The effects of the 1997–99 El Niño/La Niña events on hydrography and zooplankton off the central Oregon coast

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Abstract

Hydrographic data and nutrient, chlorophyll and zooplankton samples were collected biweekly at a hydrographic station off Newport, Oregon during the 1997–98 El Niño and 1998–99 La Niña event. Our monitoring in 1997 showed that coastal upwelling was initiated in April, the usual time. However, a series of southwesterly storms in May and June 1997 led to a prolonged warming event and reductions in copepod biomass. Though El Niño-driven atmospheric teleconnections might have been responsible for these storms, the coastal ecosystem returned to normal with the resumption of coastal upwelling in mid-July 1997. A downwelling event began on 20 August 1997 resulting in onshore movement of offshore waters. This event appeared to mark the passage of the first Kelvin wave. At this time the shelf became flooded with low-nutrient waters and offshore, 'warm-water' copepod species were transported shoreward. The abundance of local endemic boreal neritic copepod species was reduced greatly, presumably because they were transported out of the system and to the north as a result of the strong poleward flows. Poleward flows strengthened during autumn, and the ocean off Oregon remained anomalously warm through the winter of 1997, spring, and early summer of 1998. Species composition of the coastal copepod assemblage remained anomalous for about a year; species with offshore and subtropical affinities dominated from late August 1997 through late July 1998. During this same period, nitrate concentrations were reduced by a factor of 4.5 (11-month mean of 1.5 µM for August 1997–July 1998 versus 6.9 µM for August 1998–July 1999), copepod biomass was reduced by a factor of 2.1 (4.9 µg carbon l^{-1} versus 10.5 for the same time periods), but chlorophyll concentrations were similar (2.0 versus 2.5 µg l^{-1}). Perhaps the most dramatic effect on copepods during the El Niño period was the nearly complete disappearance of the normally dominant boreal neritic copepod species (*Pseudocalanus mimus*, *Calanus marshallae* and *Acartia longiremis*) and their replacement by subtropical species such as *Calanus pacificus*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Corycaeus anglicus* and several species of *Clausocalanus*. These species persisted in the coastal waters through the end of 1998. Although most of the subarctic species began to increase in numbers in August 1998, the impact of the El Niño on *Pseudocalanus mimus*, normally the numerical dominant in coastal waters, was longer lasting. The *P. mimus* population did not recover to normal abundance levels until summer of 1999. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: El Niño; Nutrients; Chlorophyll; Copepod community structure; Pseudocalanus; Calanus

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Contents

1. Introduction

Seasonal variations in copepod abundance and species composition in the coastal regions of the northern California Current are well known from Peterson and Miller (1975–1977). The canonical pattern is that of dominance by boreal neritic ('cold water') species in summer and dominance by subtropical neritic ('warm water') species in winter. These changes in species composition correspond to seasonal changes in coastal circulation patterns. Equatorward flow and coastal upwelling in summer bring cold water and boreal zooplankton species to the coast of Washington and Oregon. The poleward-flowing Davidson current and southwesterly winds in winter bring warm water and zooplankton species with southern and offshore affinities to the coast.

The dominant copepod species during summer include *Pseudocalanus mimus*, *Calanus marshallae*, *Centropages abdominalis*, *Acartia longiremis*, and *Acartia hudsonica.* These species are common along the Oregon, Washington and British Columbia coasts (Mackas, 1992) as well as in the coastal Gulf of Alaska (Coyle, Paul, & Ziemann, 1990) and the Bering Sea (Smith & Vidal, 1986). Warm-water neritic species dominate during winter months, i.e. *Pa. parvus*, *Ct. vanus*, *Clausocalanus arcuicornis*, *Clausocalanus pergens*, *Acartia tonsa* and *Co. anglicus*. These same species are common throughout the year in coastal waters off central and southern California, and at least as far south as northern Baja California (Fleminger, 1967; Barnett & Jahn, 1987; Hopcroft & Chavez, 2002).

The dominance of one set of species over the other indicates whether ocean conditions are of the 'summer' or 'winter' type. Other copepod species that are indicators of ocean conditions include *Metridia pacifica* (a subarctic species that lives chiefly in deep water beyond the shelf break), *Eucalanus californicus* and *Mesocalanus tenuicornis* (indicators of Transition Zone water), and *Calanus pacificus*, *Calocalanus styliremis*, *Clausocalanus parapergens*, *C. paululus*, and *Acartia danae* (species that are typical of the offshore California Current) (Fleminger, 1967). The presence of large numbers of these species in continental shelf waters in any season indicates onshore movement of offshore waters.

One effect of equatorial El Niño events on the coastal waters of the northern California Current is a shift in the coastal copepod assemblages during the summer upwelling season from a 'summer' assemblage to a 'winter' assemblage. Miller, Batchelder, Brodeur and Pearcy (1985), reported that although the usual 'summer species' were present off Newport Oregon in summer during the 1983 El Niño, the 'winter species' continued to persist throughout the summer and into the autumn of 1983. The winter species that occurred in greatest abundance were *P. parvus* and *A. tonsa*.

Another expected effect of equatorial El Niño events on coastal waters of the Pacific Northwest is a

reduction in nutrient concentrations and subsequent reductions in phytoplankton and zooplankton biomass. This could happen through two mechanisms. Firstly, atmospheric teleconnections associated with El Niño events may modify the strength and location of large-scale atmospheric pressure cells such that coastal upwelling is reduced in magnitude and intensity (Simpson, 1984; Huyer & Smith, 1985; Simpson, 1992). Secondly, in response to the passage of Kelvin waves, coastal transport reverses from being southward and offshore in summer to northward and onshore, advecting in relatively nutrient-poor waters. Subsequently relatively oligotrophic waters appear over the continental shelf. For example, during the summer of the 1983 El Niño, coastal upwelling was reduced in strength (e.g. the Bakun upwelling index for that summer was the second lowest ever measured at that time), zooplankton abundance fell to 30% of normal in coastal waters off Oregon (Miller et al., 1985) and total zooplankton biomass in the southern California Current was reduced by 4 to 5 fold (McGowan, 1985), possibly because the lower nutrient concentrations resulted in decreases in both primary and secondary production.

To understand the response of copepod communities to El Niño events, one must consider changes in biomass, species composition and in productivity resulting from possible decreases in nutrient supply and reductions in phytoplankton biomass. The changes observed in copepod community structure and species composition along transects off central-southern Oregon and northern California are discussed in Peterson and Keister (2002). Changes in copepod production during the summer of 1997 are discussed in Gomez-Gutiérrez and Peterson (1998). In this paper we present a description of changes in copepod biomass and species composition in response to the 1997–98 El Niño and 1998–99 La Niña events in waters off central Oregon. The data shown are from a time series of cruises made at biweekly intervals beginning in 1996 during which CTD casts were made and water and plankton net samples were collected for later analysis of nutrients, chlorophyll and zooplankton. Observations were made at several hydrographic stations located from 1 to 15 miles off the central Oregon coast; but only data from the 5 mile station are reported here because only these samples have been completely analyzed. The stations sampled were the same as those sampled by Peterson and Miller (1975–1977) and Miller et al. (1985), therefore, we have a climatology of sea surface temperature (SST), zooplankton biomass and species composition to use as a basis for comparisons with the 1997–98 El Niño event.

