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Zonal and seasonal variations in zooplankton community structure off the central Oregon coast, 1998–2000

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Abstract

Previous studies of zooplankton communities off the central Oregon coast have been primarily descriptive or have focused on only a few taxa. To more formally explore patterns in zooplankton community structure, we used cluster analysis, Non-metric Multidimensional Scaling (NMDS) ordination, and Indicator Species Analysis to examine seasonal, El Niño/La Niña, and onshore/offshore differences in community composition. Hydrographic and zooplankton data were collected off Newport, Oregon (44.7°N) at eight stations between 8 and 105 km from shore (60-2900 m water depth), on 15 cruises between Jan 1998 and Sept 2000 as part of the US GLOBEC Northeast Pacific Long-Term Observation Program. Zooplankton were collected with a 202 μm, 0.5 m diameter ring net lifted vertically at 30 m min^{-1} from 100 m, to the surface.

The 1997/1998 El Niño played an important role in structuring the zooplankton community from the beginning of our sampling in January 1998 through November 1998. The "El Niño" group identified by cluster analysis and NMDS ordination was highly diverse and was characterized by taxa with offshore and subtropical neritic affinities. When the El Niño group was present, there was no onshelf-offshelf gradient in community composition as was seen during "normal" summers. The "El Niño" group was preceded and followed by a "Transitional" group with slightly lower diversity that existed through the spring of 1999. By summer 1999, conditions had returned to "normal."

Summer upwelling strongly affected the structure of zooplankton assemblages in the "normal" years of 1999 and 2000, leading to differences between nearshore and offshore zooplankton groups. The zooplankton assemblages sampled on the continental shelf during these summers were unique, composed of boreal neritic species (such as the copepods *Calanus marshallae*, *Pseudocalanus mimus*, and *Acartia longiremis*) and larvae of several meroplanktonic taxa, whereas the off-shelf assemblages resembled the winter zooplankton assemblages which were comprised of subtropical neritic and Transition Zone species. The spatial extent of the continental shelf group present during the summer upwelling season varied between early and late summer; differences may be related to the integrated strength and duration of the north winds over the upwelling season.
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1. Introduction

The zooplankton community found off Oregon is influenced strongly by seasonal variations in wind and current patterns. During late spring and summer, northwesterly winds set up equatorward flow and coastal upwelling. Northwesterly winds dominate from April/May–September; periodic relaxations or southwesterly storms rapidly affect the hydrography of nearshore areas, but offshore of about 30 km, conditions are less variable. Boreal neritic copepods such as *Pseudocalanus mimus*, *Calanus marshallae*, *Centropages abdominalis*, *Acartia longiremis*, and *Acartia hudsonica* dominate the coastal plankton during summer (Peterson & Miller, 1977). In early fall, winds reverse and upwelling ceases; during autumn and winter, winds are predominantly southwesterly, the Davidson Current flows poleward, and offshore surface waters are transported onshore. In winter, the coastal zooplankton is populated by warm-water species such as *Mesocalanus tenuicornis*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus spp.*, *Acartia tonsa*, and *Corycaeus anglicus* (Peterson & Miller, 1977).

No previous study has formally examined the seasonal and cross-shelf changes in the full zooplankton community off Oregon. Previous studies of zooplankton communities have been primarily descriptive (Laurs, 1967; Lee, 1971; Peterson & Miller, 1975; Peterson & Miller, 1976; Peterson & Miller, 1977), have focused solely on copepods (Hebard, 1966; Peterson, 1972; Peterson, Miller & Hutchinson, 1979; Peterson & Keister, 2002; Peterson, Keister & Feinberg, 2002; Morgan, Peterson & Emmett, in press), or have focused solely on the nearshore environment and have not compared on- and off-shelf communities (Meyers, 1975; Peterson & Miller, 1975; Peterson & Miller, 1977; Peterson, Miller & Hutchinson, 1979). Aside from Miller, Batchelder, Brodeur and Pearcy (1985); Brodeur (1986); Peterson and Keister (2002), and Peterson, Keister and Feinberg (2002), little has been reported about the effect of El Niño events on zooplankton community structure off Oregon.

Zonal differences in zooplankton community structure are expected during summer because shelf waters

out to 25 km are strongly influenced by upwelling whereas at and beyond 40 km upwelling has less effect. Beyond 70 km, upwelling is not detectable (Hebard, 1966). During upwelling, the on-shelf copepod community differs from the off-shelf community (Peterson & Keister, 2002; Morgan et al., in press). Morgan et al. found that the on-shelf (defined as <180 m depth) copepod community in mid-summer is characterized by *Calanus marshallae, Pseudocalanus mimus, Acartia longiremis,* and sometimes by *Acartia hudsonica,* and *Centropages abdominalis*. The off-shelf community is characterized by *Mesocalanus tenuicornis, Calocalanus styliremis,* immature *Clausocalanus spp.,* and *Ctenocalanus vanus*.

Mackas and Sefton (1982) and Mackas (1992) sampled the zooplankton off Vancouver, BC during the summers of 1979–1980 and 1979–1989 respectively. They found that nearshore and mid-shelf samples were dominated by *Calanus marshallae*, *Acartia longiremis,* and *Pseudocalanus spp*. whereas offshelf samples were dominated by *Neocalanus plumchrus* and *N. cristatus*. In 1962–1964, Hebard (1966) studied seasonal and distributional shifts in the zooplankton community at stations 24-105 km off Newport. He found that on-shelf stations were dominated by *Metridia pacifica*, *Calanus marshallae*, and *C. pacificus* whereas off-shelf stations were dominated by *Metridia pacifica* and *Eucalanus bungii*. *Neocalanus plumchrus* (then called *Calanus plumchrus*) were common in Hebard's samples offshore during March and April. *Pseudocalanus spp*. and *Acartia longiremis* were not common in Hebard's samples, perhaps because he used nets with 571 μm mesh.

The 1997/1998 El Niño was the strongest El Niño event on record (McPhaden, 1999). Anomalously warm water was noted off central Oregon as early as May 1997 and warmer, saltier water was noted at depth by September 1997. Sea surface temperature exceeded 18 °C in nearshore water in September (Peterson et al., 2002). Sea surface temperatures >2 °C warmer than average persisted through April 1998 (Huyer, Smith, & Fleischbein, 2002). Poleward surface flows were >30 cm s^{-1} stronger in winter 1997/1998 than in 1998/1999 (Kosro, 2002). Peterson et al. (2002) found that the effects of the El Niño on the nearshore copepod community were delayed somewhat from the physical signal; the biological signal seen in the copepod community at a station 8 km off Newport, Oregon was strongest from October 1997 through June 1998.

A primary objective of the study reported here was to look for differences between on-shelf/off-shelf zooplankton community structure during the summer upwelling and winter downwelling seasons and to examine how the El Niño/La Niña affected those differences. Using multivariate statistical techniques, we examine seasonal and cross-shelf differences to obtain a more complete and rigorous idea of cross-shelf and seasonal effects on the zooplankton community.

2. Methods

Hydrographic, nutrient, and zooplankton data were collected along the Newport Hydrographic (NH) Line (44.6°N) (Fig. 1) at eight stations between 8 and 105 km from shore; water depths of the stations are 60, 80, 90, 140, 295, 700, 670, and 2850 m respectively. Additional stations at 30, 50, 2890, and 2900 m depth were surveyed for hydrographic and nutrient data. Since 1998, cruises have been conducted five times per year as part of the US GLOBEC Northeast Pacific Long-Term Observation Program; a total of 15 cruises (Jan. 1998–Dec. 2000) have been analyzed for zooplankton.

