Effects of the 1997–1999 El Niño and La Niña events on zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system

B.B. Marinovic [a,*], D.A. Croll [a], N. Gong [a], S.R. Benson [b], F.P. Chavez [c]

[a] *Institute of Marine Sciences, University of California, Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95960, USA*
[b] *Moss Landing Marine Laboratories, 8272 Moss Landing Road, CA 95039, USA*
[c] *Monterey Bay Aquarium Research Institute, 7700 Sandholt Road, Moss Landing, CA 95039, USA*

Abstract

Zooplankton abundance and euphausiid community composition were sampled seasonally (spring, summer, fall) within Monterey Bay, California, between 1997 and 1999. Measurements of sea surface temperature (SST), mixed layer depth, and upwelling indices provided concurrent data on physical oceanographic parameters. Both total zooplankton and krill abundance dramatically declined in the summer of 1997 coincident with a rapid increase in SST and mixed layer depth. Changes in euphausiid community composition occurred in concert with the decline in overall abundance. The relative abundance of the southern neritic *Nyctiphanes simplex* increased from August to November in 1997, the abundance of cold temperate *Euphausia pacifica* decreased significantly, and that of the northern neritic *Thysanoessa spinifera* declined dramatically. The sudden appearance of an adult cohort of *N. simplex* in July 1997 suggests that rapid poleward flow characteristic of coastally trapped Kelvin waves occurred between June and July of 1997. The persistent presence of warm temperate and subtropical taxa in samples collected between August 1997 and October 1998 indicates that this poleward flow continued in 1998. Zooplankton abundance, euphausiid community composition, and physical oceanographic parameters gradually returned to a more typical upwelling-dominated state in the spring and summer of 1998. *E. pacifica* and *T. spinifera* abundances gradually increased during the summer and fall of 1998, while *N. simplex* abundance abruptly declined in the spring of 1998. However, this recovery was confined to a narrow coastal band as a result of the onshore movement of the oceanic waters of the California Current. This was reflected by higher than normal numbers of the oceanic *Nematoscelis difficilis* within samples collected during the spring and summer of 1998. By the spring and summer of 1999, both zooplankton and euphausiid abundance had increased to the highest levels recorded during the 3-year study. Both *E. pacifica* and *T. spinifera* abundance increased relative to 1998 while *N. simplex* was completely absent in all samples. These changes reflected the cooler, highly productive environmental conditions associated with the 1998/1999 La Niña. © 2002 Elsevier Science Ltd. All rights reserved.

* Corresponding author. Present address: Long Marine Lab, 100 Shaffer Road, Santa Cruz, CA 95060, USA. Fax: +1-831-459-4882.
  E-mail address: marinovic@biology.ucsc.edu (B.B. Marinovic).

Contents

1. Introduction

There is wide consensus that marine ecosystems in the northeast Pacific respond strongly to acute climatic events such as El Niño Southern Oscillations (ENSO) (Barber & Chavez, 1983; Chelton, Bernal, & McGowan, 1982; Lenarz, Ven Tresca, Graham, Schwing, & Chavez, 1995; McGowan, Cayan, & Dorman, 1998; Wooster & Fluharty, 1985). Within the nearshore pelagic ecosystem off Central California, El Niño events are characterized by increases in ocean temperature and sea level (Lenarz et al., 1995; Ramp, McClean, Collins, Semtner, & Hays, 1997), enhanced onshore and poleward flow (Emery, Royer, & Reynolds, 1985), a deeper mixed layer, deeper nutricline, negative anomalies in coastal upwelling (Chavez, 1996; Hayward, Mantyla, Lynn, Zmith, & Chereskin, 1994), decreases in primary productivity (Chavez, 1996; Lenarz et al., 1995), and decreased zooplankton abundance (Lenarz et al., 1995; Smith, 1985).

Considerable debate exists as to whether El Niño-related impacts off the west coast of North America result as a consequence of remotely forced oceanographic mechanisms linked to the eastern tropical Pacific or from locally forced mechanisms associated with atmospheric phenomena. Several studies suggest sea level and ocean temperature anomalies can be linked to coastally trapped Kelvin waves generated in the equatorial Pacific (Chavez, 1996; Huyer & Smith, 1994; Norton & McLain, 1994). Alternatively, there is evidence that warming in the northeast Pacific associated with El Niño events can result from either changes in local atmospheric pressure systems (Simpson, 1985) or from a combination of remotely and locally forced mechanisms (Huyer & Smith, 1994; Norton & McLain, 1994). McGowan (1984) suggested that the community structure of zooplankton could be used to investigate whether El Niño impacts off California resulted as a consequence of poleward flow, onshore flow, or in situ mechanisms.