2. Methods

Hydrographic, nutrient and plankton data were collected at a station located five miles (8 km) from shore along the Newport Hydrographic (NH) Line (Fig. 1). This station has historically been referred to as NH 5 and we will continue to use that convention in this paper. Cruises were conducted biweekly from May 1996 until September 1999 and twice weekly in July and August of 1997; a total of 83 visits were made between May 1996 and September 1999. Vertical profiles of temperature, salinity and density were taken with a Seabird SBE-19 CTD lowered and retrieved at a rate of 30 m min^{-1}. Secchi depth measurements were made with a white 30 cm diameter disc. Chlorophyll and nutrient samples were collected from the surface with a plastic bucket. For chlorophyll analyses, 100 ml of water was filtered through GF/F filters; the filtrate was saved and frozen for later analysis of nitrate, nitrite, ammonium, phosphate and silicate. We show here only the nitrate data. Zooplankton was sampled with a 0.5 m diameter, 202 µm mesh net hauled vertically from 5 m above the bottom to the sea surface at a rate of 30 m min^{-1}. The net was fitted with a TSK flowmeter, and its mouth area:filtration area ratio was 6.5. CTD data were averaged into 1 m bins using the Seabird Seasoft software. Chlorophyll was analyzed with a Turner Designs Fluorometer (Model 10AU) and concentrations were calculated using standard equations (Strickland & Parsons, 1972). Nutrients were analyzed with a Technicon Autoanalyzer. Zooplankton samples were analyzed following the protocols described by Peterson and Miller (1975). Two 1 ml subsamples, taken from the sample with a piston pipette, were enumerated to species and developmental stage. All data were
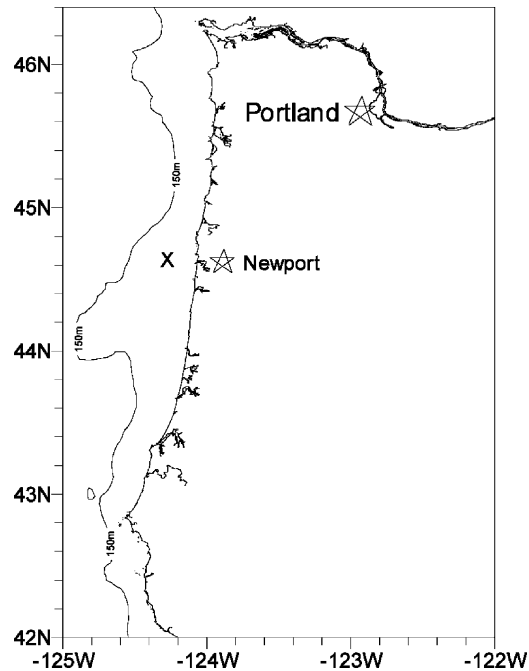
Fig. 1.   Chart showing the Oregon coastline, 150 m isobath, and location of the station NH 5 (X) off Newport, Oregon.

entered into a Microsoft Access database and numbers and biomass per cubic meter calculated. Biomass of a given species was calculated by multiplying the number m^{-3} by the carbon weight of individuals of a given developmental stage. Values for carbon are derived either from literature values or from our own estimates of weight.

To explore changes in community structure, a species density by sampling date matrix was analyzed by multivariate analyses. Multi-Response Permutation Procedure (MRPP) and a Euclidean distance measure were employed to evaluate whether species composition changed during the El Niño. Non-Metric Multidimensional Scaling (NMS) ordination was used to examine similarities among sample dates; Sorensen's (Bray–Curtis) distance measure was employed and a two-dimensional solution was found that explained 84.5% of the variance with 70.3% explained by Axis 1. In addition, cluster analysis was used to validate objectively the naturalness of the groupings produced by the NMS ordination. For cluster analysis, a Euclidean distance measure and Ward's Linkage Method were used; for presentation the cluster dendogram is scaled both by Wishart's (1969) objective function and by percentage of information remaining. Wishart's objective function is a measure of information loss as the clustering proceeds, and is calculated as the sum of the error sum of squares from the centroid of each group to the items in that group. All multivariate analyses were conducted in PC-ORD for Windows 4.36B (McCune & Mefford, 1999). Rare species defined as those occurring in <5% of samples were not included in the analyses. The data were $\log_{10}(Y+1)$ transformed to reduce the bias of high density species.

3. Results

3.1. Hydrography

The year 1997 began with 'normal' winter conditions. SSTs in January and February 1997 were 9–10°C; vertical temperature gradients were slight and sub-surface salinity ranged from 31–32.5. Northerly

winds began to blow in early April and cold salty water appeared on the shelf at the NH 5 station ($T=8$ °C, salinity> 33.0), which signalled the beginning of the upwelling season (Huyer, 1977).

But in early May, hydrographic conditions changed abruptly when several large southwesterly storms passed through the area. These storms resulted in warming at the surface and deepening of isotherms, conditions that were consistent with downwelling. These conditions persisted for two months, through mid-July (Fig. 2) keeping SSTs at 13–15°C and the water column highly stratified. In mid-July (Fig. 2) the only strong upwelling event of the summer began, and it lasted until late-August 1997 as indicated by the presence of cool, relatively salty (>33) water at the sea surface. No further upwelling took place after late August, thus there was only five weeks of upwelling during the 1997 May–September upwelling season. The Bakun Upwelling Index (http://www.pfeg.noaa.gov) cumulated over the May–September period in 1997 was only 73, the lowest index value on record (since 1946). Prior to 1997, the three lowest values observed over the May–September period had been 127 in 1993, 131 in 1976, and 135 in 1983.

On 20 August 1997 another southwesterly storm moved up the coast, not only stopping the upwelling but initiating intense downwelling (Strub & James, 2002b). SSTs rose to 13.5°C on 21 August and still further to 15.8°C and 16.2°C on 27 and 28 August, respectively. The first Kelvin wave passed through in late August/early September (Kosro, 2002), downwelling continued and the warmest temperatures on record were measured in September at NH 5, when surface temperatures reached 18.4°C in mid-September, an anomaly of +8°C (Smith, Huyer, Kosro, & Barth, 1999; Huyer, Smith, & Fleischbein, 2002).

Secchi depths, which are usually 3–6 m during the upwelling season, deepened to 10 m on 21 August then to 16 m on 9 September 1997. The water column remained transparent through most of September. It was during this period that dorado, yellowtail, yellowfin tuna and striped marlin were taken by sports fishermen in Oregon waters (Pearcy, 2002).

SSTs remained about 2°C above normal throughout the winter of 1997 and the following spring (Smith et al., 1999; Huyer et al., 2002). The coastal upwelling season was initiated in early May 1998 (indicated by water <10 °C on the shelf, see Fig. 2), but strong upwelling was not observed until mid-June when 8°C water first appeared on the shelf. However, once again the upwelling process was disrupted by a southwesterly storm that moved through the area in mid-June 1998, and coastal upwelling did not become well established again until the first week of August (Fig. 2). Smith et al. (1999) and Huyer et al. (2002) reported that both the shelf and oceanic waters off Oregon returned to normal temperatures by July 1998. Thus, anomalously warm conditions persisted in shelf waters from late-August 1997 until July 1998.

