCS were expanded coastal poleward current, and unusually warm and saline water in the upper 100 m and deeper (Lynn et al., 1998). Despite the strong climatic anomalies in the upper layer, the biological response was less clear. For the southern California region, phytoplankton biomass during 1998 was typical of the 1984–1997 time series, suggesting little affect. In contrast, macrozooplankton biomass in the same region indicated a strong impact of ENSO, as manifested by some of the lowest values recorded since 1951 (Lynn et al., 1998).

IMECOCAL surveys in the Baja California region of the CCS started in fall 1997, just when the ENSO was peaking and the expanded poleward current was particularly strong south at Punta Eugenia (Fig. 20 in Lynn, Bliss, & Eber, 1998). Anomalies of temperature and salinity, estimated from 1950–1978 historical data (Lynn, Bliss & Eber, 1982) were high, reaching maximum values of 8°C and 0.8 respectively (Lynn et al., 1998). Chlorophyll concentrations recorded in southern California during 1998 were comparable with concentrations reported in the present study for Baja California (Fig. 5), but in 1999 chlorophyll showed a notable increase in Baja California that was not observed in southern California. The presence of apparently average values of chlorophyll in both California Current regions during the ENSO peak is in contrast with the impoverishment observed in the equatorial Pacific. In that region, Chavez et al. (1999) reported values of 0.05 mg/m³ or lower, while in Baja California, median values were 0.19 and 0.17 mg/m³ (i.e. 28 and 26 mg/m²) off northern and central Baja California. The values off Baja California were close to the mean chlorophyll concentration reported for the equatorial Pacific during non-ENSO periods (Chavez et al., 1999). Furthermore, the increase of chlorophyll in Baja California after El Niño (October 1998–October, 1999) was coincident with the trend observed in the equatorial Pacific. As the depth of the mixing layer was inversely related to surface temperature in Baja California it seems reasonable to suppose that is related to the influence of vertical stratification on nutrient supply (e.g. Chavez et al., 1999; González, Sobarzo, Figueroa, & Nothig, 2000).

Zooplankton biomass during the ENSO cycle showed important differences between the Baja California and southern California regions of the CCS. While displacement volumes were extremely low in southern California during 1998, typical values were recorded in the Baja California region. Even during the ENSO peak, when volumes for southern California were the lowest in the 50 year historical record (Lynn et al., 1998), volumes for Baja California were close to their historical mean (Fig. 6; see also Lavaniegos, Gómez-Gutiérrez, Lara-Lara, & Hernández-Vázquez, 1998a). In contrast, with the onset of La Niña, when coastal waters in both Californias were cold (Hayward et al., 1999), a strong increase of macrozooplankton volume occurred in southern California but not in Baja California. In fact, a decreasing trend was observed in Baja

California for 1999. This suggests differing plankton dynamics or circulation patterns exist between Baja California and southern California.

The absence of correlation found between surface temperature and zooplankton in Baja California was unexpected, because Roesler and Chelton (1987) had found an inverse relationship between these two variables in the CCS for the period of 1951–1982. They considered that the low-saline and cold water that had originated from the subarctic, was rich in zooplankton compared to other waters originating to the west and south of the CCS. Our results, however, indicate that high zooplankton volumes in Baja California were associated with warm and saline waters, whose possible sources are central Pacific water and the coastal countercurrent (Lynn & Simpson, 1987). Durazo and Baumgartner (this issue) found a strong input of subtropical water entering the region from the southwest.

The presence of normal to high chlorophyll concentrations in the CCS would suggest a favorable food supply for zooplankton. However, the taxonomic composition of food may have changed during El Niño, with subsequent impact on zooplankton community structure. Between fall 1997 and fall 1998 copepod abundance declined 11%, which could be explained if there were a decrease in the larger type of food preferred by copepods. In contrast, salp abundance increased 4%, perhaps because of their ability to remove minute particles at high filtration rates (Andersen, 1998). Empirical determinations of particle retention by salps, indicate that particles from 3–7 μm are retained with 100% efficiency (Kremer & Madin, 1992). Thus, salps may have increased during 1998, as a result of their capacity to exploit a wider size range of the spectrum of food particles. Regrettably, we lack the data on phytoplankton sizes to test this hypothesis.