Monterey Bay, located on the central California coast, is a large, non-estuarine embayment with unrestricted access to the open ocean. It is further distinguished by the presence of a large, submarine canyon that runs along the central axis of the bay (Shepard, 1973). Strong northwest winds drive seasonal upwelling in the spring and early summer, which results in a cool, nutrient rich band of water that supports high levels of primary productivity, zooplankton, and higher trophic levels (Pennington & Chavez, 2000). This highly productive zone is typically tens of kilometers wide during the peak of the upwelling season and collapses coastward in the late summer and falls as a consequence of weakening winds and reduced upwel-

ling (Abbot & Barksdale, 1991; Chavez, 1996; Olivieri & Chavez, 2000; Pennington & Chavez, 2000). Southwesterly winds associated with winter storms cause upwelling to cease in the winter and the water column becomes well mixed. Three distinct marine climates have been described for the Monterey Bay region based on these physical/chemical oceanographic characteristics: a spring/summer upwelling period, a fall oceanic or 'relaxation' period, and a winter or 'Davidson' period (Bolin & Abbott, 1963; Pennington &Chavez, 2000; Rosenfeld, Schwing, Garfield, & Tracy, 1994).

Long-term observations within the Monterey Bay (Chavez, Pennington, Herlein, Jannasch, Thurmond, & Friedrich, 1997; Olivieri & Chavez, 2000; Pennington & Chavez, 2000) have allowed researchers to assess the impacts of El Niño events on physical oceanography and primary productivity within this region. However, there is a lack of comparable studies for zooplankton and higher trophic levels. Limited data suggest that seasonal fluctuations in zooplankton abundance lag several months behind productivity cycles associated with the distinct marine climates within Monterey Bay. In typical years, maximum abundances of zooplankton occur in the summer and early fall (Barham, 1957; Bauduini, 1997; Silver & Davoll, 1975, 1976, 1977). Lenarz et al. (1995) and Bauduini (1997) reported lower than normal zooplankton abundance off central California during the 1992–1993 El Niño, but they were unable to attribute these as El Niño-related effects because of a lack of suitable climatologies. Even less is known about euphausiid population dynamics within the Monterey Bay region. To date there has been only one seasonal investigation on this subject (Barham, 1957) and no information is available during El Niño events.

In this article, we present seasonal data on zooplankton abundance and krill population dynamics from the nearshore pelagic ecosystem off Monterey Bay, California, for 1997–1999. This time frame is of particular interest as it includes two acute yet distinctively different climatic events: the 1997/1998 El Niño and the 1999 La Niña. We use these data to examine whether changes in zooplankton community structure are consistent with remote or locally forced physical oceanographic mechanisms.

2. Methods

2.1. Study area

The Monterey Bay study area comprised a grid of seven transect lines spaced 3 nautical miles apart and covering an area of approximately 909 km² (Fig. 1). Transect lines began inshore at the 30 fathom curve (55 m) and extended WNW to 122.08°W. Transects ranged in length from 10 km (5.4 nmi) to 22 km (11.9 nmi). Monthly oceanographic surveys were conducted within this grid monthly from May to November in 1997–1999. Two supplementary surveys were conducted in March and April of 1998 in order to extend seasonal coverage into the late winter/early spring during the El Niño event.

2.2. Physical oceanography

Temperature/salinity profiles of the water column were obtained at 10 hydrographic stations distributed systematically throughout the survey grid (Fig. 1) using a Sea-Bird 19 conductivity–temperature–depth (CTD) probe lowered to a depth of 200 m or to within 10 m of the bottom. In order to obtain a measure of the relative strength of coastal upwelling during the study period, monthly mean upwelling indices at 36°N 122°W were obtained from NOAA's Pacific Fisheries Environmental Group (http://www.pfeg.noaa.gov/).

2.3. Zooplankton sampling

Seasonal (spring, summer, and fall) zooplankton abundance was estimated using both hydroacoustic and conventional net sampling. Zooplankton backscatter was measured continuously along the survey track
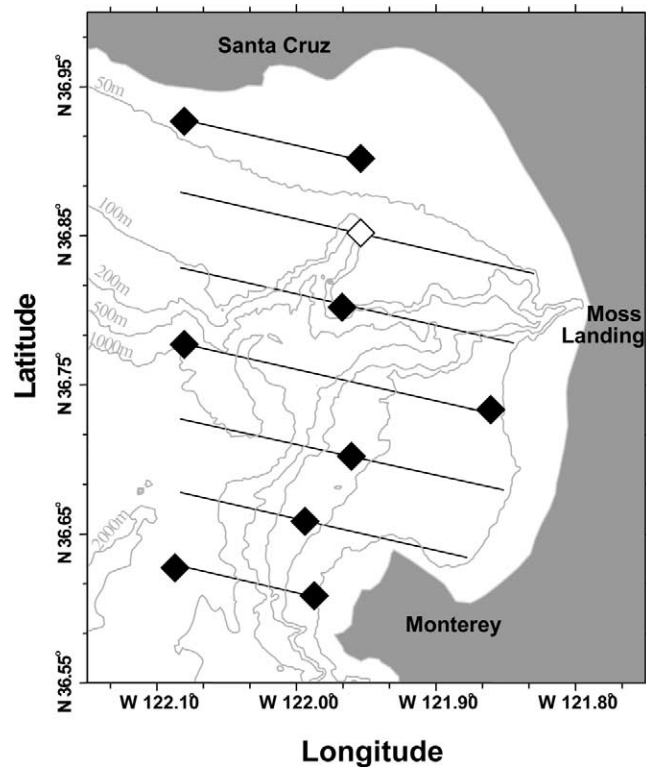
Fig. 1. Study grid within the Monterey Bay, California. Lines indicate cruise tracts for hydroacoustic sampling of zooplankton abundance. Diamonds indicate oceanographic stations. Solid diamonds indicate both hydrographic (CTD) and net sampling stations. Open diamonds indicate hydrographic stations only.

