Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem

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Abstract

We evaluated copepod taxonomic diversity as a potential biological indicator of ocean conditions in the northeast Pacific Ocean using data collected biweekly between May 1996 and December 2004 and from 1969 to 1973 and 1983 off Newport, Oregon. During the summer, low copepod biodiversity is accompanied by high biomass, with the opposite patterns prevailing in the winter. High biodiversity, and associated low biomass, is also observed during the summers of major El Niño events (1983, 1997–1998) and during years when the Pacific Decadal Oscillation is in a positive phase. From 1996 to the present, seasonally adjusted monthly anomalies of taxa richness and the Shannon–Weiner diversity index were compared to hydrographic and meteorological variables and to basin-wide climatological indices. Correlations of biodiversity with physical variables were strongest during the summer months for the Multivariate El Niño/Southern Oscillation Index, temperatures at a water depth of 50 m, and the Pacific Decadal Oscillation. During a 4-year cool period (1999–2002), biodiversity was low, likely a result of the increased transport of coastal subarctic waters into the northern California current. In recent years (2002–2005), however, there has been a dramatic increase in biodiversity. These increases may be attributable to the influence of a weak El Niño event in 2003; yet, high biodiversity persisted through the summer of 2005 and at times was higher than during the strongest El Niño events of the 20th century (1983 and 1997–1998). Our analyses suggest that changes in source waters, driven by remote basin scale forcing and not local environmental events, cause interannual-to-decadal variations in copepod biodiversity in the northern California current.

Numerous ecological studies have established the critical role that climate variability may play in controlling ecosystem dynamics in the north Pacific. Some classic examples include the influence of El Niño cycles; the Pacific Decadal Oscillation (PDO); and climate regime shifts on intertidal, planktonic, and fish communities (Francis and Hare 1994; Dayton et al. 1998; McGowan et al. 1998). Less well established are the subtle mechanisms by which ecosystem dynamics are influenced by event scale, seasonal and interannual variations in winds, hydrography, and transport. Zooplankton are excellent candidates for the study of the ecosystem response to climate variability because their life cycles are short (on the order of weeks), thus populations have the potential to respond to and reflect event-scale and seasonal changes in environmental conditions (Mackas et al. 2001). Moreover, many zooplankton taxa are known to be indicator species whose presence or absence may represent the relative influence of different water types on ecosystem structure. Thus zooplankton may serve as sentinel taxa that reflect changes in marine ecosystems by providing early indications of a biological response to climate variability (Hays et al. 2005). In this article, we use each of these attributes of zooplankton to investigate the effects of large-scale changes in atmospheric forcing on water circulation patterns and on subsequent changes in local copepod abundance patterns.

Biodiversity is a key biological parameter influencing multiple aspects of ecosystem structure and function (McGowan and Walker 1985; Hooper et al. 2005), yet studies investigating temporal variability in marine pelagic diversity have been limited. Notable exceptions, however, have provided important insights regarding the relationship between diversity and productivity (Irogoien et al. 2004) as well as zooplankton response to changes in the ocean environment. Recent analyses of a continuous plankton recorder time series suggest that copepod biodiversity may be an important indicator of latitudinal shifts of biological communities in response to oceanic warming in the North

Atlantic (Beaugrand et al. 2000; 2002). Similarly, Beaugrand and Ibanez (2004) have shown that dramatic shifts in North Sea copepod community structure can be the result of both local and regional hydroclimatic forcing. These and other studies in marine systems (e.g., Francis and Hare 1994) have demonstrated the importance of long-term data records for investigating the ecological response to interannual and interdecadal variability.

Here, we focus on copepods in the Oregon coastal upwelling zone of the northern portion of the California current ecosystem, a region of the northeast Pacific that appears to be particularly sensitive to environmental forcing (Batchelder et al. 2002). Zooplankton dynamics in the coastal zone of the northern California current display strong seasonal patterns (Peterson and Miller 1977; Peterson and Keister 2003). During the upwelling season (typically May through September), the copepod community tends to be dominated by cold-water neritic species that are representative of waters from the Bering Sea and coastal Gulf of Alaska (e.g., Cooney et al. 2001; Mackas et al. 2001). This is primarily the result of equatorward winds and subsequent southward transport of subarctic waters out of the coastal Gulf of Alaska, south along the coasts of Vancouver Island (British Columbia, Canada), Washington, and Oregon. Species composition on the continental shelf during upwelling conditions is characterized by low species diversity, with only a few dominant species (e.g., *Calanus marshallae, Psuedocalanus mimus, Acartia longiremis,* and *Centropages abdominalis*) (Peterson and Miller 1977). However, because of the close proximity of warm transition zone waters off Oregon, species diversity is high in waters immediately offshore of the continental shelf (Morgan et al. 2003). In fact, summer season sampling only 60–90 km from shore yields two to four times the species diversity observed in the coastal upwelling zone (Keister and Peterson 2003; Morgan et al. 2003). When upwelling winds weaken, offshore waters move shoreward, resulting in above average levels of copepod biodiversity on the shelf.