Temperature, salinity, density, and fluorescence were taken with a Seabird SBE 911 CTD equipped with a Sea Tech fluorometer lowered and retrieved at a rate of 50 m min^{-1}. CTD data were collected, processed, and averaged into 1 m bins by A. Huyer (Oregon State University). Wind data were provided by the National Data Buoy Center (http://www.ndbc.noaa.gov), buoy 46050, located at 44.6 °N 124.5 °W—near our 140 m-depth station. Buoy 46050 did not sample during 27 February–27 April and 25 July–22 August, 1998, so data for those dates are taken from a C-MAN station—NWP03 (44.6 °N 124.1 °W) —a jetty location at Newport which typically registers slightly lower wind speeds than buoy 46050. The daily average
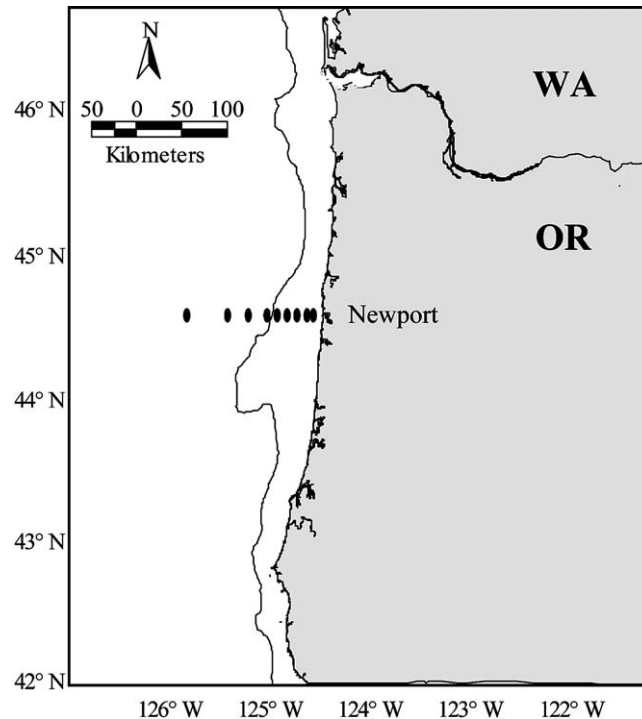
Fig. 1. Chart of the coast of Oregon USA showing the transect off Newport, sampling stations, and the 150 m depth contour.

northerly component of the winds was calculated and the cumulative percent of the non-negative northerly component of the winds was calculated for the summer upwelling season, here defined as 1 May–30 September. The cumulative percent of the non-negative northerly component represents the progression of the upwelling system.

Zooplankton was sampled with a 0.5 m diameter, 202 μm mesh ring net hauled vertically from 100 m (or near-bottom in shallower water) to the sea surface at a rate of 30 m min^{-1}. The net was fitted with a TSK flowmeter; the mouth area/filtration area ratio for this net was 6.5. Zooplankton samples were analyzed following Peterson and Miller (1975)—the sample was diluted to 5–10 X its settled volume and two 1 ml subsamples were taken from the sample with a piston pipette. Copepods were enumerated by species, but other zooplankton were grouped by larger taxonomic groups (e.g. chaetognaths, amphipods, doliolids, etc.) except for some common genera such as the pteropod *Limacina helicina* and the cladocerans *Evadne nordmanni* and *Podon leukarti*. Abundance (ind. m^{-3}) of animals was calculated. All life-history stages were counted; copepod eggs were not included in analyses.

Due to ship-time constraints, stations were occupied at any hour of day or night during each cruise. Previous studies focusing only on copepods have found no statistically significant day/night differences in either biomass or abundances of the dominant copepod species found off Oregon (Peterson, 1972; Mackas, Washburn, & Smith, 1991; Peterson & Keister, 2002). However, other groups, which may exhibit diel vertical migration beyond the 100 m depth sampled by our net, were examined for day/night differences in abundance. Of all the groups analyzed here, no mean daytime abundance differed from mean nighttime abundance by more than one standard deviation, so day and night samples were grouped for analyses. However, day/night occupations are indicated in Fig. 7 so the reader may judge the potential bias.

To explore the patterns in community structure, "species abundance" × "sample" matrices were analyzed by multivariate analyses. Rare species defined as those occurring in <5% of samples were not included

in the analyses. All data were $\log_{10}(N + 1)$ transformed. Cluster analysis was used to identify natural groupings of sampling stations based on similarity in zooplankton community structure; the 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 clustering proceeds, and is calculated as the sum of the error sum of squares from the centroid of each group relative to the items in that group.

Non-Metric Multidimensional Scaling (NMDS) ordination was used to examine similarities among samples; Sorensen's (Bray–Curtis) distance measure was employed. NMDS is considered one of the most robust ordination methods when dealing with zero–zero species abundance pairs (Field, Clarke, & Warwick, 1982; Gray et al., 1988). All multivariate analyses were conducted in PC-ORD for Windows 4.36B (McCune & Mefford, 1999). For the ordination, the final stress (a measure of the goodness-of-fit between the data and the final ordination) was examined in relation to the dimensionality to help choose the fewest number of dimensions necessary to adequately describe the data.

Indicator Species Analysis (ISA) (Dufrene & Legendre, 1997) was used to investigate which species were driving the differences among the groups identified in cluster analyses. The Indicator Value for a species in a group is calculated as the product of the relative abundance of the species in the group (i.e. the mean abundance in the group/the sum of the mean abundances in all groups) and the frequency of occurrence of the species in samples in the group. Indicator Values (IV) can range from 0 (no indication) to 100 (perfect indication, meaning the species was present in all samples in the group and was absent from all samples in other groups). A Monte Carlo simulation was used to determine significance of species IVs. Because many species in this study had significant IVs, the best indicators were defined as those indicator species whose IV was significant and whose IV in a cluster was arbitrarily defined as at least 5X higher than its IV in any other cluster.

To investigate differences among communities, we also calculated species richness (number of taxa in a sample) and the Shannon–Wiener Diversity index, calculated as

$$H' = \sum_{i}^{S} p_i(\log_2 p_i),$$

where p_i is the proportion of individuals in a sample unit belonging to species i, S is the number of species, and the summation is from $i = 1$ to S, for each sample.

3. Results

3.1. Winds

In 1998, winds over the 1 May–30 September season were northerly during 87 days of the 153-day season, whereas winds were northerly on only 51 and 62 of the 153 days in 1999 and 2000, respectively. In 1998, northerly winds commenced in early March, but the intensity was low until late April/early May (Fig. 2). Northerly winds peaked in July and remained at moderate levels until mid-September when winds became primarily southerly. The cumulative percent of the non-negative northerly winds (Fig. 2, upper right panel) shows moderate northerly winds until mid-June then steady northerly winds through July with 80% accumulation by mid-August. Northerly winds decreased by early September.

In 1999, northerly winds commenced in early April with a sudden strong (8 m s^{-1}) transition, but winds in May were dominated by strongly downwelling-favorable (southerly) winds. Northerly winds were sporadic through the summer and were infrequent after late July. The cumulative percent of the non-negative northerly component of the winds shows two strong periods of upwelling-favorable winds between 25
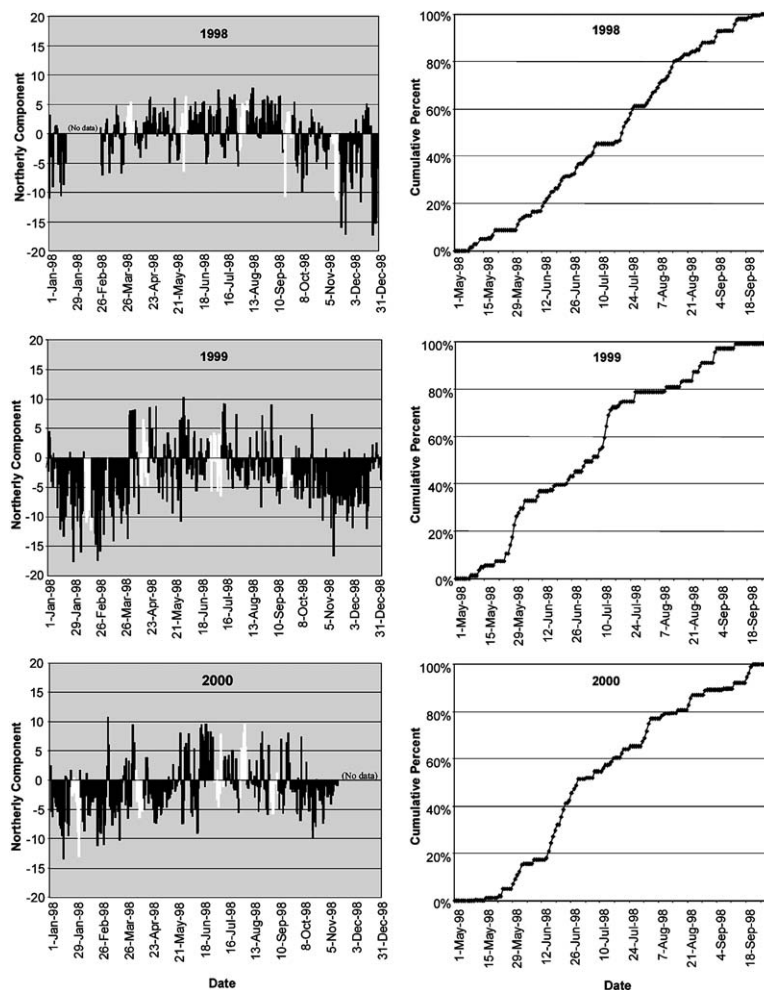
Fig. 2.   Left panels: Northerly component (m s^{-1}) of the local winds from buoy 46050. Data for 1998 include data from buoy NWP03 when 46050 was not sampling. Sampling dates and the seven days prior are in white. Right panels: Cumulative percent of the non-negative northerly component of the local winds.