using a Simrad EY-500 echosounder operating at 200 kHz. Plankton tows, using 0.7 m Bongo nets fitted with 333 μm mesh, were conducted at 6–10 sampling stations systematically distributed throughout the survey grid (Fig. 1). Nets were towed obliquely either to 200 m or to within 10 m of the bottom and the volume filtered was estimated using a calibrated analog General Oceanics flowmeter. All samples were immediately preserved in 10% buffered formalin for subsequent analysis in the laboratory. Six stations were sampled for July–November 1997 and March–November 1998. Four additional stations (10 total) were sampled May–November in 1999.

Analysis of echosounder data followed the methodology of Croll, Tershy, Hewitt, Demer, Fiedler, Smith, and Armstrong (1998) and Hewitt and Demer (1993). Zooplankton surface area backscatter (S_a) (S_a m^2/nmi^2), integrated to 200 m, was calculated for each 0.5 nmi transect segment and averaged for the entire survey. In addition, echograms were scrutinized for euphausiid scattering layers and euphausiid integrated backscatter was calculated in the same manner. Euphausiid scattering layers were periodically verified for taxonomic composition via targeted net tows. A total of 26 such targeted net tows were opportunistically sampled in 1997 and 1998.

Total zooplankton displacement volumes (ml/m^3) were determined for all oblique net tows and converted to depth integrated values (ml/m^2) by multiplying the displacement volume value with the tow depth. All post-larval euphausiids in the samples were identified to species, enumerated and measured to the nearest mm. In instances where euphausiids were abundant, samples were subdivided with a Motoda splitter to reduce their numbers to between 100 and 200 individuals. In addition, any atypical warm temperate/subtropical zooplankton taxa encountered during sample analyses were noted.

3. Results

3.1. Physical oceanography

Mean sea surface temperature (SST) values were near the long-term average for the May–July 1997 surveys. Temperatures increased from 13.8 to 17.0 °C between July and August 1997 and remained anomalously warm through November 1997 (Fig. 2). Temperatures gradually declined during the winter months, but remained warmer than normal during the spring of 1998. SST decreased dramatically in July 1998 in conjunction with an increase in coastal upwelling but increased again in the late summer/early fall. SST decreased substantially in October 1998 following the onset of strong coastal upwelling and remained anomalously low through the spring and early summer of 1999. Detailed information on mixed layer depth is presented in Benson et al. (this issue). Briefly, mixed layer depth increased throughout the 1997 season, especially in August, reaching a maximum of 41 m in November 1997. In contrast, mixed layer depths were shallower during the 1998 (2–15 m) and 1999 (0–10 m) seasons. There were distinct differences in the strength of coastal upwelling between 1997 and 1999 (Fig. 2B). Values were near the long-term mean for the spring and early summer of 1997 but declined rapidly in August concurrent with the rapid increase in SST. They remained anomalously low into the spring and early summer of 1998, with intermittent pulses of coastal upwelling between April and September. Stronger than normal coastal upwelling associated with the development of La Niña conditions in Central California were observed in the late fall of 1998 and
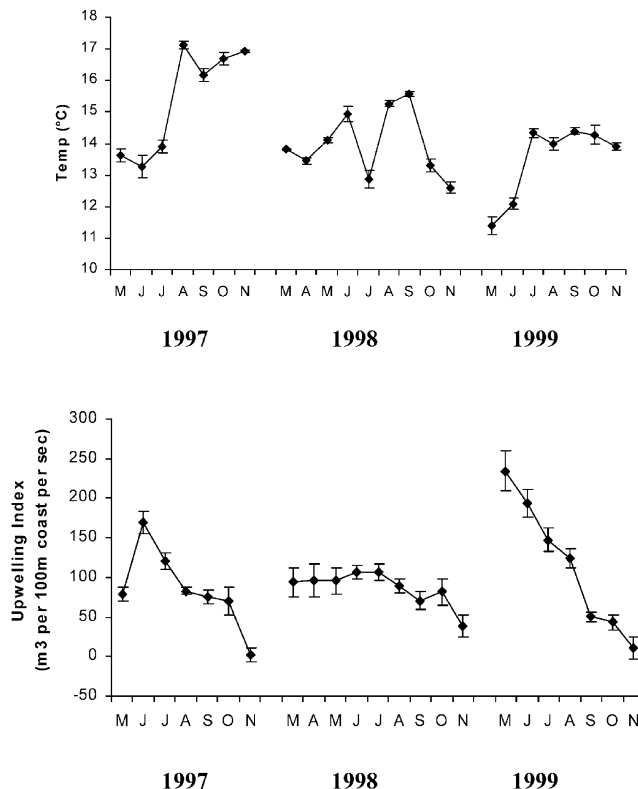