We have been monitoring the hydrography and zooplankton at several stations off Newport, Oregon, biweekly since May 1996 (Fig. 1). We visited the same stations that were sampled from 1969–1973 (Peterson and Miller 1977) and during the 1983 El Niño event (Miller et al. 1985). In an earlier article, Peterson and Keister (2003) used ordination and cluster analyses to describe variability in copepod community composition from 1996–2001. Here, we analyze temporal patterns of copepod species composition from our updated 9-year time series, and, in combination with historical samples from previous decades, we show dramatic increases in species biodiversity during recent years. These patterns provide evidence suggesting that copepod species composition in the early part of the 21st century is considerably different from that observed in the 1970s.

Methods

Samples were collected biweekly along the Newport Hydrographic (NH) line (Fig. 1), where a single station (NH05) has been visited more frequently than others,
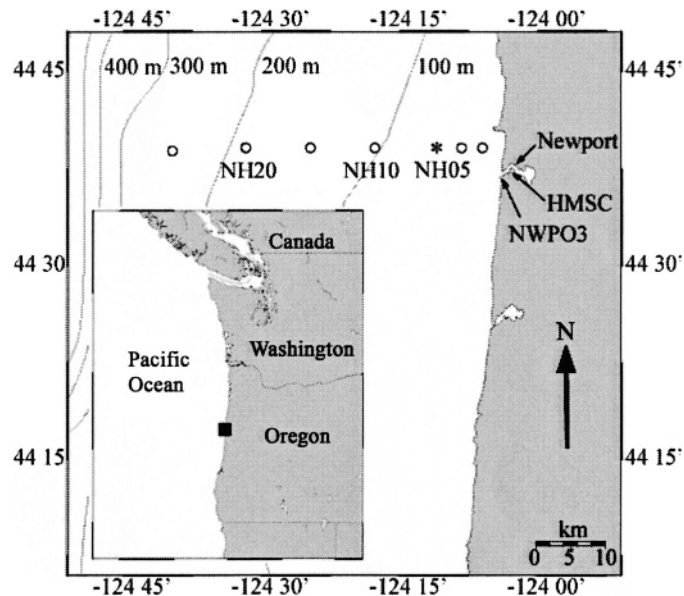

Fig. 1.   Chart of the Oregon coast, showing the location of the Newport Hydrographic line (sampling station NH05), the NH10 oceanographic mooring, NOAA buoy 46050 located near NH20, C-MAN Weather Sta. NWP03, and the Hatfield Marine Science Center (HMSC).

resulting in a more complete long-term time series and thus serving as the baseline station. Here, we report on data from NH05 (44.65°N, 124.18°W), a coastal shelf station 9 km offshore from Newport, Oregon, at 62-m water depth. Hydrographic sampling included surface temperature measurements (1969–1973 and 1996) and water column profiles using a Seabird SBE-19 conductivity–temperature–depth (CTD) meter (1997–2004). From 1969 to 1973, zooplankton were collected by oblique bongo net hauls (20-cm diameter) with 239-μm mesh. More recently, samples were collected as vertical hauls with a 75-cm (1983) and 50-cm diameter (1996–2005) ring net with 202-μm mesh. Of the 290 samples analyzed, >90% were collected during daylight hours, and in all cases, nets were hauled from 5 m off the bottom to the surface. For analysis, net samples were first diluted to 5–10 times the settled volume, and then two 1-mL aliquots were removed with a piston pipette. Zooplankton was enumerated by species and developmental stage from each subsample: this protocol resulted in the enumeration of ~300–500 individuals per aliquot. Taxa-specific biomass was estimated from literature values (e.g., Uye 1982) and our own unpublished data of carbon weights. More than 95% percent of the samples were processed by the same person (W.T. Peterson), thereby limiting any potential taxonomic inconsistencies or bias among plankton counters.

Copepod species richness (S) was calculated as the number of taxa observed in a given sample. We also calculated the Shannon–Weiner diversity index (H'; MacArthur and MacArthur, 1961)

$$H' = -\sum p_i \log p_i \qquad (1)$$

where p_i is the proportion of individuals from a sample unit

belonging to species *i*, and Pielou's J (Pielou 1969), which indexes equitability (or evenness) of taxa abundance in a given sample as