Although the numerical increase in salp contribution was low compared to the decrease in copepods, differences in typical body sizes of both groups would mean a much larger change in terms of biomass and ecosystem function (González, Sobarzo, Figueroa & Nothig, 2000). Salps are ubiquitous in the world oceans, yet it remains unclear why they change from low densities to dense swarms so fast (but see Menard, Dallot, Thomas, & Braconnot, 1994). In the Bay of Villefranche-sur-Mer, salp blooms occur either at the end of winter or the beginning of spring apparently promoted by the breakdown of the vertical stratification in the upper layer of the water column (Menard et al., 1994). In our study higher abundances of salps (Fig. 10) were observed during cruise 9801/02, when mean MLD was at its deepest (82 m) for the period 1997–98. Furthermore, the response of salps to ENSOs has been variable. During the ENSO of 1958–1959, salps declined throughout the California Current (Smith, 1985). This produced a strong decrease in zooplankton volumes because in years prior to that ENSO, salps were in high abundance. For the ENSO of 1982–1983, southern California zooplankton was rich in *Salpa fusiformis* (Lavaniegos, unpublished data), despite relatively low total biovolumes (McGowan, 1984).

Few studies have examined shifts of grazers in the ocean. Montú and Ritter-Oliveira (1986) reported salps and large carnivorous copepods were dominant in the zooplankton near Elephant Island in the Antarctic Ocean in February–March 1984 and then one year later (February–March, 1985) the zooplankton community had become impoverished in salps but rich in euphausiids and small copepods. In the present study, we did not find evidence to suggest a climatic related alternation of groups, as has been hypothesized for Antarctic waters (Montú & Ritter-Oliveira, 1986; Loeb et al., 1997). The proportion of euphausiids was similar during the four cruises analyzed, but the proportions of copepods and salps changed. Copepods were more abundant during the ENSO peak, and salps more abundant in the transition phase. A more complete taxonomic analysis would illuminate the biological affinity of the copepod and salp species present in the region during El Niño. Preliminary evidence indicated a marked increase in the abundances of the tropical copepod species *Nannocalanus minor*, *Undinula darwini* and *Undinula vulgaris* during fall 1997 (Lavaniegos, Jiménez-Pérez & Baumgartner, 1998b). *N. minor* and *U. darwini* are oceanic species, while *U. vulgaris* is a coastal species restricted to the eastern tropical Pacific. In comparison, the warm-temperate species, *Calanus pacificus*, was abundant only in the northwest area, where it was associated with low salinity water (Lavaniegos, Jiménez-Pérez, & Baumgartner, 1998b). In Monterey Bay, *Calanus* and other

temperate copepods were negatively affected compared to smaller bodied copepods (Hopcroft, Clarke, & Chavez, this issue).

The species varied in their responses to El Niño, so although total euphausiid abundance did not change through 1997–1998, temperate species declined in abundance during the El Niño (Linacre-Rojas, 2001). Off central Baja California, *Euphausia pacifica* was absent during fall 1997, and captures of *Nematoscelis difficilis* were low, being surpassed by *Euphausia eximia* (a species from the eastern tropical Pacific). The dominant species, *Nyctiphanes simplex*, presented similar abundance to that recorded in the typical fall of 1966 (Lavaniegos, 1993). However, beyond its home range in southern California and Baja California, *N. simplex* underwent an extraordinary expansion northwards during El Niño 1997–1998 (Mackas & Galbraith, this issue; Marinovic, Croll, Gong, Benson, & Chavez, this issue; Peterson, Keister, & Feinberg, this issue).

Other important changes in zooplankton structure observed were the higher proportions of chaetognaths and heteropods observed during El Niño phase, relative to the post El Niño phase. In the Humboldt Current, off northern Chile, Gonzalez et al. (2000) recorded a similar increase in chaetognaths in January 1998, maybe the result in the concurrent increases in numbers of small copepods. In Peru during the ENSO of 1972–1973, a similar increase of chaetognaths and other large predators (such as medusae) was observed (Arntz & Fahrbach, 1996), yet we did not find changes in abundance of either siphonophores or medusae in Baja California.

