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Interannual variability in copepod community composition at a coastal station in the northern California Current: a multivariate approach

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Abstract

We sampled a single station in the coastal zone off Newport OR (9 km from shore; 60 m water depth) on 206 occasions during 12 years: 1969–1973, 1983 and 1996–2001. We used cluster analysis, ordinations, and indicator species analysis (ISA) to describe temporal variations in copepod community composition. Copepod community structure during summer was distinctly different from winter. Cluster analysis showed that the transition between winter and summer communities occurred early March/April in the 1970s, late (May/June) in the late 1990s, but in (March/April) since spring 2000. Seven copepod assemblages were identified: four were found during the summer upwelling season, two during large El Niño events, and one during winter. Interannual variations in the composition of the summer assemblages was seen: most sampling dates from the summers of 1970, 1973, 2000 and 2001 clustered into one group, and dates from 1971, 1972, and 1999 clustered into a second group. The 1983 and 1998 El Niño events clustered together, but subdivided into "early El Niño" and "late El Niño" communities. The summer of 1969 corresponded with a weak El Niño event but clustered differently from both the other El Niño events and other summer clusters. Samples collected during the 1972 El Niño event clustered with "normal" summers. Non-metric multidimensional ordination analysis showed that two axes accounted for 87% of the variability in community composition; Axis 1 was associated with the influence of El Niño events and seasonal downwelling, and Axis 2 was associated with upwelling-induced productivity. ISA showed *Centropages abdominalis*, *Acartia longiremis*, and *Microcalanus pusillus* as indicators of upwelling; *Corycaeus anglicus*, *Calanus pacificus*, and *Ctenocalanus vanus* as good indicators of El Niño; and *Ctenocalanus vanus*, *Clausocalanus*, and *Calocalanus styliremis* as good indicators of winter conditions.

1. Introduction

Copepod abundance and biomass in continental shelf waters of the northern California Current varies annually, and is highest during the summer upwelling season when phytoplankton biomass is highest, and lowest during winter months. Although changes in copepod abundance and biomass are linked to the seasonal cycle of phytoplankton growth, the greatest temporal changes in copepod species composition and

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community structure are driven by seasonal changes in coastal circulation patterns. These patterns have been described in a general way by Peterson and Miller (1975, 1977). During the summer upwelling season, coastal waters are transported equatorward due to wind-driven upwelling. As a result, the nearshore zooplankton species composition off the Washington and Oregon coasts resembles that of the coastal waters to the north in the Gulf of Alaska and along the southern British Columbia coast (Mackas, 1992). There are differences in species dominance among and within summers, and these are likely related to the strength and frequency of upwelling and downwelling events. Downwelling events in summer (caused by southwesterly winds) transport offshore species shoreward, modifying the nearshore community structure (Peterson and Miller, 1975). Upwelling winds weaken in September or October, and with the strengthening of the Aleutian Low Pressure system in the Gulf of Alaska in autumn, prevailing winds off the Pacific Northwest begin to blow from the southwest. Associated with this seasonal reversal in winds is a reversal in coastal currents. Thus, in autumn/winter, northward coastal flow transports a subtropical neritic zooplankton community to the northern California Current region (Peterson and Miller, 1977).

The summer and winter copepod communities are well defined by their dominant species: in summer, dominance is usually shared by *Pseudocalanus mimus*, *Calanus marshallae*, and *Acartia longiremis*. All of these species are common in summer in coastal waters to the north of Oregon (Mackas, 1992; Mackas et al., 2001; Mackas and Galbraith, 2002) and the Gulf of Alaska (Coyle et al., 1990; Cooney et al., 2001); thus in this paper, we refer to these as boreal or cold-water species. In winter, the community is composed of *Paracalanus parvus*, *Ctenocalanus vanus*, several species of *Clausocalanus*, *Calanus pacificus, Mesocalanus tenuicornis*, *Metridia pacifica* and *Corycaeus anglicus*. These species are common in the offshore waters of the California Current (Fleminger, 1967), or in coastal waters off central and southern California (Barnett and Jahn, 1987). Thus, we refer to them as warm-water species. *Oithona similis* is a ubiquitous species, an important member of both summer and winter communities (Peterson and Miller, 1977).

Community composition is disrupted during major El Niño events, becoming a mixture of cold-water and warm-water species. For example, during the most recent El Niño event of 1997/98, the five most abundant copepod species were *Paracalanus parvus*, *Pseudocalanus mimus*, *Acartia longiremis*, *Ctenocalanus vanus* and *Calanus pacificus* (Peterson et al., 2002).

In this paper, we discuss seasonal and interannual differences in copepod community composition using the multivariate techniques of ordination (non-metric multidimensional scaling—NMDS) cluster analysis, and indicator species analysis (ISA). We compare patterns in community composition to strength of upwelling in each year (using the Bakun upwelling index as a measure of upwelling strength) and to the strength of the Pacific Decadal climate Oscillation (PDO, Mantua et al., 1997). The analysis is based on 12 years of sampling off Newport, OR. Some of the samples were collected over a 5-year period in 1969–1973, and many of these have been described by Peterson and Miller (1975, 1977). Sampling also was carried out in 1983 (Miller et al., 1985) and from 1996 to 2001. Since 1969, eight El Niño events have originated at the equator, and we sampled the zooplankton during four of those events (the two strong El Niño events of 1983 and 1998, and two weaker events in 1969 and 1972). Thus consideration of the influences of strong and weak El Niño events on zooplankton in the northern California Current is also discussed in this paper.

2. Methods

Plankton data were collected on cruises made at biweekly intervals in summer and monthly intervals in winter at a station located 9 km from shore in 60 m water depth (44.65°N, 124.18°W) along the Newport Hydrographic (NH) Line. This station is referred to as NH 05. Charts showing the location of this station have been published elsewhere (Peterson et al., 2002). Zooplankton was collected using a 20-cm diameter bongo fitted with 239-μm mesh nets towed obliquely from near the sea floor to the sea surface (during the years 1969–1973), and a 50-cm diameter, 202-μm mesh net towed vertically from near the sea floor to surface, at a rate of 30 m/min (all other samples). A TSK flowmeter was used to monitor the amount of water filtered. Samples were preserved in a 5% buffered formalin/seawater solution.

In the laboratory, zooplankton samples were diluted to 8–10 times the settled volume and subsampled with a 1.1-ml stempel pipette. Two to five subsamples were counted. Copepods were identified by species and developmental stage and the abundance of each taxonomic group (number of individuals m^{-3}) was calculated. Though sampling was done with two somewhat different mesh sizes (202- vs. 239-μm mesh), we assumed that the mesh sizes were sufficiently similar to preclude bias in the presence/absence of species. However, there could be a difference in abundance of some of the copepodite stages. Slight differences in mesh sizes have little-to-no effect on our community structure analysis because community types are typically separated by large differences in both species density and the presence/absence of indicator species, not by subtle differences in density.

To explore the patterns in community structure, "species density" × "sample date" matrices were analyzed by multivariate analyses. Rare species, defined as those occurring in $<5\%$ of samples, were not included in the analyses. Data were $\log_{10}$ transformed before being analyzed. Cluster analysis was used to identify natural groupings; a Euclidean distance measure and Ward's Linkage Method were used. For presentation, the cluster dendogram is scaled both by Wishart's (1969) objective function and by percentage of information remaining. Wishart's objective function is a measure of information loss as clustering proceeds, and is calculated as the sum of the error sum of squares from the centroid of each group to the items in that group.

NMDS ordination was used to examine similarities in copepod community composition among sampling dates; Sorensen's (Bray-Curtis) distance measure was employed. NMDS is considered one of the most robust ordination methods when dealing with zero-zero species density pairs (Field et al., 1982; Gray et al., 1988). All multivariate analyses were conducted in PC-ORD for Windows 4.36B (McCune and 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 dimensions necessary to adequately describe the data.

A common set of environmental variables (such as CTD profiles, chlorophyll concentration, secchi depths) was not available for all sampling dates. Therefore we were not able to include such environmental variables in the ordinations. We did, however, look at simple bi-variate correlations between proportion of sampling dates that were grouped into the dominant summer clusters and (i) the value of the Bakun upwelling index (http://www.pfeg.noaa.gov), and (ii) the value of the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997). The Bakun index is a measure of the strength and variations in local coastal upwelling along latitude 45°N. The PDO is a climate oscillation that occurs over the northeastern Pacific ocean. It is an index based largely on the leading principal component of the North Pacific monthly sea-surface temperature variability from 20°N to 60°N and on the strength of the Aleutian Low pressure cell. Negative values indicate anomalously cool waters and vice versa.