May–3 June and 9–15 July. Nearly 80% of the upwelling-favorable winds over the May–September period occurred by the end of July.

In 2000, two short episodes of northerly winds occurred in early March and early April, followed by an extended period of southerly winds. Persistently strong upwelling-favorable winds commenced in late May and endured through late September with frequent but short breaks of southerly winds. Fig. 2, lower right panel, shows that nearly 60% of the northerly winds occurred by early July, with 80% accumulation by early August.

3.2. Hydrography

During winter and spring cruises, surface temperatures, salinity and fluorescence were low and uniform along the entire Newport Hydrographic line (Figs. 3–5). Due to the El Niño, temperatures in winter 1998
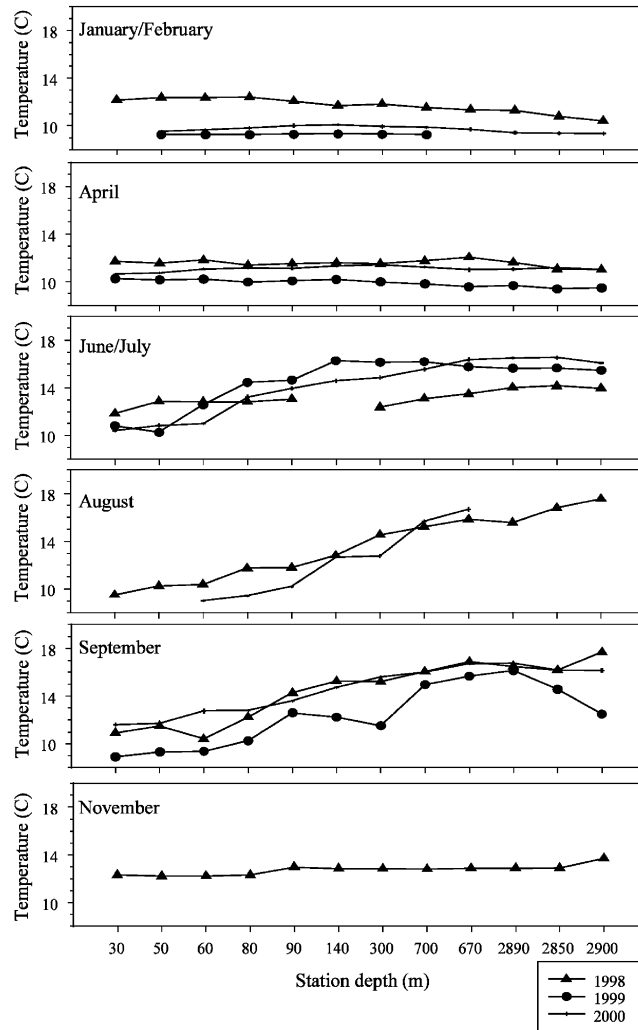
Fig. 3.   3 m temperature data from CTD casts.

were several degrees warmer than in winter 1999 and 2000 (Fig. 3). In each summer, upwelling caused strong cross-shelf temperature gradients. Sea surface temperatures nearshore were typically 9–12 °C; offshore, temperatures were as high as 17 °C. Summer sea surface temperatures during 1998 were similar to other years in nearshore waters, but offshore, temperatures tended to be cooler in early summer, and warmer in late summer than in subsequent years. Salinity increased from onshore to offshore during fall, winter, and early spring, but decreased from onshore to offshore during summer in all years due to nearshore coastal upwelling displacing the fresher surface water offshore (Fig. 4). During July 1999, the Columbia River plume was pronounced; salinity in the plume was <24 PSU. Fluorescence was much higher nearshore than off the shelf during summer of all years (Fig. 5). Fluorescence peaked at the shallowest stations in early summer, but the fluorescence peak was at mid-shelf stations in late summer.
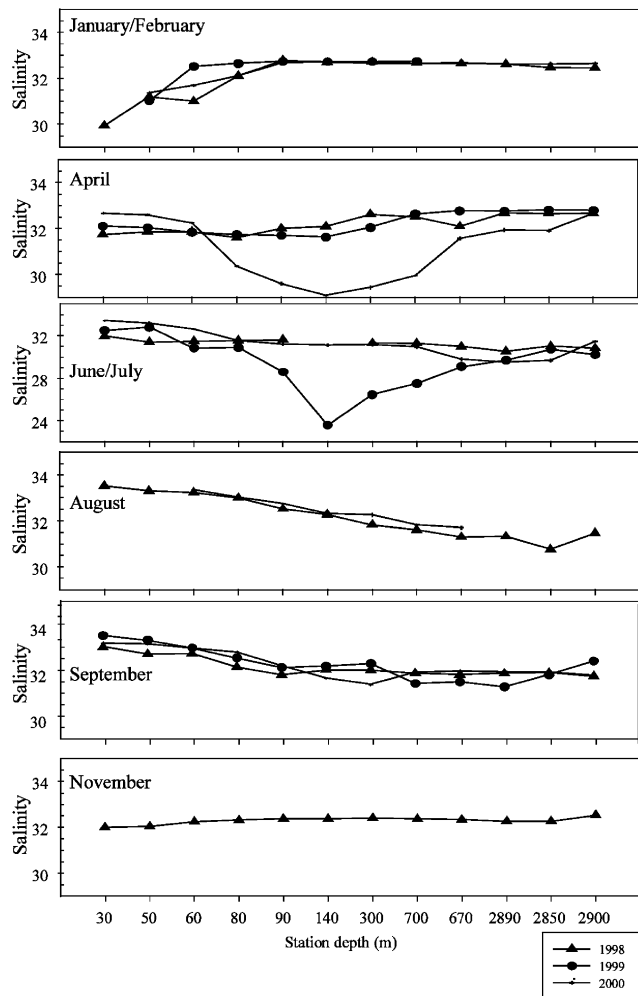
Fig. 4.   3 m salinity data from CTD casts. Note the different scale for June/July.

3.3. Zooplankton

Cluster analysis identified four primary groups (clusters) of stations based on similarities in zooplankton community structure (Fig. 6): Cluster 3—an "El Niño" group present from April 1998 through November 1998; Cluster 1—a "Transitional" group present across the continental shelf and slope only before and after the El Niño; Cluster 2—a group found in deep off-shelf waters in summer and at all stations in winter ("offshore summer/everywhere winter group") present during 1999 and 2000; and Cluster 4—a primarily on-shelf group present during summers of 1999–2000. Examination of Figs. 6 and 7 reveals a strong time-progression in zooplankton communities, possibly stabilizing into a seasonal cycle by summer 1999. Two subgroups, Clusters 2a and 3a, are also identified (Fig. 6): group 2a was present primarily nearshore during spring 2000 and at mid and off-shelf stations in summer 2000 (Fig. 7); group 3a separated the El Niño group to early (Cluster 3) and late-stage (Cluster 3a) groups.

