

Changes in dominance of copepods off Baja California during the 1997–1999 El Niño and La Niña

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ABSTRACT: Changes in copepod species composition were analyzed from September–October 1997 to April 1999. The community changed substantially between El Niño 1997–1998 and La Niña 1998–1999, following trends in oceanographic conditions. The warm period was characterized by a community rich in equatorial, tropical/subtropical and warm-temperate cosmopolites, but almost lacking in subarctic copepods. The widespread presence of *Undinula vulgaris* appears to be due to the strong poleward jet that developed in the coastal region during autumn 1997. Although the coastal jet dispersed in early 1998, the strong influence of equatorial water continued, as indicated by the record abundance of *Subeucalanus subtenuis*, an equatorial species in oceanic eutrophic waters. The community during the cold period comprised very few copepods with equatorial affinity, few tropical/subtropical and warm-temperate cosmopolites, and an increased relative importance of subarctic species. Copepods typical for the California Current (transition zone group) displayed no significant differences between the extremes of El Niño/La Niña during the fall and winter seasons. A strong La Niña increase in the transition zone group (particularly in *Calanus pacificus*) was observed until spring 1999, and was probably related to a record coastal upwelling during the La Niña conditions at this time. El Niño 1997–1998 had a greater influence on equatorial species in the region than the previous El Niño event of 1957–1959.

KEY WORDS: Copepods · El Niño · La Niña · Baja California · California Current

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INTRODUCTION

The El Niño event of 1997–1998 and the subsequent La Niña event of 1998–1999 were, respectively, the warm and cold phases of a very strong El Niño Southern Oscillation (ENSO) cycle affecting the Pacific Ocean. Unprecedented surface warming occurred during spring 1997 throughout the tropical eastern Pacific (Webster & Palmer 1997) due to a weakening and reversal of the trade winds in the western and central equatorial Pacific (McPhaden 1999). The temperature anomalies spread eastward and poleward through a Kelvin wave, reaching the California Current System (CCS) in summer 1997 (Lynn et al. 1998). The El Niño changes in the CCS were characterized by extreme water-mass characteristics and a strengthening and broadening of the poleward nearshore flow from Baja California (Durazo & Baumgartner 2002), along the

coasts of California (Collins et al. 2002, Lynn & Bograd 2002) and Oregon (Huyer et al. 2002).

Although the physical evolution of El Niño showed a clear extension eastward along the equatorial Pacific, and poleward in the CCS, the biological response displayed notable regional differences throughout the ENSO cycle. Nutrients and chlorophyll decreased sharply in the equatorial Pacific (Chavez et al. 1999) and relatively strongly in central California (Chavez et al. 2002), Oregon (Corwith & Wheeler 2002), and the Gulf of Alaska (Whitney & Welch 2002). In contrast, in southern California and Baja California chlorophyll remained within the usual range of values (Hayward 2000, Lavaniegos et al. 2002). Moderate phytoplankton blooms were observed off Baja California (Kahru & Mitchell 2000).

Low zooplankton biomass was recorded during El Niño 1997–1998 along transect line P (from Vancouver

Island to 50°N, 145°W), off the Canadian coast (Mackas & Galbraith 2002) and off southern California (Hayward 2000, Lavaniegos & Ohman 2003). In contrast, relatively high zooplankton biomass was observed off Baja California during the warm phase of the ENSO, sustained mainly by the presence of salp blooms (Lavaniegos et al. 2002). Evidence of reduced populations of copepods and euphausiids with affinity to cold-temperate water has been provided for Line P (Mackas & Galbraith 2002), Oregon (Peterson et al. 2002), Monterey Bay (Hopcroft et al. 2002, Marinovic et al. 2002) and the Southern California Bight and its offshore region (Rebstock 2002). Simultaneously, some subtropical species occurred in northern sectors of the CCS, such as the euphausiid *Nyctiphanes simplex*, the hyperiid amphipod *Primno brevidens* and the copepods *Acartia danae* and *Eucalanus hyalinus* (Mackas & Galbraith 2002, Tanasichuk & Cooper 2002).

The invasion of subtropical taxa did not persist. The 1997-1998 El Niño was short, rapidly switching from warm to cold conditions through spring of 1998. An abrupt intensification of the easterly trade winds over the eastern equatorial Pacific Ocean (McPhaden & Yu 1999) combined with the already shallow equatorial thermocline in the central and eastern Pacific Ocean (Takayabu et al. 1999) marked the onset of La Niña. In the CCS, the weakening of El Niño occurred in April 1998 with the disappearance of the Inshore Countercurrent and extreme reduction in deep poleward transport (Collins et al. 2002, Lynn & Bograd 2002), with early 1999 marking the peak of La Niña. A record coastal upwelling occurred in the spring and summer of 1999 throughout much of the CCS (Schwing et al. 2000), which promoted high chlorophyll concentrations (Hayward et al. 1999, Chavez et al. 2002, Corwith & Wheeler 2002, Lavaniegos et al. 2002, Wilkerson et al. 2002).

Similarly to chlorophyll, zooplankton biomass increased in southern California (Hayward 2000, Lavaniegos & Ohman 2003) and Monterey (Marinovic et al. 2002), but not in Baja California, where biomass decreased with the diminution in tunicate blooms (Lavaniegos et al. 2002). In 1999, the expected recovery of the boreal copepod populations off Oregon was observed (Peterson et al. 2002), but not the typical spring-time dominance of large-bodied copepods in Monterey Bay (Hopcroft et al. 2002), although in both areas subtropical species decreased during La Niña. The trends for euphausiids were the expected resurgence of subarctic *Euphausia pacifica* and *Thysanoessa spinifera* in spring and summer of 1999, while the subtropical *Nyctiphanes simplex* was completely absent in the Monterey area as usual (Marinovic et al. 2002).

Biological responses to the oceanic events of 1997 to 1999 show interesting differences in the region off Baja California. This most southern sector of the CCS has

the greatest tropical influence, but has been studied less than the other sectors. The Baja California area appears to be a source-region for species that expand their ranges northward during warm events, but little is known about how these species respond within their own home range. The purpose of the present study was to analyze the changing species composition of copepods during El Niño 1997-1998 and La Niña 1998-1999 in the oceanic ecosystem off Baja California.

MATERIALS AND METHODS

Study area and sampling. The California Current System (CCS) is a dynamic system formed by the mixing of Pacific Subarctic, North Pacific Central, and Equatorial Pacific water masses, and coastal upwelled water (Lynn & Simpson 1987). The surface currents of the CCS show seasonal variability, with a weakening of the main current flowing to the equator and the development of the coastal countercurrent during fall and winter (Hickey 1979, Lynn & Simpson 1987). The California Undercurrent is less well known, but apparently undergoes changes in intensity similar to those in the coastal countercurrent. In the present study, the sampling site was in the southernmost sector of the CCS.

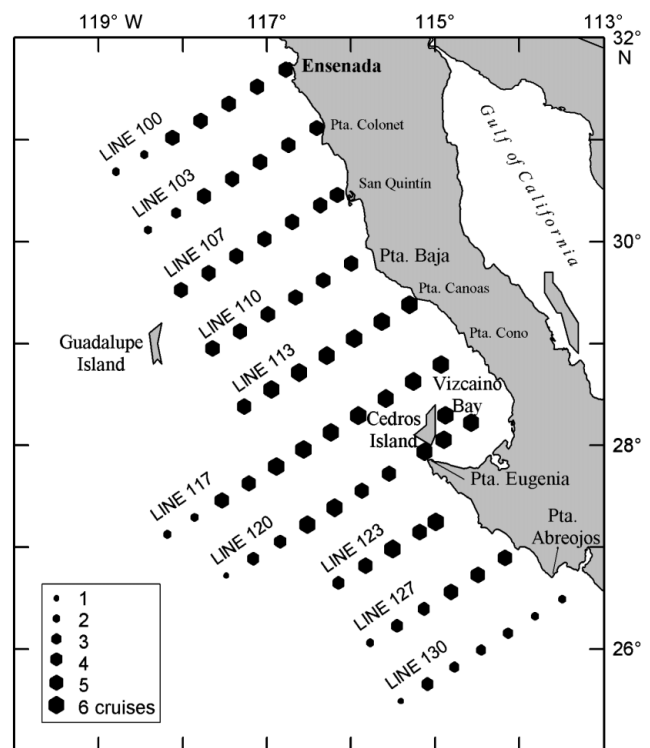


Fig. 1. Sampling stations of IMECOCAL cruises during 1997 to 1999. Symbols indicate number of cruises (i.e. number of times sampled). IMECOCAL cruises are based on the same positions and nomenclature of the CalCOFI cruises

Temperature data were taken with CTD casts during 6 IMECOCAL (Investigaciones Mexicanas de la Corriente de California) cruises designated 9710 (September-October 1997), 9801 (January-February 1998), 9807 (July 1998), 9810 (September-October 1998), 9901 (January 1999), and 9904 (April 1999). The cruises were conducted on the RV 'Francisco de Ulloa'. The station grid consisted of 10 lines approximately perpendicular to the coast, corresponding to CalCOFI transect lines 100 through 130 (Fig. 1). On Cruise 9710 only transect lines 110 to 127 were sampled. Transect 127 was missing during Cruise 9901, and transect 130 during Cruises 9810 and 9901.

Zooplankton was collected with a 61 cm diameter bongo net of 505 µm mesh-width. Oblique tows were done from 210 m to the surface when bottom depth permitted and from 10 m above the bottom to the surface at shallow stations. The volume of water strained was measured with a flowmeter in the mouth of the net (Smith & Richardson 1977). A total of 342 zooplankton samples were collected. Subsamples of 1/8 or 1/16 of the original samples were taken using a Folsom splitter. Adult copepods in the subsample were identified to species after Grice (1961), Brodsky (1967), Geletin

(1976), Dawson & Knatz (1980) and Palomares et al. (1998).

Data processing. In order to adjust for seasonal variability of temperature and salinity, the seasonal means of the period 1950 to 1978 were subtracted to calculate temperature and salinity anomalies in the IMECOCAL cruises. These historical means were estimated by Lynn et al. (1982) from the CalCOFI data for the Baja California region. This procedure was done for temperatures (or salinities) at 10 and 150 m depth for transect lines 110 and 120. For some line stations (110.45, 110.55, 120.40, 120.55, 120.65) the seasonal mean was extrapolated using data from the nearest stations. For IMECOCAL Cruise 9904 Stns 110.35 to 110.50 were missing; therefore data from Stns 107.35 to 107.50 were used instead.

Copepod abundance was standardized to individuals m⁻³. In this study only dominant species were considered, defined as those species present in 50% of the samples in 1 or more cruises. The species abundances were converted to carbon biomass based on length-carbon (C), length-dry weight (DW), or length-ash free dry weight (AFDW) regressions from the literature (Table 1). DW and AFDW were converted to carbon

Table 1. Length-weight regressions for copepod species used to estimate carbon (C), ash-free dry weight (AFDW) and dry weight (DW). PL: prosome length, TL: total length. Length parameter not indicated when a regression was not available and female weight was used instead

Species	Length parameter	Regression for female weight	Source
<i>Acartia clausi</i> ^a	PL	log µg C = 3.08 (log µm) - 8.51	Uye (1982)
<i>Calanus pacificus</i> ^b	PL	ln µg DW = 2.5 (ln mm) + 2.99	Runge (1980)
<i>Candacia/Paracandacia</i>	PL	ln µg DW = 3.38 (ln µm) - 20.48	Webber & Roff (1995)
<i>Centropages furcatus</i> ^c	PL	ln µg C = 3.82 (ln µm) - 24.58	Satapoomin (1999)
<i>Clausocalanus furcatus</i> ^d	PL	ln µg DW = 3.68 (ln µm) - 22.86	Chisholm & Roff (1990)
<i>Eucalanus californicus</i> ^e	PL	log µg DW = 3.09 (log mm) - 0.0026	Hopcroft et al. (2002)
<i>Subeucalanus pileatus</i> ^f		36.97 µg C	Tester & Turner (1988)
<i>Euchaeta</i> spp.	PL	ln µg C = 3.82 (ln µm) - 25.19	Satapoomin (1999)
<i>Haloptilus longicornis</i>	PL	ln µg DW = 4.27 (ln µm) - 29.00	Webber & Roff (1995)
<i>Heterorhabdus tanneri</i> ^g	PL	log µg AFDW = 3.463 (log mm) + 0.943	Yamaguchi & Ikeda (2000)
<i>Labidocera trispinosa</i> ^h		33 µg C	Barnett (1974)
<i>Mesocalanus tenuicornis</i>		23.29 µg C	Lindley et al. (1997)
<i>Metridia pacifica</i>		101 µg DW	Ohman (1988)
<i>Paracalanus parvus</i>	PL	ln µg DW = 2.78 (ln µm) - 16.52	Webber & Roff (1995)
<i>Pleuromamma scutullata</i> ⁱ	PL	log µg AFDW = 2.812 (log mm) + 1.09	Yamaguchi & Ikeda (2000)
<i>Rhincalanus nasutus</i>	TL	log µg C = 4.30 (log mm) - 0.47	Mullin & Brooks (1967)
<i>Scolecithrix danae</i> ^j	PL	ln µg DW = 3.57 (ln µm) - 21.36	Webber & Roff (1995)
<i>Temora discaudata</i>	PL	ln µg C = 3.55 (ln µm) - 22.07	Satapoomin (1999)
<i>Undinula vulgaris</i> ^k	PL	ln µg DW = 3.65 (ln µm) - 22.89	Chisholm & Roff (1990)
<i>Oithona plumifera</i>	PL	log µg AFDW = 3.16 (log µm) - 8.30	Hopcroft et al. (1998)
<i>Corycaeus</i> spp. ^l	PL	log µg AFDW = 2.80 (log µm) - 7.17	Hopcroft et al. (1998)