$$J = H'/\log S \qquad (2)$$

The three biodiversity parameters (species richness, Shannon–Weiner diversity index, and Pielou's J) were first smoothed by converting biweekly data to monthly averages and then calculated as monthly anomalies (i.e., climatological monthly mean subtracted from the year-specific monthly average). This was done to remove cyclical seasonal patterns and to generate a standardized time span (May 1996–December 2004) by which to facilitate regression analyses with a variety of environmental covariates, many of which are only calculated as monthly averages (e.g., the PDO and the Multivariate El Niño/Southern Oscillation Index [MEI]). Because multiyear variability is of interest to this study, we did not remove lower frequency variability by detrending the data. To explore the null hypothesis that increased copepod biodiversity is the result of local physical forcing, pairwise linear regression analyses compared the relationship of copepod biodiversity (dependent variable) to local environmental variables (independent) such as sea surface temperature (SST), sea surface height (SSH), alongshore water transport as pseudodisplacement anomalies (Kosro 2003), upwelling index anomalies, and Ekman transport. SST and Ekman transport were calculated as monthly averaged anomalies from hourly measurements at National Oceanic and Atmospheric Administration (NOAA) Buoy 46050 (36 km off Newport and 27 km west of baseline station NH05) from the National Data Buoy Center (http://seaboard.ndbc.noaa.gov). To achieve a continuous daily wind time series for calculating monthly Ekman transport values and northerly component (V) winds at Buoy 46050, missing data were replaced with measurements from the NOAA weather station NWP03 (south jetty, Newport) and the weather station at the Hatfield Marine Science Center (http://weather.hmsc.oregonstate.edu). Monthly SSH values from South Beach (Newport), Oregon, were obtained from the University of Hawaii Sea Level Center (http://ilikai.soest.hawaii.edu). Upwelling index anomalies for 45°N were obtained from the Pacific Fisheries Environmental Laboratory Live-Access Server (http://www.pfeg.noaa.gov). Cumulative alongshore pseudodisplacement anomalies, based on Acoustic Doppler Current Profiler measurements from 14-m depth at the NH10 mooring (Fig. 1; Kosro 2003), were converted to monthly estimates by calculating the difference between the mid-point value of a given month and the mid-point value of the preceding month. As a measure of variability in water column structure at NH05, CTD profile data were used to calculate a thermal gradient index—the difference between temperature at 10-m and 50-m depth. All regression analyses between biodiversity indices and environmental variables were based on monthly anomalies (monthly averaged value minus month-specific climatological mean based on the 1996–2004 sampling period).

We also explored the relationship between biodiversity and the PDO (http://jisao.washington.edu/pdo), and the MEI (http://www.cdc.noaa.gov/people/klaus.wolter/MEI). The MEI (Wolter and Timlin 1998) is derived from six oceanographic measures from the tropical Pacific as a monthly estimate of El Niño/La Niña conditions. Although the El Niño/Southern Oscillation (ENSO) cycle clearly has widespread teleconnection impacts throughout the Pacific basin and beyond (Wooster and Fluharty 1985), mechanistic influences on the northeast Pacific are still poorly understood. The PDO describes a low-frequency ENSO-like climate pattern in the north Pacific that is defined as the leading principle component of SST variability (Mantua et al. 1997).

To assess the role of advection on biodiversity, we categorized all copepod taxa into one of five biogeographical assemblages based on published zoogeographic studies from the Oregon coast (Cross and Small 1967; Peterson and Miller 1977; Morgan et al. 2003) and other studies from the broader California current region (Fleminger 1967; Mackas et al. 2001; Jimenez-Perez and Lavaniegos 2004). The five assemblages are: (1) cold-water neritic, (2) subarctic, (3) warm-water neritic, (4) warm-water oceanic, and (5) other/unresolved (Table 1).

Pairwise linear regressions and multiple regression analyses were performed to assess the relative importance of local physical variables (e.g., upwelling indices and Ekman transport) and regional measures (e.g., MEI and PDO) as potential mechanisms influencing copepod biodiversity patterns. To be conservative with respect to potential autocorrelation in the dataset, statistical significance criteria was based on high alpha values ($p < 0.01$ and 0.001). Multiple linear regression models were based on backward elimination of independent variables. Only one basin-wide parameter was included in any given multiple regression analysis. That is, each basin-wide indicator used in our analyses (MEI, MEI_3 mo lag, PDO, PDO_5 mo lag, etc) was run independently with the other environmental covariates, and then the best fit model was reported.

Results

Seasonal changes in biomass and biodiversity—Coastal upwelling during the summer months results in increased copepod biomass and relatively few copepod species (Fig. 2), whereas winter conditions are characterized by low biomass and high species richness. Mean taxa richness during the winter (Dec–Jan–Feb) and summer (Jun–Jul–Aug) months of 1996–2004 was 14.0 (± 0.66 SE) and 9.1 (± 0.82 SE) species, respectively. A total of 56 copepod taxonomic categories were identified (Table 1), with taxa richness ranging from three species in a sample (03 Jun 2000) to 20 species (15 Nov 2002) (Fig. 3).

Interannual variations in biodiversity and species composition—Periods of high biodiversity often reveal a strong correspondence to ENSO cycles. Compared to the upwelling seasonal mean (9.3 $\pm$ 0.23 SE), May–September values of copepod species richness during the strong El Niño events of 1983 (15.1 $\pm$ 0.83) and 1997–1998

Table 1. Observed copepod species grouped by water-type affiliation.