A 2-dimensional NMDS ordination (Fig. 8) explained 82.7% of the variance in zooplankton community structure. The clusters identified in Fig. 6 separate cleanly from each other in the ordination with the
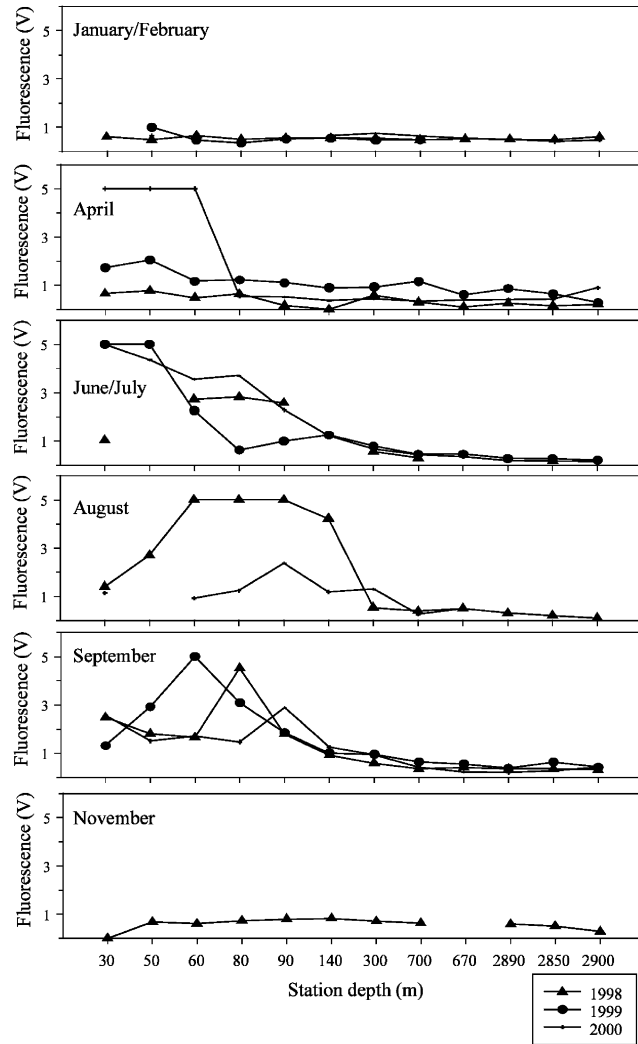
Fig. 5.   3 m fluorescence data from CTD casts.

exception of the subgroup 2a which had some overlap with Cluster 4. In the cluster dendogram (Fig. 6), Cluster 2a is only distantly related to Cluster 4, as indicated by the high level at which it joins to Cluster 2.

Correlations of the NMDS ordination with environmental factors revealed that the primary factor associated with the ordination of zooplankton communities along Axis 1 was the date of sampling ($R^2 = 0.71$) (Fig. 8 upper right panel) indicating a progression in community structure over time. No other environmental factor had an $R^2 > 0.2$ with Axis 1. Although clusters 2 and 4 seem from Fig. 7 to differ primarily by on-shelf/off-shelf differences, longitude did not correlate strongly with either axis in the NMDS (R^2 with Axis 1 $= 0.08$; R^2 with Axis 2 $= 0.25$), although, of the environmental variables we measured, longitude was the variable which explained the greatest amount of variability along Axis 2. Other than longitude, only fluorescence was correlated with Axis 2 ($R^2 = 0.22$).

Abundances of some of the dominant copepod species (*Pseudocalanus mimus*, *Paracalanus parvus*,
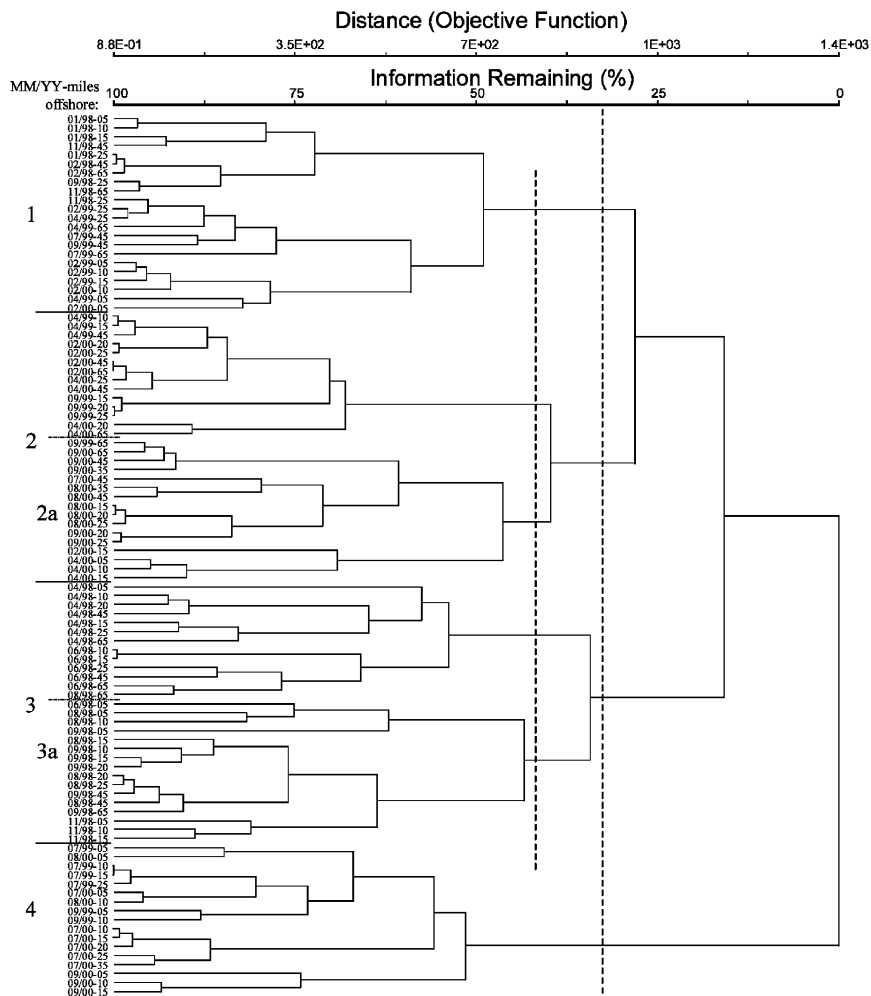
Fig. 6.   Dendogram from cluster analysis of zooplankton composition. Four primary clusters and two secondary clusters are identified.

Acartia longiremis, *Calanus marshallae*, and *C. pacificus*) from spring and summer 1998 and 1999 have been previously published in Peterson and Keister (2002), and thus are not shown here.

3.3.1. El Niño group (Cluster 3)

Most of the taxa that had significant Indicator Species values (Table 1) were indicative of the El Niño group (Cluster 3). The zooplankton assemblages sampled during the El Niño were very diverse: the average number of taxa in a sample during the El Niño was 23.8 ± 0.06 compared to 21 ± 1.08 in the "Transitional" cluster (Cluster 1), 14.7 ± 0.76 in the "off-shore summer/everywhere winter" cluster (Cluster 2), and 12.8 ± 0.93 in the "nearshore summer" cluster (Cluster 4). Of 104 taxa identified overall, 16 occurred only in the "El Niño" group and another 20 occurred only in the "Transitional" or "El Niño" and "Transitional" groups combined. Average abundance of 46 taxa was higher during the El Niño than any other time. Fig. 8, lower right panel, shows that diversity was strongly correlated with the NMDS ordination. Species richness (R^2 with Axis 1 = 0.71) and Shannon's Diversity Index (R^2 with Axis 1 = 0.72) (Fig. 8) were correlated more strongly than other variables.

