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# The effect of a large cape on distribution patterns of coastal and oceanic copepods off Oregon and northern California during the 1998–1999 El Niño–La Niña

William T. Peterson <sup>a,\*</sup>, Julie E. Keister <sup>b</sup>

<sup>a</sup> National Marine Fisheries Service, Hatfield Marine Science Center, 2030 S. Marine Science Drive, Newport, OR 97365, USA

<sup>b</sup> Cooperative Institute for Marine Resource Studies, Oregon State University, Hatfield Marine Science Center, 2030 S. Marine Science Drive, Newport, OR 97365, USA

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## Abstract

Hydrographic and ocean drifter measurements made along the Oregon coast indicate that the spatial structure of the coastal upwelling system differs in waters to the north and the south of Cape Blanco, Oregon. North of the Cape, a 10–30 km wide zone of coastal upwelling parallels the coast, but south of the Cape, increased wind stress leads to a seaward expansion of the upwelling system and cold upwelled water extends 50–100 km offshore. Because the hydrography and the transport differ, we hypothesize that zooplankton distributions will differ as well. In this paper we investigate differences in copepod distributions and copepod community composition between the waters north and south of Cape Blanco. Five cruises were conducted in 1998 and 1999, which were years of contrasting ocean conditions; there was a strong El Niño in 1998, which was followed by a strong La Niña in 1999. Copepod biomass did not differ between the El Niño and La Niña periods; however, species composition of the copepod assemblages differed vastly. During the 1998 El Niño, the copepod community was dominated by subtropical neritic and warm-water offshore species. During the 1999 La Niña, the zooplankton community was dominated by cold water boreal neritic species. The warm water species were widely distributed in shelf and slope waters in 1998, whereas in 1999, they were found primarily offshore of central Oregon, but over the shelf off northern California. During the summer upwelling season of both years, copepod community composition in shelf waters differed significantly from slope waters in the region to the north of the Cape, however, community composition was the same in shelf and slope waters in the region south of the Cape. These results lead us to suggest that offshore transport by the upwelling jet may be an important mechanism controlling copepod community structure south of Cape Blanco. When we examined these patterns in community composition on a species-by-species basis, among the dominant boreal copepod species, *Pseudocalanus mimus* and *Acartia longiremis* were displaced offshore and maintained high population densities in the waters south of Cape Blanco whereas densities of *Calanus marshallae* and *Centropages abdominalis* declined in the waters south of the Cape. Thus, the interaction between the boreal copepods and the waters north versus south of Blanco is species-specific. Species may be either lost or retained depending upon interactions between vertical current shear and their vertical distributions. Alternatively, there may be a differential ability among species to survive and reproduce in waters offshore and south of Cape Blanco. © 2002 Published by Elsevier Science Ltd.

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\* Corresponding author.

E-mail address: [bill.peterson@noaa.gov](mailto:bill.peterson@noaa.gov) (W.T. Peterson).

## Contents

1. Introduction . . . . .	390
2. Methods . . . . .	392
3. Results . . . . .	393
3.1. Physical data . . . . .	393
3.1.1. Winds . . . . .	393
3.1.2. Temperature/salinity/fluorescence . . . . .	394
3.2. Zooplankton density and distribution . . . . .	397
3.2.1. Day/night differences . . . . .	397
3.2.2. Variations in biomass and abundance . . . . .	399
3.2.3. Interannual variation in species composition . . . . .	399
3.2.4. Spatial variations in species composition . . . . .	399
3.2.5. Effect of Cape Blanco on community composition . . . . .	406
4. Discussion . . . . .	406

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## 1. Introduction

Zooplankton are not distributed uniformly in the cross-shelf and alongshore directions in continental shelf waters. Rather, they often form distinct patterns of zonation in both biomass and species composition. For the waters off Newport Oregon, Peterson and Miller (1975) and Peterson, Miller and Hutchinson (1979) described patterns in cross-shelf distributions. There is a nearshore group of species composed of all life stages of the copepods *Acartia hudsonica* and *Centropages abdominalis*, eggs, nauplii and adults of *Calanus marshallae*, all stages of cladocerans and larvae of benthic invertebrates; a midshelf group dominated by the copepods *Pseudocalanus mimus*, *Acartia longiremis*, juveniles of *Calanus marshallae*, and the euphausiid *Thysanoessa spinifera*. There is also an outershelf/slope group composed of the preceding three species along with the copepods *Eucalanus californicus*, *Metridia pacifica* and the euphausiid *Euphausia pacifica*. Landry and Lorenzen (1989) reported similar patterns for the coastal waters off Washington as did Mackas (1992) for the shelf/slope waters off southwestern Vancouver Island, Canada. We do not know if these same patterns exist in waters off southern Oregon or California.

One of the key hypotheses driving research in the US GLOBEC Northeast Pacific program is that intensification of the north winds in the vicinity of Cape Blanco, a cape off southern Oregon at 42°50'N (Fig. 1), results in a seaward expansion of the upwelling zone south of the Cape, which in turn results in a wider area of high primary and secondary production. A corollary is that growth and survival of juvenile salmonids and other small pelagic fishes is higher in waters south of Cape Blanco because of the expansion of the region of high secondary production. As a step towards testing these hypotheses, we examine in this paper whether Cape Blanco influences alongshore and cross-shelf distributions of California Current zooplankton resulting in differences in zooplankton biomass and species composition in waters off southern Oregon and northern California as compared to southern British Columbia, Washington and northern/central Oregon. We expect that distribution patterns may be altered by Cape Blanco because large capes in other upwelling systems have been shown to displace shelf-species offshore and, in some cases, even to act as faunal boundaries. The effect of capes in redistributing species has been shown by Shannon and Pillar (1986) and Shillington, Peterson, Hutchings, Probyn and Waldron (1990) for capes in the northern and southern Benguela region, by Mittelstaedt (1983) and Weikert (1983) for Cape Blanc off northwest Africa, and by Valentin and Monteiro-Ribas (1993) for Cabo Frio, southern Brazil.

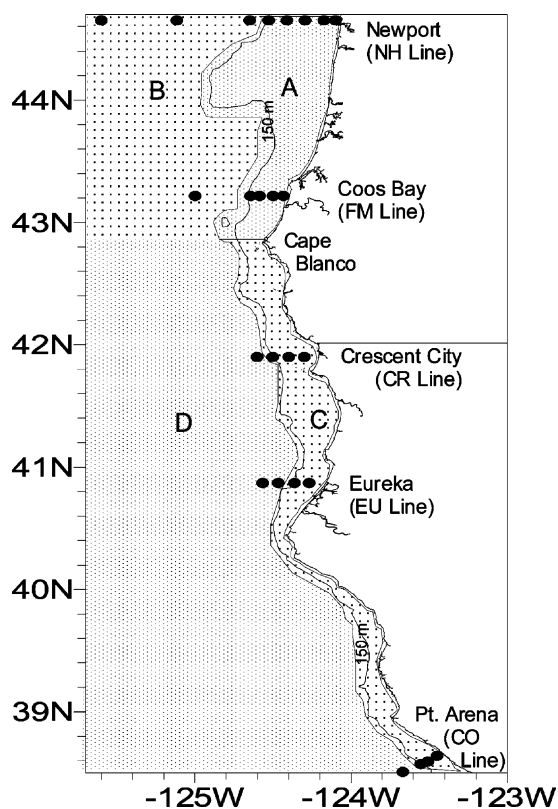


Fig. 1. Map of the sampling area showing sampling stations and the 150 m isobath. Patterned regions A, B, C, and D designate the ecological zones compared in Multi-Response Permutation Procedure analyses and correspond to (A) onshelf, north of Cape Blanco, (B) offshelf, north of Cape Blanco, (C) onshelf, south of Cape Blanco, and (D) offshelf, south of Cape Blanco.

In the vicinity of Cape Blanco Oregon, energetic coastal jets, filaments and current meanders can extend several hundred kilometers from shore (Strub, Kosro, Huyer & CTZ Collaborators, 1991). These mesoscale features originate on the continental shelf, and so they may transport zooplankton off the shelf of southern Oregon and northern California and into offshore waters. Hydrographic sections and high-resolution Seasoar surveys indicate that the spatial structure of the coastal upwelling ecosystem changes significantly near Cape Blanco (Barth & Smith, 1998; Barth, Pierce, & Smith, 2000). North of the Cape, the upwelling front and associated coastal jet lie over the mid- or outer-continental shelf, with relatively fresh waters from the Columbia River immediately offshore; south of the Cape the front and jet often lie far offshore, well beyond the shelf-break. Because waters inshore of the jet have higher nutrient and chlorophyll concentrations (Hayward & Mantyla, 1990), the offshore shift of the coastal front and jet south of Cape Blanco may extend the coastal zone of high biological productivity offshore, thus creating an extended area in which coastal zooplankton can flourish.

We report here on five cruises conducted in 1998 and 1999 during which hydrographic properties and zooplankton biomass and species composition were measured along several transects off central Oregon and northern California. Copepods are the focus of this research because they comprise the majority of the zooplankton biomass in our study area. Our goal was to test the hypothesis that copepod community composition differs between the waters to north and to the south of Cape Blanco because of the greater

degree of offshore transport of coastal water in the region south of the Cape. The expectation is that coastal copepod species that are common in shelf waters off southern British Columbia, Washington and central Oregon are advected offshore in the water being transported offshore to the south of Cape Blanco, resulting in marked differences in the copepod communities north and south of the Cape. The five cruises coincided with the strong 1997/1998 El Niño and the subsequent 1999 La Niña, and so we will also examine the spatial and temporal response of the zooplankton to those strongly contrasting oceanic conditions.

## 2. Methods

Cruises were conducted in spring (April 1998 and 1999) and summer (August 1998, and July & September, 1999). During each of these five cruises, zooplankton and environmental data were collected along a series of latitudinal transect lines off Oregon and northern California, five lines being sampled in 1998, and four in 1999. Lines sampled were the Newport Hydrographic line (44.6°N), Coos Bay line (43.2°N), Crescent City line (41.9°N), Eureka line (40.9°N), and the Point Arena line (38.6°N) in 1998 only (Fig. 1). Cape Blanco lies between the Coos Bay and Crescent City lines. Samples were taken from 1 to 85 miles offshore. Surface (3 m depth) fluorescence, temperature (SST), density, and salinity (SSS) were obtained from the 3 m bin of CTD casts (Seabird 911). Zooplankton were collected using a 0.5 m diameter, 202  $\mu\text{m}$  mesh net towed vertically from within 5 m of bottom (to a max. depth of 100 m) to the surface at a rate of 30  $\text{m min}^{-1}$ . A TSK flowmeter was used to monitor the amount of water filtered. The samples were preserved in a 5% buffered formalin/seawater solution.