ISA (Dufrêne and Legendre, 1997) was used to investigate which species were driving the differences among the clusters identified in cluster analysis. The Indicator Value for a species in a group is calculated as the product of the relative abundance of the species in the group (the mean abundance in the group divided by the sum of the mean abundances in all groups) and the frequency of occurrence of the species in samples in the group. Indicator Values 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 indicator values.

The hydrographic station NH 05 has been visited 206 times over the course of 12 years. Note that our cruises are unbalanced during the year. We sampled during 12 summers (1969–1973, 1983, 1996–2001), but winter months were sampled only during eight seasons (1969–1970, 1970–1971, 1971–1972, and each winter from 1996–1997 until 2001). Also, winter sampling was typically monthly (due to stormy weather) whereas summer sampling was typically biweekly.

3. Results

3.1. Community structure

At the highest grouping level, cluster analysis revealed strong seasonal variations in copepod community composition (Fig. 1). Most samples collected during the upwelling season, which spans calendar months in spring, summer, and autumn (henceforth referred to as "summer") clustered separately from those collected in winter. The summer group contained sampling dates from all years except for those taken during the two large El Niño events of 1983 and 1997–1998. Samples assigned to the summer group were dominated by copepod species typical of a boreal (cold-water) neritic community (Table 1). The summer group also included samples taken from April through October, and are representative both of the summer upwelling season (May–September), and the transitional months (April and October) that precede and follow the upwelling season. Four sampling dates fell outside this period (in March 1971, and November 1969, 1971 and 1999).

The winter group included 35 of the 40 sampling dates between November and March of all years sampled, as well as all of the samples collected during the 1983 and 1997/98 El Niño events. Samples assigned to the winter group were dominated by species typical of a 'warm-water community' (Table 1).

At our lowest grouping level, we identified seven groups (see Table 2):

- Cluster 1A contained all of the dates from summer 1969. This summer coincided with a moderate El Niño event (Fig. 2). The only other dates that were associated with Cluster 1A was 28 July 98 (during the 1997/98 El Niño) and 22 May 1970. We have named this cluster the "Weak El Niño Cluster".
- Cluster 1B contained samples collected primarily during June–July 1970 and June–September 1973, 2000 and 2001 (see frequency distributions in Fig. 3). We name this cluster "Summer/High Biomass".
- Cluster 2A contained sampling dates chiefly in August–October 1970, all months of the summers of 1971, 1972, 1999, and spring/early summer 1973, 1997, and 2000 (Fig. 3). We name this cluster, "Summer/Low Biomass".
- Cluster 2B was restricted to spring and autumn months of most years (Fig. 3) but included some dates from the summer of 1997 (Table 2). We name this the "Transitional Cluster".
- Cluster 3A contained samples collected early in the two strong El Niño events of 1983 and 1997/98. This is the "Early El Niño Cluster".
- Cluster 3B contained all samples from the middle and end of each large El Niño event. This is the "Late El Niño Cluster".
- Cluster 4 contained samples from non-El Niño winters, as well as some samples from spring 1996 and 1997. This is the "Winter Cluster".

3.2. Species abundances within clusters

Cluster Group 1B (Summer/High Biomass) had the highest abundances of *Acartia longiremis*, *Pseudocalanus mimus*, and C*entropages abdominalis* (Table 1). Warm-water species were virtually absent from this cluster group. In every case, average abundances of the five dominant cold-water species in Cluster 1B were significantly greater than abundances in Cluster 2A, based on non-overlapping 95% confidence intervals of the geometric mean abundances. Cluster Group 2A (Summer/Low Biomass) had moderate numbers of all dominant copepod species. Moderate abundances resulted because samples that grouped here came early in the seasonal production cycle (spring 1973, 1997, 2000) or during summers of apparent low productivity (1971, 1972 and 1999). Hence our designation of Cluster 1B as Summer/High Biomass and 2A as Summer/Low Biomass.

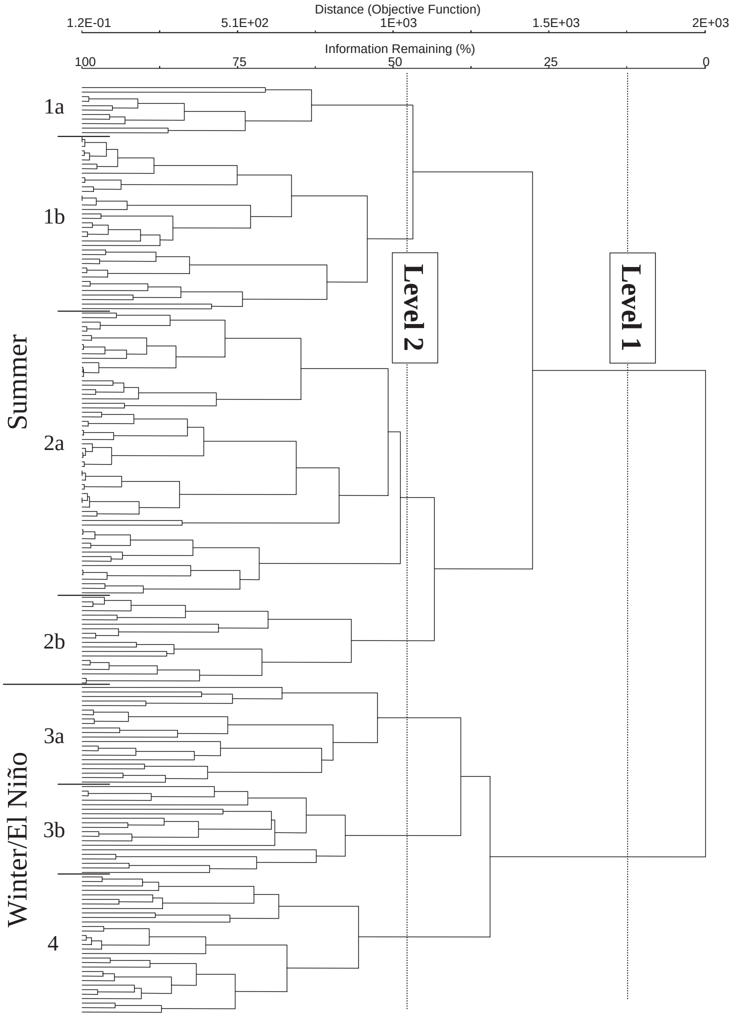

Fig. 1. Clustering dendogram. The end of each line on the left side of the dendogram represents one sampling data; a list of dates associated with each cluster is given in Table 2. The dendogram is scaled both by Wishart's (1969) objective function and by percentage of information remaining. Wishart's 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 to the items in that group.

Cluster Group 2B (Transitional cluster) represents a transitional assemblage of copepods, observed during September, October and November 1971, 1996, 2000; March–April 2001 and summer of 1997 (prior to arrival of the 1997–1998 El Niño). This group had moderate numbers of cold-water species but was distinguished chiefly by relatively high numbers of warm-water species compared to other non-El Niño summers. The highest abundances of *Paracalanus parvus, Ctenocalanus vanus, Clausocalanus* spp*., Calocalanus styliremis, Mesocalanus tenuicornis* and *Corycaeus anglicus*, and the second highest abundances of *Eucalanus californicus* were associated with Cluster Group 2B.