Km offshore/ Water depth (m)	8km/ 60m	16km/ 80m	24km/ 90m	32km/ 140m	40km/ 295m	56km/ 700m	72km/ 670m	105km/ 2850m
Jan 98	1	1	1	--	1	--	1	1
Apr 98	3	3	3	3	3	--	3	3
Jun 98	3a	3	3	3	3	--	3	3
Aug 98	3a	3a	3a	3a	3a	--	3a	3
Sep 98	3a	3a	3a	3a	1		3a	3a
Nov 98	3a	3a	3a	1		1	1	1
Feb 99	1	1	1	--	1	--		--
Apr 99	1	2	2	--	1	--	2	1
Jul 99	4	4	4	--	4	--	1	1
Sep 99	4	4	2	2	2	--	1	2a
Feb 00	1	1	2a	2	2		2	2
Apr 00	2a	2a	2a	2	2	--	2	2
Jul 00	4	4	4	4	4	4	2a	--
Aug 00	4	4	2a	2a	2a	2a	2a	--
Sep 00	4	4	4	2a	2a	2a	2a	2a

Fig. 7. Cluster groups arranged by cruise and station with clusters circled to show temporal and spatial patterns. – = Not Sampled. Daytime sampling is indicated by italics; nighttime by bold.
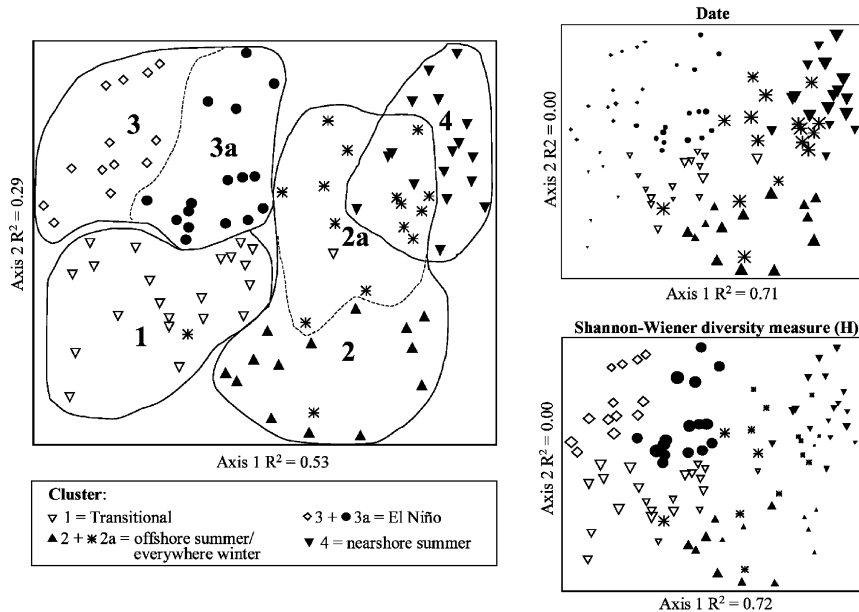

Fig. 8. Left panel: NMDS ordination of samples coded by cluster groupings defined in Fig. 5. Clusters generally correspond to 1) "Transitional" zooplankton group, 2) "normal" summer offshore/winter group, 3) El Niño group, and 4) "normal" summer nearshore group. The proportion of the overall variance in zooplankton species abundances explained by each axis is given. Upper right panel: The ordination showing the relationship of sampling date to the ordination of samples. The size of the symbol is related to the date—smallest symbols are the earliest sampling dates; largest symbols are the latest sampling dates within the study period. Lower right panel: Relationship between the NMDS ordination and the Shannon–Wiener diversity measure. Larger symbols indicate more diversity in the zooplankton sample. The correlation of the index with each axis is given.

Six taxa—the copepods *Calanus marshallae*, *Calocalanus styliremis*, *Corycaeus anglicus*, *Ctenocalanus vanus*, *Oncaea spp.*, and *Pseudocalanus spp.* (mostly *Pseudocalanus mimus*)—were highly correlated with Axis 1 of the NMDS (Fig. 9). All but *C. marshallae* and *Pseudocalanus spp.* were negatively correlated with Axis 1, indicating that most taxa were more abundant in 1998 (during the El Niño) than in 1999 or

Table 1
Taxa with significant Indicator Species Values. (Indicator values are giving in brackets.) Clusters are those identified in Fig. 5. Taxa names in **bold** are very good indicators for that cluster—their indicator value is >5× higher for that cluster than for any other cluster in the group

Cluster 1: Transitional group	Cluster 2: Offshore summer/winter	Cluster 3: El Niño	Cluster 4: Nearshore summer
Acartia danae (22)	*Scolecithricella minor* (21)	Barnacle larvae (26)	***Acartia hudsonica*** (20)
Calocalanus styliremis (45)	*Pseudocalanus spp.* (28)	Bivalve larvae (28)	*Acartia longiremis* (54)
Calocalanus tenuis (38)		*Calocalanus styliremis* (29)	***Calanus marshallae*** *(60)*
Chaetognaths (23)		***Calanus pacificus*** *(60)*	***Centropages abdominalis*** (65)
Clausocalanus arcuicornis (28)		*Candacia bipinnata* (14)	Euphausiids (31)
Clausocalanus parapergens (37)		Chaetognaths (43)	***Evadne nordmanni*** (33)
Clausocalanus pergens (48)		***Coelenterates*** *(56)*	Larvaceans (28)
Clausocalanus spp. (46)		***Corycaeus anglicus*** *(64)*	***Microcalanus pusillus*** (26)
Ctenocalanus vanus (41)		*Ctenocalanus vanus* (43)	*Pseudocalanus spp.* (39)
Lucicutia flavicornis (23)		Doliolids (29)	
Metridia spp. (28)		**Echinoderm larvae** *(43)*	
Oncaea spp. (20)		***Eucalanus californicus*** (38)	
Ostracods (27)		Euphausiids (30)	
Paracalanus parvus (32)		Larvaceans (33)	
		Lucicutia spp. (23)	
		Metridia spp. (35)	
		Microsetella spp. *(25)*	
		Muggiaea spp. (48)	
		Oncaea spp. (35)	
		Paracalanus parvus (33)	
		Pleurobrachia spp. *(55)*	
		Pteropods (58)	
		Siphonophores (21)	

2000. *Pseudocalanus spp.*, though one of the dominant taxa at all times (Table 2), was present during the El Niño in <5% of its "normal" nearshore summer abundance. Another numerically dominant taxon, *Oithona spp.* (>98% *Oithona similis; <2% Oithona spinirostris*) was found in greatly diminished numbers during the El Niño. Other taxa, particularly *Ctenocalanus vanus*, *Calanus pacificus*, *Paracalanus parvus*, *Metridia spp.* and pteropods, were in much higher abundances in 1998.

3.3.2. Transitional group (Cluster 1)

The "Transitional" group was present only before and after the El Niño. Assemblages defining the "Transitional" group stations dominated in January 1998 and in February and April 1999; by summer 1999 the transition from El Niño to "normal" had essentially been completed nearshore, but the "Transitional" group was still present offshore through summer 1999. The "Transitional" group assemblages disappeared during the following winter.