In the laboratory, the zooplankton samples were diluted and subsampled with a 1.1 ml Stempel pipette. Two to four such subsamples, about 2% of the total sample, were counted at 25–50 $\times$  magnification. Copepods and euphausiids were identified to species and developmental stage; other zooplankton were assigned to broad taxonomic groups (e.g. polychaetes, medusae, larvaceans, chaetognaths). All euphausiids, pteropods, salps, and chaetognaths were measured. In each sample, the population density of each taxonomic group (number of individuals  $\text{m}^{-3}$ ) was calculated. Copepod densities were converted to biomass estimates using dry weight/developmental-stage values found in the literature; biomasses of euphausiids, pteropods, salps, and chaetognaths were calculated from densities using length–weight regressions found in the literature.

Wind data are from the National Data Buoy Center (<http://seaboard.ndbc.noaa.gov>) for the CARO3 (Cape Arago, OR, 43.34°N 124.38°W) C-MAN station and data buoy 46027 (St Georges, CA, 41.85°N 124.38°W). These stations correspond to our Coos Bay and Crescent City lines respectively (Fig. 1). Temperature and salinity data shown in this paper are gridded and contoured using kriging and a linear variogram model in Surfer 7 software (Golden Software Inc.).

Ship–time constraints resulted in stations being occupied at any hour of day or night during each cruise. Because some copepods are known to exhibit diel migrations or net-avoidance during day, we evaluated the need to adjust densities for potential day–night bias. To examine the effect of sampling at different times of day, 11 day/night pairs of samples were examined for differences in biomass of important species and taxonomic groups. Generally, any particular station was not sampled both during day and night within a cruise, so sample pairs were chosen for comparison by finding one day and one night sample that were taken from stations with similar bottom depths and SST and SSS characteristics along adjacent transect lines within a cruise (Table 1). One pair of samples (Pair 4) included sampling of the same station (44.7°N 124.4°W) during both day and night on a cruise. Each common (i.e. present in >20% of samples) species of copepod was examined for consistently higher densities during the night. Additionally, Wilcoxon tests were employed on all samples combined ( $n=120$ ) to test for day/night differences in total copepod biomass, and in densities of some dominant species of copepods.

Table 1  
Pairs of samples used to evaluate the effect of time-of-day on biomass results

Pair No.	Cruise	Sample date	Time sampled	Bottom depth (m)	Latitude (°N)	Longitude (°W)	Day/Night
1	Apr 98	4/5/1998	1950	158	43.2166	−124.6443	Day
		4/5/1998	0038	140	44.6517	−124.5283	Night
2	Apr 98	4/9/1998	0608	117	41.9	−124.5025	Day
		4/8/1998	2317	62	40.87	−124.2683	Night
3	Apr 98	4/4/1998	1701	670	44.6517	−125.1167	Day
		4/6/1998	0143	1078	43.2166	−124.9995	Night
4	Apr 98	4/10/1998	1617	90	44.6517	−124.4117	Day
		4/5/1998	0317	90	44.6517	−124.4117	Night
5	Apr 98	4/4/1998	1133	2850	44.6517	−125.6	Day
		4/6/1998	0418	1722	43.2166	−125.166	Night
6	Aug 98	8/9/1998	1023	117	41.9	−124.5025	Day
		8/9/1998	2114	115	40.87	−124.3627	Night
7	Aug 98	8/10/1998	1950	75	38.64	−123.4497	Day
		8/10/1998	2116	109	38.593	−123.5085	Night
8	Apr 99	4/20/1999	0820	2850	44.6517	−125.6	Day
		4/20/1999	2116	1722	43.2166	−125.166	Night
9	Jul 99	7/5/1999	0400	1078	43.2166	−124.9995	Day
		7/4/1999	0120	670	44.6517	−125.1167	Night
10	Jul 99	7/9/1999	0440	296	44.6517	−124.65	Day
		7/5/1999	0130	336	43.2166	−124.8353	Night
11	Sep 99	9/23/1999	0920	2850	44.6517	−125.6	Day
		9/23/1999	2130	1722	43.2166	−125.166	Night

We used ANOVAs to test for differences in total copepod biomass between years and among four ecological zones: (A) onshelf north of Cape Blanco, (B) offshelf north of Cape Blanco, (C) onshelf south of Cape Blanco, and (D) offshelf south of Cape Blanco (Fig. 1). We defined the shelf break as being at a water depth of 180 m. We used the Multi-Response Permutation Procedure (MRPP), a multivariate test designed for species data, to test for differences in copepod community structure between the four zones. Data from each cruise was analyzed separately. Species present in <5% of samples within each cruise were removed; densities were  $\log_{10}(Y+1)$  transformed for the analyses. A Euclidean distance measure was used, and samples were weighted by  $C(i)=n(i)/\sum(n(i))$ , where  $C$  is the weight given to group  $i$ ,  $n(i)$  is the number of samples in group  $i$ , and  $n$  is the total number of samples.

Throughout this paper, we discuss species and their distributions with respect to their affinities to different water types, such as ‘southern’ or ‘warm water neritic’ species; ‘northern’, ‘cold water’ or ‘boreal neritic’ species; ‘Transition Zone species’ and so on. Assignment of affinities have been largely based on Johnson and Brinton (1963); Fleminger (1976) and Peterson & Miller, 1975, 1977). We also use the terms ‘shelf’, ‘onshelf’ and ‘onshore’ interchangeably along with ‘slope’, ‘offshelf’ and ‘offshore’ to differentiate between stations located on the continental shelf (at water depths <180 m) and those situated over deeper waters off the shelf.

### 3. Results

#### 3.1. Physical data

##### 3.1.1. Winds

Winds prior to and during the April 1998 and 1999 cruises were similar; short periods of alternating strong northerly and southerly winds were seen prior to each cruise (Fig. 2). Winds blew steadily from the north prior to, and throughout, the August 1998 cruise. Winds were strong from the north preceding and during the July 1999 cruise; winds in September 1999 were variable both before and during the cruise.

##### 3.1.2. Temperature/salinity/fluorescence

In April 1998, sea surface temperature over the sampling area ranged from 10.9 to 12.7°C, which was about 2°C higher than normal as a result of the El Niño (A. Huyer, Oregon State University, personal communication); temperatures were fairly uniform throughout the study region (Fig. 3) although SSTs were slightly lower near shore. In April 1999, SSTs were lower (9.2–10.4°C) and less variable than in 1998. Sea surface salinity was similar during both spring cruises (Fig. 4), ranging from 31.3 to 33.0 in April

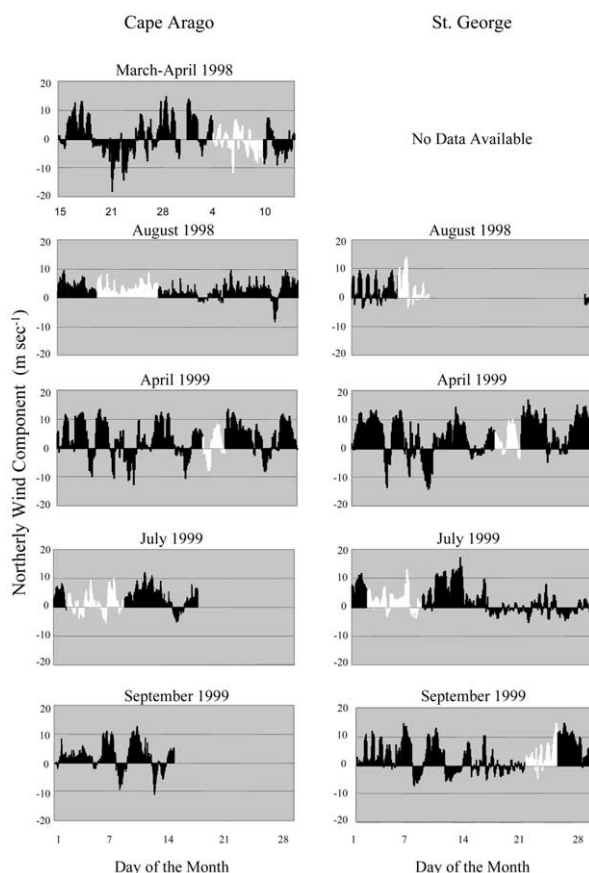


Fig. 2. North component of the wind. Data from Cape Arago (43.3°N 124.4°W) and St. Georges (41.9°N 124.4°W) buoys. Winds during the cruise periods are in white.