Assemblage	Taxa
Cold neritic	*Acartia hudsonica*
	Acartia longiremis
	Calanus marshallae
	Centropages abdominalis
	Epilabidocera amphitrites
	Pseudocalanus mimus
	Tortanus discaudatus
Subarctic	*Metridia pacifica*
	Microcalanus pusillus
	Neocalanus plumchrus
	Scolecithricella minor
Warm neritic	*Acartia tonsa*
	Corycaeus anglicus
	Ctenocalanus vanus
	Paracalanus parvus
Warm oceanic	*Acartia danae*
	Calanus pacificus
	Calocalanus pavo
	Calocalanus tenuis
	Candacia bipinnata
	Clausocalanus arcuicornis
	C. furcatus
	C. lividus
	C. mastigophorus
	C. parapergens
	C. paululus
	C. pergens
	Eucalanus hyalinus
	Euchirella rostrata
	Mesocalanus tenuicornis
	Pleuromamma abdominalis
	Rhincalanus nasutus
	Sapphirina sp.
Other	*Aetideus pacificus*
	Centropages bradyi
	Clytemnestra rostrata
	Eucalanus spp.
	Euchaeta spp.
	Lucicutia flavicornis
	Metridia lucens
	Microsetella spp.
	Oithona similis
	Oithona spinirostris
	Oncaea spp.
	Paracalanus sp.
	Racovitzanus antarcticus

Fig. 2. Monthly climatogy (based on 1996–2004 time period) of biomass (dashed line) and species richness (mean ±SE). The number of observations per month is indicated at the base of each bar.

(14.9 ± 0.57) were 62% and 60% greater (Table 2). Figure 3 shows that species richness levels observed during the 1997–1998 winter (15.0 ± 0.86) were similar to the samples collected during the El Niño summer of 1998 (because samples were not collected during the winter of the 1983 event we cannot compare winter with summer).

Not all El Niño events result in increases in biodiversity: a strong El Niño event occurred at the equator during 1972, but showed no response in terms of copepod biodiversity off the Oregon coast (Fig. 3). In fact, the summer of 1972 represents the most consistent period of low biodiversity values in our time series. During the moderate El Niño
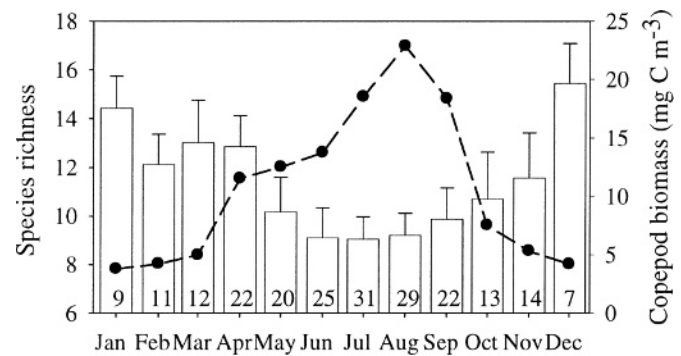
events of 1969 and 2002–2003, species richness values during the summer were only 8% and 16% greater than the seasonal mean, respectively (Table 2).

In contrast to elevated biodiversity observations associated with warm ocean conditions observed in the winter and during El Niño events, low levels of copepod species richness tend to correspond with the summer upwelling season and anomalously cool conditions. During the summers of 1970–1973 copepod species richness values (8.2 ± 0.36) were below the long-term mean (9.3 ± 0.23). Similarly, the La Niña event that immediately followed the 1997–1998 El Niño was characterized by summer season species richness values (6.9 ± 0.36) substantially lower than the seasonal mean. Anomalously low biodiversity following the 1997–1998 El Niño warm event persisted through summer 2002 (Fig. 3), with species richness similar to the early 1970s (Table 2).

Beginning in early 2001, however, the low biodiversity signal initiated in the summer of 1999 began to weaken and a significant increase in biodiversity followed. By November 2002, biodiversity values were comparable to those observed during both the 1983 and 1997–1998 El Niño events and have remained anomalously high through the winter of 2004–2005 and the spring of 2005 (W. Peterson, pers. obs.). When compared to the long-term mean (all years of 1969–1973, 1983, 1996–2004 combined), the most recent 4 years (May 2001–Dec 2004) represent a significant increase in taxa richness values ($t = -2.88$, $p < 0.01$).

To further explore the patterns exhibited by species richness and other biodiversity measures, we examined changes in species composition during the 15-year data record based on changes in proportional biomass of the five taxonomic assemblages listed in Table 1 (Figure 4). High taxa richness corresponds with winter months wherein a substantial amount of the total copepod biomass is composed of taxa with biogeographical affinities other than cold neritic. The same is true for the samples collected during the 1983 El Niño event and for the 16-month El Niño period of September 1997 through November 1998. In contrast, dominance by cold-water neritic taxa is indicative of the summer upwelling season when biodiversity is low. Note also that the period from the winter of 1999–2000 through 2004–2005 shows a trend toward
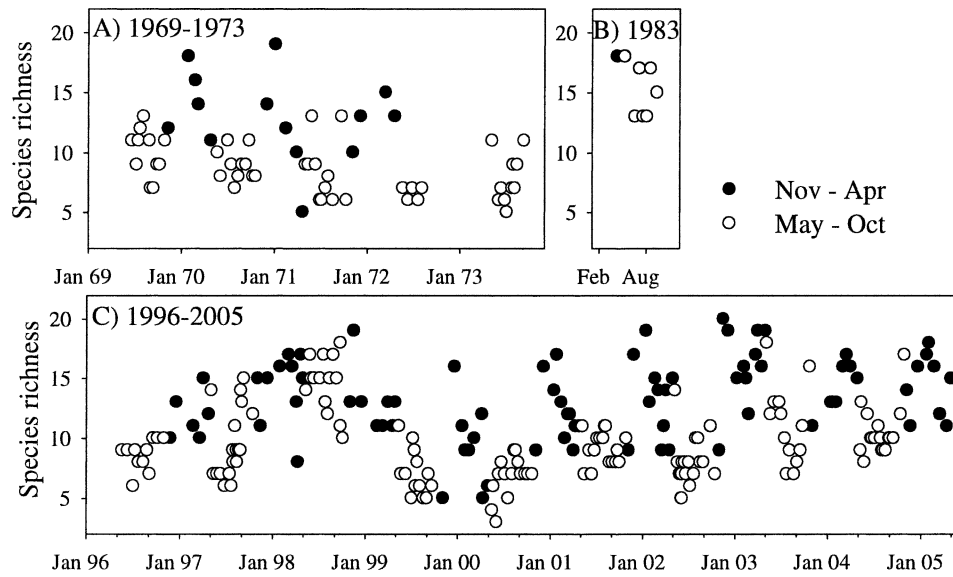
Fig. 3. Biodiversity time series from (A) 1969–1973 and 1983, (B) 1983, and (C) 1996–2005. Species richness of individual samples from November–April (filled circle) and May–October (open circle).