^a Applied to *A. danae* and *A. negligens* in present study
^b Also used for *Nannocalanus minor*, *Neocalanus cristatus*, *Neocalanus gracilis*, and *Aetidius bradyi* in present study
^c Also used for *C. bradyi* and *C. elongatus* in present study
^d Applied to *Clausocalanus* spp. in present study
^e Also used for *E. hyalinus* and *Pareucalanus attenuatus* in present study
^f Also used for *S. subcrassus* and *S. subtenuis* in present study
^g Applied to *H. papilliger* in present study
^h Applied to *L. acutifrons* in present study
ⁱ Applied to *P. abdominalis*, *P. borealis*, *P. gracilis*, *P. piseki*, and *Lucicutia flavicornis* in present study
^j Also used for *S. bradyi* and *Scolecithricella ovata* in present study
^k Also used for *U. darwini* in present study
^l Also used for *Copilia mirabilis* and *Sapphirina nigromaculata* in present study

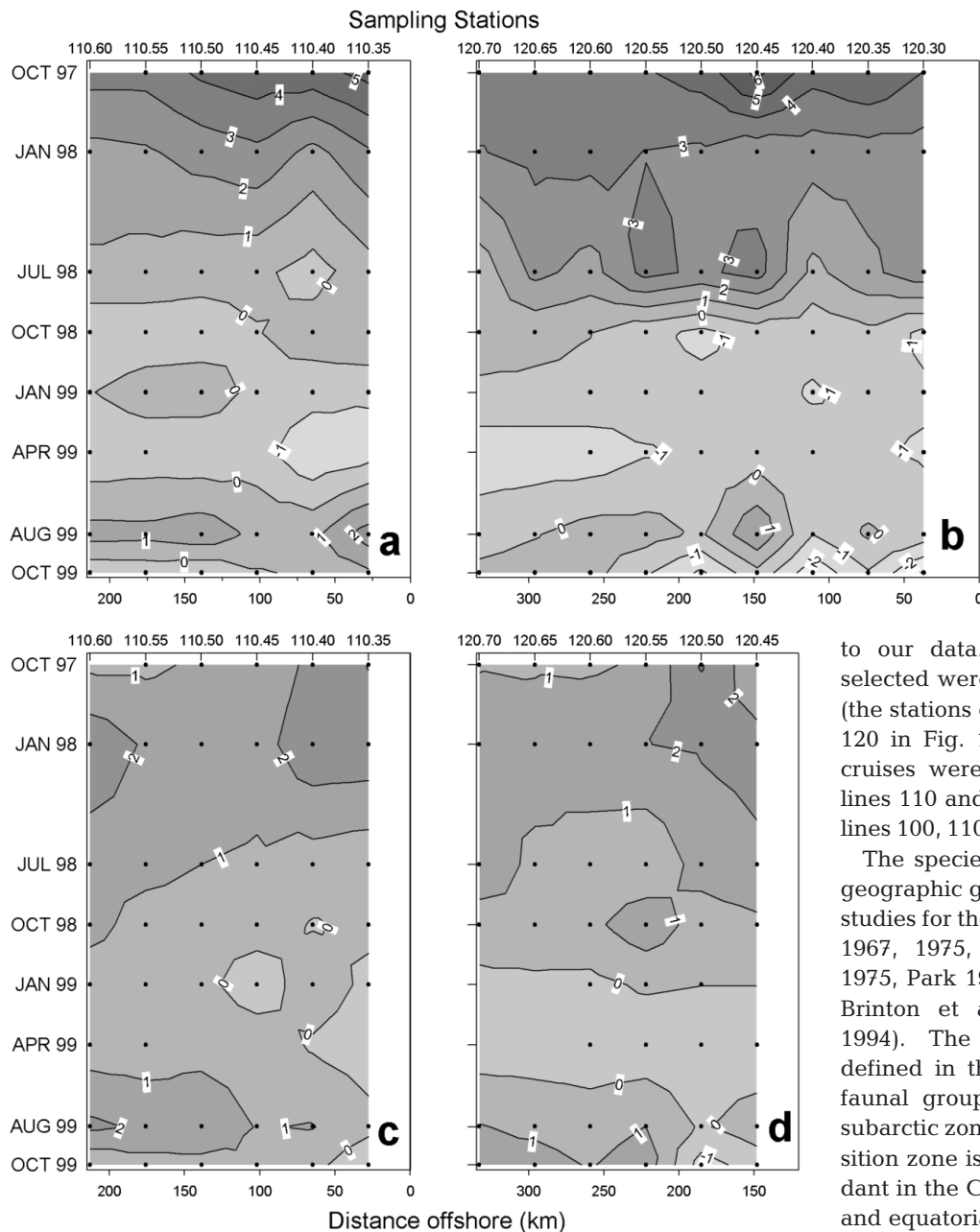


Fig. 2. Time–distance plots of temperature anomalies (-2 to 6°C) at (a, b) 10 m and (c, d) 150 m for stations along (a, c) transect line 110 and (b, d) transect line 120 (see Fig. 1). Anomalies estimated by $X_i - X$, where X_i is value measured during 1 IMECOAL cruise and X is seasonal mean for the period 1950 to 1978

assuming that carbon corresponds to 50% DW and 45% AFDW. Abundance and carbon-content data were $\log(x+1)$ -transformed before calculating the mean and 95% confidence interval. Statistical comparisons between pair of cruises were done using the Mann-Whitney U -test on raw data from nighttime samples. The results of the U -test will be expressed as z (normal approximation).

Additional comparisons were made between the 1997–1998 El Niño and the previous 1957–1959 El Niño. Ranks-of-abundance categories were assigned from distribution charts of calanoid species from Fleminger (1964, 1967) and compared with similar ranks applied

to our data. The CalCOFI cruises selected were Cruises 5810 and 5901 (the stations on transect lines 100 and 120 in Fig. 1), and the IMECOAL cruises were Cruises 9710 (transect lines 110 and 120) and 9801 (transect lines 100, 110, 120, 130).

The species were arranged in biogeographic groups based on previous studies for the Pacific Ocean (Brodsky 1967, 1975, Fleminger 1967, 1973, 1975, Park 1968, 1995, Nishida 1985, Brinton et al. 1986, US GLOBEC 1994). The category subarctic is defined in the present study as the faunal group inhabiting mainly the subarctic zone, and the category transition zone is the group mostly abundant in the CCS. Tropical/subtropical and equatorial groups are both found in the tropics *sensu stricto*, but the tropical/subtropical group differs from the equatorial group in that it also occurs in subtropical regions. The warm-temperate group is widespread throughout the tropical and temperate regions.

RESULTS

Thermohaline anomalies

Temperature at 10 m depth peaked in October 1997, with a mean and standard deviation of $24.4 \pm 0.9^{\circ}\text{C}$. In January 1998 the mean temperature decreased to $18.7 \pm 1.1^{\circ}\text{C}$, but positive temperature anomalies of 2 to 6°C

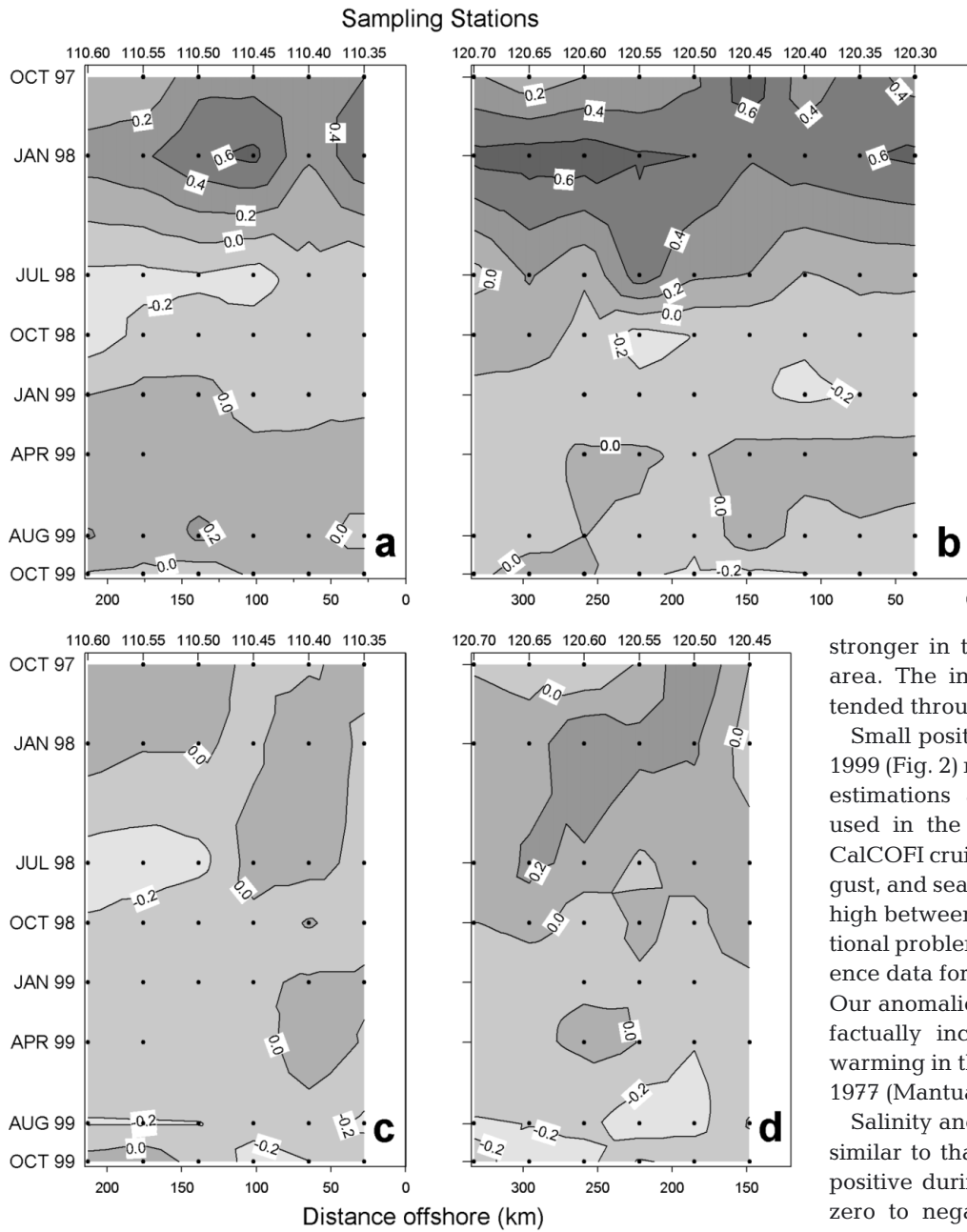


Fig. 3. Time-distance plots of salinity anomalies (–0.2 to 0.6) at (a,b) 10 m and (c,d) 150 m for stations along (a,c) transect line 110 and (b,d). Further details as in Fig. 2

indicated that both October 1997 and January 1998 were strongly influenced by El Niño (Fig. 2a,b). The anomalous warming affected a relatively thick upper layer, as anomalies as high as 3°C were recorded at 150 m depth (Fig. 2c,d).

By July 1998, temperature anomalies had dissipated for transect line 110 at 10 m depth, but remained as high as 3°C for line 120 (Fig. 2a,b). Along both transect lines, anomalies at some stations at 150 m surpassed 1°C (Fig. 2c,d). By October 1998, a rapid and intense cooling occurred along both lines. On transect line 120 the drop in temperature was 3°C compared to the previous season (Fig. 2b), indicating that La Niña was

stronger in the southern part of the area. The influence of La Niña extended throughout 1999.

Small positive anomalies in August 1999 (Fig. 2) must be considered overestimations as the seasonal means used in the calculations were from CalCOFI cruises in July instead of August, and seasonal warming is usually high between these months. An additional problem is the absence of reference data for the period 1979 to 1997. Our anomalies could have been artefactually increased due to decadal warming in the northeast Pacific after 1977 (Mantua et al. 1997).