Fig. 2. (A) Seasonal mean (±s.e.) monthly SSTs within the Monterey Bay, California, for 1997–1999. (B) Seasonal mean monthly (±s.e.) upwelling indices for 36°N 122°W for 1997–1999. (Data courtesy: Pacific Fisheries Environmental Group, SWFSC-NOAA).

persisted through to the summer of 1999. Mean upwelling indices (m^3/100 m coastline/s) for May–November 1997–1999 varied significantly between years (one way ANOVA $F = 8.667$, $P < 0.001$). Post hoc multiple comparison tests revealed that mean upwelling indices for 1999 were significantly greater (116.9) than for both 1998 (84.4) and 1997 (86.0) (Tukey Test, $P < 0.05$), with no difference in the mean seasonal values for 1997 versus 1998.

3.2. Seasonal/interannual zooplankton abundance

Both total zooplankton integrated backscatter (zS_a) and zooplankton displacement volume (zd$v$) abundance data demonstrated distinct interannual and seasonal patterns that differed between 1997 and 1999. zS_a varied significantly between years (ANOVA $F = 4.62$, $P = 0.024$) and seasons (ANOVA 1997: $F = 5.60$, $P < 0.001$; 1998: $F = 13.62$, $P < 0.001$; 1999: $F = 9.93$, $P < 0.001$) (Fig. 3A). The highest overall zS_a values were measured in 1999 while the lowest values were measured in 1997. Values decreased dramatically in August 1997 and remained low through November 1997. Values increased throughout the spring and early summer of both 1998 and 1999, but only persisted at high levels into the fall in 1999. Similar patterns were observed in interannual and seasonal zd$v$ values (Fig. 3B). Mean annual zd$v$ differed significantly between years (ANOVA: $F = 28.86$, $P < 0.001$), with the highest values observed for 1999 and the lowest values recorded for 1997. Seasonal patterns in zd$v$ were also similar to zS_a values, although there was considerably more variation in mean monthly values because of the smaller sample sizes. Nevertheless, a dramatic reduction in zooplankton abundance in the summer/fall of 1997 was apparent. Values gradually increased throughout the spring and summer of 1998 whereas those for 1999 were the highest recorded during the 3-year study. Monthly mean zS_a and zd$v$ values for 1997–1999 were positively and significantly correlated ($zS_a = 5509.3 + 814.64$(zd$v$); $r^2 = 0.36$, $P = 0.007$).

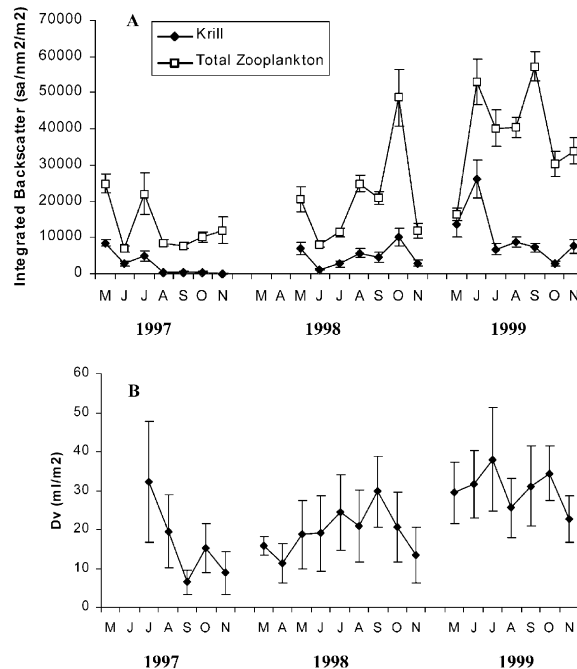Fig. 3. (A) Seasonal mean (±s.e.) monthy integrated zooplankton acoustic backscatter and euphausiid (krill) acoustic backscatter within the Monterey Bay, California, for 1997–1999. (B) Seasonal mean (±s.e.) integrated zooplankton displacement volume within the Monterey Bay, California, for 1997–1999.