Long-term changes have been documented for the zooplankton biomass of the CCS (Roemmich & McGowan, 1995; Brodeur, Frost, Hare, Francis, & Ingraham, 1996; Lavaniegos, Gómez-Gutiérrez, Lara-Lara & Hernández-Vázquez, 1998a), related to climate regime shifts (Ebbesmeyer et al., 1991; Latif & Barnett, 1996). The decline in zooplankton biomass observed in the southern California region (McGowan, 1995) appears to have been related to lower abundances of gelatinous forms (Lavaniegos & Ohman, 1999). Such long-term decreases were less evident in Baja California (Lavaniegos, Gómez-Gutiérrez, Lara-Lara & Hernández-Vázquez, 1998a), and gelatinous forms remained well represented in this region during our study. It would appear that more extensive retrospective analyses of the zooplankton community, in this and other regions of the CCS, are required to resolve such issues fully. This is further highlighted by our finding of clear regional differences in planktonic responses to climatic changes.

Acknowledgements

The work at sea of students and technicians during the IMECOCAL cruises is greatly appreciated. Thanks also to the crew of R/V *Francisco de Ulloa* and Daniel Loya-Salinas for his help in the organization of cruises. Data of zooplankton volumes from early CalCOFI cruises were provided by Paul Smith, and from CICIMAR cruises by Jaime Gómez-Gutiérrez. Support was provided by the Consejo Nacional de Ciencia y Tecnología (grants G0041-T9607, G3532-GT, and 017PÑ-1297), the Inter-American Institute for Global Change Research (grant ISP 2-124), the Centro de Investigación Científica y Educación Superior de Ensenada (project 'Efectos del ENSO 1997-1998 sobre el zooplankton de la Corriente de California'), and by a US GLOBEC grant from NSF and NOAA.

References

- Andersen, V. (1998). Salp and pyrosomid blooms and their importance in biogeochemical cycles. In Q. Bone (Ed.), *The Biology of Pelagic Tunicates* (pp. 125–137). Oxford: Oxford University Press.
- Arntz, W. E., & Fahrbach, E. (1996). *El Niño—Experimento climático de la naturaleza*. México, D.F: Fondo de Cultura Económica.
- Barber, R. T., & Chavez, F. P. (1983). Biological consequences of El Niño. *Science*, 222, 1203–1210.
- Brodeur, R. D. (1986). Northward displacement of the euphausiid *Nyctiphanes simplex* Hansen to Oregon and Washington waters following the El Niño event of 1982–83. *Journal of Crustacean Biology*, 6, 686–692.