Salinity anomalies followed a trend similar to that of temperature, being positive during the warm phase and zero to negative in the cool phase (Fig. 3). The extension of the positive

anomalies offshore during Cruises 9710 and 9801 indicates that the source was probably not coastal upwelled water. The anomalies were more likely due to Equatorial Pacific water entering the CCS from the west (Lynn & Simpson 1987).

In July 1998, an intrusion of low-salinity (subarctic) water was observed along transect line 110 (Fig. 3a), but only at the most offshore station on transect line 120 (Fig. 3b). This low-salinity core was present even at 150 m on Cruise 9807 (Fig. 3c). Contrary to expectations, few salinity anomalies were found during the first part of 1999, but were observed in August and October in subsurface waters (Fig. 3c,d).

Copepods

The total number of copepod species identified was 169 for the complete study period (see Appendix 1). They belonged to the orders Calanoida (70%), Poecilostomatoida (25%), Cyclopoida (4%), and Harpacticoida (1%). The only genus not identified to species was *Clausocalanus*. Copepodites of different genera were also present in samples, but those of *Euchaeta* and *Candacia* were particularly abundant. Considering as dominant species those collected in 50% or more samples during one or more cruises, the number is reduced to 47 plus *Clausocalanus* spp. (Table 2).

Dominant species (ordered by biogeographic groups) displayed changing proportions through the warm period (Cruises 9710 and 9801), the transition phase (Cruise 9807), and the cool period (Cruises 9810, 9901, and 9904). An unusually low percentage of Transition Zone copepods (9%) was recorded in fall 1997 compared to Equatorial, Tropical/Subtropical, and warm-temperate groups which, combined, comprised 90% of the total (Fig. 4a). The percentages are based

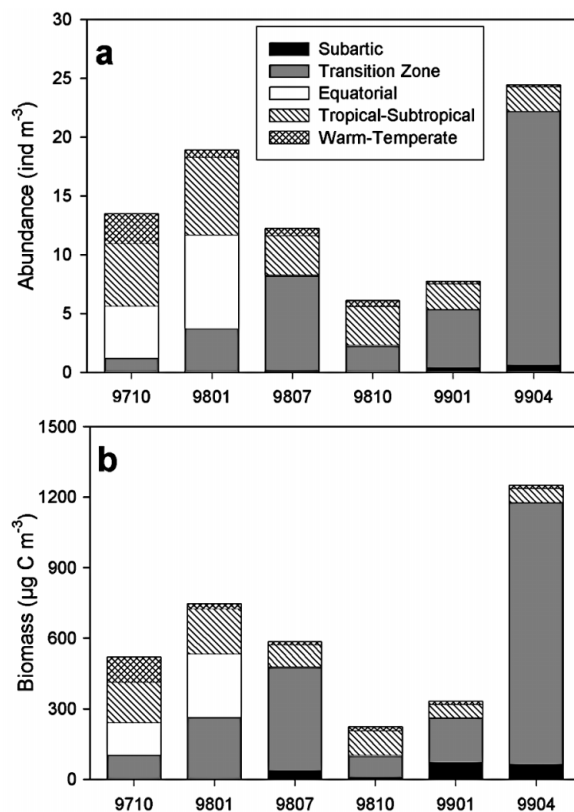


Fig. 4. Proportional contribution of biogeographic groups of copepods as (a) abundance and (b) carbon biomass, in nighttime samples, averaged per cruise. Proportions are based on anti-log means. Abscissa shows 6 IMECOCAL cruises (9710: Sep-Oct 1997; 9801: Jan-Feb 1998; 9807: Jul 1998; 9810: Sep-Oct 1998; 9901: Jan 1999; 9904: Apr 1999)

on mean abundances (antilogged mean) from nighttime samples. With regard to the biomass of the Transition Zone group, their importance increases considerably (20%), but remained low relative to their usual dominance in the California Current (Fig. 4b). During winter of 1998 the Equatorial and Transition Zone copepods increased in abundance to 19 and 42%, respectively, corresponding to 35 and 36% of the biomass.

In July 1998, the Equatorial group virtually disappeared while the Transition Zone group dominated the copepod community (65% of abundance and 74% of biomass). The Subarctic component was small (6% of the copepod biomass). The seasonal change was stronger than usual due to the extraordinarily warm winter of 1998.

Apart from the Tropical/Subtropical group and *Clausocalanus* spp., the lowest abundance and biomass of copepods occurred at the beginning of La Niña in October 1998. The small contribution of the Equatorial, Tropical/Subtropical, and warm-temperate groups was in sharp contrast to their contribution in the preceding warm fall of 1997 (Fig. 4). Further development of La Niña in January 1999 brought a strong increase in abundance of the Subarctic and Transition Zone copepods (21 and 57% of the biomass). Again, 9901 abundances were significantly lower than in the previous warm winter of 1998 for the Equatorial ($z = 6.61$, $p < 0.001$) and Tropical/Subtropical ($z = 5.49$, $p < 0.001$) groups. However, for the Transition Zone group no statistical differences were observed in biomass (or abundance) between Cruises 9801 and 9901.

From January to April 1999, the biomass of copepods increased from 331 to 1250 $\mu\text{g C m}^{-3}$ (antilogged mean), due mainly to the Transition Zone group, which increased 6-fold (Fig. 4b). Proportions of the biogeographic groups were completely inverse to those observed at the beginning of the sampling period. The Transition Zone and Subarctic groups combined represented 94% of the total copepods on Cruise 9904.

Species with limited distribution

The distribution of species is dynamic, but certainly some species are more stenothermal than others, with greater affinity for warm or cold waters. This was the case for three of the biogeographic groups:

Subarctic group. These species enter the CCS with cold northern waters. The dominant Subarctic species off Baja California were *Neocalanus cristatus* and *Metridia pacifica* (Table 2, Fig. 5). As expected, both species had the lowest biomass in the warm period (Cruises 9710 and 9801). Despite the autumn/winter dormancy of *N. cristatus*, the species was relatively

Table 2. Dominant copepod species ordered in biogeographic groups, and number of samples in which each was present in IME-COCAL Cruises 9710: Sep-Oct 1997; 9801: Jan-Feb 1998; 9807: Jul 1998; 9810: Sep-Oct 1998; 9901: Jan 1999; 9904: Apr 1999. OC: oceanic, NE: neritic. Samples collected during night time are in parentheses. Species abbreviations are used in Figs. 5, 8 & 10

Biogeographic group	Species	9710 n=39 (19)	9801 n=68 (32)	9807 n=65 (27)	9810 n=62 (33)	9901 n=54 (27)	9904 n=54 (24)	
Subarctic	OC <i>Metridia pacifica</i> (M pac)	3 (3)	14 (13)	14 (14)	19 (17)	36 (25)	28 (21)	
	<i>Neocalanus cristatus</i> (N cri)	1 (0)	0	42 (19)	24 (13)	38 (21)	19 (11)	
Transition Zone	OC <i>Centropages bradyi</i> (C bra)	6 (4)	0	29 (16)	30 (16)	14 (5)	40 (19)	
	<i>Eucalanus californicus</i> (E cal)	19 (11)	29 (13)	50 (19)	44 (22)	41 (20)	53 (24)	
	<i>Pleuromamma borealis</i> (P bor)	15 (13)	36 (27)	34 (26)	43 (32)	49 (27)	47 (24)	
	<i>Scolecithricella ovata</i> (S ova)	2 (2)	1 (0)	4 (4)	2 (2)	29 (20)	11 (6)	
	NE <i>Calanus pacificus</i> (C pac)	36 (19)	68 (32)	61 (26)	41 (24)	51 (27)	54 (24)	
	<i>Candacia bipinnata</i> (C bip)	8 (3)	29 (10)	38 (16)	27 (15)	10 (5)	35 (15)	
Equatorial	OC <i>Rhincalanus nasutus</i> ^a (R nas)	28 (14)	58 (27)	47 (16)	41 (19)	40 (22)	48 (22)	
	OC <i>Pareucalanus attenuatus</i> (P att)	33 (17)	66 (31)	17 (4)	36 (18)	8 (3)	7 (2)	
	<i>Subeucalanus subtenuis</i> (S sut)	32 (15)	68 (32)	16 (6)	22 (15)	6 (3)	6 (2)	
	<i>Undinula darwini</i> (U dar)	37 (19)	61 (28)	34 (18)	38 (19)	22 (11)	15 (6)	
	NE <i>Subeucalanus pileatus</i> (S pil)	28 (12)	68 (32)	2 (1)	9 (6)	0	1 (1)	
	<i>Subeucalanus subcrassus</i> (S suc)	15 (7)	48 (22)	11 (3)	8 (6)	1 (0)	7 (2)	
	<i>Undinula vulgaris</i> (U vul)	36 (19)	4 (3)	0	0	0	0	
	Tropical-Subtropical	OC <i>Acartia danae</i> (A dan)	21 (9)	33 (18)	61 (25)	52 (25)	38 (15)	35 (15)
		<i>Acartia negligens</i> (A neg)	15 (6)	11 (6)	20 (8)	34 (16)	18 (8)	6 (1)
<i>Centropages elongatus</i> (C elo)		2 (1)	10 (5)	12 (6)	31 (14)	13 (6)	5 (3)	
<i>Eucalanus hyalinus</i> (E hay)		11 (4)	22 (10)	19 (6)	39 (19)	27 (9)	28 (9)	
<i>Euchaeta indica</i> (E ind)		20 (9)	14 (9)	1 (1)	2 (1)	0	0	
<i>Haloptilus longicornis</i> (H lon)		19 (10)	42 (23)	22 (9)	44 (22)	34 (16)	33 (16)	
<i>Heterorhabdus papilliger</i> (H pap)		16 (9)	30 (16)	47 (24)	52 (30)	46 (25)	41 (21)	
<i>Labidocera acutifrons</i> (L acu)		23 (16)	2 (2)	0	4 (1)	0	0	
<i>Lucicutia flavicornis</i> (L fla)		8 (6)	21 (12)	15 (10)	31 (18)	39 (21)	16 (8)	
<i>Nannocalanus minor</i> (N min)		38 (19)	67 (32)	42 (18)	58 (30)	35 (17)	28 (13)	
<i>Neocalanus gracilis</i> (N gra)		6 (2)	47 (22)	0	46 (24)	11 (4)	1 (0)	
<i>Paracandacia simplex</i> (P sim)		5 (1)	23 (11)	33 (16)	29 (13)	18 (7)	17 (7)	
<i>Pleuromamma abdominalis</i> (P abd)		21 (13)	38 (28)	35 (23)	42 (31)	45 (27)	37 (22)	
<i>Pleuromamma gracilis</i> (P gra)		24 (14)	52 (30)	35 (25)	43 (32)	49 (26)	31 (21)	
<i>Pleuromamma piseki</i> (P pis)		10 (7)	45 (26)	22 (18)	23 (19)	26 (15)	16 (11)	
<i>Scolecithrix bradyi</i> (S bra)		19 (13)	48 (24)	34 (17)	39 (24)	35 (17)	25 (14)	
<i>Scolecithrix danae</i> (S dan)		36 (19)	57 (30)	56 (24)	53 (26)	41 (21)	37 (13)	
NE <i>Aetideus bradyi</i> (A bra)		19 (9)	27 (15)	21 (14)	39 (21)	21 (12)	29 (16)	
<i>Centropages furcatus</i> (C fur)		21 (9)	8 (4)	0	0	0	0	
<i>Temora discaudata</i> (T dis)		30 (13)	63 (31)	1 (0)	11 (5)	4 (1)	3 (1)	
Warm-Temperate	OC <i>Corycaeus flaccus</i> (C fla)	20 (9)	21 (9)	50 (20)	43 (20)	35 (17)	32 (13)	
	<i>Corycaeus furcifer</i> (C fuf)	13 (5)	17 (8)	22 (9)	29 (14)	29 (10)	20 (6)	
	<i>Euchaeta media</i> (E med)	28 (14)	23 (9)	13 (12)	30 (22)	23 (20)	23 (16)	
	<i>Euchaeta rimana</i> (E rim)	36 (18)	24 (12)	16 (8)	26 (16)	5 (3)	3 (2)	
	<i>Mesocalanus tenuicornis</i> (M ten)	6 (5)	0	37 (17)	34 (16)	35 (17)	20 (7)	
	<i>Oithona plumifera</i> (O plu)	34 (16)	43 (21)	57 (22)	60 (32)	32 (14)	14 (6)	
	NE <i>Copilia mirabilis</i> (C mir)	37 (18)	31 (16)	5 (1)	19 (11)	2 (0)	1 (0)	
	<i>Corycaeus amazonicus</i> (C ama)	30 (13)	4 (2)	2 (2)	3 (1)	0	0	
	<i>Corycaeus speciosus</i> (C spe)	29 (14)	50 (21)	8 (3)	23 (8)	6 (3)	3 (1)	
	<i>Euchaeta longicornis</i> (E lon)	18 (10)	54 (27)	8 (3)	3 (2)	1 (0)	2 (1)	
Unknown	<i>Paracalanus parvus</i> (P par)	32 (14)	6 (2)	7 (2)	9 (4)	1 (1)	0	
	<i>Sapphirina nigromaculata</i> (S nig)	23 (12)	2 (0)	11 (5)	7 (3)	0	0	
	<i>Clausocalanus</i> spp. (Claus)	34 (16)	55 (24)	53 (23)	59 (31)	41 (20)	29 (16)	

^aAlthough circumglobal, this species, was retained in this group because it is primarily from temperate boundary currents (Goetze 2003)

abundant in winter 9901. *M. pacifica* was more clearly an indicator of La Niña conditions, with higher biomass in January and April 1999.