Cluster 1A (Weak El Niño cluster) was characterized by high abundances of *Pseudocalanus mimus* and *Calanus marshallae*, the second highest abundances of *Acartia hudsonica* and *A. longiremis*, but low abundances of *Centropages abdominalis*. A unique characteristic of Cluster Group 1A was that abundances of some of the warm-

Table 1
Average abundance (geometric mean) of the dominant species within each of the seven clusters with the upper and lower 95% confidence levels below. Arithmetic data were log $(Y + 0.1)$ transformed for averages and back-transformed for presentation; back-transformation sometimes resulted in negative lower confidence limits

	Summer				El Niño		Winter
	1A	1B	2A	2B	3A	3B	4
Cold-water Species							
Neritic							
Acartia hudsonica	55.9	31.7	1.5	0.2	0.3	0.9	0.0
	17.47–178.33	13.90–71.94	0.68–2.99	0.04–0.77	0.03–0.82	0.19–3.43	−0.01–0.13
Acartia longiremis	179.3	326.7	31.1	27.3	0.9	67.3	0.8
	63.61–505.31	233.82–456.47	16.69–58.06	8.48–87.17	0.17–3.37	38.70–117.03	0.30–2.12
Calanus marshallae	314.1	100.8	27.5	48.6	0.6	5.8	2.6
	152.65–646.17	73.34–138.58	18.43–41.13	27.47–86.08	0.13–1.89	1.96–16.88	0.89–7.51
Centropages abdominalis	15.2	155.6	1.0	34.3	0.4	0.5	0.0
	3.85–59.38	98.35–245.99	0.51–2.02	19.49–60.41	0.07–1.65	0.12–1.58	−0.01–0.11
Pseudocalanus mimus	1656.1	1757.1	596.7	672.4	5.2	404.6	261.4
	721.70–3800.10	1351.68–2284.07	461.63–771.20	435.43–1038.46	1.56–16.56	209.16–782.41	162.45–420.47
Offshore							
Metridia pacifica	0.8	1.2	1.0	0.5	12.6	6.6	3.8
	0.10–4.19	0.52–2.58	0.53–1.79	0.08–1.73	5.02–31.22	2.60–16.27	1.94–7.47
Microcalanus pusillus	0.0	0.3	0.0	0.0	0.0	0.0	0.1
	−0.04–0.25	0.12–0.78	0.01–0.09	0.00–0.00	0.00–0.00	0.00–0.00	0.01–0.23
Warm-water Species							
Neritic							
Acartia tonsa	26.8	0.0	0.0	0.0	0.6	9.1	0.2
	13.80–52.06	−0.01–0.04	0.00–0.04	−0.02–0.10	0.14–1.80	2.24–36.22	0.06–0.55
Ctenocalanus vanus	0.2	0.9	0.1	1.0	62.9	14.1	14.1
	−0.03–1.39	0.90–0.90	0.03–0.15	0.26–3.00	29.59–133.67	5.06–38.94	6.52–30.22
Paracalanus parvus	7.8	1.9	0.7	82.0	139.9	192.7	36.8
	1.75–33.64	0.67–5.33	0.31–1.29	49.20–136.48	85.30–229.53	78.79–470.90	25.98–52.15
Corycaeus anglicus	0.0	0.0	0.0	1.1	73.8	8.2	1.0
	−0.03–0.14	0.00–0.00	0.03–0.03	0.26–3.95	52.00–104.77	2.80–23.94	0.35–2.64
Offshore							
Acartia danae	0.0	0.0	0.0	0.0	0.3	0.1	0.2
	0.00–0.00	0.00–0.00	0.00–0.00	0.00–0.00	0.06–0.71	0.00–0.50	0.05–0.46
Calocalanus styliremis	0.0	0.0	0.0	0.0	3.2	0.3	1.4
	0.00–0.00	0.00–0.00	−0.01–0.02	−0.02–0.10	0.93–10.49	0.04–0.84	0.57–3.27
Calanus pacificus	2.1	0.0	0.0	0.3	18.6	97.9	0.3
	0.17–16.93	−0.01–0.07	0.01–0.08	0.04–0.93	6.80–50.30	68.58–139.69	0.11–0.80
Mesocalanus tenuicornis	0.0	0.0	0.0	0.2	0.3	0.5	0.2
	0.00–0.00	−0.01–0.03	0.01–0.08	0.02–0.55	0.08–1.01	0.15–1.56	0.06–0.48
Clausocalanus spp.	0.1	0.0	0.1	0.8	26.3	6.4	42.2
	−0.04–0.34	0.00–0.00	0.05–0.21	0.21–2.67	12.12–57.03	2.33–17.24	25.60–69.45
Eucalanus californicus	0.6	0.0	0.0	0.1	1.5	0.0	0.0
	0.04–2.95	−0.01–0.06	0.01–0.06	−0.01–0.29	0.36–5.43	−0.01–0.09	0.00–0.11
Ubiquitous Species							
Oithona similis	83.0	295.2	118.5	507.5	243.8	215.9	301.1
	38.07–180.59	166.49–523.44	77.25–181.62	338.78–760.27	132.94–446.95	61.62–755.60	152.35–595.06

water copepod species were anomalously high, as expected during an El Niño event. For example, abundances of *Calanus pacificus* and *Acartia tonsa* were significantly higher during the summer of 1969 than during winters. *Paracalanus parvus* abundances in summer 1969 were

Table 2
Chronological order of sample dates coded by cluster number

Date	Cluster	Date	Cluster	Date	Cluster	Date	Cluster
06/22/69	1a ▽	05/09/73	2a ○	09/09/97	3b ✳	**12/20/99**	**4** ■
07/10/69	1a ▽	06/04/73	2a ○	10/15/97	3a ▲	**01/20/00**	**4** ■
07/18/69	1a ▽	06/14/73	2a ○	11/03/97	3a ▲	**02/01/00**	**4** ■
07/25/69	1a ▽	**07/05/73**	**1b** ▼	11/15/97	3a ▲	**02/16/00**	**4** ■
08/06/69	1a ▽	07/26/73	2a ○	12/12/97	3a ▲	**03/07/00**	**4** ■
08/30/69	1a ▽	**07/30/73**	**1b** ▼	01/30/98	3a ▲	04/11/00	2a ○
09/03/69	1a ▽	**08/06/73**	**1b** ▼	03/05/98	3a ▲	04/30/00	2a ○
09/14/69	1a ▽	**08/16/73**	**1b** ▼	03/18/98	3a ▲	05/17/00	2a ○
09/28/69	1a ▽	**09/12/73**	**1b** ▼	04/05/98	3a ▲	05/22/00	2a ○
10/29/69	3a ▲	04/13/83	3a ▲	04/10/98	3a ▲	06/03/00	2a ○
11/11/69	2a ○	05/12/83	3a ▲	04/21/98	3a ▲	06/12/00	2a ○
01/29/70	3a ▲	06/20/83	3b ✳	04/29/98	3a ▲	**06/23/00**	**1b** ▼
02/25/70	**4** ■	07/07/83	3b ✳	05/12/98	3a ▲	07/07/00	2a ○
03/09/70	**4** ■	07/21/83	3b ✳	05/27/98	3a ▲	07/19/00	2a ○
04/27/70	2a ○	08/04/83	3b ✳	06/02/98	3a ▲	**08/04/00**	**1b** ▼
05/22/70	1a ▽	08/19/83	3b ✳	06/12/98	3a ▲	**08/12/00**	**1b** ▼
06/04/70	**1b** ▼	09/13/83	3b ✳	06/23/98	3a ▲	**08/18/00**	**1b** ▼
07/02/70	**1b** ▼	**05/21/96**	**4** ■	07/06/98	3a ▲	**08/28/00**	**1b** ▼
07/16/70	**1b** ▼	**06/11/96**	**4** ■	07/20/98	3a ▲	**09/07/00**	**1b** ▼
07/29/70	2a ○	07/03/96	2a ○	07/28/98	1a ▽	09/23/00	2a ○
08/13/70	**1b** ▼	07/11/96	2a ○	08/06/98	3b ✳	09/25/00	2b ●
08/27/70	2a ○	**07/25/96**	**1b** ▼	08/14/98	3b ✳	10/06/00	2a ○
09/11/70	2a ○	**08/12/96**	**1b** ▼	08/27/98	3b ✳	10/23/00	2a ○
09/25/70	**1b** ▼	08/26/96	2a ○	09/10/98	3b ✳	11/07/00	4 ■
10/09/70	2a ○	**09/05/96**	**1b** ▼	09/24/98	3b ✳	12/06/00	3b ✳
10/20/70	2a ○	09/19/96	2b ●	09/26/98	3b ✳	**01/16/01**	**4** ■
12/04/70	**4** ■	10/07/96	2b ●	10/05/98	3b ✳	**01/27/01**	**4** ■
01/06/71	**4** ■	10/31/96	3b ✳	11/03/98	3b ✳	**02/14/01**	**4** ■
02/16/71	**4** ■	**11/26/96**	**4** ■	11/16/98	3b ✳	**02/28/01**	**4** ■
03/30/71	2a ○	**12/19/96**	**4** ■	12/17/98	4 ■	**03/12/01**	**4** ■
04/22/71	2a ○	**02/24/97**	**4** ■	02/17/99	4 ■	03/20/01	2b ●
05/03/71	2a ○	**03/21/97**	**4** ■	03/11/99	4 ■	04/03/01	2b ●
05/14/71	2a ○	**04/04/97**	**4** ■	04/01/99	3b ✳	04/11/01	2b ●
05/29/71	2a ○	**04/25/97**	**4** ■	04/19/99	4 ■	04/25/01	2b ●
06/12/71	**1b** ▼	**05/05/97**	**4** ■	04/29/99	2a ○	**05/09/01**	**1b** ▼
06/28/71	2a ○	05/15/97	2a ○	05/14/99	2b ●	05/18/01	2a ○
07/06/71	2a ○	05/28/97	2a ○	05/23/99	2a ○	**06/04/01**	**1b** ▼
07/21/71	2a ○	06/11/97	2a ○	06/10/99	2a ○	**06/13/01**	**1b** ▼
08/02/71	2a ○	06/27/97	2b ●	**06/23/99**	**1b** ▼	06/16/01	2a ○
08/19/71	2a ○	07/15/97	2b ●	**07/03/99**	**1b** ▼	**06/26/01**	**1b** ▼
09/23/71	2a ○	07/17/97	2b ●	**07/09/99**	**1b** ▼	**07/01/01**	**1b** ▼
10/11/71	2a ○	**07/23/97**	**1b** ▼	07/15/99	2a ○	**07/06/01**	**1b** ▼
11/06/71	2b ●	07/29/97	2b ●	07/19/99	2a ○	**07/18/01**	**1b** ▼
12/07/71	**4** ■	07/30/97	2b ●	07/26/99	2a ○	**07/30/01**	**1b** ▼
03/15/72	**4** ■	08/06/97	2b ●	08/05/99	2a ○	**08/05/01**	**1b** ▼
04/20/72	2a ○	08/12/97	2b ●	**08/19/99**	**1b** ▼	**08/09/01**	**1b** ▼
05/22/72	2a ○	08/14/97	2b ●	09/01/99	2a ○	**08/24/01**	**1b** ▼
06/11/72	2a ○	08/21/97	2b ●	09/08/99	2a ○	**09/05/01**	**1b** ▼
06/28/72	**1b** ▼	08/27/97	2b ●	09/22/99	2a ○	**09/18/01**	**1b** ▼
07/21/72	2a ○	08/28/97	2b ●	09/29/99	2a ○	09/25/01	2a ○
08/05/72	2a ○	09/02/97	3b ✳	11/04/99	2a ○	10/02/01	2a ○