increased biodiversity with increased dominance of warm-oceanic species. The past two winters (and summers) were different from earlier years in that warm-water neritic species made up a greater proportion of the biomass (along with warm-water oceanic species).

The abundance patterns of two warm-water neritic taxa (*Acartia tonsa* and *Corycaeus anglicus*) further illustrate the recent changes in biodiversity (Fig. 5A). These taxa are indicators of subtropical coastal waters (Fleminger 1967; Barnett and Jahn 1987), which off Oregon have typically been associated with the poleward-flowing Davidson current during winter downwelling conditions and during large El Niño events (Peterson et al. 2002, Keister and

Peterson 2003). These two species have become increasingly abundant during all months of 2003–2005, presumably because of increased northward advection of warm coastal waters year around. Apart from the occurrence in most winters, neither species was observed with any regularity during the summers of 1970–1973 or from 1999–2002. Beginning in late 2002, however, *A. tonsa* appeared in our samples at abundances only previously observed during El Niño events (1969, 1983, and 1997–1998). The abundance of *A. tonsa* persisted on the Oregon shelf, even during the summer months of 2003 and 2004, and remained at historically high levels during the latter part of 2004 (Fig. 5A). Before 2003, *C. anglicus* had only exhibited

Table 2. Interannual comparison of seasonal differences in average copepod species richness (±SE) during the summer (May–September) and winter (November–March) of the sampling periods 1969–1973, 1983, and 1996–2004 (n/a indicates that no samples were collected). Description of predominant El Niño-Southern Oscillation (ENSO) conditions are included.