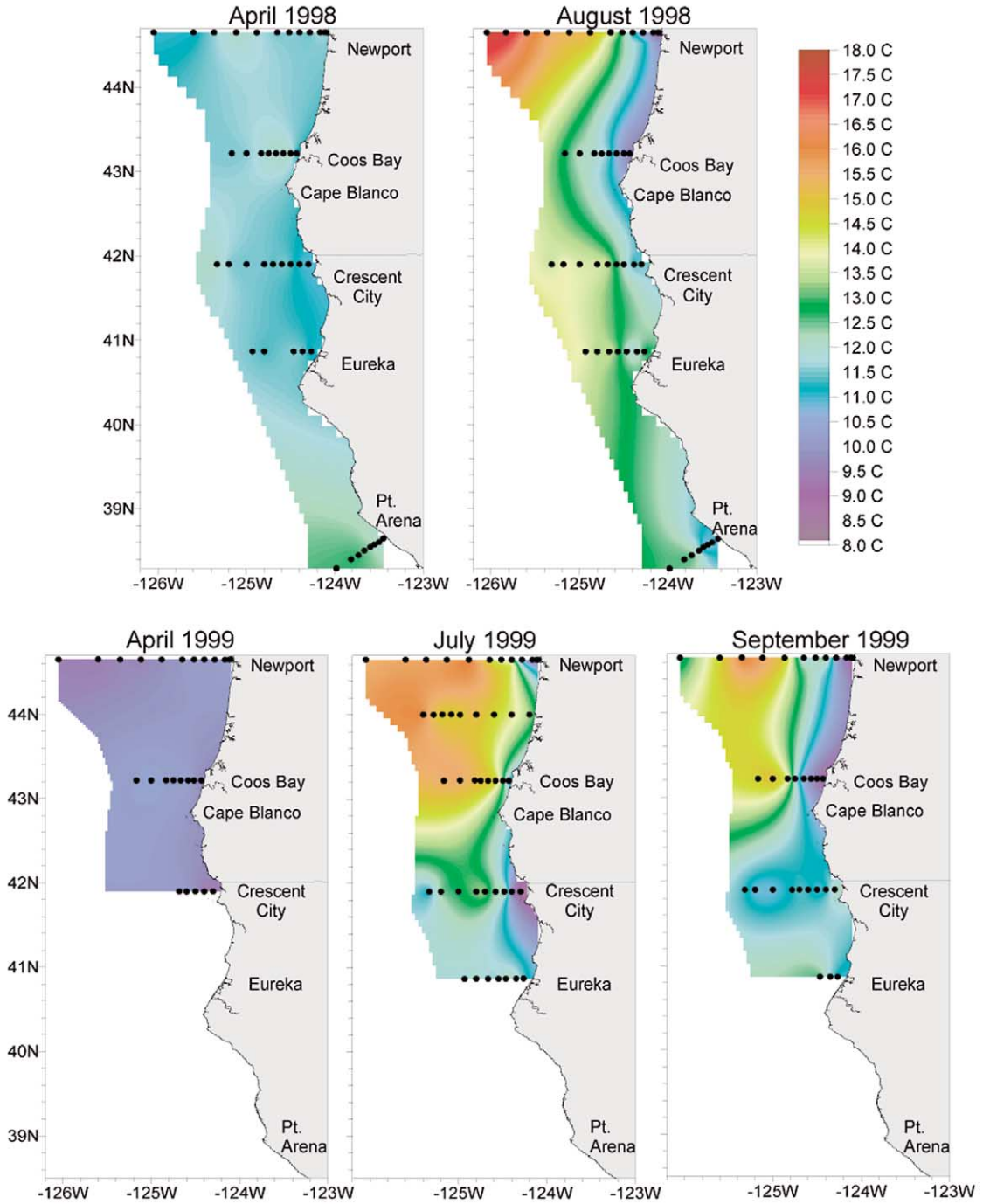


Fig. 3. Sea surface temperature (°C) during the study periods.

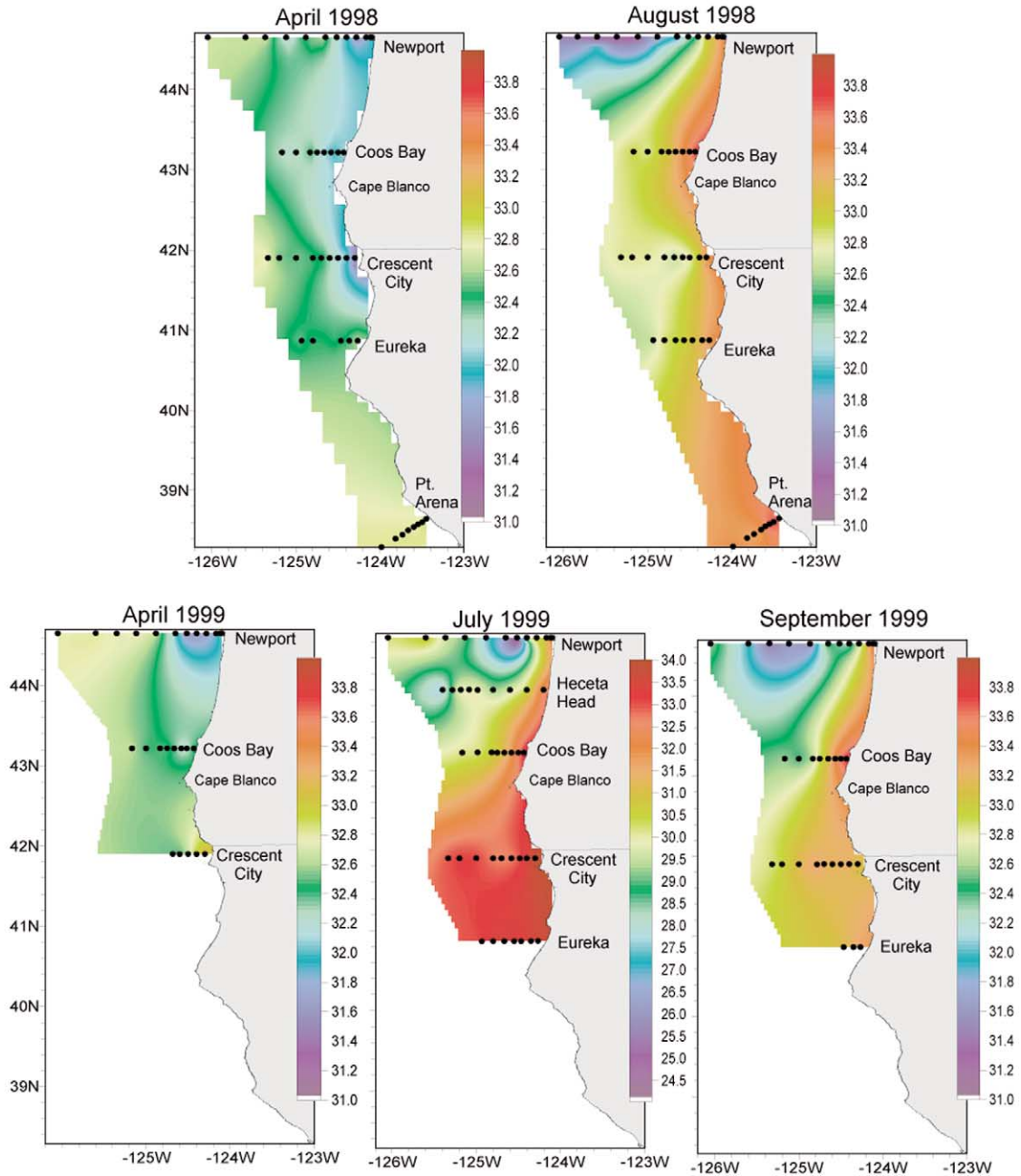


Fig. 4. Sea surface salinity during the study periods. Note the different scale for July 1999.

1998, and from 31.6 to 33.1 in April 1999. During both years, SSS was lower nearshore, probably as a result of river runoff, and increased to the south and offshore. The hydrography did not indicate that upwelling had started by the time of the April cruises started in either of the two years.

Sea surface temperatures and salinities during summers 1998 and 1999 (Figs. 3 and 4) indicated there



was strong upwelling. There was a narrow band of upwelled water in the north, and a broader, more diffuse area of upwelled water to the south of Cape Blanco. In 1998 SST ranged from 8.7 to 17.5°C and was about 1.4°C higher offshore than in 1999 (range of 8.9–16.1°C). SSS ranged between 30.8 and 33.7 in 1998 and between 31.4 and 33.7 in 1999. Offshore of Newport there were low salinity waters associated with the Columbia River plume, which originates from the discharge approximately 250 km to the north of Newport. In July and September 1999, SST and SSS off Crescent City and Eureka indicated there had been a seaward displacement of the cool, more saline upwelled water, which was not evident in 1998.

Fluorescence was low during spring of both years (Fig. 5). Highest fluorescence was seen very near shore, although in July 1999 it was also high offshore to the south of Cape Blanco. There was no apparent difference between years.

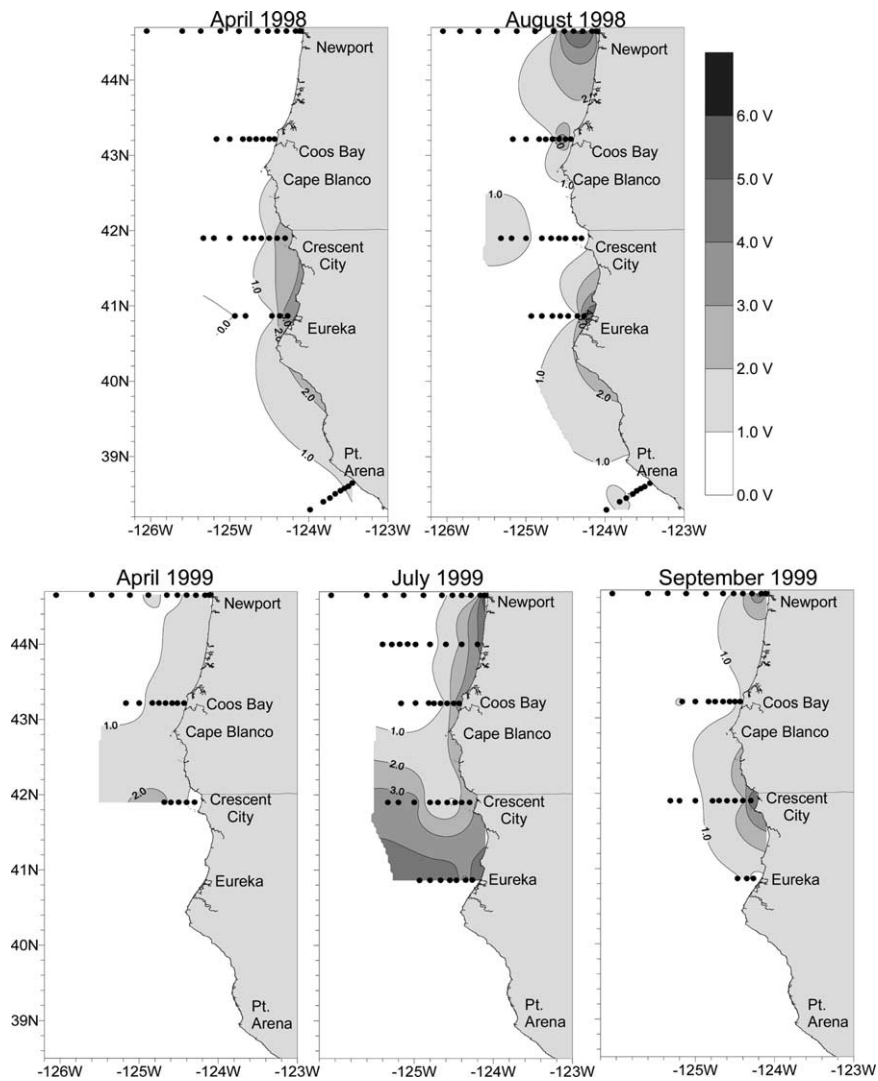


Fig. 5. Fluorescence (V) at 3 m depth during the study periods.