Breaks in sampling > 3 months are indicated by dashed lines. Symbols for each cluster are the same as those in Figs. 4, 6, and 7.

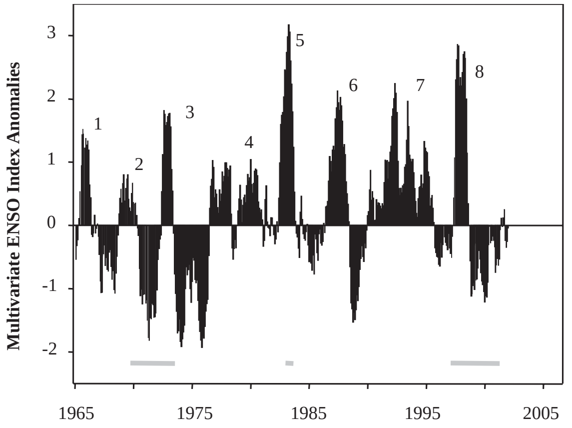

Fig. 2. A time series of the value of the monthly Multivariate ENSO Index (from Wolter and Timlin, 1998; and http://www.cdc.noaa.gov/ENSO/enso.current.html/indices). The eight El Niño events since 1965 are numbered. During this study, we sampled during event numbers 2, 3, 5 and 8. The grey bars indicate the sampling periods.

similar to average winter abundances (5 vs. 37 m^{-3}). Each of these three "warm-water" species have their greatest abundances during strong El Niño events.

Cluster 3 (Early El Niño and Late El Niño clusters), which included the two large El Niño events, differed from "normal" summers and winters by having higher abundances of warm-water species and greatly reduced abundances of boreal species (Table 1). Though many of the warm-water species listed in Table 1 appear commonly off Oregon during the wintertime, their abundance during the El Niño was generally 2X-10X higher than during a 'normal' winter. Cluster 3A, which was observed early during the two major El Niño events, contained low abundances of boreal species and high numbers of warm-water species. Cluster 3B, which was observed later in the events, contained higher abundances of boreal species than in cluster 3A suggesting that cluster 3B represents a transition from El Niño conditions to "normal" conditions. Cluster 3B continued to be well represented by warm-water species, however, with *Acartia tonsa*, *Calanus pacificus* and *Paracalanus parvus* being about twice as abundant during the late-phase (3B) than the early-phase (3A).

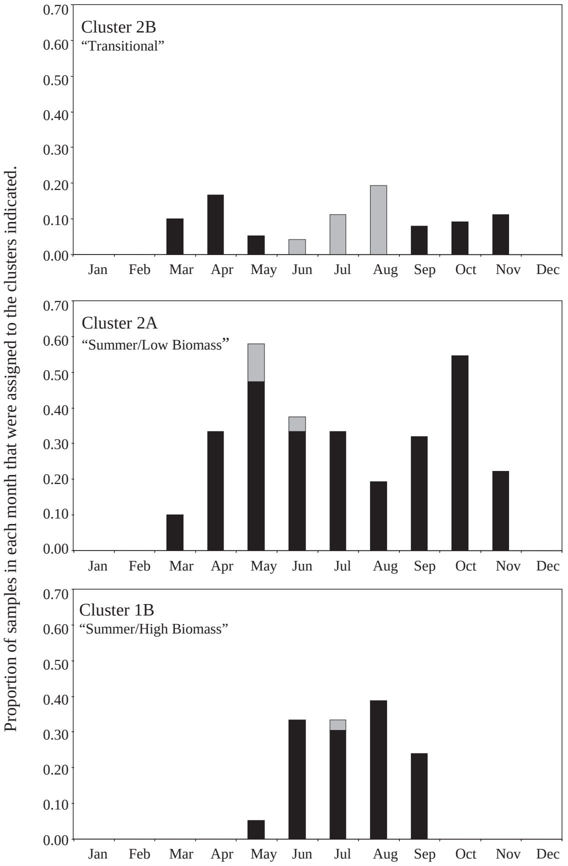

Fig. 3. Frequency distribution of sampling dates by cluster group pooled by month. Data are proportion of samples in a given month that were classified into the indicated cluster group. Shading indicates samples collected in May–August 1997.

Cluster 4 ('normal' winter) is characterized by a copepod assemblage dominated by warm-water species *Paracalanus parvus*, *Ctenocalanus vanus* and three species of *Clausocalanus* (including *C. pergens*, *C. arcuicornis* and *C. parapergens*), a cold-water species, *Pseudocalanus mimus* and a ubiquitous species, *Oithona similis*.

3.3. Timing of spring and fall transition

Cluster analysis allows one to determine the date of transition between winter and summer communities. Although it is not possible to establish the exact date due to our biweekly-to-

Table 3
For each year of sampling: proportion of sampling dates in each of the four summer clusters (1A, 1B, 2A, 2B); the value of the Bakun upwelling index at 45°N (Bakun index) summed for May–September of each year; the value of the PDO summed over January–September of each year; the period of time between which the transition from a winter community to summer community occurred (indicated by the date the last winter community was observed/the date the first summer community was observed); and the dates between which the community transitioned from a summer to a winter community (last summer observation/1st winter observation)

Year	Proportion in cluster group				Bakun index	PDO	Last winter observation/first summer observation	Last summer observation/first winter observation
	1A	1B	2A	2B				
1969	1.00	—	—	—	226	−3.8	[a]	28 Sept./29 Oct.
1970	0.11	0.55	0.33	—	223	−1.6	9 March/23 April	20 Oct./4 Dec.
1971	—	0.10	0.90	—	168	−12.2	16 Feb./30 March	6 Nov./7 Dec.
1972	—	0.17	0.83	—	197	−11.4	15 March / 20 April	[b]
1973	—	0.56	0.44	—	231	−6.2	[a]	[b]
1983	—	—	—	—	107	16.1	[a,c]	[b]
1996	—	0.27	0.27	0.18	321	7.8	11 June/20 June	7 Oct./31 Oct.
1997	—	0.07	0.20	0.73	73	14.1	5 May/15 May	[c]
1998	0.07	—	—	—	269	5.3	[c]	16 Nov./20 Dec.[d]
1999	—	0.26	0.67	0.07	196	−6.9	19 April/29 April	4 Nov./20 Dec.
2000	—	0.43	0.50	0.07	187	−5.8	12 March/20 March	23 Oct./7 Nov.
2001	—	0.81	0.19	—	264	−1.9	18 April/30 April	7 Nov./27 Nov.