Assuming that 1999 was indeed a 'normal' year, the contrasts between its hydrography and that of the abnormal El Niño affected years of 1997 and 1998, are particularly striking. During 1999, upwelling began in early April and persisted with little interruption through mid-October as indicated by the presence of cold water (≤9 °C) at most depths at NH 5 (Fig. 2). During 1997 water <9°C was absent from NH5 after late August, and in 1998 was recorded only during one cruise in April, and then during July–August 1998. Subsurface water, as cold as 7°C, was observed at NH 5 on several cruises in 1999 but never in either 1997 or 1998.

3.2. Nutrients and chlorophyll

Sea surface nitrate concentrations are highly variable during the upwelling season because of the episodic upwelling events. These increase nitrate concentrations in the wind mixed layer, which subsequently stimulate phytoplankton blooms that then reduce nitrate concentrations. During 1997, nitrate values ranged from 0 to 23 μM (May–August average of 8.4 μM) (Fig. 3). At the end of August, commensurate with the onshore movement of warm waters described above, nitrate levels dropped to near zero and remained there through September. Winter-time values were relatively low (3 μM during 1997/98 as compared to 6–8 μM during winter of 1998/99). Average values during the spring and summer of 1998 were lower than spring/summer of 1997 and 1999 by a factor of two. Table 1 compares nitrate concentrations over two
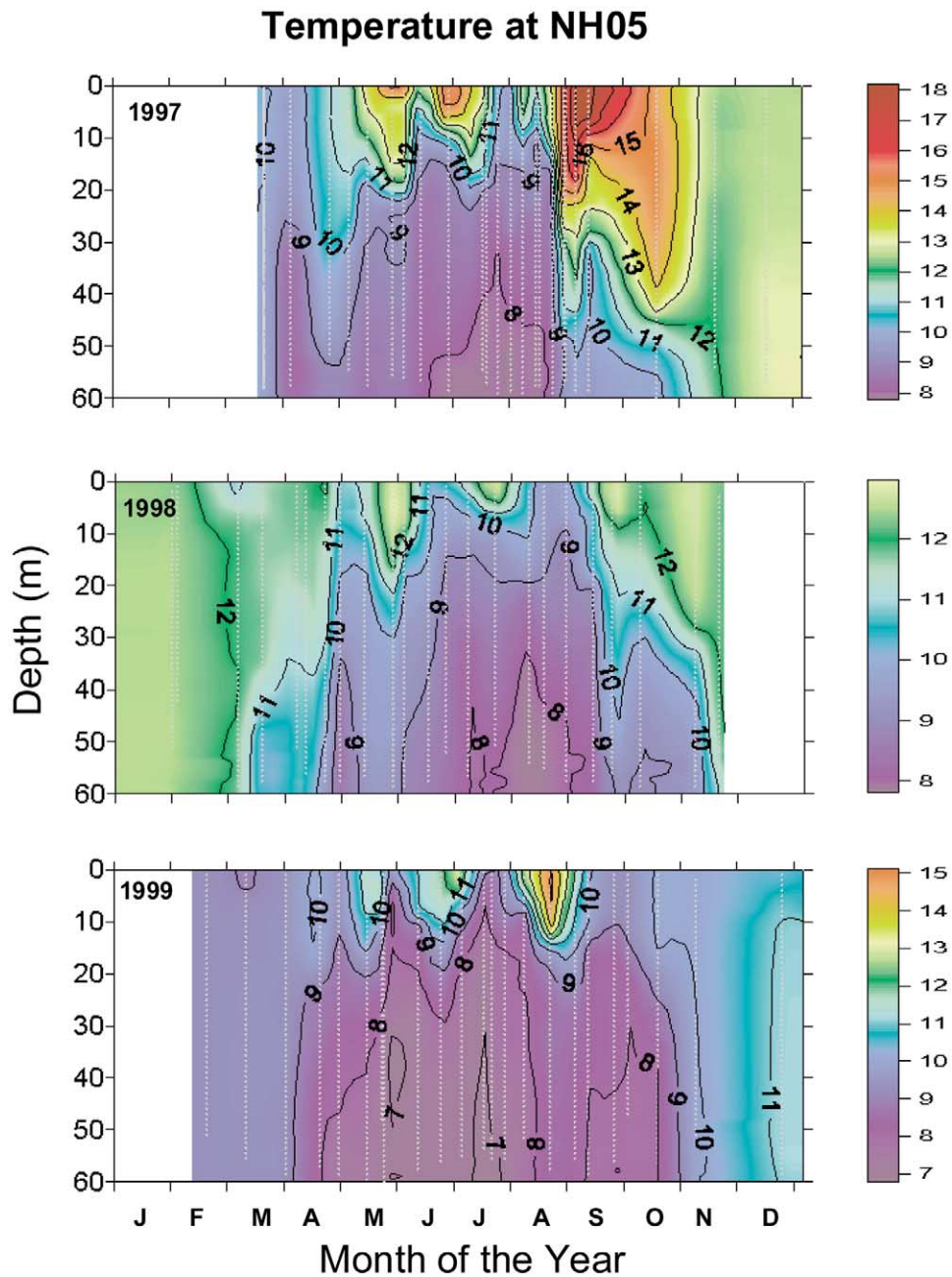
Temperature at NH05

Fig. 2. Temperature-depth sections at the station NH 5 for the years 1997, 1998 and 1999. Vertical lines indicate sampling dates.

different time periods, the 'summertime' of May–September 1997–1999, and 'the El Niño period', which we define to be late August 1997 through late July 1998. Comparing the summer periods of the three years, we find no significant differences in average nitrate concentration among years. However, when the August 1997–July 1998 El Niño period was compared to the August 1998–July 1999 La Niña period,
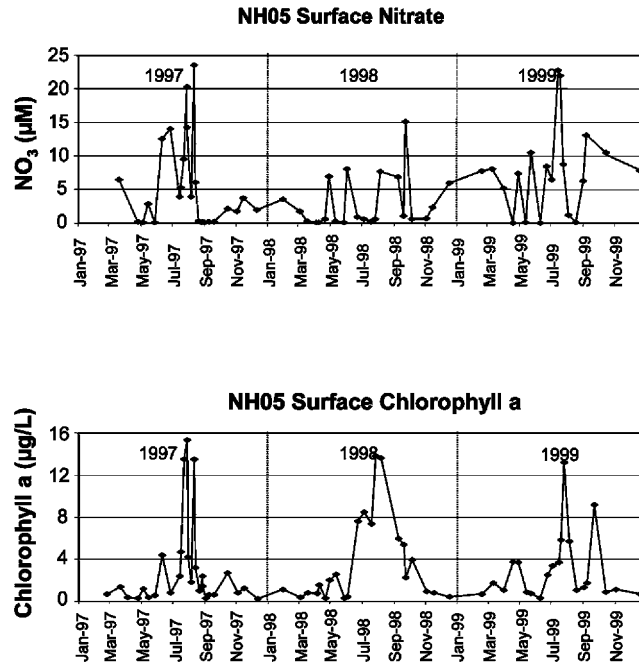
Fig. 3.   Sea surface nitrate and chlorophyll concentrations at the station NH 5 for 1997–1999.