3.3. Euphausiid abundance and community composition

Seasonal euphausiid integrated backscatter (eS_a) closely tracked zS_a (Fig. 3A). Peaks in eS_a were found in the spring (May, June) of all 3 years, however, in August 1997 values declined to near zero and remained so through November 1997. In contrast, eS_a values persisted throughout the summer and fall of both 1998 and 1999. Of the 26 targeted net samples taken in designated euphausiid scattering layers between 1997 and 1998, 25 (96%) yielded high densities of euphausiids. The density of euphausiids within targeted tows was significantly greater than comparable values for standard oblique tows conducted off the shelf break (Mann–Whitney Rank Sum Test; $T = 524$, $P < 0.001$). Mean values in targeted net tows were over an order of magnitude higher than those of standard oblique tows (mean targeted = 16591 individuals per m^3, range = 2.67–50.91; mean standard = 1.397 individuals per m^3, range = 0.003–7.30).

In general, overall euphausiid densities within oblique net tows followed the same pattern as eS_a, although different species displayed distinctly different patterns (Fig. 4). *Euphausia pacifica* was present in samples during the entire study, and it was typically the dominant species. However, its abundance declined dramatically in September 1997 and remained low until April 1998 (Fig. 4A). *E. pacifica* abundance increased sharply in the spring of 1998 and then declined in subsequent months, though unlike the previous year, it remained stable throughout the summer and fall. *E. pacifica* abundance peaked again in the spring of 1999 when the highest values for the entire study were recorded. Abundance declined again in the summer and fall but remained higher in general than the previous year. Demographic analysis revealed that juveniles comprised the bulk of the population in the spring of 1997 and 1998 and a substantial portion in 1999 (Fig. 5A). Juveniles were largely absent from the population in the fall of 1997. In contrast, about one-third of all individuals in the fall of 1998 were juveniles and they dominated the population in the fall of 1999.

A distinctly different pattern was seen for *Thysanoessa spinifera* (Fig. 4B). Low numbers of *T. spinifera* were present in the early summer of 1997, but by September its abundance had declined to near zero and it remained virtually absent until the spring of 1998, when its abundance increased slightly but remained low until November. In contrast, *T. spinifera* abundance increased in the spring of 1999 and remained relatively stable into the fall. Demographic analysis of *T. spinifera* populations between 1997 and 1999 similarly revealed a high proportion of juveniles in the spring of all 3 years (Fig. 5B). During the fall of 1998, the population was composed exclusively of adults. However, during the same period in 1999, the population was persistently dominated by juveniles.

Nyctiphanes simplex abundance displayed a pattern that was virtually opposite to that of *T. spinifera* (Fig. 4C). Individuals appeared suddenly within samples in July 1997 and its abundance increased and remained relatively high through the early spring of 1998. Its abundance then declined rapidly to near zero in the summer and fall of 1998 and in 1999 it was absent from all samples. In July 1997, the population consisted almost entirely of adults (Fig. 5C). However, by September, juveniles dominated the population. In October, the population was again entirely adult, but once again in November juveniles dominated the population. This pattern continued through May of 1998, but by June and July the few remaining individuals were almost all adults.

Nematoscelis difficilis was present in low numbers throughout the entire study period. However, abundance increased slightly during the spring and summer of 1998 (Fig. 4D). Both adults and juveniles were present in all months, and there was no clear seasonal or interannual pattern to their relative abundance.