[a] 1st cruise in this year was after the summer community was established.
[b] No winter cruises this year.
[c] No transition during the El Niño.
[d] Transitioned from El Niño to winter community.

monthly cruise frequency, we can establish the date *by which* the community composition had switched from a winter-assemblage to a summer-assemblage, and vice-versa. The spring transition in community type can come as early as March and as late as June (Table 3). The years 1970–1973 and 2000–2001 were characterized by a transition during March–April. In 1996 and 1997, the transition was late, in May or June. An intermediate transition date was seen in 1999 (late-April). There was no transition during spring of the two strong El Niño years (1983, 1998). The date of the fall transition was variable but appears to come between late-October and early-December (Table 3).

3.4. Non-metric multidimensional scaling (ordinations)

Ordination of the plankton samples allows one to look for patterns to visualize similarity in community composition among sampling dates. The two ordination axes (Fig. 4) explained 87.1% of the variability in copepod community structure. Axis 1 explained 58.5% of the variability and Axis 2, 28.6%.

Several patterns in the arrangement of cluster groups are apparent in the ordination. First, the dissimilarity between summer and winter dates is evident (Groups 1A, 1B, 2A, 2B vs. 3A, 3B, and 4). Second, note that Groups 1B, 2B and 4 are ordered along a diagonal trend (Fig. 4) that runs from upper left to lower right quadrants. This illustrates a continuum between "Summer/High Biomass" through "Transitional", to "Winter" copepod assemblages. Note also that the other summer cluster (2A), "Summer/Low Biomass", merges directly towards the "Winter" cluster (4) without a transition. Third, a similar trend is seen with the three groups representative of the 1969, 1983 and 1997/98 El Niño events (1A, 3B and 3A; Fig. 4), but offset to the right of Axis 1. Note also that the samples from the large El Niño events (clusters 3A, B) are distinctly different from

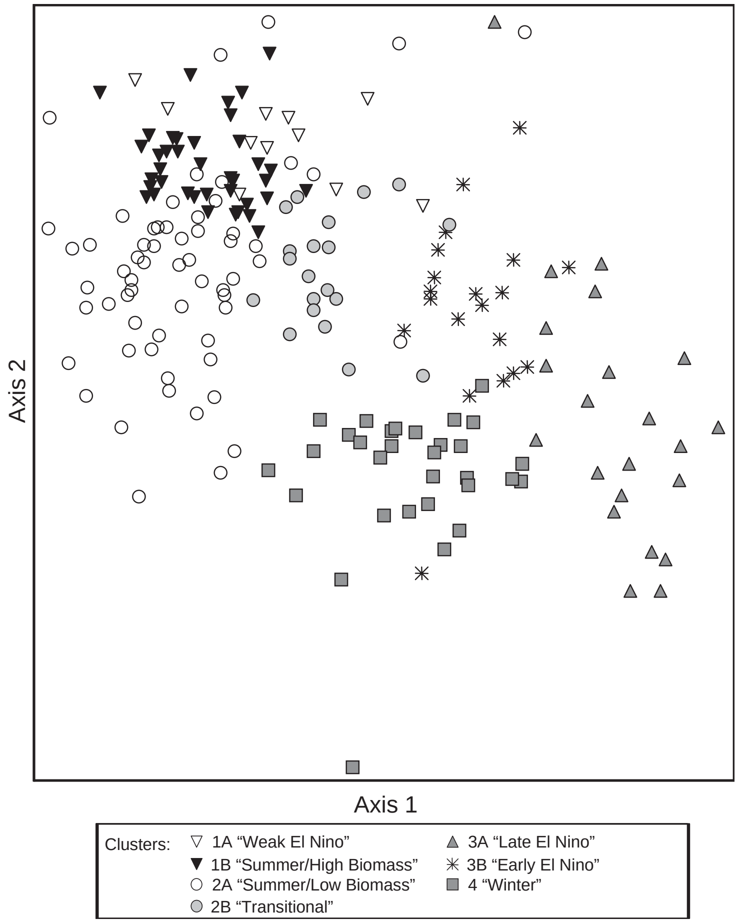

Fig. 4. Ordination of copepod communities for the 12-year data set. Each symbol is a sampling date, and the shape of each symbol identifies its corresponding cluster number, as in Table 2. Symbols adjacent to each other indicate the greatest similarity in community composition between two samples; the greatest separation between symbols indicates the greatest dissimilarity.

'winter' samples (cluster 4), but are more similar to winter than to summer groups.

Possible relationships between the summer copepod clusters and environmental variables such as the strength of upwelling (as measured by the Bakun upwelling index) and the PDO were analyzed with correlation analysis. The proportion of total sampling dates in a given summer that clustered into Cluster 1B (Summer/High Biomass) or 2A (Summer/Low Biomass) (Table 3) was compared to each of the environmental indices. The only significant correlation was with proportion of samples in 2A (the "Summer/Low Biomass" cluster) and the value of the PDO (Fig. 5; $R^2 = 0.50$; $F = 10.0$, $p = 0.01$). Summers in which a high proportion of the sampling dates were assigned to Cluster 2A had strongly negative values of the PDO (1971, 1972, and 1999–2001). Summers that had a low proportion of dates in Cluster 2A (1970, 1996, 1997, and 2001) were summers during which the PDO was either strongly positive or had a slight negative value (Table 3). The correlation of the proportion of samples clustering in cluster 1B with the PDO was not significant ($p = 0.12$). The Bakun upwelling index was uncorrelated with the proportion of sampling dates in either Cluster 2A ($r = 0.39$, $p = 0.20$) or 1B ($r = 0.09$, $p = 0.77$).

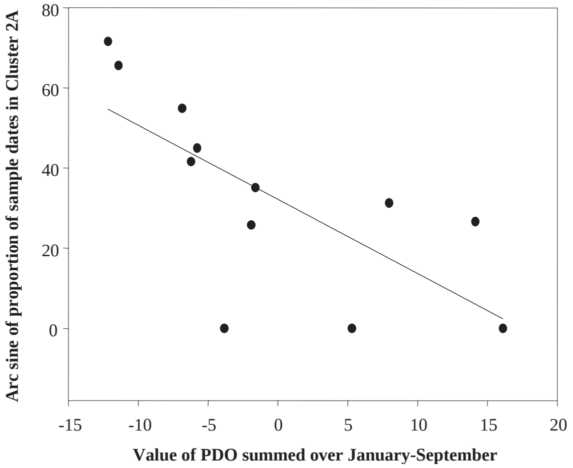

Fig. 5. Relationship between (arc sine transformed) proportion of sampling dates that grouped with Cluster 2A (Summer/Low Biomass cluster) and the PDO summed over the period January–September.

Many of the dominant copepod species were strongly correlated with Axis 1 or 2 of the ordination (Table 4). All of the dominant cold-water neritic species were strongly positively correlated with Axis 2, whereas the many of the warm-water copepod species were negatively correlated with Axis 2 and were positively correlated with Axis 1.

Examination of the way that the dominant copepod species relate to the ordination (Figs. 6 and 7) reveals several patterns related to season and El Niño events. For example, among the 'cold-water species', *Acartia longiremis* and *Calanus marshallae* have a similar pattern (Fig. 6). They are important members of summer communities and are present in relatively high numbers during the late-phase of strong El Niño events. *Centropages abdominalis* is an important member of the community only during summer months, and only in certain years (chiefly in Clusters 1B and 2B). *Pseudocalanus mimus* differed from *A. longiremis* and *C. marshallae* in that it appears to be an important component of the winter communities. *P. mimus* also appeared in relatively high numbers (compared to the other cold-water species) in a greater number of samples collected during the two strong El Niños and the weak El Niño of 1969 (Clusters 1A and 3B).

Among the warm-water species (Fig. 7), *Paracalanus parvus* had a higher degree of association with the 'summer' samples as compared to the other warm-water species. *Calanus pacificus* had a closer association with samples collected during both the two strong El Niño events of 1983 and 1998 (Cluster 3A, 3B) and the weaker event in 1969 (Cluster 1A) than during a 'normal' winter (Cluster 4). *Ctenocalanus vanus* is associated as strongly with El Niño events (3A, 3B) as with 'normal' winter months (Cluster 4). *Calocalanus styliremis* is a species that is more typical of 'winter' (Cluster 4) with lesser association with El Niño events.