|	May–Sep	Nov–Mar	ENSO conditions
1969 (69/70)	10.0 (0.71)	15.0 (1.29)	Weak El Niño
1970	9.1 (0.45)	13.8 (1.93)	
1971	8.6 (0.88)	12.7 (1.45)	
1972	6.6 (0.27)	n/a	El Niño
1973	7.8 (0.66)	n/a	
1983	15.1 (0.83)	n/a	El Niño
1996	8.3 (0.41)	11.0 (0.71)	
1997	9.2 (0.69)	15.0 (0.86)	El Niño
1998	14.9 (0.57)	13.4 (1.47)	El Niño
1999	7.1 (0.54)	10.0 (1.46)	La Niña
2000	6.7 (0.50)	12.9 (0.97)	
2001	9.0 (0.38)	13.4 (1.28)	
2002	8.0 (0.51)	15.4 (1.19)	Weak El Niño
2003	10.8 (0.91)	14.1 (0.83)	Weak El Niño
2004	10.0 (0.32)	14.9 (0.99)	
All observations	9.3 (0.23)	13.6 (0.37)	
1969–1973	8.4 (0.34)	13.8 (0.89)	
Nov 2002–Mar 2005	10.4 (0.44)	14.8 (0.58)	
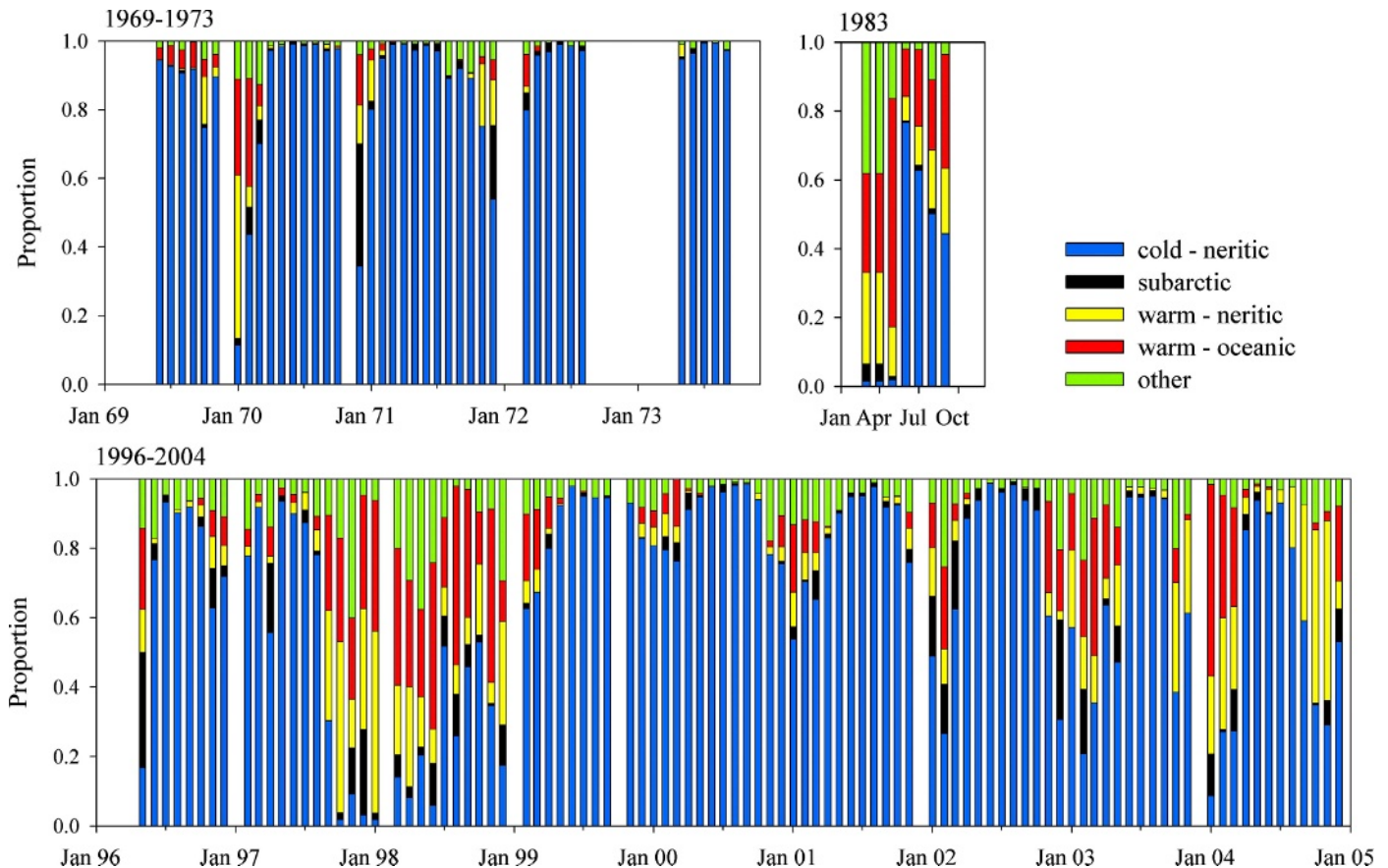
Fig. 4.   Species composition based on biogeographical affinities of five copepod assemblages listed in Table 1. Stacked bars represent the monthly averaged proportional contribution of each assemblage to total copepod biomass.

substantial summer season abundance during major El Niño events (1983 and 1997–1998). The frequency of occurrence and abundance of *C. anglicus* during the summers of 2003 and 2004 was comparable to these previous major ENSO events and had not been observed during earlier moderate events (i.e., 1969). Similarly, *Clausocalanus parapergens*, also a predominantly winter-time species, showed increases in frequency of occurrence and abundance beginning in winter 2000–2001 and was a more frequent member of the summertime community in both 2003 and 2004 (Fig. 5A).

Complementary examples are seen with three cold water taxa, *Tortanus discaudatus, Microcalanus pusillus*, and *Scolecithricella minor* (Fig. 5B). The presence of these three indicator species illustrates the strong influence of subarctic waters flowing southward from the Gulf of Alaska during the summers of 2000 through 2002 (Freeland et al. 2003; Huyer 2003).

A more detailed analysis of recent changes in biodiversity and ocean-climate variability—Because of significant gaps in the historical data set and a lack of corresponding hydrographic and meteorological data for the two earlier time periods (1969–1973, 1983), the remainder of this article focuses on copepod biodiversity response to environmental variability during the most recent 9-year