Other euphausiid species were occasionally identified in samples taken between August 1997 and July 1998, which included *Thysanoessa gregaria, Euphausia gibboides*, and *Euphausia mutica*. Several other warm temperate zooplankton taxa were also identified in samples collected between July 1997 and October 1998. Juvenile pelagic red crabs (*Pleuroncodes planipes*) were commonly found in samples collected between November 1997 and July 1998. Four post-larvae (puerulus) of the California spiny lobster (*Panulirus interruptus*) were collected in July 1998 and one in September 1998. Numerous larval and post-
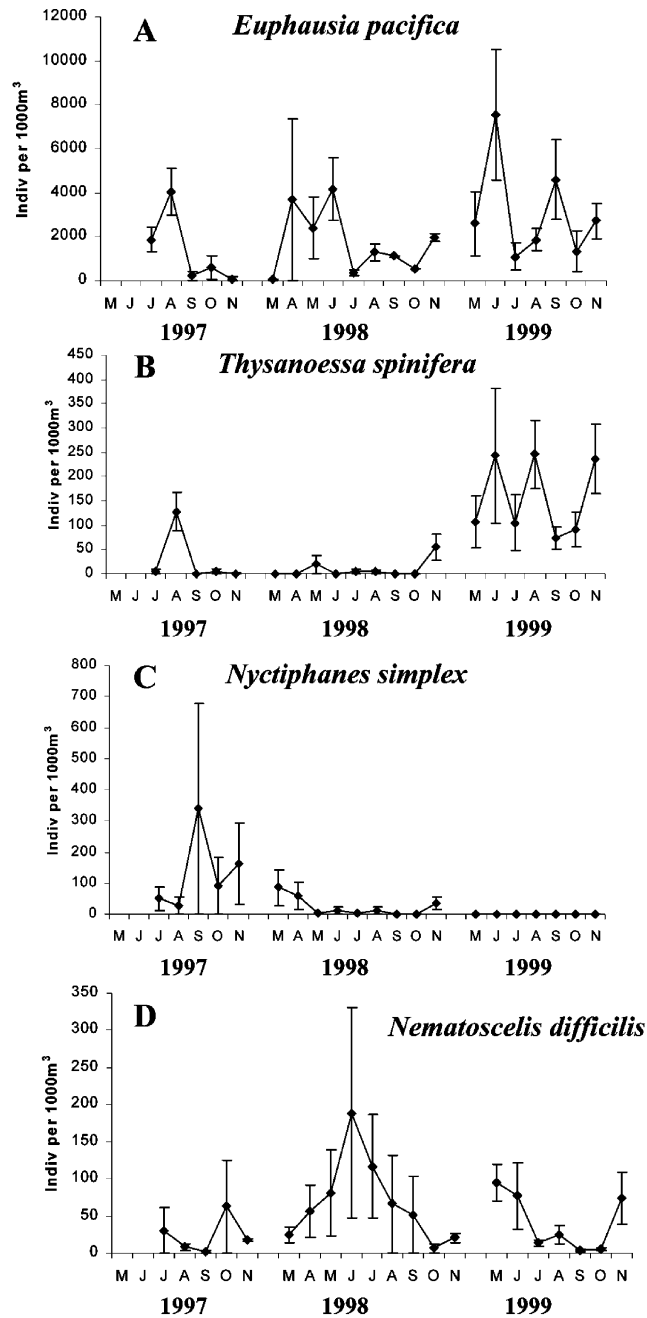
Fig. 4.   Seasonal mean abundance (±s.e.) of euphausiid species within the Monterey Bay, California, for 1997–1999. (A) *E. pacifica*, (B) *T. spinifera*, (C) *N. simplex*, and (D) *N. difficilis*. Note different density scales for each species.
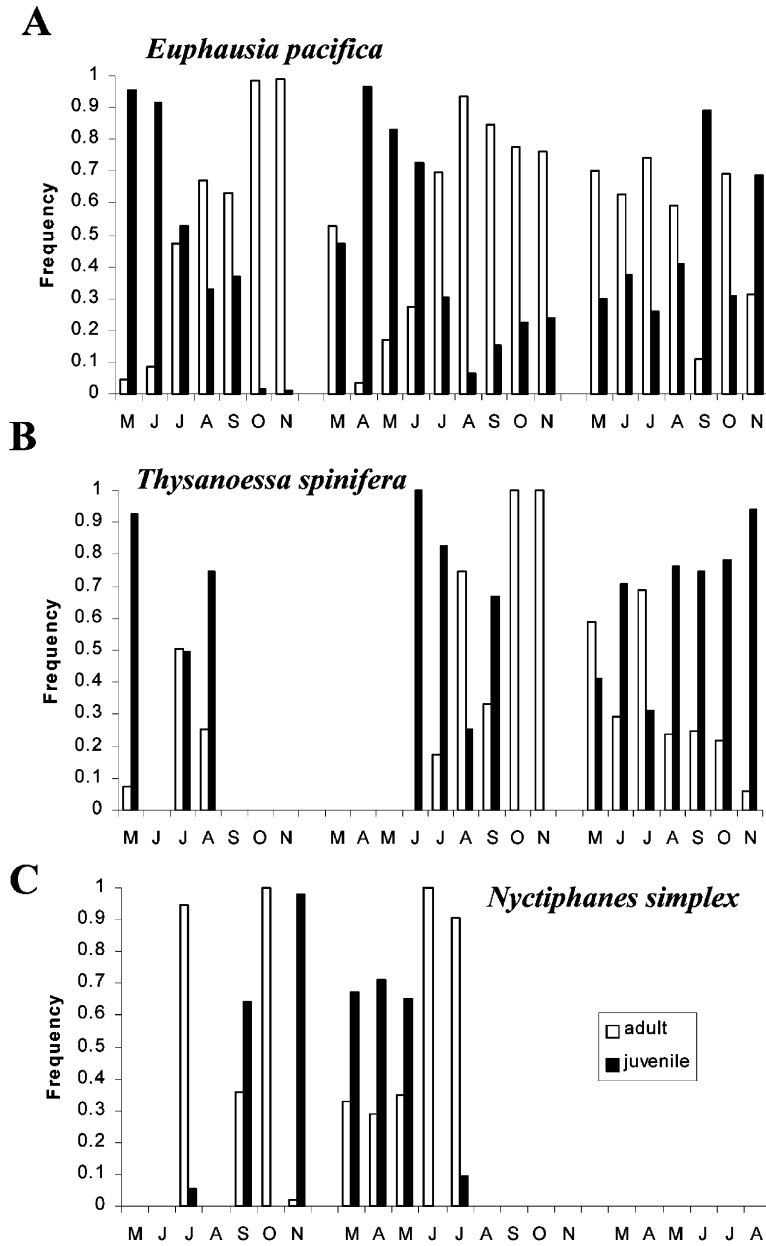
Fig. 5. Proportions of juveniles (black bars) and adults (white bars) for euphausiid species collected in samples from the Monterey Bay, California, between 1997 and 1999. (A) *E. pacifica*, (B) *T. spinifera*, and (C) *N. simplex*.

larval stomatopods, most likely *Pseudosquillopsis marmorata*, were in samples collected in September and November 1997 and July and October 1998. All these warm water species were absent from samples collected in early 1997 and throughout 1999.