Table 1
Nitrate (μmolar), chlorophyll concentrations (μg chlorophyll-a l^{-1}), and copepod biomass (mg carbon m^{-3}) averaged over the summer upwelling seasons of 1996–1999 at the hydrographic station NH5, five miles off Newport Oregon (upper table), and averaged over the August–July period of the El Niño (and non- El Niño years), along with the 95% confidence interval for each value (NS, not sampled)

	Nitrate (μM)		Chlorophyll-a (μg l^{-1})		Copepod biomass (mg Carbon m^{-3})	
	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.
May–September 1996	NS		NS		9.2	2.54
May–September 1997	6.19	3.57	3.80	2.31	9.7	1.35
May–September 1998	3.76	3.32	6.15	3.14	10.1	1.51
May–September 1999	8.3	5.01	3.82	2.30	11.0	2.31
October 1997–April 1998	2.09	1.38	1.08	0.51		
October 1998–April 1999	4.21	2.54	1.91	1.12		
26 August 1996–17 July 1997	NS		NS		8.2	1.23
27 August 1997–20 July 1998	1.54	0.99	1.99	1.10	4.9	0.53
27 August 1998–19 July 1999	6.90	3.29	2.54	0.91	10.5	2.00

nitrate concentrations were on average 4.5 times lower during the El Niño period than during the La Niña period.

The effect of the El Niño on chlorophyll concentrations was subtle (Fig. 3). There were no pronounced differences in the peak concentrations in 1997, 1998 or 1999 and any differences in concentration among years were not significant (Table 1). The lack of large differences among years may be related to the fact that the seasons when the El Niño was influencing local waters (fall, winter and spring) were not those when high concentrations of chlorophyll are generally observed (i.e. in summer). For the three-year period of 1997–1999, highest chlorophyll values were usually observed in July and August with a modest bloom in the fall. Thus the only effect of the El Niño was the disappearance of chlorophyll during the late August–September 1997 downwelling event, and a possible suppression of the fall bloom in October 1997. Chlorophyll concentrations were high in summer 1998, with the first major bloom occurring in late June 1998 following the mid-June upwelling event described above.

3.3. Copepods

Copepod biomass in May 1996–September 1999 ranged from 1 to 32 mg carbon m^{-3} (Fig. 4). The mean biomass was 10.1 mg carbon m^{-3} during the upwelling season of May–September and 3.7 mg carbon m^{-3} during the other six months (October–April). The mean biomass during May–September was similar between years, being 9.2, 9.7, 10.1, and 11.0 mg carbon m^{-3} for 1996 through 1999, respectively (Table 1). However, when averaged over the El Niño period (late-August of one year through late-July of the next) significant differences were found. Copepod biomass during the El Niño period was 4.9 mg carbon m^{-3}, approximately half that observed during the similar periods in 1996–97 and 1998–99 (Table 1).

The greatest changes in the zooplankton were seen in the community structure. The NMS ordination and cluster analysis showed that four distinct copepod communities occurred during our study period (Fig. 5A,C). One community type (Cluster 3), which we designate as the 'El Niño' community, was primarily present when the El Niño was at its strongest during fall 1997 through spring 1998. A second community type (Cluster 4), which we designate the 'summer upwelling' community, was present during 'normal' summers (May–September) in 1996, early summer in 1997, and in 1999. A third community (Cluster 1),

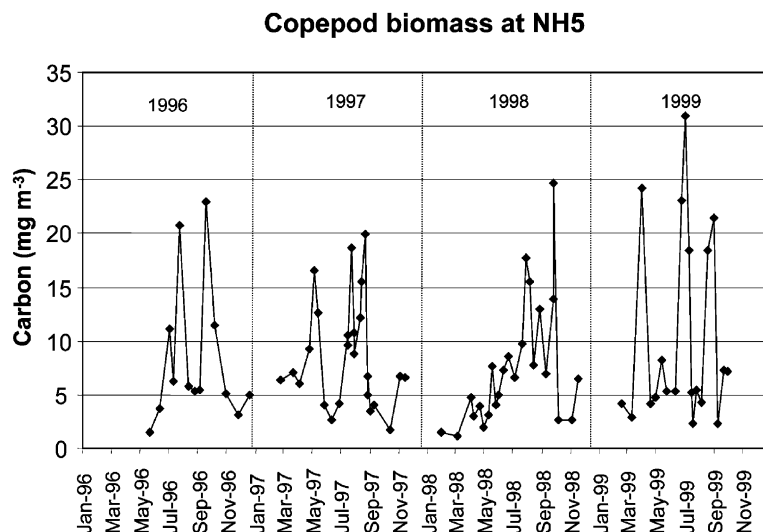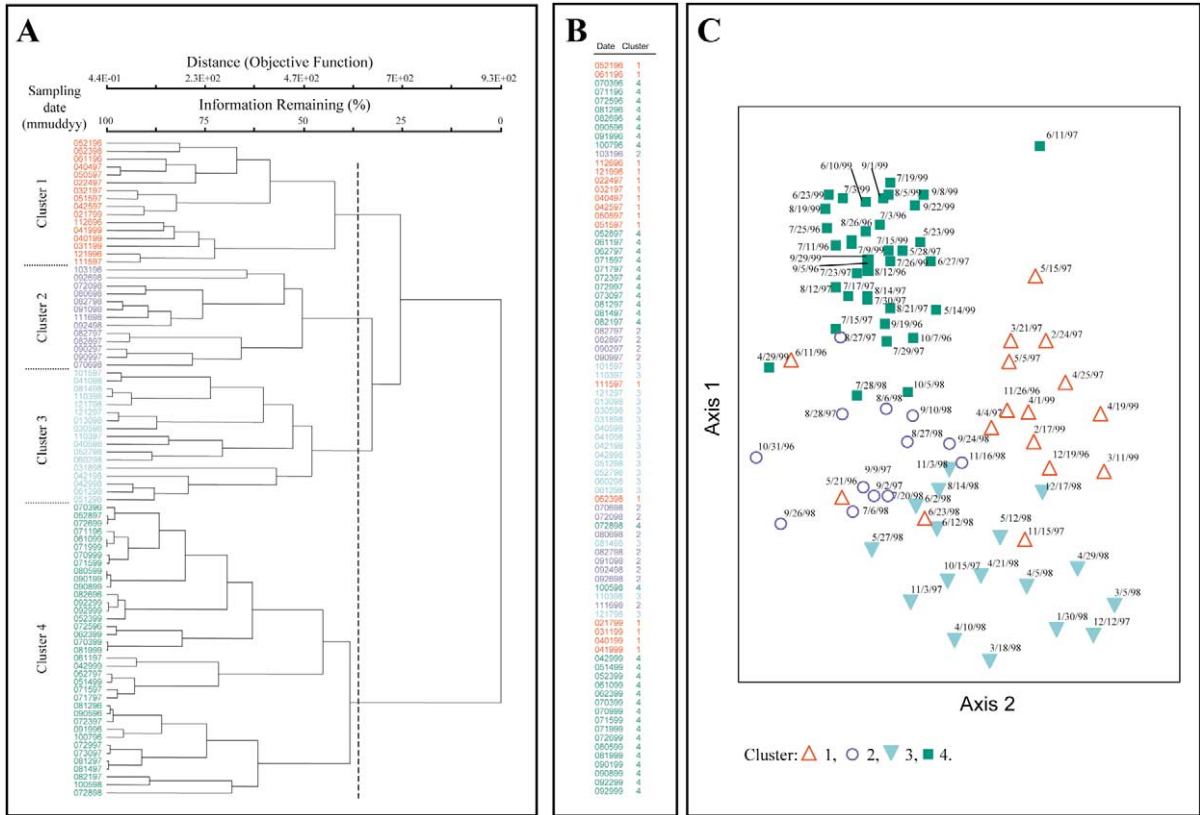Fig. 4. Copepod biomass at the station NH 5 for the years 1996–1999.