sampling period (1996–2004). Figure 6 shows monthly anomaly time series of biodiversity indices (species richness, Shannon–Weiner index, and Pielou's J) and a variety of physical variables. Visually, correlations between the bio-diversity time series and some physical variables are apparent. In particular, the interannual patterns of species richness (Fig. 6A) track both the PDO and the MEI (Fig. 6C). That is, when the PDO and MEI were in a positive (i.e., warm) phase during the 1997–1998 El Niño, greater than average numbers of taxa were observed. In August 1998, the PDO shifted to negative (i.e., cool) phase and remained negative for 41 of the following 48 months, a pattern not observed since the years before 1977 (Mantua et al. 1997). This transition from positive (and warm) climate index values to negative (and cool) values, was mirrored by a dramatic downward shift in species richness from anomalously high "winter-like" levels in September 1998 (18 spp.) to below average monthly values beginning in October 1998 (10 spp.). This decline in richness may be attributed to both a La Niña response and to a longer-term climate shift to cool conditions as reflected by the persistence of negative values of the PDO for the following 4 years (Fig. 6C). The Shannon–Weiner diversity index and Pielou's J index of equitability (Fig. 6B) also reveal patterns of interannual variability similar to those observed in species richness.
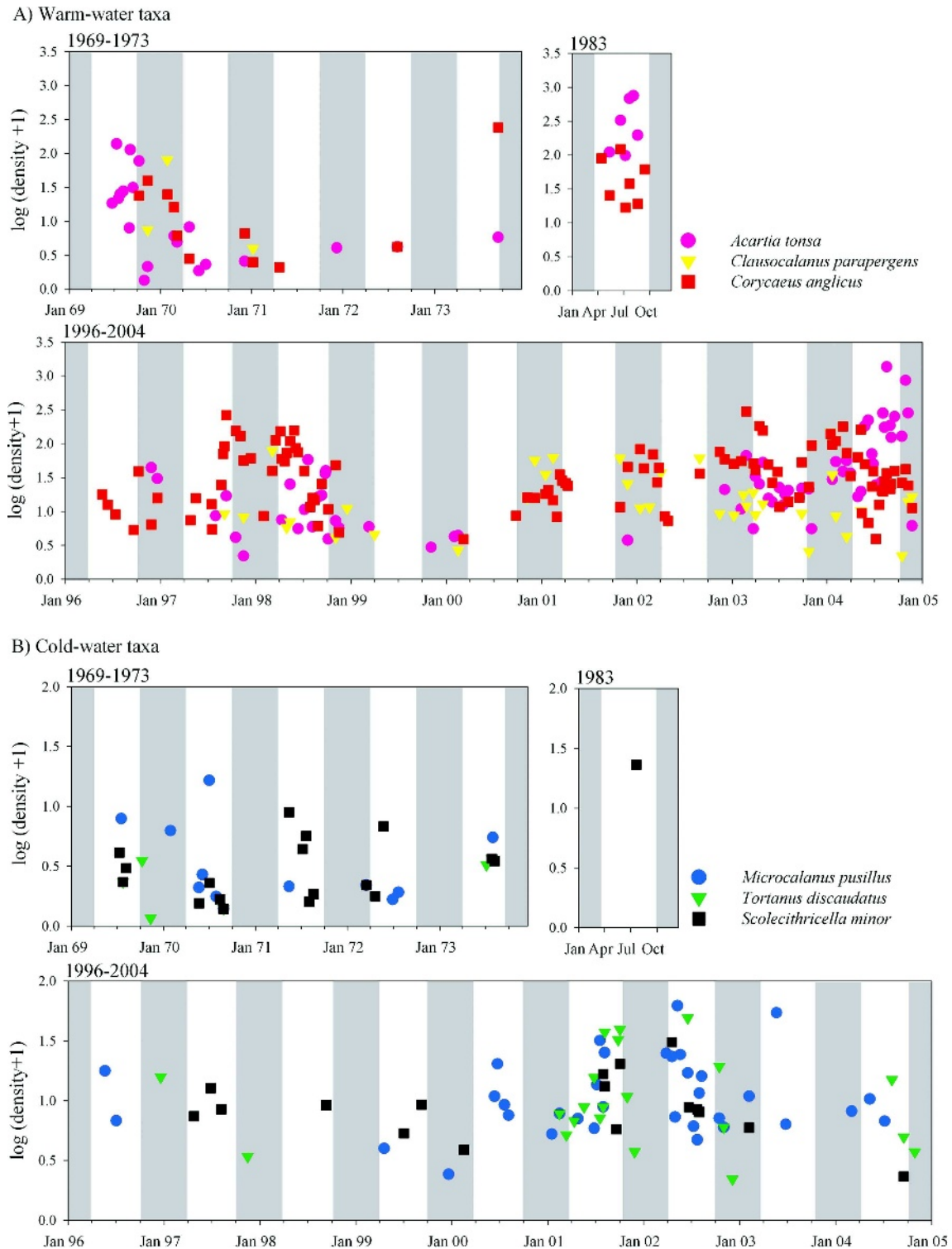
Fig. 5. Species-specific time series (1969–1973, 1983, 1996–2004) of representative (A) warm-water and (B) cold-water taxa. Gray portions of the time series represent winter months (Nov–Mar). Note: zero abundance observations are not included; sampling frequency identical to observations in Fig. 3.