### 3.2. Zooplankton density and distribution

#### 3.2.1. Day/night differences

In the 11 day/night pairs of samples examined, total copepod biomass averaged 1.12 times higher at night than during day (Table 2). Wilcoxon tests on the day/night differences indicated that neither total copepod biomass nor the density of any individual species differed between day and night (all  $p > 0.05$ ). Mackas, Washburn and Smith (1991), who also assessed day/night differences in the upper 100 m, concluded that there was no difference in copepod biomass between day and night, except for *Metridia pacifica*, which exhibited diel migration. Huntley, Zhou and Nordhausen (1995) estimated zooplankton abundance and biomass in the mesoscale eddy fields off central California in June 1993 with an optical plankton counter, and again did not find a difference in copepod biomass between day and night in the upper 300 m. Therefore, we have not separated day from night samples when comparing distributions and abundances, but, in Fig. 6, samples taken during day are differentiated from those taken during night so that the effect of sample time can be subjectively evaluated.

#### 3.2.2. Variations in biomass and abundance

Copepods contributed the majority of the biomass in both years, averaging  $69 \pm 2.7\%$  in all samples. Copepod biomass was  $>70\%$  of the total biomass during all but the April 1999 cruise when salps (primarily *Salpa fusiformis*) comprised  $59 \pm 9.2\%$  of the biomass. Chaetognaths made up the next most important group averaging  $5 \pm 1.0\%$  of the overall biomass, and contributed a larger portion of the biomass in 1999 than 1998. Pteropods and euphausiid larvae together averaged 3% of the total biomass; both these groups contributed a larger portion of the biomass in 1998 than 1999. Other taxonomic groups (polychaetes, shrimp, crabs, etc.) made up the remainder of the total biomass.

Copepod biomass did not differ between years ( $F=0.47$ ,  $p=0.49$ ) or among zones ( $F=1.57$ ,  $p=0.20$ ). During some cruises their biomass tended to be highest the nearshore zone (July, 1999) and in others, biomass tended to be higher in the southern zones (August 1998 and September, 1999) (Fig. 6). For all cruises, copepod biomass fluctuated by over one order of magnitude, ranging from  $0.3 \text{ g carbon m}^{-2}$  (65 miles off Newport in September, 1999) to  $2.4 \text{ g carbon m}^{-2}$  (19 miles off Eureka in August, 1998).

#### 3.2.3. Interannual variation in species composition

Although we did not find any differences in copepod biomass between years, copepod community composition differed vastly between years. For example, species diversity (richness) was much higher in 1998 with 9 species of copepods making up 90% of the total numbers whereas only 3 species comprised 90% of the numbers in 1999. In general, species with southern warm-water or offshore affinities were more abundant in 1998, whereas species with cold-water affinities increased in density in 1999 (Table 3). Most notably, *Corycaeus anglicus*, (a subtropical neritic species) almost disappeared from all stations in 1999 and densities of *Paracalanus parvus* (a subtropical neritic species) and *Eucalanus bungii californicus* (an offshore Transition Zone species) declined by  $>90\%$  from 1998 to 1999. Three species with northern affinities, *Pseudocalanus mimus*, *A. longiremis*, and *Neocalanus plumchrus*, were much more abundant in 1999 than 1998. However, *C. marshallae*, a species with northern affinities, and *Metridia pacifica*, a species of uncertain affinity, were about equally abundant in the two years. Several species of *Clausocalanus*, all with warm-water associations, increased slightly in their average densities between 1998 and 1999.

#### 3.2.4. Spatial variations in species composition

Most species were not distributed evenly across the study area. *Oithona similis*, one of the commonest species, was fairly uniformly distributed, but the other dominants, such as *Pseudocalanus mimus*, *Paracal-*

Table 2  
Day/Night comparison of total biomass (mg Carbon m<sup>-3</sup>) of common (present in >20% of samples) species of copepods. Bold boxes indicate biomass differences of >2 mg carbon m<sup>-3</sup>. Biomass values of 0.00 mg m<sup>-3</sup> indicate very small values whereas blank cells indicate true zero values

Pair	Day	Night	<i>Artia longiremis</i>	<i>Calanus marshallae</i>	<i>C. pacificus</i>	<i>Calocalanus styliremis</i>	<i>C. tenuis</i>	<i>Candacia bipinnata</i>	<i>Clausocalanus spp.</i>	<i>Corcaeus anglicus</i>	<i>Cenocalanus vanus</i>	<i>Eucalanus bungii californi</i>	<i>Mesocalanus tenuicornis</i>	<i>Metridia pacifica</i>	<i>Microsetella spp</i>	<i>Necocalanus plumchrus</i>	<i>Oithona spp</i>	<i>Oncaea spp</i>	<i>Paracalanus parvus</i>	<i>Pseudocalanus mimus</i>
1	0.19	0.15	0.03	0.00	0.29	0.11	0.04	0.13	8.76	6.94	1.02	0.01	0.51	0.03	0.01	0.01	0.01	0.01	0.01	0.01
2	0.09	0.37	0.01	0.00	0.08	0.04	0.01	0.14	2.56	0.02	1.23	0.01	0.32	0.02	0.00	0.03	0.00	0.03	0.03	0.03
3	0.16	1.85	0.02	0.00	0.05	0.11	0.02	0.35	0.00	0.02	2.16	0.01	0.51	0.34	0.01	0.05	0.01	0.03	0.03	0.02
4	0.30	0.77	0.01	0.00	0.05	0.08	0.04	0.09	2.83	0.02	0.42	0.00	2.08	0.42	0.00	0.02	0.00	0.02	0.02	0.02
5	0.08	0.08	0.05	0.00	0.02	0.07	0.01	0.15	0.07	0.02	0.93	0.00	4.01	0.93	0.00	0.04	0.00	0.01	0.11	0.02
6	0.16	0.01	0.00	0.00	0.02	0.13	0.01	0.09	2.85	0.03	1.33	0.01	1.21	1.12	0.00	1.44	0.03	0.01	0.03	0.03
7	0.00	0.01	0.00	0.00	0.02	0.00	0.37	0.91	0.67	0.01	0.61	0.01	0.02	0.02	0.00	0.07	0.02	0.00	0.07	0.07
8	0.01	0.00	0.00	0.05	0.05	0.21	0.95	3.65	0.06	0.06	0.06	0.00	0.01	0.06	0.00	0.01	0.06	0.00	0.01	0.01
9	7.67	0.04	0.15	0.29	1.41	6.13	0.02	0.02	1.31	0.02	1.31	0.02	0.17	0.00	0.62	0.06	0.01	0.28	0.02	0.02
10	8.11	0.03	0.12	0.03	0.50	0.52	0.02	0.02	3.46	0.02	3.46	0.02	5.37	0.05	0.02	0.02	0.08	0.00	0.01	0.05
11	0.15	0.07	0.00	0.68	0.12	1.03	0.20	0.65	0.43	0.43	0.43	0.20	7.75	0.08	0.00	0.01	0.10	0.01	0.16	0.05
12	0.04	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
13	0.36	2.07	0.06	0.00	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
14	0.02	0.06	0.00	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
15	0.04	0.04	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
16	0.04	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
17	0.41	2.80	0.26	0.01	0.29	1.22	0.39	2.42	27.37	0.40	7.68	0.05	8.77	0.05	0.02	0.97	0.56	0.02	0.97	11.22
18	0.04	6.41	0.45	0.00	0.20	2.81	0.09	1.82	17.49	0.20	16.88	0.01	15.30	0.57	0.05	0.56	0.05	0.56	11.19	11.19