Fig. 5. (A) dendogram from cluster analysis of copepod species composition on each sampling date at NH 5, (B) list of sampling dates in chronological order with cluster color-coded, (C) NMS ordination with sample dates coded by clusters identified in (A). Clusters roughly correspond to (1) 'normal' winter, (2) transition, (3) El Niño, and (4) 'normal' summer upwelling periods.

which we designate as the 'normal winter' community, was present during 'normal' fall/winter/early spring periods in winter/spring of 1996/1997 and winter 1999. The final community type (Cluster 2) we designate as a 'transitional' community type since it was composed of a mixture of subarctic and subtropical copepods, which was primarily found at the onset of the El Niño in late August–early September 1997 and towards the end of the El Niño in late summer 1998.

   Examination of the chronological progression of community changes (Fig. 5B) shows that at the start of our time series in May 1996, the copepod community was in a 'normal winter' state. A 'summer upwelling' assemblage appeared from early July 1996 through early October 1996, and the ecosystem reverted to a 'normal winter' state from late November 1996 through mid May 1997 and then changed again to a normal 'upwelling' state from late May through late August. In late August and early September 1997, the copepod community was transitional and in October 1997 through June 1998, the period of strongest El Niño influence, became the full 'El Niño' community. The system re-entered a 'transitional' phase between about July and late December 1998, and not until February 1999 did copepod community structure returned to 'normal'.

   The copepod community present at station NH5 during the1997/98 El Niño proved to be unique for the area. In the NMS ordination, the samples taken during the El Niño lie at one extreme of Axis 1. The El Niño community more closely resembled the winters of 'normal' years than the summers of 'normal' years, but the El Niño community lies even further along Axis 1 than 'normal' winter samples. Additionally,

MRPP analysis found that copepod communities differed significantly between samples taken during the El Niño (defined for the MRPP as late August 1997 through July 1998) and samples taken on all other sampling dates ($T=-27.4$, $A=0.10$, $p<0.0001$).

The radical changes in community composition observed with the onset of the El Niño were driven in part by the dramatic declines in the abundance of two of the dominant local boreal copepod species, *C. marshallae* and *P. mimus*, from September 1997 through July 1998 (Figs. 6 and 7). Prior to the beginning of the El Niño in 1997, these two boreal species began to increase in abundance in April, and by May, the *C. marshallae* population had reached 150 individuals m^{-3}, and *P. mimus* had reached 2500 individuals m^{-3}. These values are higher than our 8-year climatology values of 75 and 1500 m^{-3}, respectively. Their abundances declined during the May/June 1997 downwelling event, rebounded during the brief July/August upwelling period, but then declined to near zero with the onset of downwelling in late-August 1997. Their abundances remained persistently low throughout the winter of 1997/98 and most of 1998.

Another factor contributing to changes in community structure during the El Niño period was that *C. marshallae* and *P. mimus* were replaced by two warm-water species, *C. pacificus* (an offshore California Current species) and *Pa. parvus* (a subtropical neritic species) (Figs. 6 and 7). During 1998, *Pa. parvus* was, on average, the most abundant calanoid copepod, and *P. mimus* was the second most abundant. *C. pacificus* was ranked fourth and *C. marshallae* was ranked tenth (Table 2).

Several other warm-water copepod species occurred commonly during the El Niño period (Table 2). Two of these species, *Ct. vanus* and *Co. anglicus* (Fig. 8), became common after late August 1997, and were among the most abundant species in the Oregon coastal zone. As with *Pa. parvus* and *C. pacificus*,
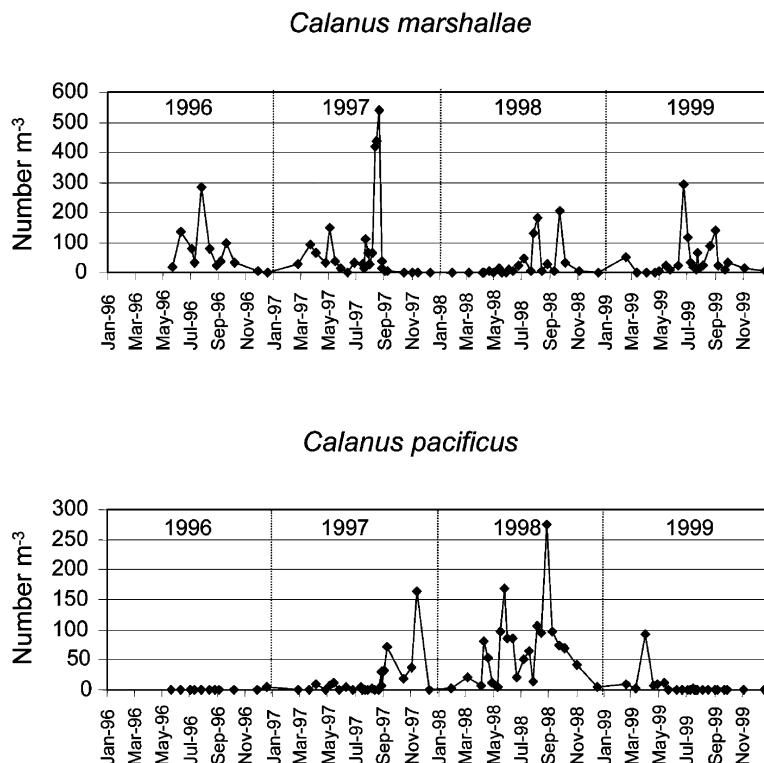

Fig. 6.   Abundance (number per cubic meter) of the copepods *C. marshallae* and *C. pacificus* at the station NH5 from May 1996 through September 1999.

Pseudocalanus mimus
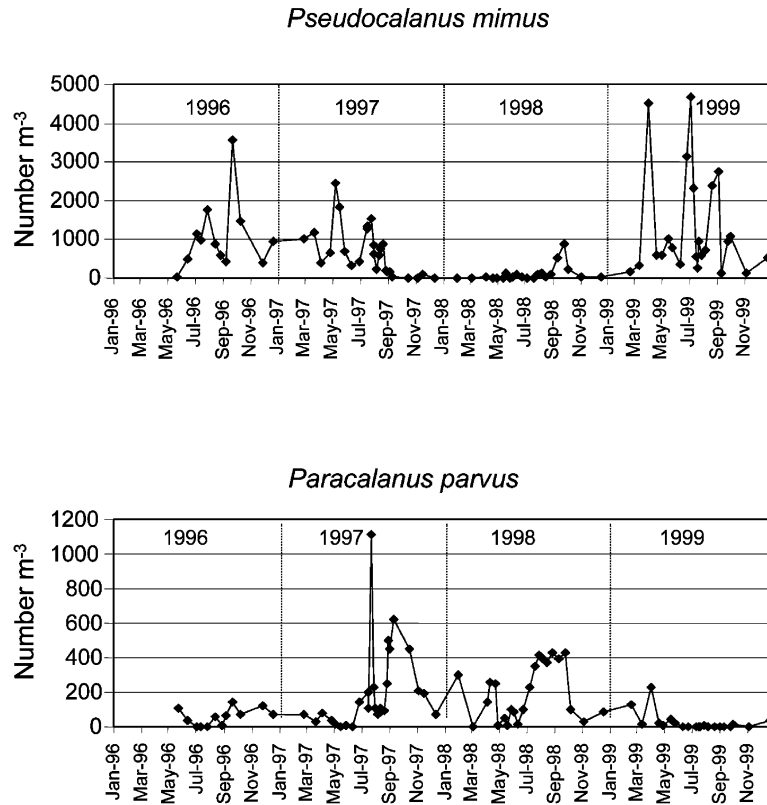

Paracalanus parvus

Fig. 7.   Abundance (number per cubic meter) of the copepods *P. mimus* and *Pa. parvus* at the station NH5 from May 1996 through September 1999.