Two species, *Acartia danae* and *Calocalanus tenuis*, were strong indicators of the "Transitional" group (Table 1). Several other taxa (such as *Calocalanus styliremis*, *Ctenocalanus vanus*, and *Oncaea spp.* among others) that were indicators of the El Niño community were also indicators of the "Transitional" group. All species of *Clausocalanus* were, on average, more abundant in the "Transitional" group than in any other group.
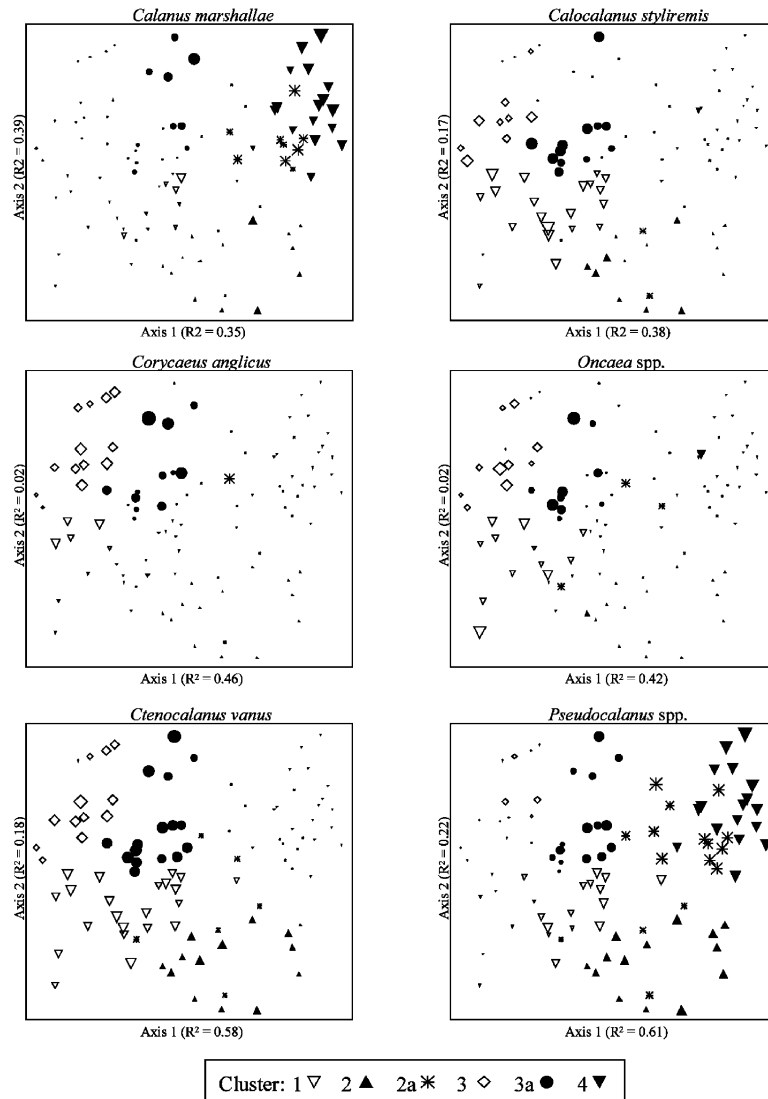
Fig. 9. NMDS ordination overlaid with abundances of taxa that were strongly correlated ($R^2 > 0.35$) to Axis 1. Within each plot, the size of the symbol is proportional to the abundance ; symbol sizes (eg. abundance of animals) among plots cannot be compared. The correlation of each species with the axes is given.

3.3.3. "Normal" summer offshore/everywhere winter group (Cluster 2)

Only two taxa (*Scolecithricella minor* and *Pseudocalanus spp.*) were indicative of the summer offshore/everywhere winter group (Cluster 2). Most other species tended to be in relatively moderate to low abundances and/or infrequently found in samples from that cluster. The numerically dominant species in the offshore summer/everywhere winter group were *Pseudocalanus mimus*, *Oithona similis*, and *Acartia longiremis* (Table 2). Only eight taxa (including *Neocalanus plumchrus*, *N. cristatus*, salps, and the cteno-phore *Pleurobrachia*) were in higher abundance in the summer offshore/everywhere winter group than in other groups.

Table 2
Average abundance (No. m^{-3}) of taxa that were dominant (>20 m^{-3}) in any cluster and abundance of taxa which were good indicators (indicator value $>5x$ than in any other cluster). Some taxa were both dominant and good indicators. **Bold** stands for dominant species (density >20 m^{-3}); CAPS stands for good indicator

	Cluster 1: Transitional group	Cluster 2: Offshore summer/winter	Cluster 3: El Niño	Cluster 4: Summer nearshore
Acartia hudsonica	2.0±0.41	0.0±0.00	1.1±0.10	26.3±4.14
ACARTIA DANAE	2.4±0.31	0.5±0.04	1.1±0.13	0.0±0.00
Acartia longiremis	1.5±0.18	80.0±4.42	33.4±1.92	485.9±28.1
AMPHIPODS	21.4±4.46	1.2±0.11	0.3±0.03	0.8±0.10
Calanus marshallae	4.1±0.54	16.3±1.14	9.6±1.18	118.0±9.56
Calanus pacificus	2.8±0.18	1.8±0.13	55.0±3.40	0.0±0.00
Centropages abdominalis	0.04±0.01	0.3±0.03	4.1±0.35	69.5±7.46
Clausocalanus pergens	51.7±2.07	16.6±1.59	14.3±0.97	1.2±0.16
Clausocalanus spp.	41.1±2.47	4.1±0.24	16.3±1.22	1.2±0.24
COELENTERATES	0.2±0.03	0.1±0.01	15.0±0.81	3.5±0.85
Corycaeus anglicus	4.1±0.41	1.2±0.21	29.1±1.30	0.0±0.00
Ctenocalanus vanus	55.6±1.74	6.4±0.31	94.1±3.59	0.0±0.00
ECHINODERM LARVAE	0.3±0.05	0.9±0.12	8.3±0.39	7.4±1.21
Eucalanus californicus Johnson	0.5±0.05	0.6±0.05	23.4±1.95	0.3±0.06
EUPHAUSIIDS	2.7±0.22	23.5±1.54	19.8±0.60	92.6±6.66
EVADNE NORDMANNI	0.0±0.00	0.0±0.00	1.9±0.22	17.5±2.60
LARVACEANS	18.7±1.49	42.4±2.97	85.2±4.64	59.2±3.83
MESOCALANUS TENUICORNIS	7.9±0.79	4.5±0.40	4.7±0.21	1.0±0.18
Metridia spp.	30.6±1.51	36.9±4.32	67.6±2.34	11.5±0.79
MICROCALANUS PUSILLUS	0.1±0.02	0.1±0.02	0.0±0.00	3.5±0.35
MICROSETELLA SPP.	0.1±0.02	0.1±0.01	1.0±0.06	0.0±0.00
MUGGIAEA Spp.	0.0±0.00	0.0±0.00	6.6±0.42	0.0±0.00
Oithona spp.	283.1±9.81	466.5±20.77	269.8±8.73	526.6±17.58
Paracalanus parvus	63.6±2.73	77.9±5.01	152.3±6.15	59.8±8.50
PLEUROBRACHIA	0.0±0.00	0.5±0.06	0.2±0.04	0.0±0.00
Pseudocalanus spp.	196.9±13.18	748.1±39.6	112.4±7.51	2639.7±209.18
PTEROPODS	1.9±0.14	0.9±0.07	55.7±2.24	3.4±0.45
SIPHONOPHORES	0.0±0.00	0.4±0.06	9.2±0.81	0.0±0.00

3.3.4. "Normal" summer nearshore group (Cluster 4)

Nine taxa were significant indicators of the nearshore summer group (Cluster 4) (Table 1). The nearshore summer group was characterized by very high abundances of several taxa, most notably *Pseudocalanus mimus*, *Oithona similis*, *Acartia longiremis*, and *Calanus marshallae*, and very low abundances of *Calanus pacificus*, *Clausocalanus spp.*, and *Ctenocalanus vanus* (Table 2).

3.3.5. Spatial extent of the upwelling group

Strong longitudinal differences in zooplankton assemblages were seen during the summers of 1999 and 2000 (Fig. 7). The nearshore group extended substantially farther offshore in July 1999 and 2000 than in August/September 1999 and 2000. There was no apparent correlation between longitudinal position of the change in cluster number (i.e. from cluster 4 to Cluster 2 or 2a) and any particular value of or rapid change in sea surface temperature or salinity.

4. Discussion

4.1. El Niño group

Results reported here on the events surrounding the 1997/1998 El Niño were similar to results of a study on the biweekly sampling of a single nearshore station at 60 m water depth along the Newport Hydrographic Line reported in Peterson et al. (2002). In both studies, a Transitional group was seen immediately preceding and following the El Niño. The biweekly study is useful to more finely resolve the timing of arrival of the El Niño zooplankton assemblages: at the nearshore station, Transitional zooplankton assemblages were observed before the El Niño in August–October 1997, El Niño assemblages were found from November 1997 through early June 1998, then the Transitional assemblages were again present from July through December 1998. The "normal" winter assemblages were first seen in February 1999 at the nearshore station. Because the seasonal sampling program described in the study reported here was not initiated until late-January 1998, we do not know how early the Transitional assemblages might have occurred in offshore waters, but based on results from the nearshore, biweekly time series, the transition in offshore waters probably began in late summer or early autumn of 1997.