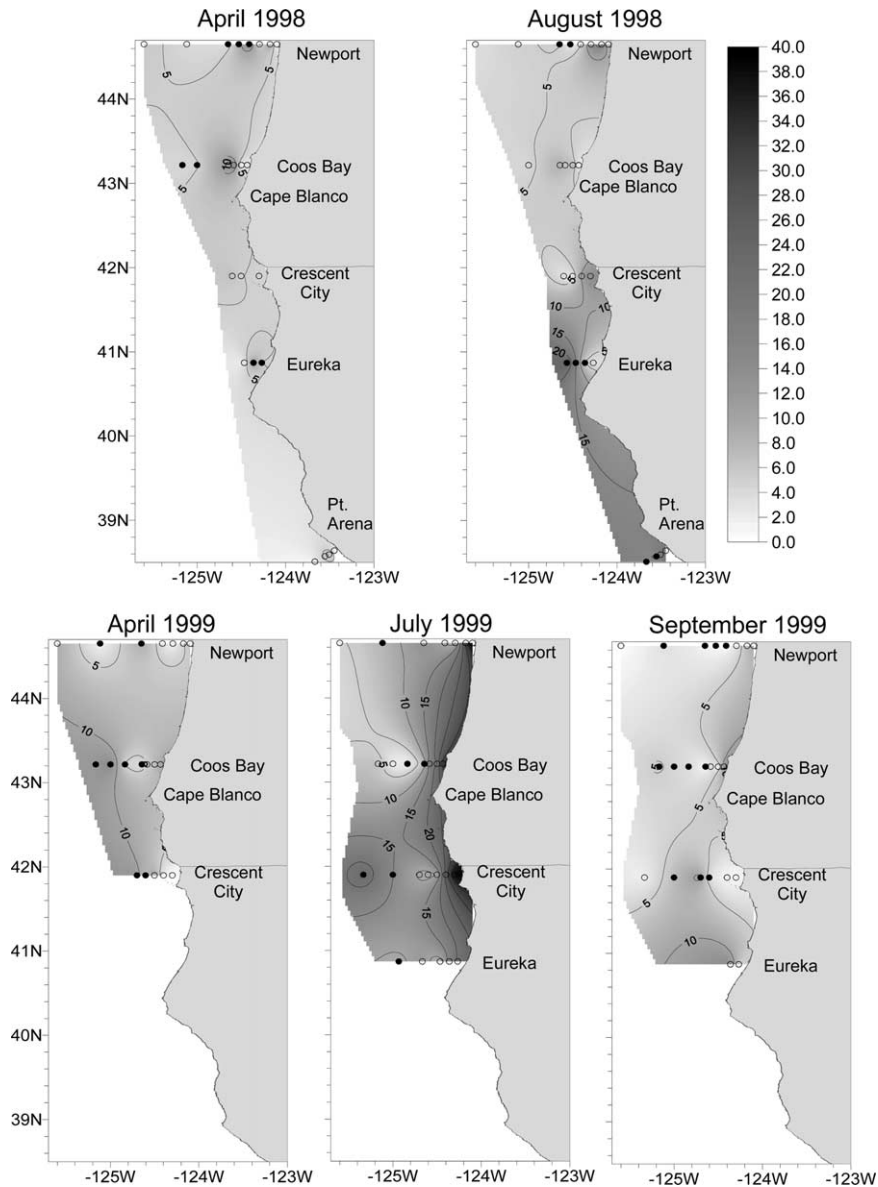


Fig. 6. Total copepod biomass ( $\text{mg carbon m}^{-3}$ ). Open symbols represent stations occupied during day; filled symbols represent stations occupied at night.

*anus parvus*, *Acartia longiremis*, *Calanus marshallae*, and *Centropages abdominalis* were not. *Pseudocalanus mimus* specimens were found chiefly near-shore and to the north in April 1998, August 1998, and April 1999, but in July and September 1999 they were more offshore and further south (Fig. 7). Similarly, the distribution of *P. parvus*, a subtropical neritic species, also differed between 1998 and 1999 (Fig. 8). During spring and summer 1998, its densities tended to be highest near-shore but in 1999 its densities

Table 3  
 Densities (No. m<sup>-3</sup>) of some copepods typically associated with offshore/northern (cold-water species) or southern waters (warm-water species) and the trend in biomass from 1998 to 1999

Genus species	Apr 98	Aug 98	Apr 99	Jul 99	Sep 99	Trend 1998–1999
<b>Cold-Water Species</b>						
<i>Acartia hudsonica</i>	0.09	5.21	2.46	19.51	47.39	↑
<i>Acartia longiremis</i>	0.09	33.86		352.83	54.52	↑
<i>Calanus marshallae</i>	0.64	17.71	0.43	26.28	4.93	–
<i>Centropages abdominalis</i>	0.05	3.52		64.01	0.62	↑
<i>Neocalanus plumchrus</i>	2.36		5.45			↑
<i>Pseudocalanus mimus</i>	2.50	13.25	446.88	1872.96	493.85	↑
<i>Acartia danae</i>	1.25		1.44		0.20	↓
<i>Acartia tonsa</i>	0.31	0.60				
<i>Calanus pacificus</i>	15.30	81.03	3.42	36.43	0.68	↓
<i>Calocalanus styliremis</i>	21.30	6.41	5.43	4.04	2.10	↓
<i>Calocalanus tenuis</i>	1.22	0.77	0.33		0.16	↓
<i>Clausocalanus arcuicornis</i>	1.65	0.54	4.22	0.76		↓
<i>Clausocalanus parapergens</i>	2.53	2.17	9.76	0.91	2.31	↑
<i>Clausocalanus paululus</i>	0.56		4.29	1.41	0.23	↑
<i>Clausocalanus pergens</i>	4.66	2.16	31.14	9.61	4.91	↑
<i>Corycaeus anglicus</i>	55.11	22.56	0.09			↓
<i>Ctenocalanus vanus</i>	43.03	88.97	16.16	33.17	14.68	↓
<i>Eucalanus bungii californicus</i>	37.74	8.96	0.40	2.54	0.27	↓
<i>Mesocalanus tenuicornis</i>	0.53	5.40	1.57	7.20	0.52	–
<i>Paracalanus parvus</i>	57.26	237.49	13.56	9.94	12.01	↓
<i>Paracalanus spp. 2</i>			1.50		0.37	↑
<i>Metridia</i>	28.17	72.51	16.77	15.24	29.50	↑
<i>Oithona</i>	196.11	336.74	392.66	661.22	489.13	↑
<b>Warm-Water Species</b>						
<b>Uncertain</b>						

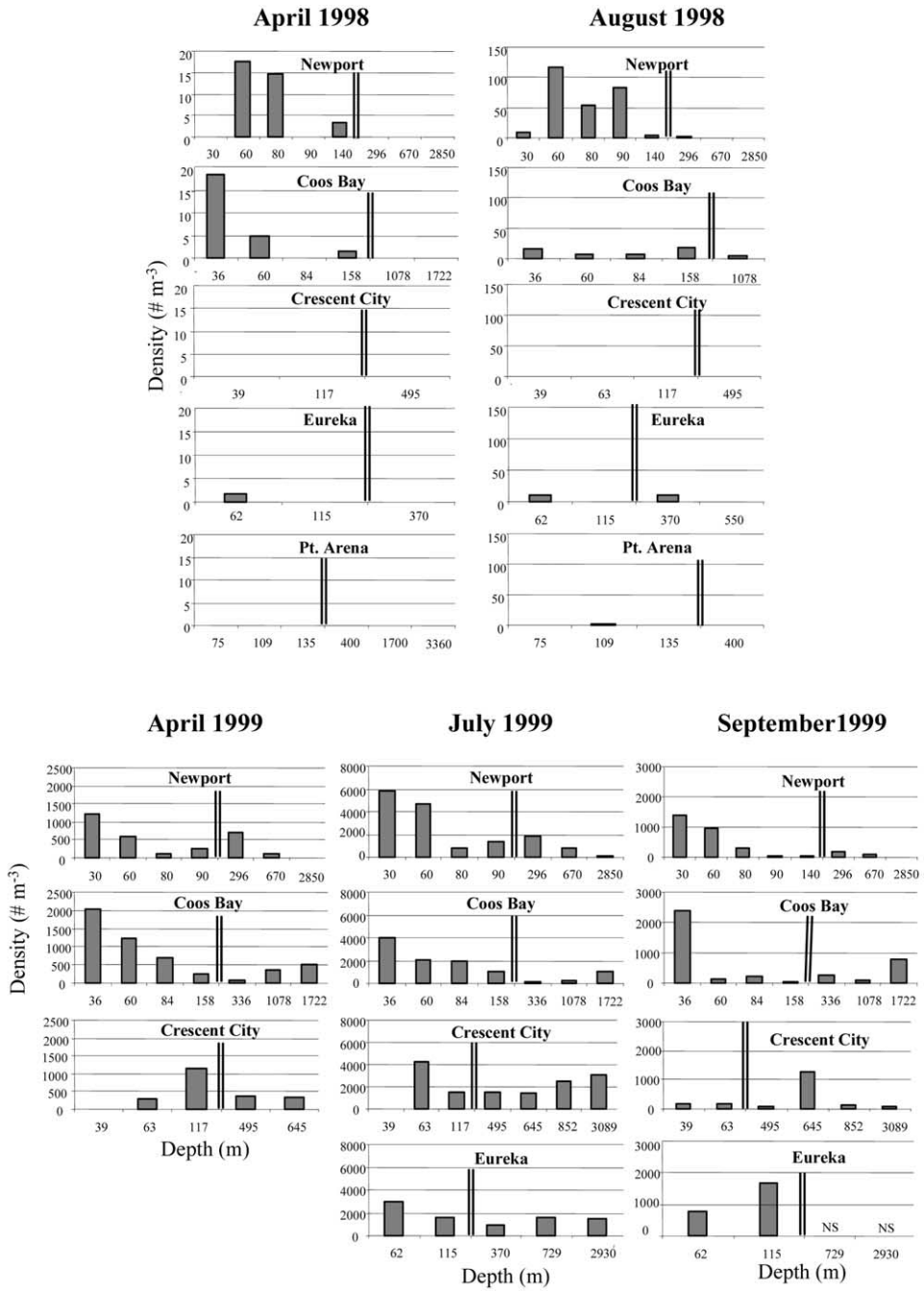


Fig. 7. Density of *Pseudocalanus mimus*. Note the different scales for each cruise. || separates onshelf and offshore stations. NS=Not sampled.