they remained common in our samples through 1998. Several species with oceanic, tropical and subtropical affinities such as *Cl. arcuicornis*, *Clausocalanus pergens,* and *Metridia* spp. (Fig. 8) also became common during the El Niño period (Table 2). Other warm-water copepod species such as *E. californicus*, *M. tenuicornis*, *Ca. styliremis*, *Calocalanus tenuis, A. tonsa* and *A. danae* occurred frequently but in low numbers. Several species persisted through the summer and winter of 1998/99, but then disappeared in spring 1999.

The boreal coastal copepod species began to recover in July/August of 1998, 11 months after the onset of the El Niño event. C. *marshallae* numbers began to increase in July, and the population appeared to have recovered from the effects of the El Niño by August 1998. Although *P. mimus* showed signs of a recovery in August 1998, its population did not reach 'normal levels' (based on historical data) until 1999, two years after the advent of the El Niño. Both of the dominant warm-water species, *C. pacificus* and *Pa. parvus*, remained abundant through the end of 1998 and persisted in coastal waters (although in low numbers) through mid-summer of 1999.

4. Discussion

The 1997–98 El Niño was arguably the largest of the century (McPhaden, 1999) and is certainly the best studied. It is unique among the strongest events of the century in that it appeared to begin at the equator in March 1997, earlier in the year than others, and lasted for at least one full year. The previous

Table 2
Abundance (number per cubic meter) of the more common copepod species which occurred in samples collected at a station five miles off Newport OR during the summer (May–September) 1996–1999

		1996	1997	1998	1999
E. californicus	W, T	0.4[a]	1.7[a]	6.0[b]	0[a]
Neocalanus plumchrus		0[a]	2.4[a]	1.3[a]	0[a]
M. tenuicornis	W, T	0[a]	3.1[b]	3.0[b]	0.2[a]
C. marshallae		87.5[a](3)	105.1[a](3)	31.8[a]	46.1[a](4)
C. pacificus	W, T	0[a]	8.9[a]	79.4[b](5)	7.2[a]
P. mimus		1095.9[a](1)	770.9[a](1)	129.7[b](2)	1389.3[a](1)
Pa. parvus	W, N	44.9[a](4)	210.7[b](2)	215.3[b](1)	20.2[a](6)
Ct. vanus	W, N	0.9[a]	6.0[a]	85.6[b](4)	1.1[a]
Cl. arcuicornis	W	2.8[a]	3.1[a]	8.3[a]	1.6[a]
Ca. pergens	W	10.6[a]	10.4[a]	11.2[a]	1.8[a]
Ca. parapergens	W	0[a]	0[a]	5.9[b]	0[a]
Ca. paululus	W	0[a]	0[a]	2.8[b]	0[a]
Ca. styliremis	W	0[a]	1.4[a]	10.7[b]	0.2[a]
Ca. tenuis	W	0[a]	0[a]	2.0[b]	0[a]
Ce. abdominalis		19.6[a](6)	45.1[a](5)	32.0[a]	65.1[a](3)
Metridia spp.		7.3[a]	8.6[a]	51.6[b]	4.1[a]
A. longiremis		345.7[a](2)	45.3[b](4)	105.8[a](3)	165.6[a](2)
A. hudsonica		37.1[a](5)	2.9[b]	15.4[a]	41.0[a](5)
A. tonsa	W, N	0[a]	0.2[a]	10.1[b]	0.41[a]
A. danae	W	0[a]	2.1[b]	0[a]	0[a]
Oithona similis		928.8[a]	614.9[a]	396.7[b]	564.1[a]
O. spinirostris		8.3[a]	4.7[a]	12.4[a]	7.6[a]
Co. anglicus	W, N	10.7[a]	11.8[a](6)	53.6[b](6)	0[a]

W indicates a 'warm water species', N 'neritic' and T 'Transition Zone'. All others are boreal, cold water species. Within a species, means with the same letter are not significantly different ($p > 0.05$). The rank order of abundance for the top six ranked calanoid species is in the parentheses.

events mostly began during summer or autumn (boreal) months at the equator and ended by the following spring or summer. Thus they had a measurable effect on the biological productivity in the northern hemisphere for only one or two seasons (spring and summer of the year following the initiation of an event). In contrast the 1997–98 event affected biological productivity during summer 1997 as well as spring and summer 1998.

Although the El Niño event is known to have begun at the equator in March 1997 and ended at the equator in April 1998 (based on the multivariate El Niño index developed by the NOAA-CIRES-Climate Diagnostic Center, Boulder CO, see http://www.cdc.noaa.gov/ ~kew/MEI/mei.html), it remains an open question as to the period of time over which the equatorial event influenced local oceanographic conditions in the Pacific Northwest. To answer that question, one has to determine the relative role that atmospheric teleconnections might play in influencing local winds and subsequent onshore transport of warmer offshore waters (sensu Simpson, 1984, 1992) versus the role that Kelvin waves may play (Huyer & Smith, 1985) in influencing poleward transport of water within the coastal region of the California Current. We will not enter into this debate here because such a discussion is best left to the meteorologists and physical oceanographers. We will, however, present a brief summary of some of the relevant atmospheric and physical oceanographic observations, then discuss what the copepods tell us about the duration of the 1997–98 El Niño event.

Overland, Bond, and Adams (1999) showed that the northeastern North Pacific (and eastern Bering Sea)

Corycaeus anglicus

Ctenocalanus vanus
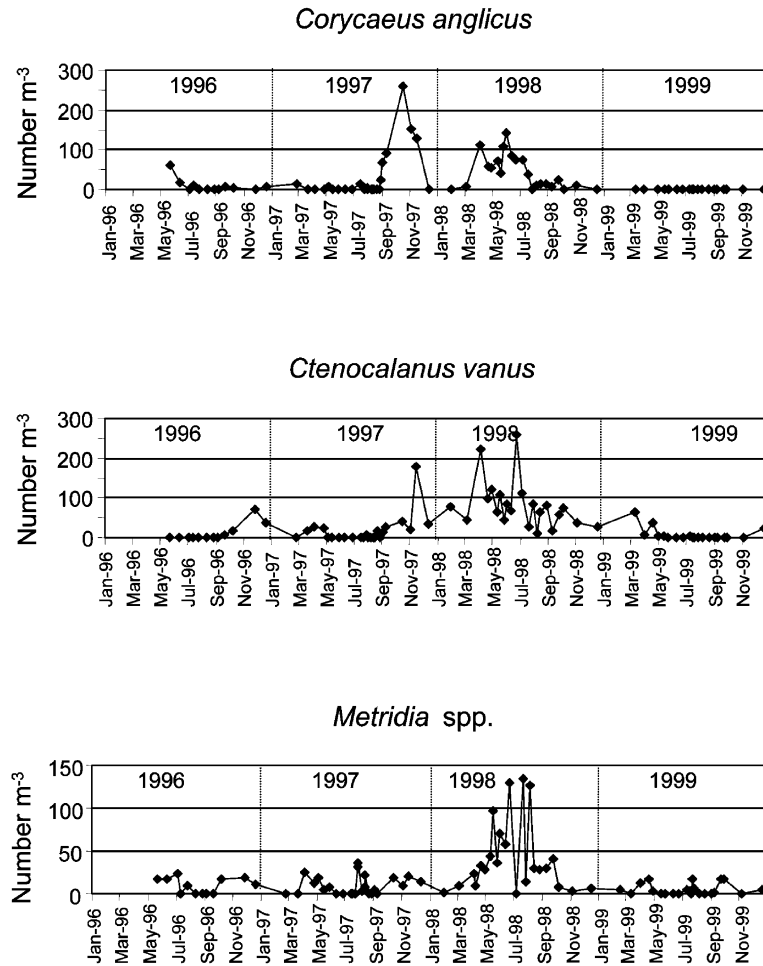
Metridia spp.