- Brodeur, R. T., Frost, B. W., Hare, S. R., Francis, R. C., & Ingraham, W. J. Jr. (1996). Interannual variations in zooplankton biomass in the Gulf of Alaska, and covariation with California Current zooplankton biomass. *California Cooperative Oceanic Fisheries Investigations Reports*, 37, 80–99.
- California Department of Fish & Game (1998). Review of some California fisheries for 1997. *California Cooperative Oceanic Fisheries Investigations Reports*, 39, 9–24.
- Chavez, F. P., Strutton, P. G., Friederich, G. E., Feely, R. A., Feldman, G. C., Foley, D. G., & McPhaden, M. J. (1999). Biological and chemical response of the equatorial Pacific Ocean to the 1997–98 El Niño. *Science*, 286, 2126–2131.
- Chelton, D. B., Bernal, P. A., & McGowan, J. A. (1982). Large-scale interannual physical and biological interactions in the California Current. *Journal of Marine Research*, 40, 1095–1125.
- Durazo, R., & Baumgartner, T. R. (2002). Evolution of Oceanographic Conditions off Baja California: 1997–1999. *Progress in Oceanography* (this issue), PII: S0079-6611(02)00041-1.
- Ebbesmeyer, C. C., Cayan, D. R., McLain, D. R., Nichols, F. H., Peterson, D. H., & Redmond, K. T. (1991). 1976 Step in the Pacific climate: Forty environmental changes between 1968–1975 and 1977–1984. In J. L. Betancourt, & V. L. Tharp (Eds.), *Proceedings of the Seventh Annual Pacific Climate Workshop, April 1990, California Department of Water Resources, Interagency Ecological Studies Program* (pp. 115–126). *Technical Report*, 26.
- Fiedler, P. C., Methot, R. D., & Hewitt, R. P. (1986). Effects of California El Niño 1982–1984 on the northern anchovy. *Journal of Marine Research*, 44, 317–338.
- González, H. E., Sobarzo, M., Figueroa, D., & Nothig, E. (2000). Composition, biomass and potential grazing impact of the crustacean and pelagic tunicates in the northern Humboldt Current area off Chile: differences between El Niño and non-El Niño years. *Marine Ecology Progress Series*, 195, 201–220.
- Hayward, L. T., Baumgartner, T. R., Checkley, D. M., Durazo, R., Gaxiola-Castro, G., Hyrenbach, K. D., Mantyla, A. W., Mullin, M. M., Murphree, T., Schwing, F. B., Smith, P. E., & Tegner, M. J. (1999). The state of the California Current in 1998–1999: Transition to cool-water conditions. *California Cooperative Oceanic Fisheries Investigations Reports*, 40, 29–62.
- Hewitt, T. P. (1988). Historical review of the oceanographic approach to fishery research. *California Cooperative Oceanic Fisheries Investigations Reports*, 29, 27–41.
- Holm-Hansen, O., Lorenzen, C., Holmes, R., & Strickland, J. (1965). Fluorimetric determination of chlorophyll. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, 30, 3–15.
- Hopcroft, R. R., Clarke, C., Chavez, F. P. (2002). Copepod communities in Monterey Bay during the 1997 to 1999 El Niño and La Niña. *Progress in Oceanography* (this issue), PII: S0079-611(02)00052-6.
- Huyer, A., & Smith, R. L. (1985). The signature of El Niño off Oregon, 1982–1983. *Journal of Geophysical Research*, 90, 7133–7142.
- Keitt, B. (1998). Seabirds and abalones, April 1998, Mexico (Baja California). In: D. Duffy & P. J. Bryant (Eds.), *The 1997 El Niño/Southern Oscillation* (ENSO 97–98), <http://darwin.bio.uci.edu/~sustain/Enso97/0498/AprMex.htm>.
- Kremer, P., & Madin, L. P. (1992). Particle retention efficiency of salps. *Journal of Plankton Research*, 14, 1009–1015.
- Ladah, L., Zertuche-González, J., & Hernández-Carmona, G. (1999). Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998. *Journal of Phycology*, 35, 1106–1112.
- Lavaniegos, B. E. (1993). *Estructura de las poblaciones de eufáusidos (Crustacea) en la zona de transición de Punta Eugenia, Baja California, con referencia particular a la producción de Nyctiphanes simplex*. Ph.D. Thesis, Departamento de Ecología, Centro de Investigación Científica y Educación Superior de Ensenada, Baja California, México.
- Lavaniegos, B. E., Gómez-Gutiérrez, J., Lara-Lara, J. R., & Hernández-Vázquez, S. (1998a). Long-term changes of zooplankton volumes in the California Current System—The Baja California region. *Marine Ecology Progress Series*, 169, 55–64.
- Lavaniegos, B. E., Jiménez-Pérez, L. C., & Baumgartner, T. (1998b). *Zooplankton volumes and calanoids from the Region IV of the California Current sampled by IMECOCAL cruises during El Niño 1997–98*. In California Cooperative Oceanic Fisheries Investigations Annual Conference, November 2–5, 1998, Monterey, California, Program and Abstracts.
- Lavaniegos, B. E., & Ohman, M. D. (1999). *Hyperiid amphipods as indicators of climate change in the California Current*. In F. R. Schram, & J. C. von Vaupel-Klein (Eds.), *Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998, Vol. 1.* (pp. 489–509). Leiden: Brill.
- Latif, M., & Barnett, T. P. (1996). Decadal climate variability over the North Pacific and North America: dynamics and predictability. *Journal of Climate*, 9, 2407–2423.
- Linacre-Rojas, L. (2001). *Estructura comunitaria de los eufáusidos en la parte sur de la Corriente de California durante octubre de 1997 (evento El Niño) y octubre de 1999 (post-El Niño)*. M.S. Thesis, Departamento de Ecología, Centro de Investigación Científica y Educación Superior de Ensenada, Baja California, México (in Spanish).
- Loeb, V., Siegerl, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., & Trivelpiece, S. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature, London*, 387, 897–900.
- Lynn, R. J., Baumgartner, T., García, J., Collins, C. A., Hayward, T. L., Hyrenbach, K. D., Mantyla, A. W., Murphree, T., Shankle, A., Schwing, F. B., Sakuma, K. M., & Tegner, M. J. (1998). The state of the California Current, 1997–1998: transition to El Niño conditions. *California Cooperative Oceanic Fisheries Investigations Reports*, 39, 25–49.
- Lynn, R. J., Bliss, K. A., & Eber, L. E. (1982). Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-