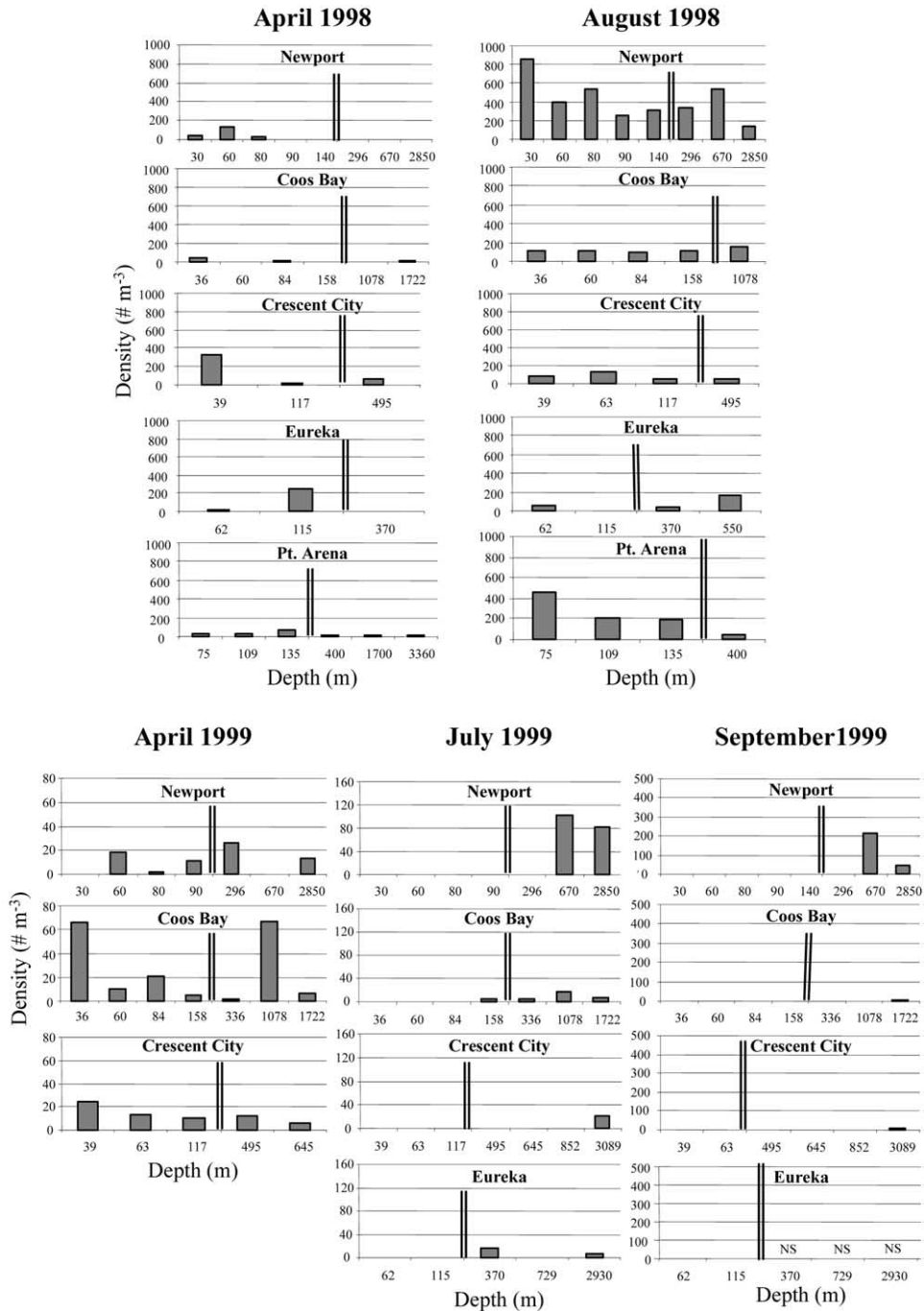


Fig. 8. Density of *Paracalanus parvus*. Note the different scales for each cruise. || separates onshelf and offshore stations. NS=Not sampled.

were generally higher offshore. The other common boreal copepod species, *A. longiremis* (Fig. 9), *C. marshallae* (Fig. 10), and *Centropages abdominalis* (not shown), displayed patterns of relatively low abundance everywhere in the spring, but higher population abundances during summer, particularly in the north.

Many of the warm-water copepod species found off Oregon in 1998 (Table 3) were broadly distributed throughout the study region and showed no clear latitudinal or alongshore pattern. However, with the advent of La Niña conditions in summer 1999, their distributions changed greatly. Most of those species occurred chiefly over deep water; some members of the group (*Clausocalanus perygens*, *C. arcuicornis*, *C. paraperygens*, *Ctenocalanus vanus* and *Calanus pacificus*) were found in coastal waters, but primarily along the transect lines to the south of Cape Blanco. *Calanus pacificus* (Fig. 11), a species that usually dominates the coastal waters off California, was common during the 1998 El Niño, but were seldom found in 1999 except at the nearshore station off Crescent City in July (892 individuals  $\text{m}^{-3}$ ).

### 3.2.5. Effect of Cape Blanco on community composition

When we examined onshelf and offshelf differences in copepod community composition for the summer cruises using MRPP analysis, we found that community structure was different between onshelf and offshelf zones in waters to the north of Cape Blanco (Zone A versus B), but was the similar in the onshelf and offshelf zones to the south of Cape Blanco (Zone C versus D; see Table 4 lower right quadrant). When we examined north versus south differences in community structure, we found that, with the exception of the offshelf samples in September 1999, community structure differed to the north and south of Cape Blanco both in shelf waters (Zone A versus C) and slope waters (Zone B versus D) (see Table 4 lower left quadrant). As for the spring cruises, community structure in April 1998 differed in both the onshelf/offshelf and the north/south comparisons (Table 4 upper quadrants). Patterns in April 1999 were unclear, possibly because of the paucity of data.

## 4. Discussion

Our estimates of copepod biomass are similar to past measurements in the continental shelf waters of the Pacific Northwest. We found a range of 0.3–2.4 g carbon  $\text{m}^{-2}$  for the upper 100 m of the water column. Peterson et al. (1979) reported copepod biomass of 0.4–1.6 g carbon  $\text{m}^{-2}$  off Newport, Oregon, in the upper 20 m of the water column, and Landry and Lorenzen (1989) observed copepod biomass of 1.6 and 1.7 g carbon  $\text{m}^{-2}$  along transects off the coast of Washington in the upper 100 m in June 1981 and August 1982 respectively. Mackas (1992) reported 1.0–2.0 g carbon  $\text{m}^{-2}$  for the shelf waters off southwestern Vancouver Island (approximately 300 km north of Oregon).

There are only a few estimates of copepod biomass reported from other upwelling systems that were either direct measurements of total copepod carbon or that calculated carbon from enumeration data (as we have done) and can, therefore, be compared to our data. These include reports of 0.3–2.1 g carbon  $\text{m}^{-2}$  off Cape Blanc, Mauritania, Northwest Africa (Vives, 1974), 1–3 g  $\text{m}^{-2}$  for the same region in another year (Postel, Arndt, & Brenning, 1995), 0.4–2.0 g carbon  $\text{m}^{-2}$  for the upwelling region off Somalia in the Arabian Sea (Smith, 1982), 3.1–4.2 g carbon  $\text{m}^{-2}$  for the upwelling region off northwestern Spain (Valdes, Roman, Alvarez-Ossorio, Gauzens, & Miranda, 1990), 0.8–3.5 g carbon  $\text{m}^{-2}$  for the upwelling region off northern California (Mackas et al., 1991), and 2–20 g carbon  $\text{m}^{-2}$  off central California (Huntley et al., 1995). Our values fall within most of these reported ranges.

There were no statistically significant differences in copepod biomass between our four ecological zones, nor were there differences in copepod biomass between the warm 1998 El Niño event and the cooler 1999 La Niña event. Peterson, Keister and Feinberg (2002) also found no difference in copepod biomass in their



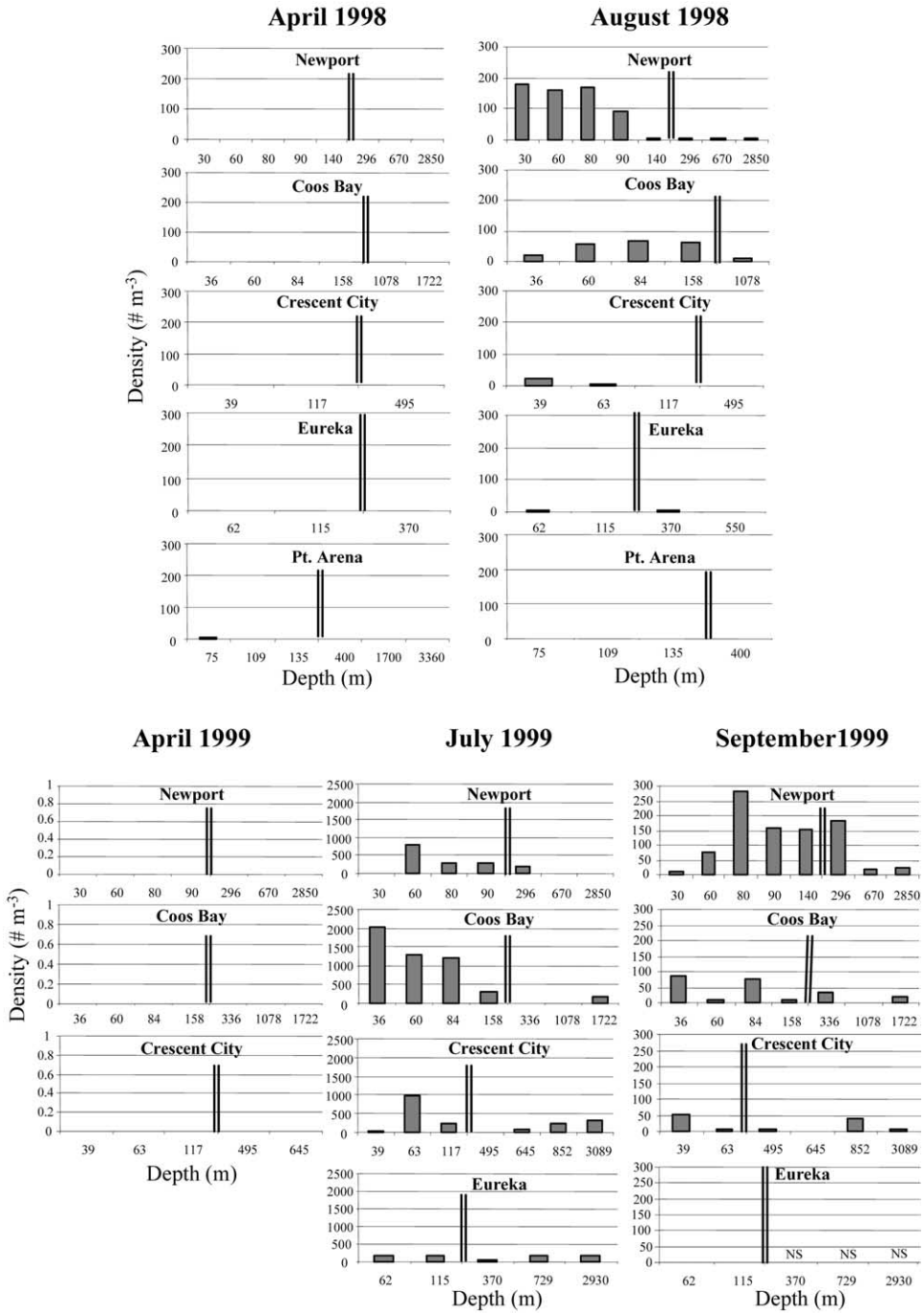


Fig. 9. Density of *Acartia longiremis*. Note the different scales for each cruise. || separates onshelf and offshore stations. NS=Not sampled.