Fig. 8. Abundance (number per cubic meter) of the copepods *Co. anglicus*, *Ct. vanus* and *Metridia* spp. at the station NH5 from May 1996 through September 1999. *Metridia* spp. includes both *M. pacifica* and *M. pseudopacifica*.

began to warm in spring 1997, with +3°C anomalies in SST being observed throughout the California Current in May 1997. They attributed this to anomalous southerly winds caused by a strong blocking ridge weather pattern in May 1997. Schwing, Murphree, de Witt and Green (2002) show that these anomalous winds were driven by atmospheric pressure gradients associated with a large pool of warm water that was positioned approximately 100 km off the coast of Oregon and California (see their Fig. 8). We present evidence here that shelf waters off central Oregon warmed in May 1997, presumably as a result of onshore movement of these warmer offshore waters (see Fig. 2).

Strub and James (2002a) show that sea levels were anomalously high from May 1997 through February 1998 for waters off California and the Pacific Northwest. This is indicative of either weak southerly flow or northerly flow in the coastal regions of the California Current. They attribute the positive sea level anomalies in May–August to downwelling at the coast caused by southwesterly winds, whereas the anomalously high sea levels in winter of 1997–98 are attributed to both a higher frequency of strong southwesterly storms as well as the passage of Kelvin waves. Strub and James (2002a) also show bimonthly composites of anomalies in geostrophic transports between altimeter crossover points. Based on their charts, weak

poleward flows were first seen in the April–May 1997 composite flows, weakened in June–July, but were very strong in coastal waters in August 1997 through January 1998.

Kosro (2002) analyzed local sea level data and SSTs from National Data Center Buoys moored off California, Oregon and Washington, and velocities from several moorings off Newport. Kosro reported that during May–June 1997, anomalously warm SST was found over the mid-shelf from the southern California Bight to the Washington coast. Cool waters returned to the coast from June to mid August. A 'warm event' propagated up the coast, beginning in southern California as early as July 1997 (Kosro, 2002, his Figs. 3 and 4), arriving off Newport in late-August. This was the first Kelvin wave event and resulted in strong downwelling at the coast. Its expression off Newport was extraordinary in that the entire water column warmed. The usual case for a strong wind-driven downwelling event is that only the waters of the upper Ekman layer become warm, i.e., the upper 10–15 m (see Fig. 2 for the May and June 1997 downwelling events, and other warming, downwelling events in 1998 and 1999). The same effect was seen in Monterey Bay (Hopcroft & Chavez, 2002, their Fig. 3); the August 1997 warming event penetrated to 150 m water depth in Monterey Bay whereas other 'downwelling' events only penetrated the upper 20–30 m of the water column.

Our observations on zooplankton abundance and species composition indicate that the changes in copepod community composition observed during spring and summer of 1997 mirrored the physical events described by Strub and James (2002) and Kosro (2002). Copepod community structure first began to change in early May 1997, at the same time as the warming event. As this event progressed, the water column warmed, nutrient and chlorophyll concentrations remained low and copepod biomass declined by a factor of three. The biomass change occurred primarily because of the decline in the abundances of two of what are normally the most abundant species, *P. mimus* and *C. marshallae*. It was during this warming period that several 'subtropical neritic species' became common in our samples. The abundances of both the boreal and subtropical species remained low through the June and early July downwelling period. When upwelling resumed in mid-July, the boreal neritic copepods once again became abundant, but this upwelling event ceased in late-August.

The long-term changes in copepod biomass and the large changes in copepod species composition first became apparent in late August 1997, coincident with the large downwelling event we first observed during our 21 August cruise. It was during this warming event that the boreal neritic copepod species virtually disappeared from the central Oregon coastal ecosystem and the subtropical species began to dominate. NMS and cluster analysis show that major changes in copepod community structure began to take place sometime between our cruises of 21 and 27 August 1997. Cluster analysis shows that the copepod community observed during the late-August and September 1997 warming event was a transitional community (Cluster 2 in Fig. 5), and that, in terms of copepod community structure, the El Niño event was most extreme from October 1997 through mid June 1998.

During the October 1997–June 1998 period, the copepod community was unique. We had expected (based on the work of Miller et al., 1985) that the copepod assemblage observed during the El Niño would be similar to a 'wintertime' community. This expectation was based on the hypothesis that the physical explanation of a difference in copepod composition during El Niño events is enhanced poleward flow in the coastal zone, which in turn would transport warm-water coastal species from central California into Oregon waters. Since poleward flow occurs every winter (as the Davidson Current) one might expect all winters to be similar with regards to copepod species composition regardless of the occurrence of an El Niño event. However, the community present during the El Niño period differed from the 'normal' winter community, possibly as a result of onshore movement of offshore waters as well as poleward movement of coastal waters. The presence of species on the shelf, which are usually most abundant at and beyond the shelf break off Oregon (Peterson & Miller, 1975), supports the notion that local downwelling and shoreward transport resulting from strong southerly winds was a key agent in changing species composition.

The observations of Pearcy (2002) that the unusual species of nekton and large fishes that appeared in Oregon's coastal waters were offshore species further support our hypothesis.

With the appearance of the El Niño copepod assemblage, the boreal copepod species disappeared from the ecosystem. We suggest that this disappearance of boreal species in late-August 1997 was not necessarily a result of local mortality. Rather, we suggest that these species had been advected to the north by the poleward flows that became established at that time (Kosro, 2002). As happens in most winters, these 'cold water' species were then replaced by a mixture of transition zone species and subtropical neritic species that were advected onto the shelf from both offshore and from further south; including *C. pacificus*, *Pa. parvus*, *Metridia pseudopacifica*, *E. californicus*, *M. tenuicornis*, and several species of *Clausocalanus*. The persistence of these warm water species off Oregon for at least the next year (through summer 1998) is consistent with the maintenance of strong onshore and poleward flows in the coastal zone as discussed by Strub and James (2002b) and Kosro (2002).