- t, stability, dynamic height, oxygen and oxygen saturation in the California Current. *California Cooperative Oceanic Fisheries Investigations Atlas*, 30, 1950–1978.
- Lynn, R. J., & Simpson, J. J. (1987). The California Current system: the seasonal variability of its physical characteristics. *Journal of Geophysical Research*, 92, 12947–12966.
- Mackas, D.L. & Galbraith, M. (2002). Zooplankton community composition along the inner portion of Line P during the 1997–98 El Niño event. *Progress in Oceanography* (this issue), PII: S0079-611(02)00062-9.
- Mackas, D. L., & Yelland, D. R. (1999). Horizontal flux of nutrients and plankton across and along the British Columbia continental margin. *Deep-Sea Research II*, 46, 2941–2968.
- Marinovic, B., Croll, D.A., Gong, N., Benson, S. & Chavez, F. (2002). Effects of the 1997–98 El Niño on zooplankton within the Monterey Bay coastal upwelling system with emphasis on the euphausiid community. *Progress in Oceanography* (this issue).
- McGowan, J. A. (1984). The California El Niño, 1983. *Oceanus*, 27, 48–51.
- McPhaden, M. J. (1999). Genesis and evolution of the 1997–98 El Niño. *Science*, 283, 950–954.
- Menard, F., Dallot, S., Thomas, G., & Braconnot, J. C. (1994). Temporal fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. *Marine Ecology Progress Series*, 104, 139–152.
- Miller, C. B., Batchelder, R. D., Brodeur, R. D., & Pearcy, W. G. (1985). Response of the zooplankton and ichthyoplankton off Oregon to the El Niño of 1983. In W. S. Wooster, & D. L. Fluharty (Eds.), *El Niño North—Niño effects in the eastern subarctic Pacific Ocean* (pp. 185–187). Seattle: Washington Sea Grant Program.
- Montú, M., & Ritter-Oliveira, I. (1986). Zooplanktonic associations, trophic relations and standing stocks of krill and other groups of the community near Elephant Island (February–March 84/85). *Neritica, Pontal do Sul*, 1, 111–129.
- Pearcy, W., Fisher, J., Brodeur, R., & Johnson, S. (1985). Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. In W. S. Wooster, & D. L. Fluharty (Eds.), *El Niño North—Niño effects in the eastern subarctic Pacific Ocean*, (pp. 188–204). Seattle: Washington Sea Grant Program.
- Pearcy, W. G., & Schoener, A. (1987). Changes in the marine biota coincident with the 1982–1983 El Niño in the northeastern subarctic Pacific Ocean. *Journal of Geophysical Research*, 92, 14417–14428.
- Peterson, W.T., Keister, J., Feinberg, L. (2002). The effects of the 1997–98 El Niño event on hydrography and zooplankton off the central Oregon coast. *Progress in Oceanography* (this issue), PII: S0079-6611(02)00059-9.
- Reinecker, M. M., & Mooers, C. N. K. (1986). The 1982–1983 Niño off northern California. *Journal of Geophysical Research*, 91, 6597–6608.
- Roemmich, D., & McGowan, J. A. (1995). Climatic warming and the decline of zooplankton in the California Current. *Science*, 267, 1324–1326.
- Roesler, C. S., & Chelton, D. B. (1987). Zooplankton variability in the California Current, 1951–1982. *California Cooperative Oceanic Fisheries Investigations Reports*, 28, 59–96.