ISA was used to determine which species are the best indicators of each cluster group (Table 4). Four patterns were clearly seen: (1)*Pseudocalanus mimus* and *Oithona similis* are not good indicators of any water type or oceanographic condition; (2) three other cold-water neritic species (*Acartia hudsonica*, *Calanus marshallae*, *Centropages abdominalis*) and one offshore species (*Microcalanus pusillus*) are good indicators of an upwelling community; (3) the best indicators of winter downwelling conditions were *Ctenocalanus vanus*, *Clausocalanus* spp., and *Calocalanus styliremis*; and (4) a host of warm-water neritic and warm-water offshore species are good indicators of El Niño conditions, but especially *Corycaeus anglicus* and *Calanus pacificus*.

4. Discussion

A composite picture of year-to-year variations in abundances of the dominant copepod species off central Oregon can be found by comparing Frolander (1962), Peterson (1972), Peterson and Miller (1975, 1976, 1977), Peterson et al. (1979), and Peterson et al. (2002). The earlier papers were highly descriptive and considered only differences in abundance among species and among years. The combined use of cluster analysis, NMDS, and ISA in this paper allows a more objective analysis of seasonal and interannual changes in community structure. This is the third paper in a series that

Table 4
Indicator values (IV) for the most common copepod species collected at the station NH 05, arranged by cluster group; and Spearman's correlation coefficient (r) for correlation of the species abundance with the two axes of the NMDS ordination

	Cluster								
	1A	1B	2A	2B	3A	3B	4	r_{Axis1}	r_{Axis2}
Cold-water species									
Neritic									
Acartia hudsonica	34	27	7	1	1	5	0	−0.28	0.64
A. longiremis	21	33	13	13	2	17	2	−0.46	0.77
Calanus marshallae	26	20	14	17	1	9	5	−0.55	0.64
Centropages abdominalis	19	34	4	24	2	2	0	−0.28	0.70
Pseudocalanus mimus	18	18	15	16	3	15	13	−0.59	0.50
Offshore									
Metridia pacifica	5	7	7	3	22	20	13	0.39	−0.10
Microcalanus pusillus	1	20	1	0	0	0	4	−0.15	−0.25
Warm-water species									
Neritic									
Acartia tonsa	43	0	0	0	5	26	2	0.33	0.03
Ctenocalanus vanus	2	0	0	5	32	24	21	0.83	−0.48
Paracalanus parvus	9	4	2	19	21	21	15	0.77	−0.16
Corycaeus anglicus	0	0	0	7	44	21	7	0.80	−0.31
Offshore									
A. danae	0	0	0	0	13	7	9	0.41	−0.29
Calocalanus styliremis	0	0	0	0	32	5	21	0.63	−0.44
C. tenuis	0	0	0	0	22	0	10	0.36	−0.27
Calanus pacificus	9	0	0	2	26	40	2	0.69	−0.14
Mesocalanus tenuicornis	0	0	1	4	9	18	6	0.36	−0.24
Candacia bininnata	0	0	0	0	14	1	0	0.27	−0.17
Clausocalanus spp.	0	0	1	5	29	17	33	0.72	−0.61
Eucalanus californicus	14	0	0	1	26	0	1	0.36	0.01
Ubiquitous species									
Oithona similis	12	15	12	16	14	13	15	0.23	−0.50

The higher the IV, the better indicator that species is of that particular cluster group. Only those species whose IV was significant for at least one cluster are listed. For 204 degrees of freedom, a coefficient greater than 0.14 is significant at the $p = 0.05$ level.

uses clustering and ordination techniques to describe zooplankton community composition off Oregon. Morgan et al. (2003) discuss longitudinal and alongshore patterns in community structure from samples collected in July of 1994, 1996 and 1997 off northern, central and southern Oregon. In that study, two copepod communities were identified, one characteristic of continental shelf waters and the other characteristic of deep waters offshore of the continental shelf. Keister and Peterson (2003) describe seasonal and longitudinal changes in community composition from samples collected off Newport, Oregon at quarterly intervals in 1998, 1999 and 2000. Like Morgan et al. (2003), two assemblages were identified during summer (a shelf water, and an oceanic water, community). The shelf community expanded into offshore waters in July at the peak of the upwelling season but contracted to shelf waters in September. In addition, they showed that the warm-water community found offshore of the upwelling community in summer has the same community structure as the warm-water community found in both shelf and oceanic waters during winter. This suggests

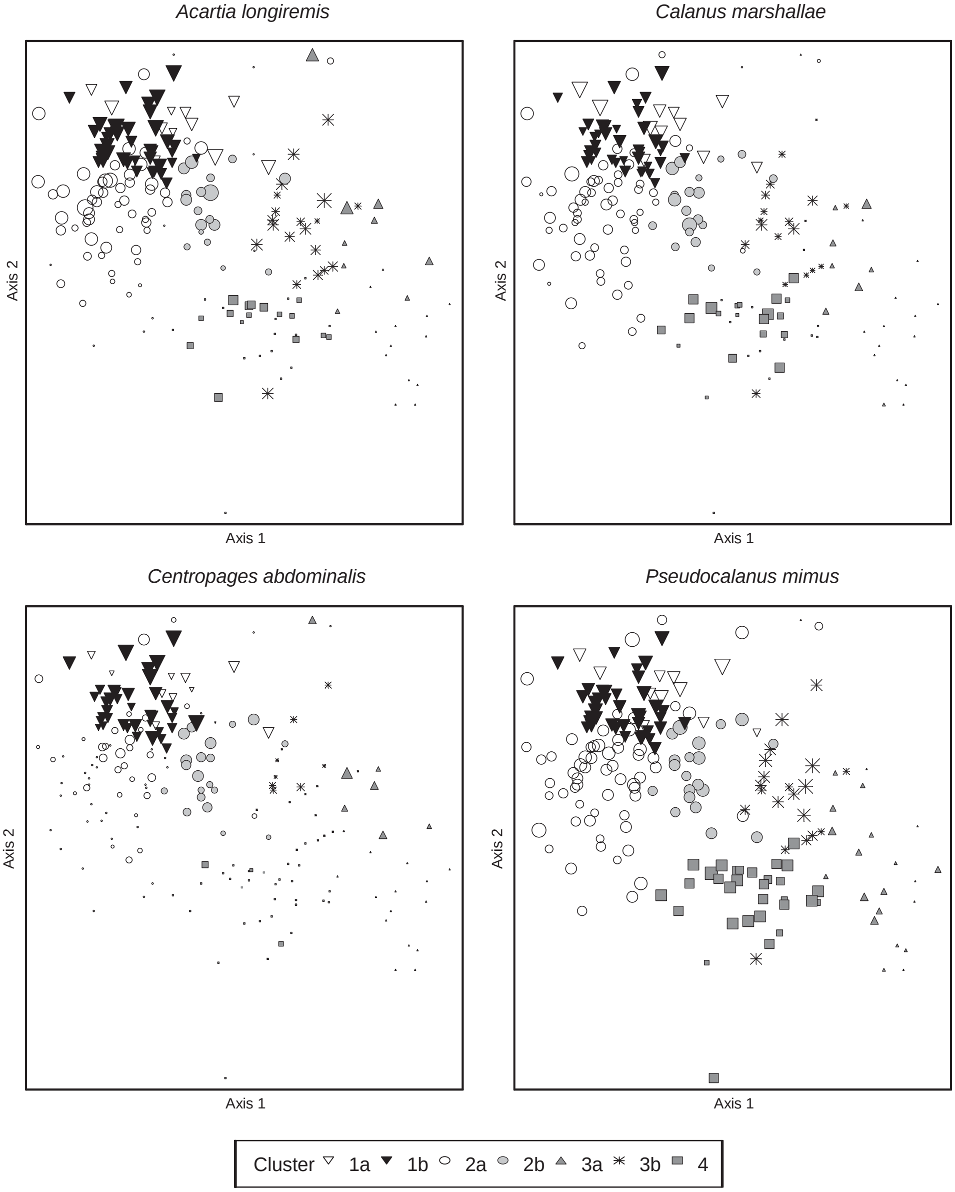

Fig. 6. Ordination of copepod communities with abundance of the dominant cold-water neritic species overlayed. Symbol indicates cluster group; size of symbol indicates relative abundance of the taxa.

that the transition from a summer to a winter community could in part be the result of the shoreward movement of offshore waters during seasonal downwelling.