Transition zone group. This group is associated with the core of the California Current and the coastal

upwelling region. *Calanus pacificus* was the dominant species during Cruises 9807 and 9904 (Fig. 5). Lower captures of *C. pacificus* during fall and winter were probably due to its dormancy in deep waters. Although some samples collected during 1997-1998 contained

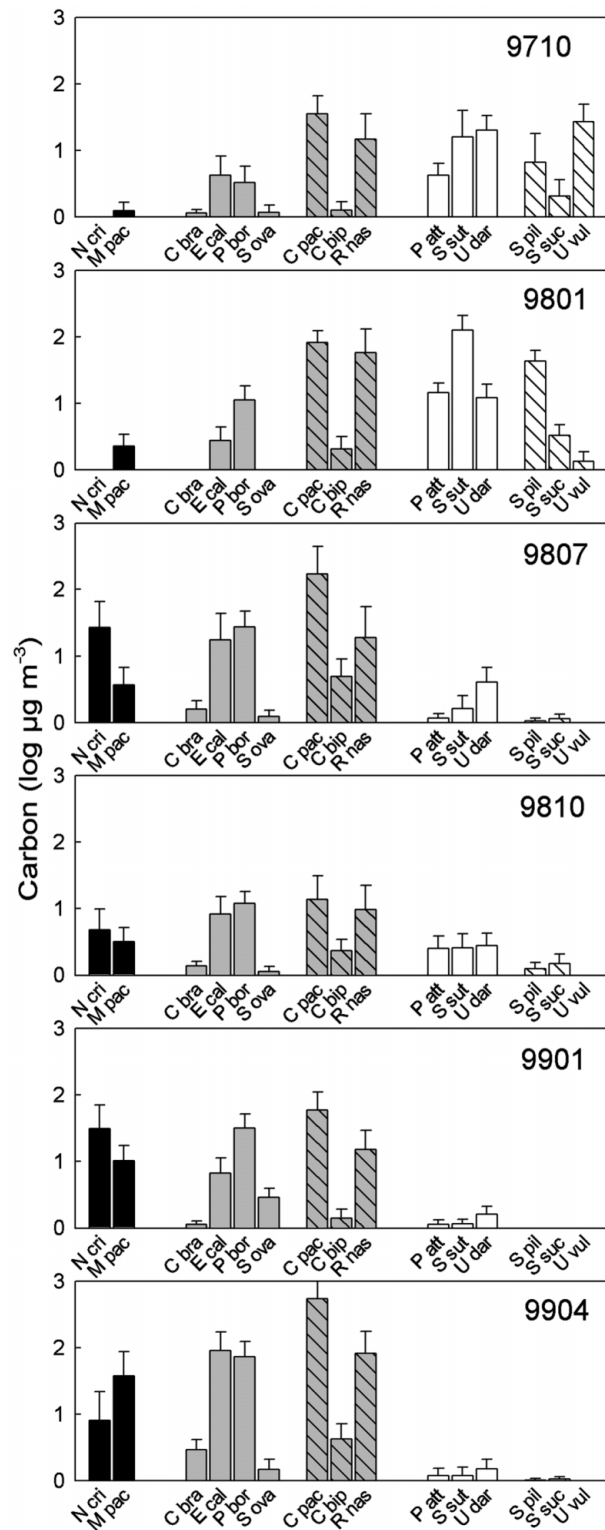


Fig. 5. Carbon biomass (mean \pm 95% confidence intervals) of copepod species from 3 biogeographic groups: Subarctic (black bars), Transition zone (gray bars) and Equatorial (white bars), in nighttime samples at IMECOAL cruises. Hatched bars indicate neritic species, remainder are oceanic. Abbreviations in the abscissa as in Table 2

high numbers of this species, most of the area had relatively low abundance compared to the La Niña spring bloom (see Fig. 9). Other species from this group with maximal capture in April 1999 were *Eucalanus californicus*, *Pleuromamma borealis* and *Rhincalanus nasutus*. The biomass of *E. californicus* and *P. borealis* was also significantly higher in the cold winter covered by Cruise 9901 than the winter covered by Cruise 801 (Table 3). However, *R. nasutus* had a higher biomass in the warm winter covered by Cruise 801.

The other 3 species in this group (*Candacia bipinnata*, *Centropages bradyi* and *Scolecithricella ovata*), although very common in the samples from some cruises, made only small contributions to the biomass.

Equatorial group. This group is transported into the region from the southwest with equatorial water. The presence of this group during the warm period was extraordinarily high, representing 27 and 36% of the copepod biomass during Cruises 9710 and 9801, respectively. The dominant neritic species were *Subeucalanus pileatus*, *S. subcrassus* and *Undinula vulgaris* (Fig. 5). These 3 species were more abundant during the warm period (Table 2). *U. vulgaris* was the second most abundant species in Cruise 9710, decreasing sharply during Cruise 9801 and disappearing later.

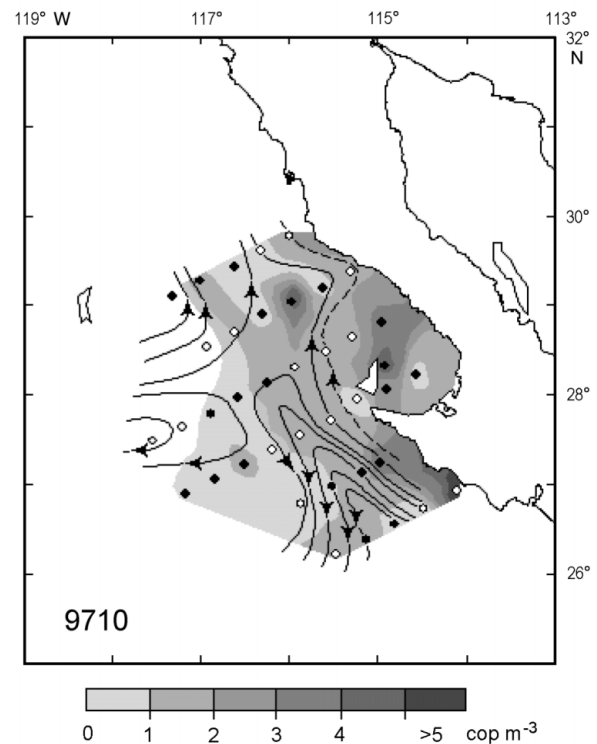


Fig. 6. *Undinula vulgaris* abundance (copepods m^{-3}) during fall 1997 (Cruise 9710). Black (white) circles are stations sampled during night (day). Arrowed lines are dynamic height anomalies (10/500 dbar) redrawn from Lynn et al. (1998)

Table 3. Comparison of carbon biomass of dominant copepods during fall (9710, 9810) and winter (9801, 9901) of 2 successive years, using the Mann-Whitney *U* test. Only the species with significant differences at $\alpha = 0.05$ are shown. Ratio of fall (9710/9810) and winter (9801/9901) medians is indicated when medians are higher than zero. Only nighttime samples were considered. (c: median from warm period = 0; w: median from cool period = 0; --: median in both periods = 0)

Biogeographic group	Species	9710 vs 9810			9801 vs 9901				
		z	p	ratio	z	p	ratio		
Subarctic	OC	<i>Metridia pacifica</i>	-2.59	0.023	c	-4.19	<0.001	c	
		<i>Neocalanus cristatus</i>	-3.09	0.018	c	-5.97	<0.001	c	
Transition Zone	OC	<i>Eucalanus californicus</i>	-1.45	0.161		-2.51	0.016	c	
		<i>Pleuromamma borealis</i>	-3.35	0.001	0.2	-2.83	0.004	0.4	
		<i>Scolecithricella ovata</i>	0.58	0.792		-5.77	<0.001	c	
	NE	<i>Rhincalanus nasutus</i>	0.91	0.386		2.60	0.009	4.6	
Equatorial	OC	<i>Pareucalanus attenuatus</i>	2.15	0.034	5.7	6.54	<0.001	w	
		<i>Subeucalanus subtenuis</i>	3.33	0.001	w	6.91	<0.001	w	
		<i>Undinula darwini</i>	4.71	<0.001	16.0	5.21	<0.001	w	
	NE	<i>Subeucalanus pileatus</i>	3.65	0.002	w	6.81	<0.001	w	
		<i>Subeucalanus subcrassus</i>	1.44	0.282		5.18	<0.001	w	
		<i>Undinula vulgaris</i>	6.90	<0.001	w	1.62	0.540		
Tropical-Subtropical	OC	<i>Acartia danae</i>	-2.94	0.003	c	0.78	0.463		
		<i>Centropages elongatus</i>	-2.21	0.027	--	-0.54	0.723		
		<i>Eucalanus hyalinus</i>	-2.44	0.014	c	0.00	1.000		
		<i>Euchaeta indica</i>	2.69	0.007	--	2.95	0.064		
		<i>Heterorhabdus papilliger</i>	-2.54	0.011	c	-2.84	0.005	0.1	
		<i>Labidocera acutifrons</i>	5.89	<0.001	w	-2.75	0.689		
		<i>Lucicutia flavicornis</i>	-1.78	0.103		-2.75	0.008	c	
		<i>Nannocalanus minor</i>	4.21	<0.001	4.8	6.59	<0.001	38.7	
		<i>Neocalanus gracilis</i>	-3.66	<0.001	c	3.68	0.001	w	
		<i>Pleuromamma piseki</i>	-0.42	0.706		3.74	<0.001	6.4	
		<i>Scolecithrix bradyi</i>	1.14	0.265		2.25	0.026	4.2	
		<i>Scolecithrix danae</i>	2.13	0.032	2.0	3.69	<0.001	3.0	
		NE	<i>Centropages furcatus</i>	2.82	0.004	--	1.89	0.419	
			<i>Temora discaudata</i>	4.04	<0.001	w	6.59	<0.001	w
		Warm-Temperate	OC	<i>Corycaeus flaccus</i>	-0.33	0.763		-2.39	0.029
<i>Euchaeta media</i>	1.48			0.145		-2.57	0.016	c	
<i>Euchaeta rimana</i>	5.03			<0.001	w	2.62	0.045	--	
<i>Mesocalanus tenuicornis</i>	-1.51			0.185		-5.18	<0.001	c	
<i>Oithona plumifera</i>	1.32			0.192		2.27	0.028	7.3	
NE	<i>Copilia mirabilis</i>		5.54	<0.001	w	4.20	0.001	w	
	<i>Corycaeus amazonicus</i>		5.07	<0.001	w	1.31	0.689		
	<i>Corycaeus speciosus</i>		3.83	<0.001	w	4.43	<0.001	w	
	<i>Euchaeta longicornis</i>		3.78	0.004	w	6.05	<0.001	w	
	<i>Paracalanus parvus</i>		4.59	<0.001	w	0.48	0.862		
		<i>Sapphirina nigromaculata</i>	4.41	<0.001	w	0.00	1.000		
Unknown		<i>Clausocalanus</i> spp.	-2.10	0.036	0.5	1.49	0.143		

This species was probably introduced from the south-eastern Pacific coast and dispersed off Baja California by the strong near-surface poleward coastal jet that developed on Cruise 9710 (Fig. 6).

A similar assemblage of 3 oceanic species (*Pareucalanus attenuatus*, *Subeucalanus subtenuis* and *Undinula darwini*) was also found in the warm period. During Cruise 9801 *Subeucalanus subtenuis* was the dominant species entering the region with equatorial water (salinity > 34 at 10 m) from the southwest (Fig. 7), and decreasing from July 1998 to the end of the study period.