4. Discussion

4.1. El Niño effects on zooplankton abundance

Summertime peaks in zooplankton abundance have been reported in Monterey Bay by a number of researchers, who have examined zooplankton abundance over limited spatial and temporal scales (Barham, 1957; Bauduini, 1997; Silver & Davoll, 1975, 1976, 1977). Our seasonal measurements of zooplankton abundance within the Monterey Bay between 1997 and 1999 (Fig. 3) confirm these observations of peak abundances occurring in the summer and early fall, i.e. several months after the observed peak primary productivity (Bolin & Abbott, 1963; Chavez, 1996; Pennington & Chavez, 2000). However, this general pattern was disrupted in August 1997, when zooplankton abundances decreased dramatically (Fig. 3A, B), coincident with an increase in SST (Fig. 2A), a decrease in coastal upwelling, (Fig. 2B) and a deepening of the thermocline (Benson et al., this issue). The recovery of zooplankton abundance within the Monterey Bay to a more typical seasonal pattern in the spring and summer of 1998 (Fig. 3A, B) appears to have been restricted to a relatively narrow productive coastal band where nearshore shoaling of the thermocline (Benson et al., this issue, Chavez et al., this issue) and intermittent periods of coastal upwelling (Fig. 2B) sustained higher levels of primary productivity relative to the adjacent offshore region (Chavez et al., this issue). Kudela and Chavez (2000) determined that moderate levels of coastal upwelling that occurred during the 1992–1993 El Niño were sufficient to sustain near normal levels of primary productivity within the Monterey Bay, but productivity both downstream and offshore of the region were lower than normal because the thermocline and associated nutricline were deeper than normal. The high values for zooplankton abundance recorded in the spring and summer of 1999 (Fig. 3A, B) followed a typical pattern of rising to peak values in the summer/early fall and reflected the highly productive coastal environment associated with La Niña conditions (Chavez et al., this issue). Thus, the most pronounced effects of the 1997–1998 El Niño on zooplankton abundance within the Monterey Bay region occurred between August 1997 and April 1998. Both Lenarz et al. (1995) and Bauduini (1997) have documented reductions in zooplankton biomass within the Monterey Bay region during the 1991–1993 El Niño. Large-scale reductions in zooplankton abundance associated with El Niño events have also been reported by a number of researchers working in the Southern California Bight. During the 1983–1984 El Niño, McGowan (1984) reported a significant reduction in macrozooplankton biomass off southern California by midsummer in 1983. Similarly, Mullin (1997) documented a decrease in mature females of the copepod *Calanus pacificus* off Southern California in the winter and spring during the 1991–1993 El Niño.

4.2. El Niño effects on euphausiid abundance and community composition

The changes in euphausiid community composition that we observed in July 1997 (Fig. 4) suggest that biological impacts related to this El Niño event preceded large-scale changes in physical oceanographic parameters. Specifically, the sudden appearance of a distinct adult cohort of the warm temperate euphausiid *N. simplex* suggests that rapid poleward advection had occurred in the nearshore region between June and July. This observation is consistent with the physical/chemical oceanographic measurements made by other investigators working in the Central California region at the same time (Chavez et al., this issue). *N. simplex* has a predominantly neritic distribution centered off the Baja California Peninsula, which is normally bounded to the north by Point Conception (Brinton, 1962). The sudden appearance of adults in our study area between June and July in 1997 could only have occurred as a result of nearshore, poleward flow at velocities similar to those reported for coastally trapped Kelvin waves (Enfield & Allen, 1980), and not as a result of local recruitment. Brinton (1981) reported similar northerly shifts in the distribution of *N. simplex* during both the 1957–1960 El Niño event and the warm oceanic winter and spring of 1977–1978. Brodeur (1986) found numerous specimens of *N. simplex* within plankton tows taken off the coast of

Oregon during the summer and fall of 1983 and similarly concluded that they had been transported far north of their normal distribution as a result of the strong poleward flow associated with that El Niño event.