This paper presents data on temporal variations in copepod community structure at a single nearshore hydrographic station. At the highest hierarchical level in the cluster analysis, seasonal differences were the most apparent. These first-order differences between summer and winter are due to seasonal variations in coastal winds and water circulation patterns. Winds are from the north and coastal waters flow south during the upwelling season (May–September),

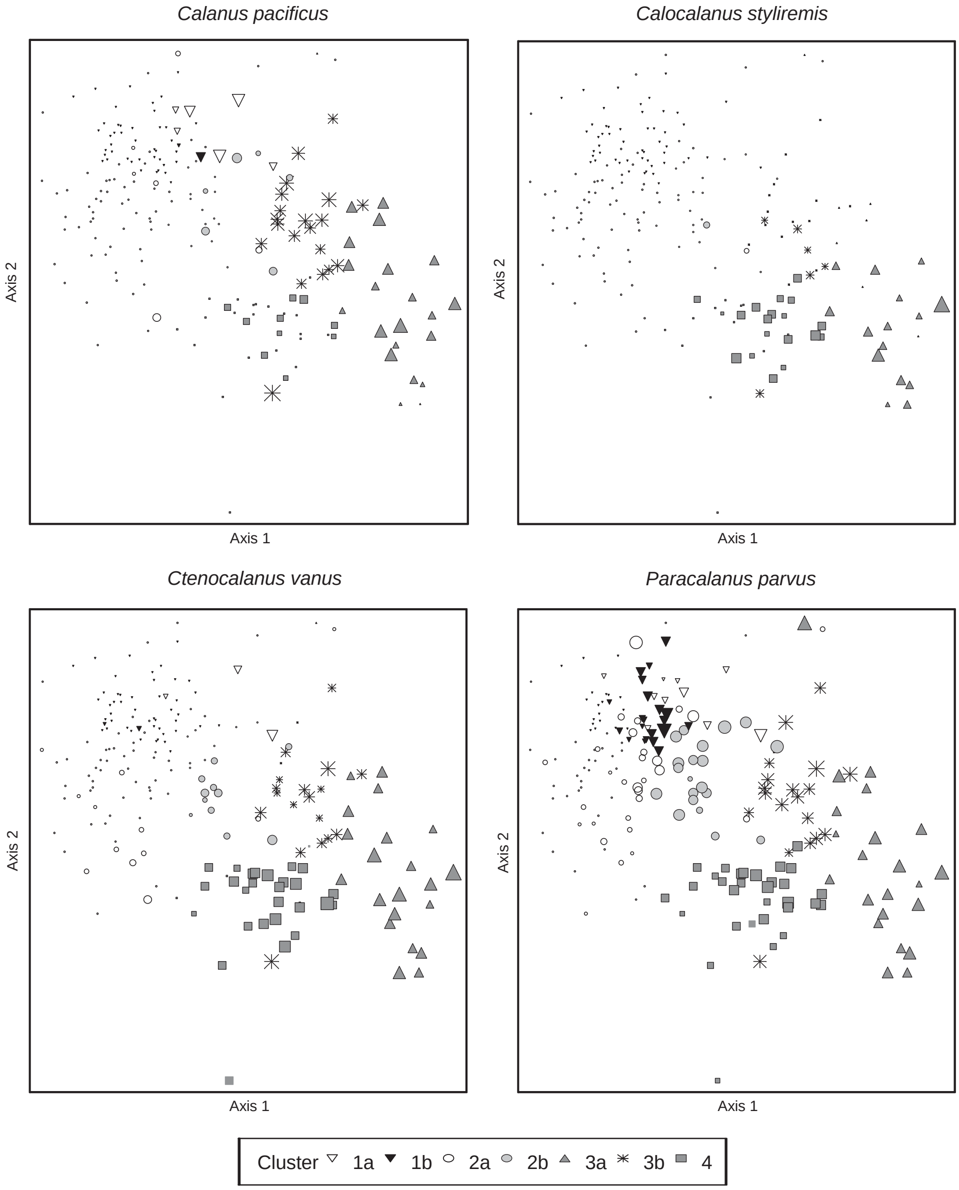

Fig. 7. Ordination of copepod communities with abundance of the dominant warm-water species overlayed. Symbol indicates cluster group; size of symbol indicates relative abundance of the taxa.

whereas winds are from the south and water flows to the north during winter months (November–March). Wind and current reversals in the California Current were first pointed out by Fleming (1955). Changes in zooplankton species composition in association with current reversals also were suggested by Frolander (1962), Cross and Small (1967) and Peterson and Miller (1977).

Winter communities (Cluster 4) were closely related to the 1983 and 1997/98 El Niño communities (Clusters 3A and 3B) in both cluster analysis and the ordination implying that, in a broad sense, winters are similar to strong El Niño events. This is probably due to common source waters during winters and El Niño events. We suggest that in winter and during El Niño events, warm-water species are brought to Oregon by a combination of increased northward transport from central California (as the Davidson Current) and onshore transport of offshore waters as shown by our recent work (Peterson et al., 2002).

The more ecologically interesting results of the clustering analysis occurred with the separation of community types into seven groups. Three groups appeared in summer, three during El Niños, and one during winter. Two clusters, 1B and 2A, dominated the 'summer' months, accounting for about 80% of the spring–summer–autumn sampling dates. The chief differences between these two clusters was in the abundance of the dominant species (*Pseudocalanus mimus*, *Acartia longiremis*, *Calanus marshallae*, and *Centropages abdominalis*): these species were significantly more abundant in Cluster 1B ("Summer/High Biomass") than Cluster 2A ("Summer/Low Biomass"). Nearly two-thirds of the sampling dates in Group 1B came in July and August at the time of peak coastal upwelling when chlorophyll concentrations are highest (Feinberg and Peterson, 2003). Samples with lower abundances of the dominant copepod species grouped into Cluster 2A in part because many of the sampling dates were outside the period of peak upwelling (April–June and September–November) when productivity is relatively low. Also, low abundances were found during some dates in the July–August period, suggesting that 2A is perhaps associated with periods of lower productivity during the upwelling season, possibly near the end of periodic upwelling events.

The cluster group 2B (the "Transitional" cluster) represents a transitional period that occurred before (or while) upwelling was first being established in spring and after (or while) upwelling was ending in fall. It differed from 2A by having a greater abundance of warm-water species. Group 2B was also the dominant group observed during June–July 1997. This was a transitional period between the initial arrival of an El Niño signal off Oregon in May 1997 through an atmospheric connection (resulting in strong southwesterly winds for a 6-week period in May and June) and the arrival of the oceanic El Niño signal in early September through the Kelvin wave connection (discussed in Peterson et al., 2002). The summer of 1997 was also one with the lowest amounts of upwelling on record (see Table 3 and http://www.pfeg.noaa.gov). Thus Group 2B is characterized by low abundances of all species and relatively high abundances of warm-water species that are common when upwelling is weak or non-existent.

The "Summer/Low Biomass" cluster, 2A, was associated with the strength of the PDO. We found that the more negative the value of the PDO, the greater the number of samples that were classified as 2A. Negative values of the PDO result because of a weak Aleutian Low pressure system in winter and cooler sea-surface temperature throughout the year, both of which could lead to an early and strong upwelling season. However, since we found no relationship between proportion of sampling dates in Group 2A and the Bakun upwelling index, we caution that the correlation of PDO with Group 2A may be spurious. On the other hand, lack of a relationship between cluster 2A and the Bakun index might have resulted because this index is a measure of 'potential' coastal upwelling, but it is not necessarily an index of coastal productivity. For example, during summer 1998, the upwelling index was among the higher values recorded (see Table 3), yet due to the lingering El Niño event, copepod biomass was low (Peterson et al., 2002) and the zooplankton species that dominated the continental shelf waters were of warm-water origin. Also, despite favorable upwelling winds, surface waters remained anomalously warm by about 1°C (Huyer et al., 2002; Peterson et al., 2002). Therefore it should not be a surprise that the strength of upwelling was unrelated to biomass and/or species composition. Another example of the failure of the Bakun Index to predict copepod abundances occurred during the summer of 1996. This summer had the highest value of the Bakun Index of any year during our 12-year study, yet (as with 1998) was also a summer characterized by low copepod biomass (Peterson et al., 2002), and low to moderate numbers of both cold-water and warm-water species. Also the transition to a cold-water community occurred very late, in June 1996. Thus, 1996 was another “outlier”. We suggest that although the Bakun Index predicts the strength of upwelling winds and thus the expected amount of upwelling, it is not a good measure of the *result* of upwelling favorable winds (that is, cooler sea-surface temperatures and increased biological productivity). We suggest that the PDO is a better indicator of upwelling and coastal productivity since the value of the index is driven chiefly by measurements of sea-surface temperatures.