Species with broad distribution

Tropical/subtropical group. Species in this group are usual residents of the CCS but maintain relatively low abundances. Most of these species had an equally low biomass in the warm and cold phases of 1997 to 1999 (Fig. 8). However, 2 oceanic species (*Nannocalanus minor* and *Scolecithrix danae*) and 1 neritic species (*Temora discaudata*) increased considerably during El Niño. *N. minor* was the major species during fall 1997 and the second in importance in winter 1998. On both warm cruises, *N. minor* invaded the coastal

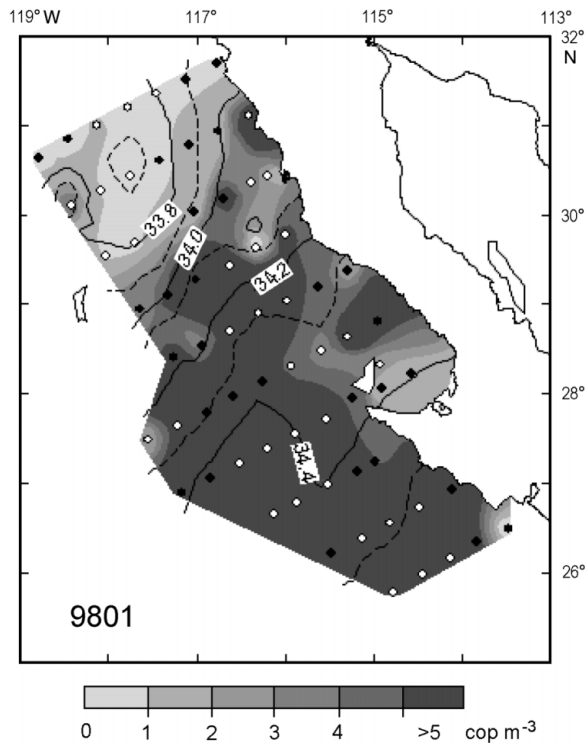


Fig. 7. *Subeucalanus subtenuus* abundance (copepods m^{-3}) during winter 1998 (Cruise 9801). Black (white) circles are stations sampled during night (day). Lines indicate isohalines at 10 m depth

zone, including Vizcaino Bay (Fig. 9). This bay is partially isolated to the west, and usually remains cooler than the central oceanic region from late summer to early winter. The distributions of *N. minor* and *Calanus pacificus* displayed opposite patterns, which could reflect interspecific competition. Although some regions of overlap between these species were observed throughout the study period, most locations with a high aggregation of *C. pacificus* had a low abundance of *N. minor*.

The biomass of *Scolecithrix danae* was high through 1998, decreasing in 1999. It differed significantly between autumn (Cruises 9710 and 9810) and winter (Cruises 9801 and 9901) (Table 3). Similar levels of biomass were found for 2 species of *Pleuromamma* (*P. abdominalis* and *P. gracilis*), which remained the same throughout the study period. In contrast, the biomass of *P. piseki* was lower than the other dominant species of the genus, only increasing on Cruise 9801.

Other tropical/subtropical oceanic copepods with low contributions to copepod biomass showed interannual differences during fall, but some were higher on Cruise 9710 (*Euchaeta indica* and *Labidocera acutifrons*) while others were higher on Cruise 9810 (*Acartia danae*, *Centropages elongatus*, *Eucalanus hyalinus*, *Heterorhabdus papilliger* and *Neocalanus gracilis*).

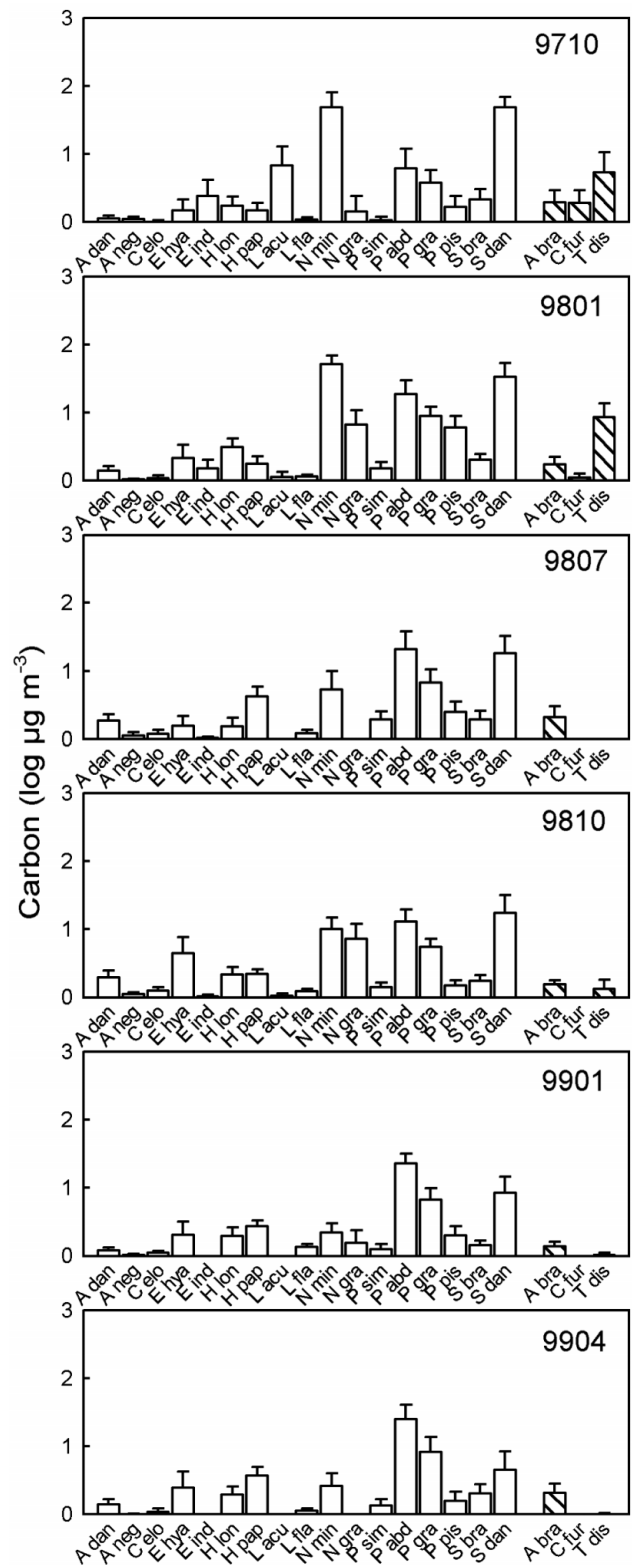


Fig. 8. Carbon biomass (mean \pm 95% confidence intervals) of tropical/subtropical copepod species in nighttime samples at IMECOAL cruises. Hatched bars indicate neritic species; remainder are oceanic. Abbreviations in the abscissa as in Table 2

However, the response of these species was not consistent in winter excepting for *Heterorhabdus papilliger*, which could be considered more temperate than tropical as it showed higher abundances on Cruises 9807 and 9904 (July and April respectively). Other minor species with interannual differences during winter were *Lucicutia flavicornis*, *N. gracilis*, and *Scolecithrix bradyi*. The first increased in abundance on Cruise 9901 while the other 2 decreased. The opposite response of *N. gracilis* in fall (Cruise 9710 < 9810) compared to winter (Cruise 9801 > 9901) indicates that this species is affected by extreme temperatures.

Apart from *Temora discaudata*, tropical/subtropical neritic copepods, had a low biomass through the study period. *Centropages furcatus* disappeared from July 1998 to April 1999 (Table 2), but *Aetideus bradyi* persisted with no significant interannual changes.

Warm-temperate group. The most abundant oceanic species during the warm fall of 1997 were 2 species of *Euchaeta* (Fig. 10). However, while the biomass of *E. rimana* showed a significant interannual decrease and a reduced abundance in Cruise 9904, *E. media* was well represented in the cooler cruises (Table 3). The remaining species in this oceanic group showed significant interannual differences only in winter, with increased biomass in January 1999, except for the decrease in *Oithona plumifera*.

In contrast, the neritic species of this group were better represented in the warm period. *Copilia mirabilis*, in particular, made a contribution similar to that of the oceanic *Euchaeta rimana* and exhibited the same progressive decrease after the El Niño peak. *Euchaeta longicornis* and *Corycaeus speciosus* also showed significant interannual differences in fall and winter, while the remaining species showed such differences only in fall.

Clausocalanus spp. *C. arcuicornis* was one of the most abundant species in this genus observed in the samples. This species has a tropical oceanic distribution and has been reported in high abundance in Baja California waters (Fleminger 1964). However, many other *Clausocalanus* species with a different biogeography occur in the area. *Clausocalanus* spp. were very abundant during the whole study period

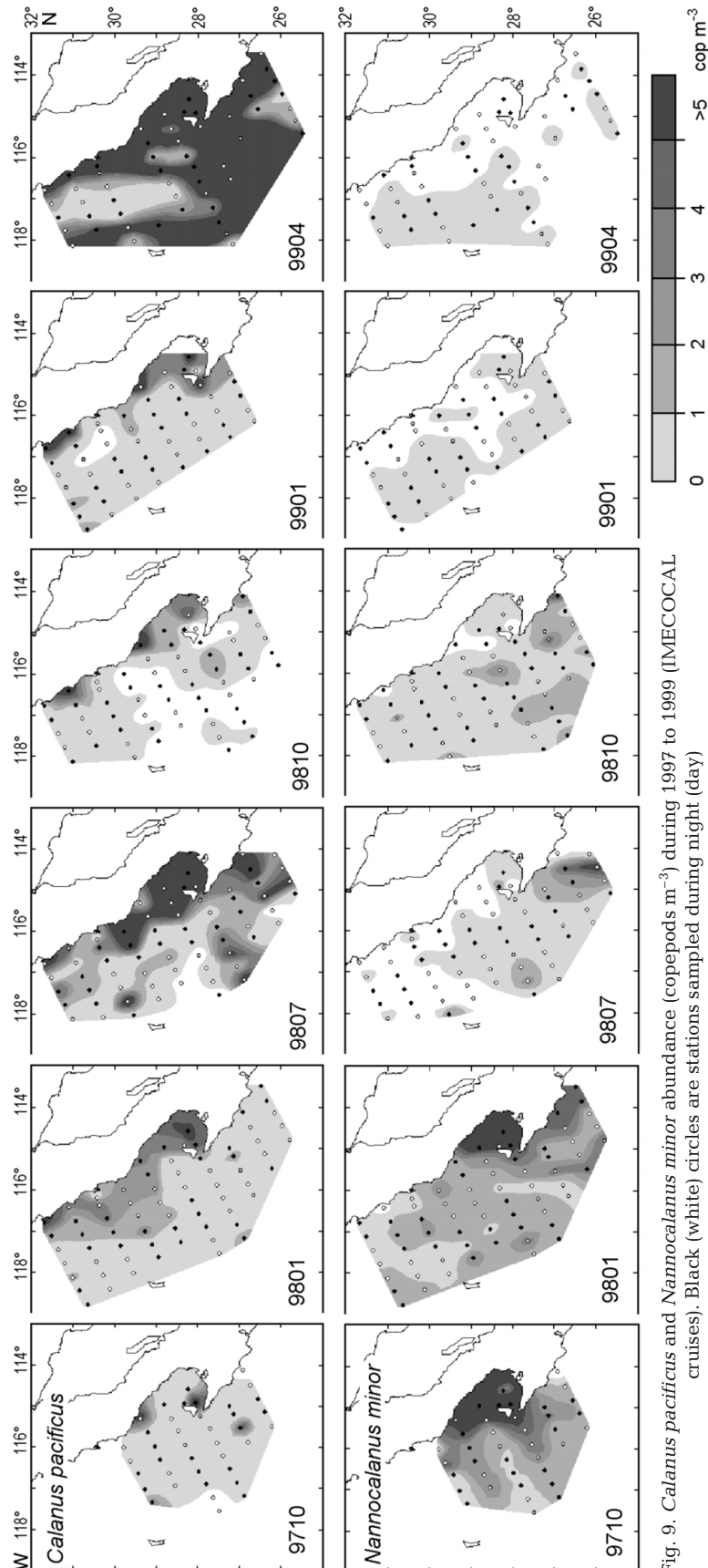


Fig. 9. *Calanus pacificus* and *Nannocalanus minor* abundance (copepods m^{-3}) during 1997 to 1999 (IMECOCAL cruises). Black (white) circles are stations sampled during night (day)