Because the physical El Niño signal had mostly disappeared by the summer of 1998 (Huyer, Smith & Fleischbein, 2002), whereas the biological signal had not, we suggest that there are time lags between the physical signals and biological responses. The hydrographical data for the upper 100 m (the depth of our sampling) are not very different between the summers of 1998 and 1999/2000, but the zooplankton community present was very different from the subsequent years. At the nearshore station, Peterson et al. (2002) found that the copepod community did not return to normal until several months after the physical El Niño signal had disappeared. We hypothesize that northerly transport during the El Niño was so strong during winter 1997/1998 that the southern waters (and the species which they contained) were transported so far north into the Gulf of Alaska that, when currents reversed in spring 1998, the animals returned to the south were those of southern origin. Some rough estimates of potential transport distances poleward during the El Niño, and equatorward afterwards, can be calculated using velocity measurements from Kosro (2002) and Huyer, Pillsbury and Smith (1975). During the period of August 1997 to February 1998, anomalous poleward displacement was ~350 km per month (18° latitude or ~2500 km over the period assuming uniform alongshore transport) (Kosro, 2002). Assuming total equatorward transport over the shelf of 10–20 cm/s during the April–September upwelling season (estimated from Huyer et al., 1975), equatorward transport in spring/summer 1998 may have totaled 1500–3000 km over the period. Though uniform poleward intensification of currents probably did not occur, it seems reasonable that boreal species were displaced far enough to the north to prevent their replenishment off the Oregon coast in summer 1998.

An alternative hypothesis for the lack of the normal upwelling assemblage of boreal neritic origin during summer 1998 is that the source of the upwelled water was not the same as in "normal" years. We do not know the source of the seed populations of the summer upwelling assemblage; our hypothesis is that alongshore transport during upwelling brings the animals along the coast from the north, but alternatively, the animals may be present in the deep water that is upwelled onto the shelf in the spring, where they then reproduce. It is noteworthy that coastal sea levels were near normal by June 1998 (Huyer, Smith & Fleischbein, 2002), and that upwelling was strong during the summer of 1998 (as indicated by the wind data shown in Fig. 2 and by the Bakun upwelling index, available at http://www.pfeg.noaa./gov/products/current-products.html), though water over the shelf remained ≥ 1 °C warmer and 0.2–0.5 fresher than normal (Huyer, Smith & Fleischbein, 2002). The characteristics of the upwelled water during 1998 indicate that the water was not coming from the same source as during normal years, so may not have carried the animals necessary to reseed the coastal waters. The source of the water upwelled off Oregon may have been affected by the anomalously strong northward displacement during the El Niño (Huyer, Smith &

Fleischbein, 2002), making a resolution between our two hypotheses (animals brought from the north or animals brought from deep water) especially difficult.

The El Niño zooplankton group observed off the Oregon coast was unique compared to groups present during "normal" years. Although many of the species sampled are found throughout the study area during normal winters and offshore during normal summers, the species compositions do not support the hypothesis that the El Niño is simply greater poleward transport of the Davidson Current, as occurs during every winter. Instead, a mix of southern neritic forms (that appear off Oregon each winter) and Transition Zone/offshore species (which are typically found up to several hundred kms from shore) were found during the El Niño, resulting in very high species diversity and indicating both poleward and onshore transport.

4.2. Transitional group

A "Transitional" group was present before the El Niño and for several months afterwards. The community composition in samples making up the "Transitional" group was a mix of species typical of the El Niño and "normal" groups: the communities were comprised of moderate numbers of many of the species found in high abundances during the El Niño, such as *Ctenocalanus vanus*, *Calanus pacificus*, and *Corycaeus anglicus*, but also had moderate abundances of species such as *Pseudocalanus spp*. and *Acartia hudsonica* that were present in very high numbers in the "normal" nearshore summer group. The "Transitional" community persisted in offshore waters during summer 1999 before the "normal" offshore summer/winter group emerged in late 1999. However, because there is a high degree of interannual variability, we can only hypothesize at this time that the zooplankton assemblages found in 2000 are "normal". Whether the seasonal differences in zooplankton assemblages had started to stabilize cannot be known until several more years are sampled. Because Cluster 2a separated Cluster 2 into winter and offshore summer 1999 versus offshore summer 2000, there is some indication that the zooplankton assemblages had not stabilized. Year-to-year variability may prevent any two years from looking identical. Our sampling program will continue through at least 2003, so we hope to answer this question in the future.

4.3. Onshore/Offshore differences

- The nearshore summer group (Cluster 4) was the most unique of the 4 groups identified, as indicated by the level at which it grouped with the other clusters (Fig. 6). The nearshore summer group differed from other groups in several ways: Boreal neritic species (e.g. *Pseudocalanus spp*., *Acartia longiremis*, *Calanus marshallae*, and *Centropages abdominalis*) dominated the zooplankton, some in very high (>100 m^{-3}) abundance. These copepods are all common species in Gulf of Alaska (Cooney, Coyle, Stockmar, & Stark, 2001), and Southern British Columbia (Mackas & Sefton, 1982) coastal waters, and their presence indicates the transport of coastal waters from the north.
- Larvae of several meroplanktonic taxa (such as bivalves, barnacles, polychaetes and echinoderms) were present in relatively high numbers in the nearshore summer assemblages.
- There was a relative absence of warm-water species, such as *Metridia pacifica*, the *Clausocalanus* species, and *Calanus pacificus*, which may have been held off the shelf by the offshore transport of surface waters during upwelling. Many of the warm-water species that appear offshore during summer (in Cluster 2) can appear nearshore during summer, but only during extended periods of downwelling-favorable winds (our unpublished data).
- Species diversity in the nearshore summer assemblages was very low as indicated by low Shannon–Wiener diversity indices (Fig. 8, lower right panel). All together, 17 taxa occurred in the offshore summer/everywhere winter group (Cluster 2) that were absent from the nearshore summer group (Cluster 4); only 5 taxa occurred in the nearshore summer group that were absent from the offshore summer/winter group. The result that the nearshore summer assemblages were less diverse than the

offshore summer/winter assemblages agrees with Hebard (1966) and Lee (1971), who both found that diversity tended to increase offshore.

Our finding, that the "nearshore summer" and "offshore summer/everywhere winter" groups differ in species composition more than just by a shift in dominance of the common species, contrasts with findings of Hebard (1966), Mackas and Sefton (1982), and Mackas (1992). Mackas, working off Vancouver Island, BC, found that onshore–offshore differences were primarily shifts in dominance of common species. Hebard, who in 1962–1964 sampled some of the same stations we sampled in this study, used an Index of Affinity developed by Sanders (1960) to examine similarities among stations. Like us, he found that during the winter, stations were similar across the continental shelf, but during the summer, stations on the shelf differed from those off the shelf. But, like Mackas and Sefton, Hebard found that seasonal and cross-shelf species assemblages differed only by the relative abundance of common species rather than by the presence/absence of a different assemblage of species.

The picture which emerges from our findings is that, were it not for the coastal upwelling process, the shelf waters in both summer and winter would be populated by offshore Transition Zone and subtropical neritic species. The zooplankton assemblages present offshore during the summer upwelling season were similar to the assemblages present all across the shelf during winter and spring (Cluster 2) indicating that the summer nearshore group displaces the otherwise omnipresent "winter" group. Alongshore transport of boreal neritic species into the area, spawning of many nearshore meroplanktonic species, and increased production of more uniformly distributed species (such as *Pseudocalanus spp.*, *Oithona spp.*, and euphausiids) in the nutrient-rich nearshore zone may lead to the unique group found nearshore during upwelling. Should climate change lead to a decreased rate of upwelling, the Oregon shelf zooplankton community could quickly come to resemble that of the shelf off central or southern California with a dominance of *Calanus pacificus*, *Paracalanus parvus*, *Ctenocalanus vanus*, and *Corycaeus anglicus*.