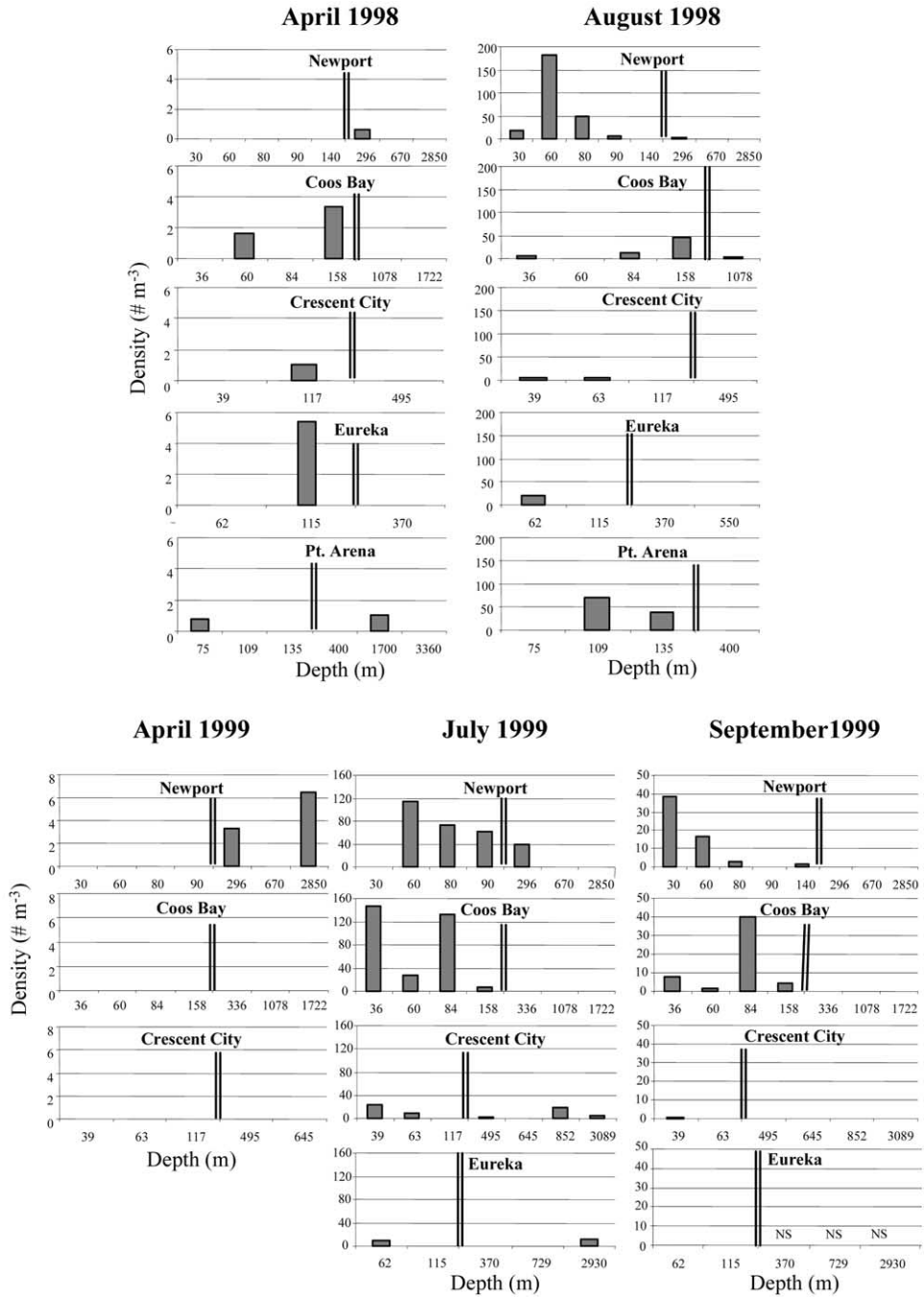


Fig. 10. Density of *Calanus marshallae*. Note the different scales for each cruise. || separates onshore and offshore station. NS=Not sampled.

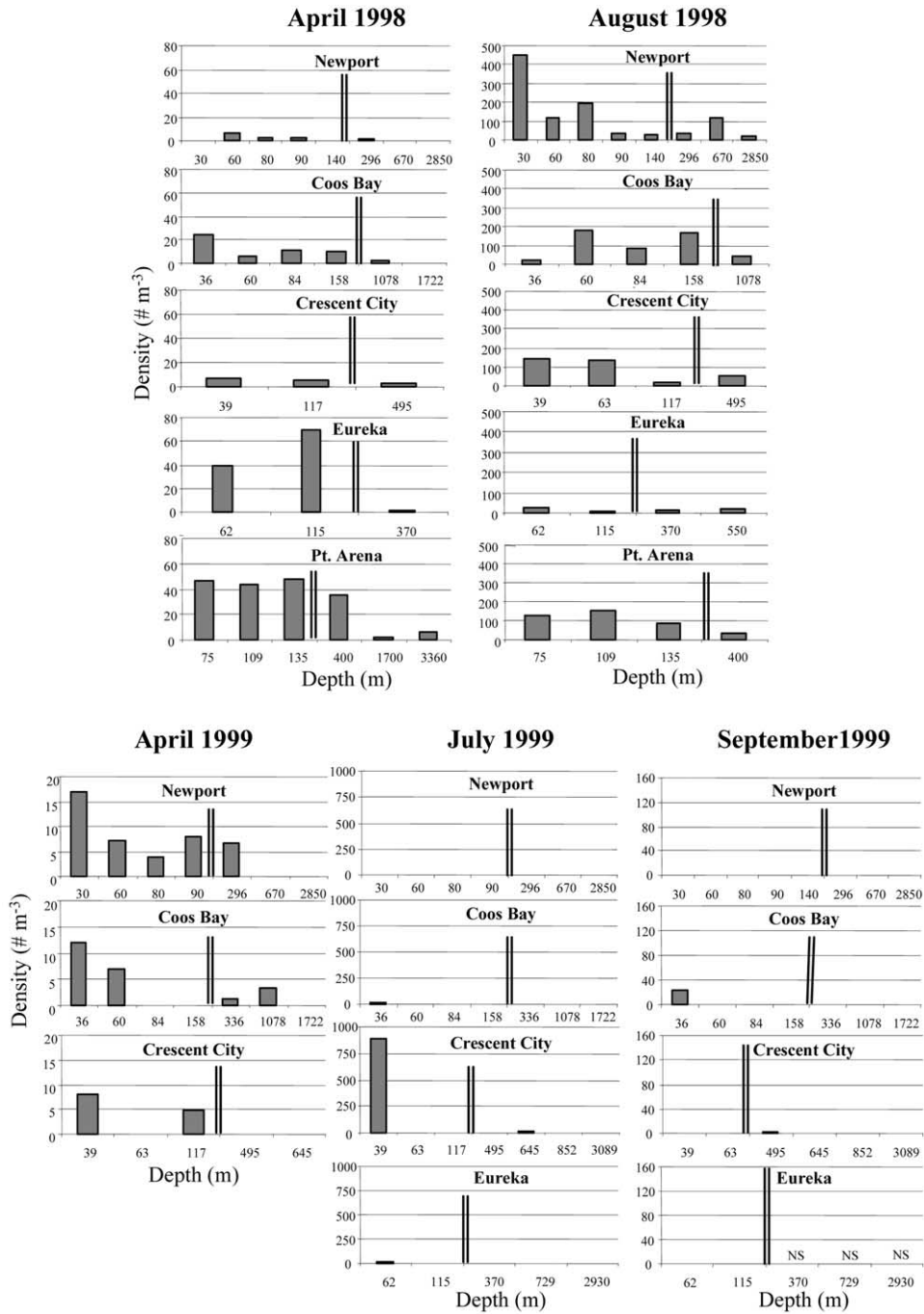


Fig. 11. Density of *Calanus pacificus*. Note the different scales for each cruise. || separates onshelf and offshore stations. NS=Not sampled.

Table 4

Probability values from MRPP analyses testing for differences in copepod community structure between ecological zones shown in Fig. 1. Significant differences are indicated by **bold**

		North vs South Onshelf (Zone A vs C)	Offshelf (Zone B vs D)	Onshelf vs Offshelf N. of Blanco (Zone A vs B)	S. of Blanco (Zone C vs D)
Spring	April 1998	<b>0.0008</b>	<b>0.04</b>	<b>0.002</b>	<b>0.002</b>
	April 1999	0.15	<b>0.007</b>	0.11	(Not enough data)
Summer	August 1998	<b>0.0002</b>	<b>0.01</b>	<b>0.005</b>	0.12
	July 1999	<b>0.002</b>	<b>0.01</b>	<b>0.0006</b>	0.30
	September 1999	<b>0.018</b>	0.57	<b>0.002</b>	0.06

time series of biweekly samples collected at a station five miles off Newport, Oregon. Their mean biomass for the May–September period was  $0.58 \text{ g m}^{-2}$  in 1997,  $0.61 \text{ g m}^{-2}$  in 1998 and  $0.66 \text{ g m}^{-2}$  in 1999. This lack of any large differences in biomass is somewhat surprising considering the conventional wisdom that El Niño events reduce zooplankton biomass (McGowan, 1985; Miller, Batchelder, Brodeur, & Percy, 1985). Our observations [and those of Peterson et al. (2002)] have shown that the chief influence of the 1998 El Niño event was a dramatic change in species composition, rather than a decline in total copepod biomass. Copepod biomass did not change, probably because phytoplankton concentrations were not limiting to copepod growth and production. Chlorophyll concentrations were actually highest during 1998 in Peterson's study (2002), averaging 3.8, 6.2 and  $3.9 \mu\text{g chlorophyll l}^{-1}$  over the May–September periods of 1997, 1998 and 1999 respectively.

The MRPP results support our hypothesis that, during summer upwelling, copepod communities differ between the region to the north and to the south of Cape Blanco. In summer the copepod communities differed between north and south of Cape Blanco in every analysis except offshelf (i.e. Zone B versus D) in September 1999 (see Table 4). One reason for this may be that no offshore samples were collected along the southernmost (Eureka) line during September 1999. Since the MRPP analysis did not find a north/south community difference during that cruise, this may indicate that changes in community structure are most marked at stations south of Crescent City.