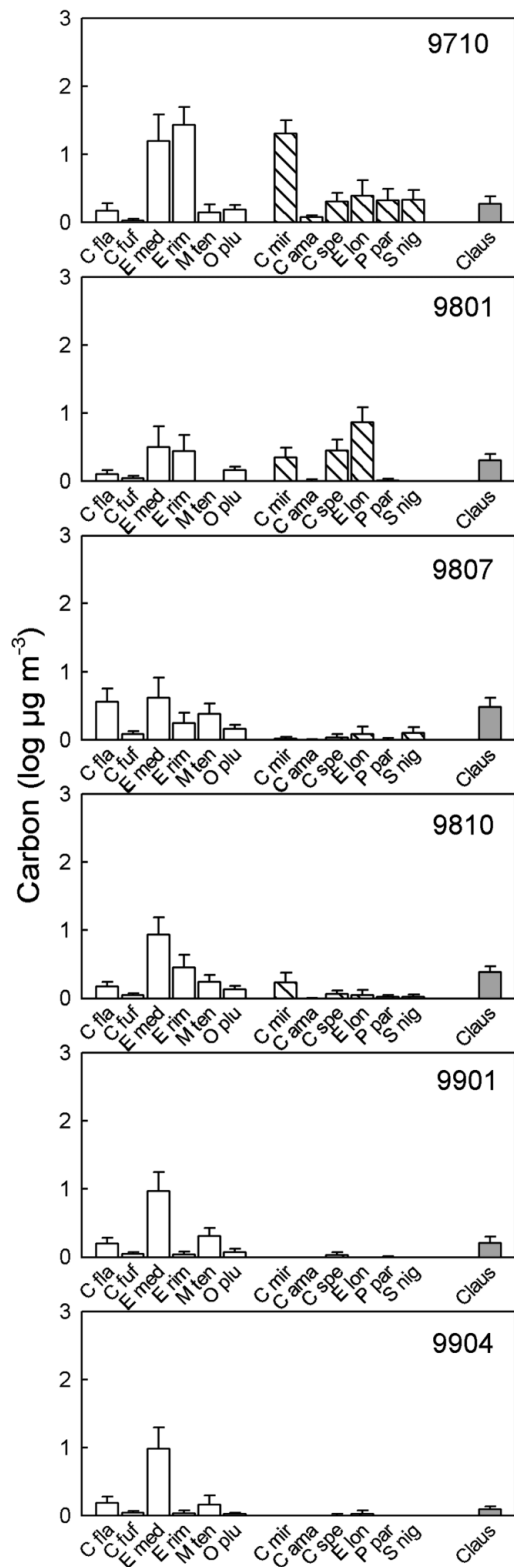


Fig. 10. Carbon biomass (mean \pm 95% confidence intervals) of warm-temperate copepod species (white bars) and *Clausocalanus* (gray bars) in nighttime samples at IMECOCAL cruises. Hatched bars indicate neritic species, remainder are oceanic. Abbreviations in the abscissa as in Table 2

(Table 2), but in fall 1998 copepods of this genus were the most abundant in the community. Because of its small body size (0.8 to 1.6 mm), the amount of biomass represented by this genus is not impressive (Fig. 10). Interannual differences were observed only in fall (Table 3).

Comparison of the 1957-1959 and 1997-1998 El Niño events

Fleminger (1964, 1967) described the distribution of calanoid copepods from April 1958 to January 1959, when another strong El Niño event was in progress. Fleminger's (1964, 1967) quantitative distributions shown on contour intervals based on a logarithmic scale, permitted us to make a nonparametric comparison with the dominant calanoid species found in the IMECOCAL cruises. El Niño 1957-1959 peaked in winter 1958 but extended through winter 1959. Therefore it appears reasonable to compare data for fall (CalCOFI Cruise 5810) and winter (CalCOFI Cruise 5901) with data for the same seasons in the IMECOCAL Cruises in 1997-1998.

Species with higher abundance during 1997-1998.

All the Equatorial species were more abundant on Cruise 9710 (September-October 1997) than on Cruise 5810 (October 1958) (Table 4). The oceanic *Pareucalanus attenuatus*, *Subeucalanus subtenuis* and *Undinula darwini* invaded Vizcaino Bay during Cruise 9710 and further north. The neritic *S. pileatus* (combined with *S. subcrassus*), although well represented along the coastal area in Cruise 5810, extended more to the west during Cruise 9710. The most marked difference was for *U. vulgaris*, which was completely absent north of transect line 120 on Cruise 5810, but was ubiquitous on Cruise 9710. Similar trends were observed for Equatorial species during winter, except for *U. vulgaris*, which almost disappeared in Cruise 9801.

The Tropical/subtropical species significantly higher in fall 1997 were *Centropages furcatus*, *Nannocalanus minor*, and *Scolecithrix danae* (Table 4). *C. furcatus* showed a more extended distribution to the north on Cruise 9710 than on Cruise 5810. *N. minor* and *S. danae* although present over the whole area during both El Niño events, ranked higher on Cruise 9710. A similar trend was observed in winter. Other species more abundant on Cruise 9801 than in Cruise 5901 were *Haloptilus longicornis* and *Pleuromamma gracilis* (the latter combined with *P. piseki*). *H. longicornis* invaded coastal waters along transect line 100 and *P. gracilis* penetrated Vizcaino Bay on Cruise 9801.

The only species to indicate that the El Niño 1997-1998 event was weaker than the event of 1957-1959 were 2 species from the Transition Zone group, *Eucalanus californicus* and *Rhincalanus nasutus* (Table 4).

Table 4. Comparison of calanoid copepod abundance during 2 strong El Niños, in fall (5810, 9710) and winter (5901, 9801), using the Mann-Whitney *U* test. Only species with significant results at $\alpha = 0.05$ for one or both seasons are shown ($n = 10, 15, 12, 28$ for 5810, 9710, 5901, 9801 respectively, NS = not significant)

Species	El Niño fall (5810 vs 9710)		El Niño winter (5901 vs 9801)	
	z	p	z	p
	More abundant in 9710		More abundant in 9801	
<i>Eucalanus californicus</i>	-2.35	0.048		NS
<i>Rhincalanus nasutus</i>		NS	-2.99	0.003
<i>Pareucalanus attenuatus</i>	-4.17	<0.001	-5.06	<0.001
<i>Subeucalanus pileatus</i> + <i>subcrassus</i>	-3.04	0.003	-4.03	0.001
<i>Subeucalanus subtenuis</i>	-3.04	0.004	-5.03	<0.001
<i>Undinula darwini</i>	-4.44	<0.001	-4.81	<0.001
<i>Undinula vulgaris</i>	-4.22	<0.001		NS
<i>Centropages furcatus</i>	-2.92	0.012		NS
<i>Haloptilus longicornis</i>		NS	-2.35	0.033
<i>Nannocalanus minor</i>	-2.40	0.023		NS
<i>Pleuromamma gracilis</i> + <i>piseki</i>		NS	-2.62	0.012
<i>Scolecithrix danae</i>	-3.41	0.001	-3.55	<0.001
<i>Euchaeta rimana</i>	-2.84	0.005		NS
	Less abundant in 9710		Less abundant in 9801	
<i>Metridia pacifica</i>	3.03	0.016		NS
<i>Candacia bipinnata</i>	4.03	<0.001		NS
<i>Pleuromamma borealis</i>	2.84	0.007	2.53	0.013
<i>Scolecithricella ovata</i>	2.71	0.031		NS
<i>Acartia negligens</i>		NS	2.75	0.031
<i>Heterorhabdus papilliger</i>	2.18	0.048		NS
<i>Lucicutia flavicornis</i>	3.25	0.002	2.38	0.045
<i>Temora discaudata</i>	2.24	0.031		NS
<i>Mesocalanus tenuicornis</i>	2.91	0.007	5.47	<0.001
<i>Paracalanus parvus</i>		NS	5.33	<0.001

The former was absent from the region during Cruise 5810, and the second was very rare on Cruise 5901.

Species with higher abundance during 1958-1959.

The subarctic *Metridia pacifica* and 3 Transition Zone species (*Candacia bipinnata*, *Pleuromamma borealis* and *Scolecithricella ovata*) were more abundant on Cruise 5810 than in Cruise 9710 (Table 4). The intrusion of these species in the Baja California region was higher during fall 1958 (moderately higher for *M. pacifica*) than in fall 1997. A similar intrusion during winter 1959 was only observed for *P. borealis*, including the invasion of Vizcaino Bay, while in the winter of 1998 was more scattered. The better representation in the region of these species with cold water affinity indicated an El Niño 1958-1959 event less intense than the event of 1997-1998.

Of the tropical/subtropical species 3 ranked higher on Cruise 5810 than on Cruise 9710, but only *Lucicutia flavicornis* had a similar trend in winter (Cruise 5901 against Cruise 9801) (Table 4). The distribution of this species was more extensive in the region during El Niño 1958-1959, entering in the shallow area of Vizcaino Bay. *Acartia negligens* also ranked higher on Cruise 5901, being well distributed in the area.

The warm-temperate cosmopolites that were better represented in the winter 1959 were *Mesocalanus tenuicornis* and *Paracalanus parvus* (Table 4). *M. tenuicornis* was absent from samples during Cruise 9801 (Table 2), while it was broadly distributed in the region on Cruise 5901. *P. parvus* was also common during Cruise 5901 and was particularly abundant along transect line 120, where it did not occur during Cruise 9801.

DISCUSSION

The physical evolution of ENSO from the warm phase in 1997-1998 to the cold phase in 1998-1999 has been extensively documented for the Pacific basin (Webster & Palmer 1997, McPhaden 1999) and in the CCS (Lynn et al. 1998, Collins et al. 2002, Durazo & Baumgartner 2002, Huyer et al. 2002, Lynn & Bograd 2002). Particularly relevant for the present study is the analysis by Lynn & Bograd (2002) for the southern California region. Based on departures of dynamic height and transport from their seasonal norms, these authors considered

that El Niño 1997-1998 showed 2 pulses, one in July 1997 and a second stronger pulse in November-December 1997. Therefore, our first 2 IMECOCAL cruises (9710 and 9801) which took place before and after the second El Niño pulse are appropriate to characterize the warming event. The abrupt change from a net poleward flow reversing to an equatorward flow was observed in southern California in April 1998, but negative temperature anomalies were not evident until October 1998 (Lynn & Bograd 2002). This is consistent with the transition to a cooler and fresher state off Baja California from October 1998 to August 1999 (Durazo & Baumgartner 2002).

During the anomalous warming of 1997-1998, the copepod community off Baja California showed pronounced changes, the most impressive being the increase in abundance of Equatorial species (*Pareucalanus attenuatus*, *Subeucalanus subtenuis*, *S. pileatus*, *S. subcrassus*, *Undinula darwini*, and *U. vulgaris*). Equatorial species, constrained to low latitudes (Fleminger 1973, 1975, Brinton et al. 1986), usually occupy a limited area at the southern edge of the CCS, and are often only evident in autumn and winter (Fleminger 1964, 1967). During the El Niño of 1997-1998, these

species expanded their distribution to the complete Baja California sector of the CCS. The group of Tropical/Subtropical species also increased during El Niño. Although the tropical species usually occur in low numbers in subtropical regions, during the warm phase of 1997–1998 they exhibited a strong increase. In particular, *Nannocalanus minor* was the dominant copepod on Cruise 9710 and the second most dominant on Cruise 9801. The preponderance of the Equatorial and Tropical/Subtropical species off Baja California during El Niño indicated that this was the most perturbed region of the CCS. None of the Equatorial species appeared in the list of 'exotic southern taxa' on transect line P, off Vancouver (Mackas & Galbraith 2002), neither in the list of warm water species off Oregon (Peterson et al. 2002), or in the list off Monterey Bay (Hopcroft et al. 2002) during El Niño 1997–1998.

Transport by the poleward flow appears to be an important factor accounting for distributional shifts, as illustrated by *Undinula vulgaris*. Although this species is usually restricted to neritic waters of the eastern tropical Pacific (Fleminger 1975, Suárez-Morales et al. 2000), it was ubiquitous off Baja California during fall 1997 (Fig. 6). The widespread presence of this species through the oceanic area appears to be due to the strong near-surface poleward coastal jet along the peninsula south of Punta Eugenia (Lynn et al. 1998). The coastal jet had disappeared by January 1998, but the poleward flow continued from the southwest, introducing saline (Equatorial) water (Fig. 3b,d) as far as southern California (Lynn & Bograd 2002). The distribution of *Subeucalanus subtennis* during January–February 1998 (Cruise 9801) (Fig. 7) matched remarkably well with 10 m isohalines, and thus is a useful marker of the strong poleward flow during El Niño. *S. subtennis*, an inhabitant of eutrophic oceanic waters (Fleminger 1973), found favorable conditions at moderate chlorophyll concentrations on Cruise 9801 (Lavaniegos et al. 2002). This species is one of the dominant species of the eastern tropical Pacific (Boyd et al. 1980, Arcos & Fleminger 1986, Chen 1986, Fernández-Alamo et al. 2000), and extends offshore along the equator (Grice 1961, Fleminger 1973, Timonin & Voronina 1977). In the southern hemisphere it is abundant off Peru, but during fall and winter 1997–1998 the presence of expatriate *S. subtennis* also was noted at Mejillones Bay, Chile (23°S) (Hidalgo & Escribano 2001).