- SIO Data Report, (1999a). Physical, chemical and biological data: CalCOFI cruise 9707, 1–18 July 1997; CalCOFI cruise 9709, 20 September–6 October 1997; CalCOFI cruise 9712, 13–16 December 1997. SIO References, 99-5. La Jolla, CA. Scripps Institution of Oceanography, University of California.
- SIO Data Report, (1999b). Physical, chemical and biological data: CalCOFI Cruise 9802, 23 January–14 February 1998; CalCOFI Cruise 9803, 11–17 March 1998; CalCOFI Cruise 9804, 2–23 April 1998; CalCOFI Cruise 9805, 16–22 May 1998; CalCOFI Cruise 9806, 17–23 June 1998. SIO References, 99-9. La Jolla, CA. Scripps Institution of Oceanography, University of California.
- SIO Data Report, (1999c). Physical, chemical and biological data: CalCOFI Cruise 9807, 9–27 July 1998; CalCOFI Cruise 9808, 12–18 August 1998; CalCOFI Cruise 9809, 13 September–1 October 1998; CalCOFI Cruise 9810, 16–22 October 1998; CalCOFI Cruise 9811, 18–24 November 1998; CalCOFI Cruise 9812, 10–15 December 1998. SIO References, 99-18. La Jolla, CA. Scripps Institution of Oceanography, University of California.
- SIO Data Report, (2000a). Physical, chemical and biological data: CalCOFI Cruise 9901, 9–29 January 1999; CalCOFI Cruise 9904, 1–20 April 1999. SIO References, 00-6. La Jolla, CA. Scripps Institution of Oceanography, University of California.
- SIO Data Report, (2000b). Physical, chemical and biological data: CalCOFI Cruise 9908, 7–29 August 1999; CalCOFI Cruise 9910, 3–21 October 1999. SIO References, 00-10. La Jolla, CA. Scripps Institution of Oceanography, University of California.
- Simpson, J. J. (1983). Large-scale thermal anomalies in the California Current during the 1982–1983 El Niño. *Geophysical Research Letters*, 10, 937–940.
- Smith, P. E. (1985). A case history of an anti-El Niño to El Niño transition on plankton and nekton distribution and abundances. In W. S. Wooster, & D. L. Fluharty (Eds.), *El Niño North—Niño effects in the eastern subarctic Pacific Ocean* (pp. 121–142). Seattle: Washington Sea Grant Program.
- Smith, P.E., Richardson, S.L. (1977). Standard techniques for pelagic fish eggs and larvae. *FAO Fisheries Technical Paper*, 175.
- Tegner, M. (1998). El Niños devastate kelp forest communities. *Current*, 15, 8–11.
- US GLOBEC (1994). *A science plan for the California Current. United States GLOBEC Ocean Ecosystem Dynamics*, Report 11. Berkeley, California: Department of Integrative Biology, University of California.

- Venrick, E. L., & Hayward, T. L. (1984). Determining chlorophyll on the 1984 CalCOFI surveys. *California Cooperative Oceanic Fisheries Investigations Reports*, 25, 74–79.
- Wang, C., & Weisberg, R. H. (2000). The 1997–98 El Niño evolution relative to previous El Niño events. *Journal of Climate*, 13, 488–501.
- Wolter, K., & Timlin, M. S. (1998). Measuring the strength of the ENSO events: How does 1997/98 rank? *Weather*, 53, 315–324.