The abrupt decline in euphausiid abundance in the summer and fall of 1997 (Fig. 3A) was primarily the result of the large decline in *E. pacifica* abundance (Fig. 4A) and was likely to have been a direct response to the increase in SSTs (Fig. 2A) and decline in primary productivity (Chavez et al., this issue) that occurred during this period. The increase in *E. pacifica* abundance recorded in the spring of both 1998 and 1999 (Fig. 4A) resulted from the influx of new recruits (Fig. 5A), although adult survival appears to have been far better in the more productive winter of 1998–1999 than in 1997–1998. Barham (1957) reported spring/early summer recruitment peaks for *E. pacifica* in Monterey over a 2 year period, while Brinton (1976) found up to three distinct recruitment periods for *E. pacifica* populations in the Southern California Bight. The relative increase in the abundance of juveniles in the Monterey Bay that we observed during the fall of 1998 and 1999 (Fig. 5A) suggests an additional recruitment peak in the fall that was not observed in 1997 when El Niño conditions were strongest.

The El Niño-related decline of *T. spinifera* that we observed between September 1997 and May 1998 (Fig. 4B) was most likely the result of both increased mortality and northern displacement. Regional declines in *T. spinifera* abundance during periods of elevated ocean temperatures have been reported in both California (Brinton, 1981) and British Columbia (Tanasichuk, 1998). The large proportion of juveniles that we observed in the spring and early summer of all 3 years (Fig. 5B) suggests that peak recruitment occurs during this period. However, new recruits during the spring and summer of 1998 were most likely produced by stocks to the north, and advected south to Monterey Bay by equatorward flow during this period (Chavez et al., this issue). Chavez et al. (this issue) report temperatures were warmer than the long-term mean in the Monterey Bay during the spring and summer of 1998, and primary productivity, while still higher than in the adjacent offshore region, was anomalously low. These factors resulted in poor growth and hence a lack of recruitment in the late summer and fall (Fig. 5B). In contrast, the cool and highly productive conditions during the spring and summer of 1999 (Fig. 2A, Chavez et al., this issue) translated to favorable conditions for growth and reproduction and recruitment was continuous throughout the 1999 season (Fig. 5B).

In contrast to both *E. pacifica* and *T. spinifera*, *N. simplex* flourished during the strongest period of the El Niño with episodic recruitment between September 1997 and May 1998 (Fig. 4C). The cooler coastal conditions associated with the shallower thermocline and resumption of coastal upwelling in the spring and summer of 1998 created less favorable conditions, leading to a decline in abundance and the lack of new recruits for this warm temperate, neritic species (Fig. 5C). Brodeur (1986) similarly found evidence of successful reproduction and recruitment for *N. simplex* off the coast of Oregon during the winter and spring of 1982/1983 and a subsequent decline during 1994.

Like zooplankton abundance, the recovery of both *E. pacifica* and *T. spinifera* stocks during the spring and summer of 1998 appears to have been limited to a narrow band along the coast. Chavez et al. (this issue) attribute this narrow productive zone to the onshore movement of relatively low nutrient California Current water, which effectively constrained upwelled nutrient rich water to a narrow region off the coast. This observation is supported by the increase in *N. difficilis* within the Monterey Bay during the spring and summer of 1998 (Fig. 4D). *N. difficilis* has a predominantly oceanic distribution within the central and transition regions of the California Current (Brinton, 1962), thus its increase in abundance during 1998 resulted from the inshore intrusion of oceanic water. Post-larval recruitment within the coastal zone for all euphausiid species was also likely enhanced as a consequence of the inshore intrusion of the California Current, as offshore, advective loss of larvae by coastal upwelling was in all likelihood reduced.

The nearshore concentration of euphausiids consisting of primarily *E. pacifica* during the summer and fall of 1998 (Figs. 3A and 4A) had impacts on the distribution of euphausiid predators. Although euphausiid abundance in 1998 was lower than in 1999 (Figs. 3A and 4A), humpback, blue, and fin whale (which are euphausiid predators) abundance within the Monterey Bay was higher than in either 1997 or 1999 (Benson

et al., this issue). The nearshore environment may, therefore, have served as a spatial refuge for mobile higher trophic levels.

5. Summary

El Niño effects on the zooplankton community within the Monterey Bay, California, were first manifested in a dramatic decline in zooplankton abundance and shift in the euphausiid species composition during the summer of 1997. The rapid appearance of southern fauna, particularly the neritic euphausiid *N. simplex*, suggests that these biological effects were caused, at least in part, by remotely forced oceanographic processes. Zooplankton abundance and community composition gradually returned to a more 'typical' state during the spring and summer of 1998, though this recovery was limited to a relatively narrow coastal band. Recovery of overall zooplankton abundance and euphausiid community composition was complete with the onset of the 1999 La Niña event when the highest biomass and backscatter of zooplankton were recorded along with a more typical 'cool temperate' assemblage of euphausiid species. Our results support previous investigations that suggested that nearshore productivity is significantly less impacted during El Niño events (Barber & Chavez, 1983; Kudela & Chavez, 2000), thus this region may provide spatial refuge for higher trophic levels during periods of environmental stress associated with climatic events.

Acknowledgements

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