Unfortunately we did not sample in April 1998, when the reversal of flow seems to have occurred in southern California (Lynn & Bograd 2002). However, by July 1998 the intensification of the California Current was evident in the low-salinity nucleus observed at oceanic stations along transect line 110 (Fig. 3a,c). Again, the transition to cool conditions had a strong effect on the copepod community, with a virtual disappearance of

equatorial copepods and a considerable reduction in the Tropical/Subtropical group. At the same time, the abundance of temperate species recovered. While *Nannocalanus minor* decreased and retreated to oceanic areas, *Calanus pacificus* became the top calanoid in July 1998 and again in April 1999.

Calanus pacificus showed different responses to El Niño, depending on latitude. Thus, while Peterson et al. (2002) noted an increase in abundance of this species off Oregon, other authors from central (Hopcroft et al. 2002) and southern California (Rebstock 2002) waters recorded a decrease. This is an expected result for a Transition zone species endemic to the California Current that has been displaced northward under warm conditions. However, we do not have sufficient evidence of a negative effect on abundance or biomass of *C. pacificus* off Baja California. It is well known that this species avoids surface waters from late summer to and early winter (Longhurst 1967, Aldredge et al. 1984, Osgood & Checkley 1997), i.e. is the time of seasonal warming and decreased primary production. Thus, through a diapause mechanism, *C. pacificus* probably avoided surface waters during El Niño and attain an advantage after that event; this was particularly marked during the productive spring of 1999 (Lavaniegos et al. 2002). A similar process could have operated in populations of other Transition zone species (*Eucalanus californicus*, *Rhincalanus nasutus*) which showed a strong rebound during Cruise 9904 (April 1999). Dormancy of these Transition zone species and the Subarctic *Metridia pacifica* was analyzed by Ohman et al. (1998), based on metabolic enzymes and lipids. While *M. pacifica* shows no evidence of dormancy, *C. pacificus* has a biphasic life history, with an actively reproducing segment of the population in surface waters overlying a deep dormant segment in winter.

One of the problems inherent in understanding the biological effects of events such as El Niño and La Niña, is the uncertainty about the seasonal norms. The CalCOFI time series has been useful in understanding the physical variability of the CCS on seasonal and interannual scales (Lynn & Simpson 1987), and even decadal scales inside the southern California region (Bograd & Lynn 2003). Bowman & Johnson (1973) described the distribution of some calanoid copepods between May and October 1949, but the southern Baja California region was not included in the first CalCOFI cruises. The distribution charts of Fleminger (1964, 1967) included a more complete number of species and better coverage for the Baja California region. However, his seasonal series was based on cruises in 1958–1959 (CalCOFI Cruises 5804, 5807, 5810, 5901), at the time when other strong ENSO was taking place.

Increasing evidence of a long-term process of warming in the North Pacific between 1976 and 1998 (Latif &

Barnett 1994, Miller et al. 1994, Roemmich & McGowan 1995, Mantua et al. 1997) and possible persistent cooling since 1999 (Lavaniegos & Ohman 2003) has renewed interest in possible changes in species composition. A retrospective analysis of the CalCOFI collection from the region off southern California was done by Rebstock (2001, 2002) who, from 1951 to 1999 found a consistent dominance of *Calanus pacificus*, *Metridia pacifica* and *Pleuromamma borealis* during spring (Rebstock 2001). Although *C. pacificus* did not change on decadal scales, it unequivocally decreased in abundance during anomalous years (i.e. El Niño years). It was also the species showing the strongest seasonal change, as a difference of 87% was found between its abundance in spring and autumn. Among the Tropical/subtropical species enriching the southern California community during fall was *Nannocalanus minor*, which was relatively abundant during 1997-1998, but was less abundant than the main Transition zone species (Rebstock 2002).

The weak response of *Nannocalanus minor* in southern California, during fall 1997, contrasts with the strong increase of this species in Baja California waters. The regional differences are sufficiently important and the long-term trends from southern California are not appropriate for resolving interannual perturbations in the Baja California region. The extent of stability of the copepod assemblages off Baja California is still unresolved and needs to be addressed, with an additional analysis of CalCOFI samples. The overwhelming presence of Equatorial species during the El Niño event of 1997-1998 compared to that of 1957-1959 could have 3 possible interpretations: (1) El Niño 1997-1998 was more intense than El Niño 1958-1959; (2) both events were similar, but climatic influences of different types affected the region during the relevant periods; (3) the comparison was influenced by the deeper sampling (210 m) in 1997-1998 than in 1957-1958 (140 m).

Certainly the 1957-1959 El Niño event was one of the strongest and longest on record. The classification of Wolter & Timlin (1998), based on the multivariate ENSO index, ranked the period between May 1957 and May 1958 highest, while that between November 1958 and March 1959 was ranked as moderate. It could be argued that the cruises under comparison (CalCOFI Cruises 5810 and 5901) did not include the warmest phase, which occurred in 1957-1958, and therefore any comparison with recent cruises (9710, 9801) would be based on different phases of the ENSO cycle. A more valid comparison would require data from fall 1957 (Cruise 5710) and winter 1958 (Cruise 5801), for which unfortunately there are no data on copepod abundance in the region. An additional complication is the influence superimposed by a different time scale. The

warm regime affecting the region during 1977 to 1998 (Mantua et al. 1997) could have induced the intrusion of tropical species. There is biological evidence from ichthyoplankton (Moser et al. 2001) and euphausiids (Brinton & Townsend 2003) that suggests colonization by tropical species off southern California, or a decline in abundance of some mid-latitude salps (Lavaniegos & Ohman 2003).

Information for other El Niños is available for Baja California coastal waters. Hernández-Trujillo (1999) reported changes in the copepod community off south Baja California throughout the period 1982 to 1989. The overlap of this area with the IMECOCAL grid is confined to the southern locations near the coast. Although some species were common to El Niño 1982-1983, El Niño 1987-1988 and El Niño 1997-1998, *Nannocalanus minor* was one of the most abundant species only during 1987-1988. *Subeucalanus subtenuis* and *S. pileatus* were not reported in Hernández-Trujillo's (1999) study on previous El Niños, and perhaps were confused with other species of the genus also abundant in the area (Fleminger 1973). In Magdalena Bay (24.5°N, 112°W), *Undinula vulgaris* was found during 1983 (Palomares-García & Gómez-Gutiérrez 1996) and again in 1997-1998 (Palomares-García et al. 2003). The strong predominance of *Acartia lilljeborgii* and *A. tonsa* in Magdalena Bay may indicate a high degree of avoidance of oceanic waters by these species.

In the Gulf of California during the spring of 1983, *Subeucalanus subtenuis* and *S. pileatus* were, together with *Pleuromamma gracilis*, the most abundant calanoids (Jiménez-Pérez & Lara-Lara 1988). *Nannocalanus minor*, although present, was less important. Similarly, during El Niño 1992-1993, a replacement of *N. minor* by the neritic *U. vulgaris* was observed in Canal San Lorenzo (24.5°N, 110.33°W). The differential response of *N. minor* inside the Gulf and *N. minor* off the western coast of Baja California could be due to the oceanic affinity of this species. The entrance to the Gulf is more influenced by eastern tropical Pacific fauna, particularly in autumn/winter, when the Costa Rica Coastal Current develops along the Central American coast (Badan-Dangon 1998). The evolution of this current is not well known. The Costa Rica Coastal Current could reach the coastal zone off western Baja California and may be associated with the coastal jet observed during fall 1997 (Lynn et al. 1998). The North Equatorial Countercurrent (NECC), from which the Costa Rica Coastal Current arises, becomes stronger during the ENSO, as was observed in 1982-1983 (Dessier & Donguy 1987). The herbivorous copepods *Undinula darwini*, *N. minor*, *Clausocalanus* spp. and *Paracalanus* spp. in the NECC domain of the eastern tropical Pacific during El Niño 1982-1983 decreased in abundance, while opposite response was

observed off Baja California during El Niño 1997–1998 for *U. darwini* and *N. minor*, which appeared to be forced northward.

In conclusion, the composition of copepods off Baja California during the period 1997 to 1999 showed a rapid transition from an Equatorial-Tropical/subtropical community during El Niño to a temperate or Transition zone community typical of the CCS during La Niña. Seasonal and interannual trends cannot be separated by means of the few historical data available, and require a renewed focus on retrospective studies for the region. The CalCOFI zooplankton collection includes samples from the Baja Californian sector for the period 1949–1984, and the similarity in sampling methods make possible future comparison with the IMECOCAL samples analyzed in the present study.

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Appendix 1. Copepod species present (+) during 1997 to 1999 El Niño and La Niña

Species	IMECOCAL cruises						Species	IMECOCAL cruises					
	9710	9801	9807	9810	9901	9904		9710	9801	9807	9810	9901	9904
Order Calanoida Sars 1903													
Family Acartiidae Sars 1903													
<i>Acartia clausi</i> Giesbrecht 1892	+	+	+	+	+	+	<i>Haloptilus ornatos</i> (Giesbrecht 1892)	+	+	+	+	+	+
<i>Acartia danae</i> Giesbrecht 1889	+	+	+	+	+	+	<i>Haloptilus spiniceps</i> (Giesbrecht 1892)	+	+	+	+	+	+
<i>Acartia negligens</i> Dana 1852	+	+	+	+	+	+	<i>Pachyptilus pacificus</i> Johnson 1936	+	-	-	-	-	-
<i>Acartia tonsa</i> Dana 1849	+	+	+	+	+	+	Family Calanidae Dana 1849						
Family Aetideidae Giesbrecht 1892													
<i>Aetideus acutus</i> Farran 1929	+	-	-	+	+	+	<i>Calanus pacificus</i> Brodsky 1948	+	+	+	+	+	+
<i>Aetideus armatus</i> (Boeck 1872)	+	+	-	-	+	+	<i>Canthocalanus pauper</i> (Giesbrecht 1888)	-	-	-	+	-	-
<i>Aetideus bradyi</i> A. Scott 1909	+	+	+	+	+	+	<i>Mesocalanus tenuicornis</i> (Dana 1849)	+	-	+	+	+	+
<i>Aetideus giesbrechti</i> Cleve 1904	+	-	-	-	-	-	<i>Nannocalanus minor</i> (Claus 1863)	+	+	+	+	+	+
<i>Euchirella amoena</i> Giesbrecht 1888	+	-	+	+	+	+	<i>Neocalanus cristatus</i> (Krøyer 1848)	+	-	+	+	+	+
<i>Euchirella bella</i> Giesbrecht 1888	+	+	-	+	-	-	<i>Neocalanus gracilis</i> (Dana 1852)	+	+	-	+	+	+
<i>Euchirella bitumida</i> With 1915	-	-	+	+	+	+	<i>Undinula darwini</i> (Lubbock 1860)	+	+	+	+	+	+
<i>Euchirella curticauda</i> Giesbrecht 1888	+	+	+	+	+	+	<i>Undinula vulgaris</i> (Dana 1849)	+	+	-	-	-	-
<i>Euchirella messinensis</i> (Claus 1863)	-	-	+	-	-	-	Family Calocalanidae Bernard 1958						
<i>Euchirella pulchra</i> (Lubbock 1856)	-	-	+	+	+	+	<i>Calocalanus pavo</i> (Dana 1852)	+	+	+	+	+	+
<i>Euchirella rostrata</i> (Claus 1866)	-	-	-	-	-	-	<i>Calocalanus styliremis</i> Giesbrecht 1888	+	-	+	+	+	+
<i>Euchirella truncata</i> Esterly 1911	+	-	-	-	-	+	Family Candaciidae Giesbrecht 1892						
<i>Gaetanus miles</i> Giesbrecht 1888	+	-	-	-	+	-	<i>Candacia aethiopica</i> (Dana 1849)	+	+	+	+	+	+
<i>Gaetanus minor</i> Farran 1905	+	+	+	+	+	+	<i>Candacia bipinnata</i> (Giesbrecht 1889)	+	+	+	+	+	+
<i>Gaidius pungens</i> Giesbrecht 1895	+	+	+	+	+	+	<i>Candacia catula</i> (Giesbrecht 1889)	+	+	-	-	-	-
<i>Undeuchaeta bispinosa</i> Esterly 1911	+	-	-	-	-	-	<i>Candacia curta</i> (Dana 1849)	+	+	+	+	+	+
<i>Undeuchaeta intermedia</i> A. Scott 1909	+	+	+	+	+	+	<i>Candacia longimana</i> (Claus 1863)	+	+	-	-	-	-
<i>Undeuchaeta plumosa</i> (Lubbock 1856)	-	+	+	+	-	-	<i>Candacia pachydactyla</i> (Dana 1849)	-	-	+	-	-	-
Family Arietellidae Sars 1902													
<i>Arietellus plumifer</i> Sars 1905	-	-	+	-	-	-	<i>Candacia tenuimana</i> (Giesbrecht 1889)	+	+	-	+	+	-
<i>Arietellus setosus</i> Giesbrecht 1892	-	+	-	+	+	-	<i>Candacia varicans</i> (Giesbrecht 1892)	+	-	-	-	+	+
Family Augaptilidae Sars 1905													
<i>Augaptilus longicaudatus</i> (Claus 1863)	-	+	-	+	+	+	<i>Paracandacia bispinosa</i> (Claus 1863)	+	+	+	+	+	+
<i>Haloptilus acutifrons</i> (Giesbrecht 1892)	+	+	+	+	+	+	<i>Paracandacia simplex</i> (Giesbrecht 1889)	+	+	+	+	+	+
<i>Haloptilus austini</i> Grice 1959	-	-	-	+	-	-	<i>Paracandacia truncata</i> (Dana 1849)	+	+	+	+	-	-
<i>Haloptilus longicornis</i> (Claus 1863)	+	+	+	+	+	+	Family Centropagidae Giesbrecht 1892						
<i>Haloptilus mucronatus</i> (Claus 1863)	-	-	-	+	-	-	<i>Centropages bradyi</i> Wheeler 1900	+	-	+	+	+	+
							<i>Centropages calaninus</i> (Dana 1849)	+	-	-	+	-	-
							<i>Centropages elongatus</i> Giesbrecht 1896	+	+	+	+	+	+
							<i>Centropages furcatus</i> (Dana 1849)	+	+	-	-	-	-
							<i>Centropages gracilis</i> (Dana 1849)	+	+	+	+	+	-
							<i>Centropages violaceus</i> (Claus 1863)	+	+	+	+	-	-