We found a longitudinal separation in zooplankton assemblages during the upwelling season, but the distance from shore where the separation fell was variable seasonally. Cluster 4 (the nearshore group) extended substantially farther offshore in early summer than in late summer. Morgan et al. (in press), who examined variations in copepod community composition along the entire Oregon coast, found that onshore–offshore differences were pronounced; a shelf community was distinct from an offshore/slope-water community, but they found that the separation between the upwelling and offshore communities fell fairly consistently at the shelf-break (by their definition, at about 180 m water depth). Our separation between sample groups came between 295 and 700 m depth during early summer, and between 80 and 150 m during late summer. A few stations that Morgan et al. sampled offshore of 180 m depth fell into their nearshore cluster—they hypothesized that those stations were in areas of particularly strong offshore transport, such as off Newport, where our samples were collected. Morgan et al. (in press) only sampled during early summer (June/July), so did not sample during times of less-intense upwelling (e.g. September) and therefore times when the nearshore community may have been compressed closer to shore.

The separation between the summer nearshore group and summer offshore group may not have been as strong during 2000 as during 1999. In the NMDS ordination (Fig. 8), five of the seven samples in Cluster 2a that overlapped with Cluster 4 were the mid-shelf stations of August and September 2000 (the 90 m, 140 m, and 295 m depth stations in August, and the 140 m and 295 m depth stations in September). That those samples lay close to samples from Cluster 4 indicates that the community composition was relatively similar. The same is not true of September 1999—the mid-shelf stations were less associated with Cluster 4 in the NMDS ordination, indicating that the separation between the nearshore and offshore groups may have been more distinct in 1999 as compared to 2000. However, diel sampling differences may have influenced the association; a shift from day to night sampling occurred at the separation in cluster groups in 1999, but not in 2000. We do not think that diel sampling differences influenced differences among clusters, since cluster number rarely changed between day and night samplings, but there may be subtle

differences between day and night samples not noticeable when examining clusters or individual species abundances that slightly affected the NMDS ordination.

Mechanisms controlling the spatial extent of the upwelling assemblages are not clear, but are important to examine. The zooplankton assemblages found in upwelling areas are likely to be of particular importance to predator species such as juvenile salmonids, which are rarely found outside of nearshore areas (R. Brodeur & R. Emmett, personal communication). In our study, two zooplankton groups (an onshore and an offshore group) were seen in summer when there were onshore–offshore gradients in temperature, salinity, and chlorophyll. When there were no gradients in hydrographic structure, as occurs in winter (Figs. 3–5), there was no onshore–offshore separation in groups. However, in summer, there was no correlation between longitudinal position of the change in cluster number (from Cluster 4 to Cluster 2 or 2a) and any rapid change in sea surface temperature, salinity, or fluorescence. Variations in sea surface temperature/salinity characteristics of the nearshore versus offshore water may not have been noticeable in relation to the zooplankton differences because our zooplankton sampling was integrated over the upper 100 m of the water column. If different species respond differently to physical gradients and/or have different vertical distributions, and therefore experience different physical fields, we may not be able to simply match changes in the physical data with changes in zooplankton when examining the zooplankton community as a whole.

The overall development of the summer upwelling system on a seasonal basis may be important in the longitudinal extent of the nearshore zooplankton group. Short-term wind events may play a role in the variation in the extent of the upwelling group, but examination of Fig. 2 (left panels) reveals little evidence of that. In 1999, northerly winds were stronger in the 7 days prior to the July sampling, when the upwelling group extended far offshore, than they were before the September sampling, when the group was compressed near shore. But in 2000, winds were southerly in the 7 days prior to the July and September samplings when the upwelling group extended far offshore, and winds were northerly prior to the August cruise when the group was compressed near shore. So, instead, we hypothesize that the upwelling assemblages are transported farther offshore during the peak of the upwelling season when northerly winds are strongest overall (typically June/July) than later in the season after northerly winds have begun to relax. Examination of the cumulative northerly wind stress (Fig. 2 right panels) supports that hypothesis: in both years, nearly 80% of the cumulative northerly wind stress occurred before August.

4.4. Indicator taxa

Because Indicator Values are based on the relative abundance of a species across groups, species that are highly abundant overall are not necessarily statistically better indicators than species with low abundances. Also, because we used a small (0.5 m diameter) plankton net, larger or rare taxa were not likely to have been captured and subsampled reliably, so taxa that may be indicators in nature may not have occurred as indicators in our samples.

Ideally, the best indicators would be both abundant and faithful to a group so that field sampling and subsampling methods reliably uncover the species when present. Alternatively, a less abundant species that is faithful to a group to the point that its mere presence in a sample is indicative would make a good indicator. *Pseudocalanus spp.*, for instance, though highly abundant in, and a significant indicator of, the nearshore summer group (Cluster 4), is not a useful indicator of that group because it is found frequently in, and is abundant in, all groups. The siphonophore, *Muggiaea spp.*, on the other hand, though not very abundant, was found in almost half of all samples from the El Niño cluster (Cluster 3) and not in any other sample, making it a good indicator of the El Niño group.

Russell (1935, in Raymont, 1983) suggested that associations of several species may be the best indication of particular water masses. Here, we only tested individual species' value as indicators, but several strong indicators of the same group may together be the best indication of that group. There were several

taxa that could be good indicators of the El Niño or nearshore summer groups. *Calanus pacificus*, coelenter-ates, *Corycaeus anglicus*, *Muggiaea spp.*, *Pleurobrachia spp.*, and pteropods served as good indicators of the El Niño group. *Calanus marshallae* and *Centropages abdominalis* had high IV's for the nearshore summer group (Cluster 4). Morgan et al. (in press) also found that *C. marshallae* was a significant indicator species of on-shelf waters, and Cross and Small (1967) suggested that *Centropages abdominalis* could be a useful indicator of nearshore waters during the summer. Frolander (1962); Cross and Small (1967), and Peterson (1972) all found that *Acartia danae* may be used as a species indicative of warm water, but *A. danae* was only an indicator of the "Transitional" group in this study and was not an indicator of either the El Niño or offshore summer/winter groups.

Three taxa, *Acartia hudsonica*, *Evadne nordmanni*, and *Microcalanus pusillus*, occurred in >25% of the nearshore summer samples (Cluster 4) and were significant indicator species for the nearshore group even though they were found in low to moderate abundance there. This indicates that their presence, although they formed a relatively small fraction of the population, may have been important in defining the clusters. Peterson, Miller and Hutchinson (1979) and Peterson and Miller (1976) found *A. hudsonica* (which they called *A. clausi*) and *Evadne nordmanni* almost exclusively within 7 km of shore off New-port, Oregon.

Most species associated with the offshore summer/everywhere winter group (Cluster 2) were found in higher abundance during the El Niño, so were better indicators for that cluster (Cluster 3) than for the offshore summer/winter group. The IV's for *Scolecithricella minor* and *Pseudocalanus spp.* (21 and 29 respectively) in the offshore summer/winter group, though statistically significant, are probably not high enough for those taxa to be useful ecological indicators. The offshore summer/winter group, though readily differentiable from other groups when examining the zooplankton community overall, had no distinguishing characteristics when examining individual species.

5. Conclusions

We have shown that zooplankton community composition off the Oregon coast varies seasonally and with El Niño events. In summer, there is a unique zooplankton assemblage that populates continental shelf waters and is boreal neritic (coastal Gulf of Alaska) in origin. Offshore of the shelf, the assemblages are a mixture of species that have subtropical neritic affinities and Transition Zone affinities. The location of the transition between shelf and slope assemblages, as indicated by cluster analysis, was not related to abrupt changes in hydrography, but may be related to seasonal changes in strength of upwelling. During the height of the upwelling season in July, the transition point was farther from shore than late in the season. During winter, the shelf assemblages were not distinguished from the offshore assemblages, and during non-El Niño years, the summer offshore assemblages were similar to the winter assemblages. The effects of the 1997/1998 El Niño on zooplankton lasted far longer than the physical effects, with the shelf and offshore assemblages not returning to normal until mid-late winter 1999.

Acknowledgements

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