When then did the system return to normal? Sea level heights and SSTs returned to normal off Oregon by March 1998 and April 1998 respectively (Kosro, 2002) suggesting that the El Niño ended in spring 1998. However, northerly winds did not begin to blow off central Oregon until much later in the year. The first upwelling event of 1998 was not initiated until early May and this event was brief, interrupted by southwesterly winds that lasted for three weeks. The coastal hydrography did not reflect the influence of coastal upwelling until late July. Based on the NMS ordination and cluster analysis, the most extreme 'El Niño' copepod community persisted through our 12 June 1998 cruise. This community type was followed by the presence of a transitional community composed of a mixture of subarctic and subtropical species, which persisted through the remainder of 1998. Subsequently, a 'normal' wintertime community was found from February through our 21 April 1999 cruise. The 'normal' summertime community was first seen on our 29 April 1999 cruise and this community remained through September 1999. Thus, in terms of winds, coastal hydrography, copepod species composition and copepod community structure, the system remained in a highly anomalous state for 10 months, from October 1997 through mid June 1998. However, in terms of copepod community structure alone, the system remained either in the El Niño state or in a transitional (but anomalous) state for 16 months, from late-August 1997 through December 1998.

The transitional period, which began in July 1998, included a return of most of the cold-water boreal neritic copepod species to the Oregon coastal zone. Curiously, the one boreal copepod, *P. mimus*, that usually dominates both numbers and biomass in coastal waters of southern British Columbia, Washington, and Oregon, did not return as a dominant member of the pelagic ecosystem until 1999. For this species, the impact of the El Niño appears to have persisted for nearly two years, from spring 1997 through spring 1999. The long time lag between relaxation of El Niño conditions and recovery of *P. mimus* may have resulted from the lack of a seed population large enough to initiate recovery. We know that the influence of the El Niño reached far into the Gulf of Alaska and the Bering Sea (Hunt et al., 1999) and though poleward transport associated with the El Niño ceased by early spring 1998, the boreal neritic copepod species were not instantly returned to Oregon waters, perhaps because they had been transported hundreds of kilometers to the north. Though small numbers of *P. mimus* appeared in August 1998, the initiation of the poleward-flowing Davidson Current in October would have transported members of this population out of the area once again. An alternate hypothesis is that ocean conditions were unsuitable for recovery of the local population of *P. mimus* until 1999, as evidenced by the persistence of subtropical copepod species throughout 1998.

In contrast to the slow recovery of *P. mimus,* populations of another dominant boreal coastal species, *C. marshallae*, did begin to recover in August 1998. We suggest that the difference in response resulted from *C. marshallae* using a different circulation pathway whereby it recruits into coastal waters as compared to *P. mimus*. If *C. marshallae* recruits from deep waters offshore (rather than with equatorward surface flows as suggested above for *P. mimus*), *C. marshallae* individuals would reappear in coastal waters more quickly because they would repopulate shelf waters with active upwelling events. This may explain why

they flourished during the brief upwelling event in July 1997 (whereas *Pseudocalanus* did not) and why they repopulated shelf waters in July–August 1998 (whereas *Pseudocalanus* did not).

Many of our findings are similar to results from observations made elsewhere in the California Current during the 1997–1999 El Niño/La Niña. Mackas and Galbraith (2002) sampled monthly along cross-shelf transects off southwest Vancouver Island, British Columbia. They found that ENSO-related changes in the zooplankton community were most apparent over the shelf break and slope, but weaker further offshore. Similar to our findings, they found that boreal species (*P. mimus*, *C. marshallae* and *Acartia longiremis*) were reduced in abundance and southern species, (*Pa. parvus*, *Ct. vanus*, *M. tenuicornis* and *Clausocalanus* spp.) became common. Strongest anomalies in species composition were observed from September 1997 through April 1998. Abundances of boreal coastal species remained anomalously low through 1998 and failed to attain 'normal' levels until 1999 (Mackas, Thomson & Galbraith, 2001).

Hopcroft and Chavez (2002) sampled the zooplankton every three weeks from March 1997 through December 1999 in Monterey Bay. They found that warm water persisted in Monterey Bay from 1 August 1997 through April 1998, similar to our observations off central Oregon. Upwelling was weak through the summer of 1998 but was stronger in 1999. A notable change in the zooplankton community included a decline in numbers of larger copepods such as *Calanus*, *Eucalanus*, *Metridia*, and *Rhincalanus*, particularly during the height of the El Niño event of December 1997 through April 1998. However, abundances of smaller-sized genera such as *Paracalanus*, *Clausocalanus*, *Corycaeus*, *Oncaea* and *Oithona* showed very little change. In contrast to our findings, the total copepod biomass in Monterey Bay did not change greatly during the El Niño event; the largest signal was a shift in dominance from large-sized copepods to small-sized copepods. They suggest that these changes were not the result of advection, but that the warmer waters that occurred in the Bay during the El Niño period preferentially favored the development of smaller copepods (that have a greater tolerance for higher temperatures than the larger copepod genera).

At the southern end of the California Current, during the 1997–1998 El Niño, Lavaniegos, Jiménez-Pérez and Gaxiola-Castro (2002) reported little change in either chlorophyll concentrations or zooplankton biomass along the Pacific Coast of Baja California. Though detailed analysis of species composition in their samples has not been completed, preliminary observations show that there was a strong increase in tropical copepods during fall 1997 and a decline in abundance of the usually common *C. pacificus*. Euphausiid species were similarly affected; the species normally dominant, *Euphausia pacifica*, was absent during fall 1997 and was replaced by a tropical species, *E. eximia*. An increase in the abundances of tropical species was also observed during the 1982–83 El Niño in Baja California waters in Magdalena Bay (latitude 25°N), resulting from northward and shoreward advection of tropical waters (Palomares-Garcia & Gómez-Gutiérrez, 1996). Similar observations were made along the Pacific coast of Baja California during both the 1982–83 and 1987–88 El Niño events (Hernandez-Trujillo, 1999) and in coastal waters near La Paz during the 1992–93 El Niño (Lavaniegos & Gonzalez-Navarro, 1999).

A common theme in the zooplankton observations made off Vancouver Island, central Oregon, central California and central/southern Baja California is that the greatest differences in species composition during El Niño were seen chiefly at the northern and southern ends of the California Current, off the coasts of Oregon and Baja California respectively, near the location of faunal boundaries. During El Niño events, the position of the California Current appears to have shifted northward by several hundred kilometers. Thus at the northern end of the Current (Oregon north to Vancouver Island, British Columbia) warm water species displaced boreal species and at the southern end (Baja California) tropical/equatorial species displaced subtropical species.

5. Conclusion

Off central Oregon, a prolonged downwelling event in May–June 1997 resulted in advection of warm, low nutrient water onto the shelf. Copepod biomass was reduced by this event and the copepod community

became a mixture of boreal coastal and offshore subtropical species. This downwelling event appeared to have been linked to the equatorial El Niño via an atmospheric teleconnection. Coastal upwelling was re-established in July and August and the ecosystem reverted to 'normal'. Persistent long term effects of the El Niño on temperature, nutrients, copepod biomass and, especially, species composition were not apparent until late August/early September 1997, which was synchronous with the passage of the first Kelvin waves. Poleward flows and downwelling associated with the late August 1997 transition to El Niño conditions flooded the Oregon coastal zone with 'warm water' copepod species. The ocean off Oregon remained anomalously warm with warm water copepod species dominating the assemblage through the spring and summer of 1998. It was not until August 1998 that the pelagic ecosystem first began to return to normal. However, full recovery was not observed until spring 1999. Thus, though the physical influence of the El Niño on Oregon coastal waters might be said to have lasted from May 1997 through July 1998, the effects on the copepod populations persisted far longer.

Acknowledgements

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