Appendix 1 (continued)

Species	IMECOCAL cruises						Species	IMECOCAL cruises					
	9710	9801	9807	9810	9901	9904		9710	9801	9807	9810	9901	9904
Family Clausocalanidae Giesbrecht 1892							<i>Scottocalanus securifrons</i> (T. Scott 1894)	-	-	-	+	+	-
<i>Clausocalanus</i> spp.	+	+	+	+	+	+	<i>Scottocalanus sedatus</i> Farran 1936	+	-	+	+	+	+
Family Eucalanidae Giesbrecht 1892							Family Temoridae Giesbrecht 1892						
<i>Eucalanus californicus</i> Johnson 1938	+	+	+	+	+	+	<i>Temora discaudata</i> Giesbrecht 1889	+	+	+	+	+	+
<i>Eucalanus elongatus</i> (Dana 1849)	-	-	-	+	-	+	Family Tortanidae Sars 1902						
<i>Eucalanus hyalinus</i> (Claus 1866)	+	+	+	+	+	+	<i>Tortanus discaudatus</i> (Herdman, Thompson & A. Scott 1897)	-	-	-	-	+	-
<i>Pareucalanus attenuatus</i> (Dana 1849)	+	+	+	+	+	+	Order Cyclopoida Burmeister 1835						
<i>Subeucalanus crassus</i> Giesbrecht 1888	+	-	-	-	-	-	Family Oithonidae Dana 1852						
<i>Subeucalanus mucronatus</i> Giesbrecht 1888	+	-	-	-	-	-	<i>Oithona attenuata</i> Farran 1913	-	+	-	+	+	-
<i>Subeucalanus pileatus</i> Giesbrecht 1888	+	+	+	+	-	+	<i>Oithona oculata</i> Farran 1913	-	-	-	+	+	-
<i>Subeucalanus subcrassus</i> Giesbrecht 1888	+	+	+	+	+	+	<i>Oithona plumifera</i> Baird 1843	+	+	+	+	+	+
<i>Subeucalanus subtenuis</i> Giesbrecht 1888	+	+	+	+	+	+	<i>Oithona similis</i> Claus 1866	+	+	+	+	-	-
<i>Rhincalanus nasutus</i> Giesbrecht 1888	+	+	+	+	+	+	<i>Oithona spinirostris</i> Claus 1863	+	+	-	+	+	+
Family Euchaetidae Giesbrecht 1892							<i>Oithona tenuis</i> Rosendorn 1917	-	-	+	-	+	-
<i>Euchaeta acuta</i> Giesbrecht 1892	+	+	-	+	-	-	Order Harpacticoida Sars 1903						
<i>Euchaeta concinna</i> Dana 1849	+	-	-	+	-	-	Family Clytemnestridae A. Scott 1909						
<i>Euchaeta indica</i> Wolfenden 1905	+	+	+	+	-	-	<i>Clytemnestra rostrata</i> (Brady 1883)	-	-	+	-	-	-
<i>Euchaeta longicornis</i> Giesbrecht 1888	+	+	+	+	+	+	Family Ectinosomatidae Sars 1903						
<i>Euchaeta media</i> Giesbrecht 1888	+	+	+	+	+	+	<i>Microsetella rosea</i> (Dana 1849)	-	+	+	+	+	-
<i>Euchaeta rimana</i> Bradford 1974	+	+	+	+	+	+	Order Poecilostomatoida Thorell 1859						
<i>Euchaeta spinosa</i> Giesbrecht 1892	+	-	-	+	+	-	Family Corycaeidae Dana 1852						
<i>Euchaeta tenuis</i> Esterly 1906	+	+	+	+	+	-	<i>Corycaeus agilis</i> Dana 1849	-	-	-	+	-	-
<i>Paraeuchaeta elongata</i> (Esterly 1913)	+	-	-	-	-	-	<i>Corycaeus amazonicus</i> F. Dahl 1894	+	+	+	+	-	-
Family Heterorhabdidae Sars 1902							<i>Corycaeus americanus</i> Wilson 1949	+	+	-	-	-	-
<i>Heterorhabdus clausi</i> (Giesbrecht 1889)	-	-	-	+	-	-	<i>Corycaeus anglicus</i> Lubbock 1857	+	+	-	-	-	-
<i>Heterorhabdus papilliger</i> (Claus 1863)	+	+	+	+	+	+	<i>Corycaeus clausi</i> F. Dahl 1894	-	+	+	+	+	-
<i>Heterorhabdus spinifrons</i> (Claus 1863)	+	+	+	+	+	+	<i>Corycaeus crassiusculus</i> Dana 1849	-	-	-	+	-	+
<i>Heterorhabdus tanneri</i> (Giesbrecht 1895)	+	+	-	-	+	-	<i>Corycaeus flaccus</i> Giesbrecht 1891	+	+	+	+	+	+
<i>Heterostylites longicornis</i> (Giesbrecht 1889)	+	+	-	+	+	+	<i>Corycaeus furcifer</i> (Claus 1863)	+	+	+	+	+	+
Family Lucicutiidae Sars 1902							<i>Corycaeus giesbrechti</i> F. Dahl 1894	+	-	-	-	+	-
<i>Lucicutia flavicornis</i> (Claus 1863)	+	+	+	+	+	+	<i>Corycaeus gracilis</i> Dana 1849	-	+	-	-	-	-
Family Mecynoceridae Andronov 1973							<i>Corycaeus latus</i> Dana 1849	+	-	-	-	-	-
<i>Mecynocera clausi</i> Thompson 1888	+	+	+	+	+	+	<i>Corycaeus lautus</i> Dana 1849	+	+	+	+	+	+
Family Metridinidae Sars 1902							<i>Corycaeus limbatus</i> Brady 1883	-	+	+	+	+	+
<i>Gaussia princeps</i> (T. Scott 1894)	-	-	+	+	+	-	<i>Corycaeus longistylis</i> Dana 1849	-	-	-	+	-	-
<i>Metridia pacifica</i> Brodsky 1950	+	+	+	+	+	+	<i>Corycaeus pacificus</i> F. Dahl 1894	+	+	+	+	-	-
<i>Metridia princeps</i> Giesbrecht 1889	-	-	-	+	+	+	<i>Corycaeus robustus</i> Giesbrecht 1892	+	-	-	+	-	-
<i>Pleuromamma abdominales</i> (Lubbock 1856)	+	+	+	+	+	+	<i>Corycaeus speciosus</i> Dana 1849	+	+	+	+	+	+
<i>Pleuromamma borealis</i> (F. Dahl 1893)	+	+	+	+	+	+	<i>Farranula gibbula</i> (Giesbrecht 1891)	-	-	-	-	+	-
<i>Pleuromamma gracilis</i> (Claus 1863)	+	+	+	+	+	+	<i>Farranula gracilis</i> (Dana 1849)	-	+	-	-	-	-
<i>Pleuromamma piseki</i> Farran 1929	+	+	+	+	+	+	Family Oncaeidae Giesbrecht 1892						
<i>Pleuromamma quadrungulata</i> (F. Dahl 1893)	+	+	+	+	+	+	<i>Conaea rapax</i> Giesbrecht 1891	-	-	-	+	-	-
<i>Pleuromama xiphias</i> (Giesbrecht 1889)	+	+	+	+	+	+	<i>Lubbockia aculeata</i> Giesbrecht 1891	-	-	-	+	-	+
Family Paracalanidae Giesbrecht 1892							<i>Lubbockia squillimana</i> Claus 1863	-	-	-	-	+	-
<i>Acrocalanus longicornis</i> Giesbrecht 1888	+	-	-	+	-	-	<i>Oncaea confiera</i> Giesbrecht 1891	+	-	-	+	-	-
<i>Paracalanus parvus</i> (Claus 1863)	+	+	+	+	+	-	<i>Oncaea dentipes</i> Giesbrecht 1891	+	+	-	-	-	-
Family Phaennidae Sars 1902							<i>Oncaea media</i> Giesbrecht 1891	+	+	+	+	+	+
<i>Amalophora smithae</i> Grice 1961	-	+	-	-	-	-	<i>Oncaea mediterranea</i> (Claus 1863)	-	-	+	+	+	-
<i>Phaenna spinifera</i> Claus 1863	+	+	+	+	+	+	<i>Oncaea venusta</i> Philippi 1843	+	+	+	-	-	-
Family Pontellidae Dana 1852							<i>Pachos punctatum</i> (Claus 1863)	-	-	+	+	+	-
<i>Labidocera acuta</i> (Dana 1849)	+	+	-	-	-	-	Family Sapphirinidae Thorell 1859						
<i>Labidocera acutifrons</i> (Dana 1849)	+	+	-	+	-	-	<i>Copilia longistylis</i> Mori 1932	-	-	-	+	-	-
<i>Labidocera euchaeta</i> Giesbrecht 1889	+	+	+	+	-	-	<i>Copilia mirabilis</i> Dana 1852	+	+	+	+	+	+
<i>Labidocera jollae</i> Esterly 1906	-	-	-	-	+	-	<i>Copilia quadrata</i> Dana 1849	+	+	+	+	+	+
<i>Labidocera trispinosa</i> Esterly 1905	-	-	+	+	-	-	<i>Copilia recta</i> Giesbrecht 1891	+	+	-	+	-	-
<i>Pontellina plumata</i> (Dana 1849)	+	+	+	+	+	+	<i>Copilia vitrea</i> (Haeckel 1864)	-	-	-	+	-	-
<i>Pontellopsis brevis</i> (Giesbrecht 1889)	-	-	-	+	-	-	<i>Sapphirina angusta</i> Dana 1849	-	+	+	+	+	+
<i>Pontellopsis occidentales</i> Esterly 1906	+	-	-	+	+	+	<i>Sapphirina darwinii</i> Haeckel 1864	+	+	+	+	+	-
<i>Pontellopsis regalis</i> (Dana 1849)	+	-	-	+	-	-	<i>Sapphirina gastrica</i> Giesbrecht 1891	+	+	+	+	+	+
Family Scolecithricidae Giesbrecht 1892							<i>Sapphirina gemma</i> Dana 1852	+	+	+	+	+	+
<i>Lophotrix frontalis</i> Giesbrecht 1895	+	+	+	+	+	+	<i>Sapphirina intestinata</i> Giesbrecht 1891	+	+	+	+	+	-
<i>Scaphocalanus magnus</i> (T. Scott 1894)	+	-	-	-	-	-	<i>Sapphirina metallina</i> Dana 1849	+	+	+	+	-	+
<i>Scolecithricella abyssalis</i> (Giesbrecht 1888)	+	+	+	+	+	-	<i>Sapphirina nigromaculata</i> Claus 1863	+	+	+	+	-	-
<i>Scolecithricella dentata</i> (Giesbrecht 1892)	+	+	+	+	+	+	<i>Sapphirina opalina</i> Dana 1849	+	+	+	+	-	+
<i>Scolecithricella ovata</i> (Farran 1905)	+	+	+	+	+	+	<i>Sapphirina scarlata</i> Giesbrecht 1891	-	+	+	+	+	+
<i>Scolecithrix bradyi</i> Giesbrecht 1888	+	+	+	+	+	+	<i>Sapphirina stellata</i> Giesbrecht 1891	+	+	+	+	+	+
<i>Scolecithrix danae</i> (Lubbock 1856)	+	+	+	+	+	+							
<i>Scottocalanus helenae</i> (Lubbock 1856)	-	-	+	+	-	-							