A unique result shown in this paper is the differential response of copepod community composition to different El Niño events. For example, the 1972 event, which was very strong off Peru (Wyrtki et al., 1976; dee Boersma, 1978), had no influence on the zooplankton (our data), sea level or sea-surface temperatures in the Pacific Northwest (Cannon et al., 1985). Also, the 1969 event, though a weak one, apparently had a large impact on copepods as shown in Tables 1 and 2. The unusual nature of the copepod community composition is intriguing since we are not aware of any publications that have shown anomalous biological events during the summer of 1969. One of the expected results of El Niño events is reduced zooplankton biomass throughout the California Current. However, there was no indication of an effect on biomass during the CalCOFI surveys in 1969 (http://www.calcofi.org/data/zooplankton/5_-_time_series.htm) off either central or southern California. In fact, zooplankton biomass observed by the CalCOFI program in 1969 was among the higher values observed over the entire 45-year time series. Therefore we question whether the weak 1969 El Niño event can explain the anomalous copepod species composition observed off central Oregon. Given that both the clustering and ordination analyses showed that the summer of 1969 was more closely associated with “normal summers” than with “strong El Niño events”, we are uncertain how this summer should be classified. Stronger El Niño events certainly have a noticeable effect on the zooplankton of the northern California Current as well as on sea level and sea-surface temperatures (such as the 1941, 1958, 1983 events (Cannon et al., 1985) as well as the 1997/98 events), but the weaker events apparently do not always express themselves in the northern California Current.

Apart from the large-scale seasonal differences, the greatest differences in copepod community structure observed over the 12-year study period were seen during the two “strong” El Niño events of 1983 and 1997/98. During onset of both of these events, the community was dominated by offshore and southern neritic warm-water copepod species (our “Early El Niño” community), whereas in what might be called the “decay” phase of El Niño, the community had evolved into a mixture of warm- and cold-water species (our “Late El Niño” community). Keister and Peterson (2003) found the same result during the 1997/98 El Niño event and noted that the early and late El Niño community types also were seen in oceanic as well as coastal waters off Newport. The observation that an El Niño community persisted into the autumn of 1998, 6 months after the physical manifestations had ended, shows that care must be taken when interpreting the effects of any El Niño event on ecosystem structure if all one has available for study are temperature, wind or sea-level data. Biological effects can last longer than physical effects, as discussed in greater detail by Peterson et al. (2002) and Keister and Peterson (2003).

A similar lag between physical forcing and biological response during El Niño events is seen with euphausiids. During the 1983 El Niño event, Brodeur (1986) noted the presence in Oregon waters of *Nyctiphanes simplex*, a neritic euphausiid species that is common in continental shelf waters off Baja California and the southern California Bight. Presence of this species off Oregon indicates strong poleward flow of coastal waters during El Niño events. This species was not observed during the 1969 or 1972 events, but was common in our samples in 1997/1998. It first appeared in December 1997 and remained in coastal waters until November 1998 (see also Tanasichuk and Cooper, 2002).

The date of spring transition is of interest to biological oceanographers because this date signals the beginning of the annual production cycle. But determining the date of the transition is not simple because variables used to determine the date do not "flip" from one steady-state to another and because different variables may indicate different dates. Through examination of changes in copepod community types, we are able to determine the date by which the transition had occurred from the zooplankton's perspective (Table 3). Determination of the date of spring transition has recently been treated rigorously by Bilbao (2000) using time series of sea level and the Bakun coastal upwelling index, for the period 1971–1998. We compared our estimated dates to his for the 5 years for which we had data in common. The results were as follows (our estimate precedes Bilbao's): <u>1971</u>, 30 March vs. 15 April; <u>1972</u>, 20 April vs. 14 April; <u>1996</u>, 20 June vs.13 March; <u>1997</u>, 15 May vs. 18 March; and <u>1998</u>, never vs. 25 March. In two of the five cases (1971 and 1972) our estimates are very similar; however, the other three differ greatly. In these cases, the date when we noted a transition in copepod community composition was much later than the date by which Bilbao estimated the physical-hydrographic transition had occurred. The lack of agreement in 1998 is likely due to the lag-time necessary for the copepod community to recover following a strong El Niño event (Peterson et al., 2002; Keister and Peterson, 2003). However, the reasons for the lack of agreement in 1996 and 1997 are unknown.

ISA combines information on the abundance of a species within a cluster group and the frequency of occurrence of the species within the cluster group. A perfect indicator species is one that is always present in a given cluster group but absent from all other groups. We had no perfect indicators (which would yield a score of 100) but several species with relatively high scores. Those with highest scores were *Corycaeus anglicus* (score of 44 in cluster 3A), *Calanus pacificus* (score of 40 in cluster 3B), and *Acartia tonsa* (score of 43 in cluster 1A); each is a "warm-water species" and is a good indicator of El Niño conditions. The three highest scores for "cold water species" were seen in three species, *Acartia hudsonica* (34 in cluster 1A), *Centropages abdominalis* (34 in cluster 1B), and *Acartia longiremis* (33 in cluster 1B). The first two species are typical of the very nearshore community, being most abundant within less than 5 km of the shore (Peterson et al., 1979), thus can indicate the presence of a nearshore community in more offshore waters. These two species, along with *A. longiremis*, are only abundant during June-September, another reason which may explain their utility as indicator species. The reason that the other two dominant "cold water species" were not good indicators of summer upwelling (*Calanus marshallae* and *Pseudocalanus mimus*) may be related to their seasonal cycles of abundance as well: *C. marshallae* breaks diapause in January, thus is present in samples collected in winter and spring samples, and *P. mimus* can be moderately abundant year around (Peterson and Miller, 1976; Peterson and Miller, 1977).

ISA is useful in assigning ecological meaning to cluster groups, and can be applied when one wishes to contrast performance of individuals of species across two or more groups. However, we found that drawing ecological conclusions about members of cluster groups can be difficult because of inadequate understanding of the biological characteristics of each species. For example, Cluster 1B ("Summer/High Biomass") was defined chiefly by *Centropages abdominalis* and *Acartia longiremis*, whereas Cluster 2A ("Summer/Low Biomass") had no strong indicator species; yet both clusters represent 'normal' summer conditions. Similarly, cluster 2B ("Transitional" cluster) had no strong indicators. *C. abdominalis*, and to a lesser extent *A. longiremis*, are characterized by strong year-to-year variations in abundance (Peterson and Miller, 1975), and, in the case of *C. abdominalis*, was dominant only in the "Summer/High Biomass" cluster. Reasons for this are unknown but may rest with underlying biological characteristics of each species.

Indicator species can be useful in determining the community type that any particular sample represents, though to be fairly confident of correct community-type classification, the species used must be a very strong indicator of the community. For instance, a hypothetical sample collected at the nearshore station containing a high abundance of *Calanus pacificus*, *Corycaeus anglicus*, or *Ctenocalanus vanus* could fairly confidently be classified as from an "El Niño" community because those species were only found in high abundances during El Niño years (Table 1). Confidently classifying a single sample without the presence of strong indicator taxa would be problematic, however. Only after several sequential samples were collected and abundances of multiple species were examined in relation to each other could the community-type possibly be classified.

If we are to understand what drives differences in community structure during the summer upwelling season, for example, then clearly we need a better understanding of the factors controlling the population dynamics of two of the better indicator species, *A. longiremis* and *C. abdominalis*, and two of the dominant and ubiquitous species, *P. mimus* and *C. marshallae*. However, so little is known about the feeding, egg production, growth rates, or losses due to predation of these (and all other epipelagic) species in the northern California Current, that we cannot yet even speculate on the reasons for their dominance in some years but not others. We do know that development times are similar for all species, so rate of development is probably not a factor controlling population dynamics so long as food-limitation of development does not become a problem (Peterson, 2001). For the cold-water species in general, two issues of interest are: (1) to what degree are abundances observed in spring dependent upon overwintering survival in local waters vs. advection of new individuals into the coastal zone from the southern Gulf of Alaska, and (2) how do variations in the strength of upwelling in any given summer manifest themselves into dominance by different sets of copepod species in different years.

An overriding question derived from our studies is, to what degree are among-year differences in abundances of the dominant copepod species driven by physical factors (e.g., advection or strength of upwelling) vs. biological factors (e.g., food quality or predation)? The strong correlation of cold-water species abundances with Axis 2 of the ordination and the correlation of warm-water species abundances with Axis 1 indicate that different mechanisms control those populations. However, the major influences on population dynamics are unknown and need to be explored before we will have a good understanding of the mechanisms controlling copepod community structure.

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