Results of community analyses for the spring cruises are not as clear. We found both north and south of Cape Blanco that the shelf communities differed from the offshelf communities in April 1998, as may be expected early in the year before upwelling has become established. Before upwelling starts, the copepod community structure reflects the linear alongshore nature of the coastal currents and the offshore California Current, each of which contain a different zooplankton assemblages. In the absence of an upwelling jet, the southerly flows do not meander and so coastal zooplankton species do not get advected offshore. However, In April 1999, the shelf communities were similar to offshelf communities. We have no explanation for this contradictory result, except to note that Fig. 3 shows that in 1999, sea surface temperatures were uniform between all three transect lines, suggesting uniform conditions out to at least 60 miles from shore. More heterogeneity was observed in the temperature fields during the 1998 El Niño period.

This pattern of similarity in copepod community composition in onshelf and offshelf waters south of Cape Blanco during the 1998 El Niño summer cruise was the result of the influence of the distribution patterns of the four dominant species (see Table 3). *Paracalanus parvus*, *Ctenocalanus vanus*, *Calanus pacificus* and *Metridia pacifica* were all most abundant on the shelf off Newport and/or Coos Bay, but to the south were more evenly distributed between on- and offshelf stations.

In 1999, during the summer cruises (La Niña conditions), the pattern of the copepod community composition was probably driven by the distribution patterns of *Pseudocalanus mimus*, and to a lesser extent, by *Acartia longiremis*. In the north, these two species only occurred in high densities in shelf waters, but to the south of Cape Blanco they occurred in high densities in both onshelf and offshelf waters. For example, in July 1999, *P. mimus* was evenly distributed between stations in both shelf and slope waters off Crescent City and Eureka California, and its abundances changed little at stations up to 100 km from shore. *Acartia longiremis* occurred in lower densities off California than off Oregon, but in both shelf and slope waters off California its densities were similar. These observations contrast with those for the other two common boreal neritic species, *Calanus marshallae* and *Centropages abdominalis*. Both these species declined in abundance offshore of Newport and along the transects to the south of Newport.

The copepods *Pseudocalanus mimus*, *Calanus marshallae*, *Acartia longiremis* and *Centropages abdominalis* are the four most common species in shelf waters from the Bering Sea, south through the Gulf of Alaska, along the coast of British Columbia to as far south as central Oregon. However, only two of these species proved to be common in the waters to the south of Cape Blanco, *P. mimus* and *A. longiremis*. Why should these species respond so differently to hydrographic changes in waters south of Cape Blanco? One possible explanation is related to their distribution patterns. Off Washington and northern Oregon, the eggs and nauplii of *Calanus marshallae* and all developmental stages of *Centropages abdominalis* are concentrated very close inshore, within 10 km of the coast (Peterson et al., 1979; W.T. Peterson, unpublished data). *Pseudocalanus mimus* is not only abundant very close to shore, but in mid-shelf and shelf-break waters; along with *Acartia longiremis*, this species dominates the biomass in the mid- and outer regions of the shelf. We hypothesize that the species that can only reproduce in the nearshore zone off Washington and northern Oregon (i.e. *C. marshallae* and *C. abdominalis*) can not prosper off northern California because there the coastal upwelling jet transports them offshore waters where (for unknown reasons) they cannot reproduce at rates that can sustain population growth. Both *P. mimus* and *A. longiremis*, which maintain high population levels in the mid- and outershelf waters off Washington and northern Oregon, may have a greater capability to feed and to reproduce further offshore, and so may also be better able to feed and reproduce in outer shelf and offshore waters off northern California.

Finally, the copepod biomass data indicate a simple pattern of similar copepod biomass throughout the study region, whereas multivariate analyses of species densities indicate there are marked differences in community composition between the waters to the north and to the south of Cape Blanco. However, no simple patterns emerge when individual species are examined. Some boreal species seem to do equally well both north and south of Cape Blanco, whereas others do not. This is consistent with the postulates of Peterson et al. (1979) and Peterson (1998) about how copepod species maintain their populations in coastal upwelling zones; they suggested that each dominant species has a unique mechanism by which they achieve population retention. However, a mechanism that enables retention off central Oregon may not necessarily be effective in the very different circulation regime in the waters south of Cape Blanco. Thus we predict that each species is interacting with the upwelling jet to the south of Cape Blanco in its own specific, yet undiscovered, way. A more detailed analysis of the physical data is required before we seek possible relationships between the hydrographic features and densities of the more common boreal species, namely *Pseudocalanus mimus*, *Calanus marshallae*, *Acartia longiremis* and *Centropages abdominalis*. Such an analysis will also require detailed data on the vertical distributions of all life history stages of these species in the waters near and to the south of Cape Blanco. Without such information we may not be able to deduce why some species flourish while others decline to the south of Cape Blanco. However, one of the long term goals of the GLOBEC program is to examine specific responses of the dominant coastal species to both the potential negative effects of offshore displacement (and dilution of population numbers) at Cape Blanco and the potential positive effects of the species' having differential abilities to feed, grow, and reproduce at high rates in offshore waters. Those mechanisms and responses will be examined during in the Northeast Pacific field studies over the next few years.

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## References

- Barth, J. A., Pierce, S. D., & Smith, R. L. (2000). A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California current system. *Deep-Sea Research II*, 47, 783–810.
- Barth, J. A., & Smith, R. L. (1998). Separation of a coastal upwelling jet at Cape Blanco, Oregon, USA. *South African Journal of Marine Science*, 19, 5–14.
- Fleminger, A. (1976). Distributional atlas of calanoid copepods in the California Current region, Part II. CalCOFI Atlas No. 7, 1–213 plates.
- Hayward, T. L., & Mantyla, A. W. (1990). Physical, chemical and biological structure of a coastal eddy near Cape Mendocino. *Journal of Marine Research*, 48, 825–850.
- Huntley, M. E., Zhou, M., & Nordhausen, W. (1995). Mesoscale distribution of zooplankton in the California Current in late spring, observed by optical plankton counter. *Journal of Marine Research*, 53, 647–674.
- Johnson, M. W., & Brinton, E. (1963). Biological species, water masses and current. In M. N. Hill (Ed.), (pp. 381–414). *The sea*, 2. New York: Interscience.
- Landry, M. L., & Lorenzen, C. J. (1989). Utilization and transformation of primary production by zooplankton. In M. L. Landry, & B. J. Hickey (Eds.), *Coastal oceanography of Washington and Oregon* (pp. 175–210). Amsterdam: Elsevier.
- Mackas, D. L. (1992). Seasonal cycles of zooplankton off southwestern British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 903–921.
- Mackas, D. L., Washburn, L., & Smith, S. L. (1991). Zooplankton community pattern associated with a California Current cold filament. *Journal of Geophysical Research*, 96, 14781–14797.
- McGowan, J. A. (1985). El Niño 1983 in the southern California Bight. In W. S. Wooster, & D. L. Fluharty (Eds.), *El Niño North: Niño effects in the Eastern Subarctic Pacific Ocean* (pp. 166–184). Seattle, WA: Washington Sea Grant Program.
- Miller, C. B., Batchelder, H. P., Brodeur, R. D., & Percy, W. G. (1985). Response of the zooplankton and ichthyoplankton off Oregon to the El Niño event of 1983. In W. S. Wooster, & D. L. Fluharty (Eds.), *El Niño North: Niño effects in the Eastern Subarctic Pacific Ocean* (pp. 185–187). Seattle, WA: Washington Sea Grant Program.
- Mittelstaedt, E. (1983). The upwelling area off northwest Africa—a description of phenomena related to coastal upwelling. *Progress in Oceanography*, 12, 307–331.
- Peterson, W. T. (1998). Life cycles of copepods in upwelling zones. *Journal of Marine Systems*, 15, 313–326.
- Peterson, W. T., Keister, J. E., & Feinberg, L. R. (2002). The effects of the 1997–99 El Niño/La Niña events on hydrography and zooplankton off the central Oregon coast, *Progress in Oceanography*, in press.
- Peterson, W. T., & Miller, C. B. (1975). Year-to-year variations in the planktology of the Oregon upwelling zone. *Fishery Bulletin US*, 73, 642–653.
- Peterson, W. T., & Miller, C. B. (1977). The seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. *Fishery Bulletin US*, 75, 717–724.
- Peterson, W. T., Miller, C. B., & Hutchinson, A. (1979). Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep-Sea Research*, 26A, 467–494.
- Postel, L., Arndt, E. A., & Brenning, U. (1995). Rostok zooplankton studies off West Africa. *Helgoländer Meeresunters*, 49, 829–847.
- Shannon, L. V., & Pillar, S. C. (1986). The Benguela Ecosystem Part III. Plankton. *Oceanography Marine Biology Ann. Rev.*, 24, 65–170.
- Shillington, F., Peterson, W., Hutchings, L., Probyn, T., & Waldron, H. (1990). A cool upwelling filament off Luderitz, Namibia: Physical and biological observations. *Deep-Sea Research I*, 37, 1753–1777.
- Smith, S. L. (1982). The northwestern Indian Ocean during the monsoons of 1979: distribution, abundance, and feeding of zooplankton. *Deep-Sea Research*, 29, 131–135.
- Strub, P.T., Kosro, P.M., Huyer, A., & CTZ Collaborators (1991). The nature of cold filaments in the California Current system, *Journal of Geophysical Research*, 96, 14743–14768.
- Valdes, J. L., Roman, M. R., Alvarez-Ossorio, M. T., Gauzens, A. L., & Miranda, A. (1990). Zooplankton composition and distribution off the coast of Galicia, Spain. *Journal of Plankton Research*, 12, 629–643.

- Valentin, J. L., & Monteiro-Ribas, W. M. (1993). Zooplankton community structure on the east-southeast Brazilian continental shelf (18–23°S latitude). *Continental Shelf Research*, 13, 407–424.
- Vives, F. (1974). Le zooplancton et les masses d'eau des environs du Cap Blanc. *Tethys*, 6, 313–318.
- Weikert, H. (1983). Zooplankton distribution and hydrography in the Mauritanian upwelling region off northwestern Africa, with special reference to the calanoid copepods. *Meeresforsch*, 30, 155–171.