The pattern of biodiversity anomalies shows three distinct phases following the relaxation of strong El Niño conditions in autumn 1998 as indicated by the vertical dotted lines in Fig. 6. Phase I, the 1999–2000 time period, represents 2 years of anomalously low species richness (Fig. 6A). Beginning in December 2000, however, biodiversity anomalies signaled a weakening trend toward neutral (average) values (phase II, Fig. 6A,B). Late in 2002,
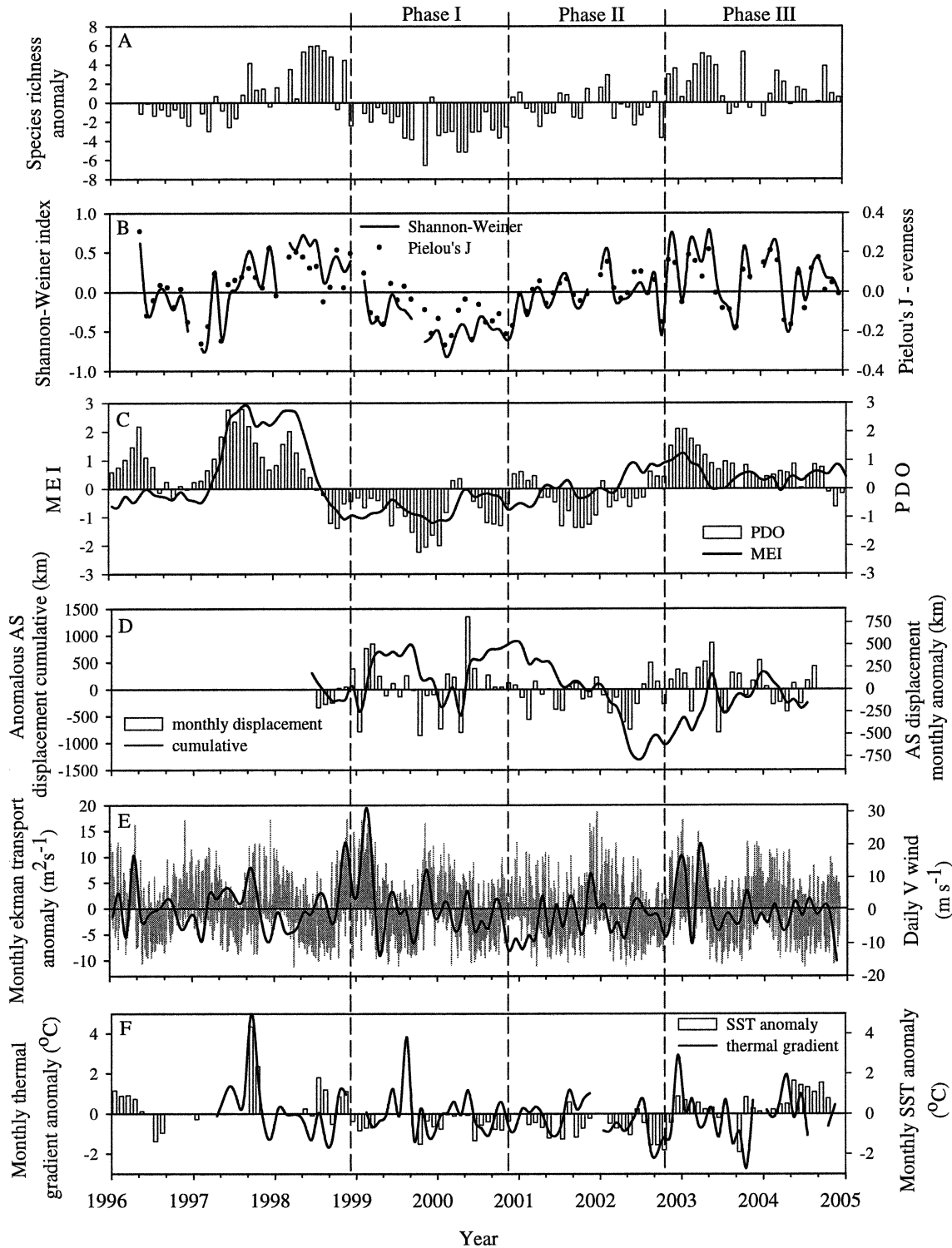
Fig. 6. 1996–2004 time series. Seasonally detrended monthly anomalies of (A) taxa richness, (B) Shannon–Weiner diversity index (circle) and Pielou's J equitablity index (line). (C) Monthly MEI (bar) and PDO (line), (D) cumulative alongshore pseudodisplacement (line) and monthly displacement values from a depth of 14 m measured at the NH10 acoustic Doppler current profiler mooring, (E) daily northern component (V) winds (bars) and monthly Ekman transport (line), (F) monthly SST (Buoy 46050) and thermal gradient (10-m temperature–50-m temperature) anomalies. Phase I (Nov 98 to Dec 00) describes a period of anomalously low species biodiversity, Phase II corresponds to neutral biodiversity; and Phase III represents a period of high biodiversity. Where applicable, the left axis is represented by spline curves and the right axis by vertical bars.

corresponding with a shift toward positive (warm) values of the MEI and PDO, biodiversity indicators again became anomalously high (phase III), a trend that persists up to the writing of this article (August 2005).

An oceanographic mooring 18 km offshore at Sta. NH10 (Kosro 2003) has resulted in a time series of ocean currents (1998 to 2004) that shows a visual correspondence between some interannual shifts in alongshore transport (Fig. 6D) and the patterns observed in our biodiversity time series. Phase I showed equatorward transport during winter 1999–2000 and brief periods of poleward transport in February–April 1999 and December 1999–February 2000, but neutral transport during both summers of 1999 and 2000. During this period, biodiversity anomalies were consistently negative and low. During phase II, a period characterized by an increased occurrence of cold-water indicator taxa and a shift toward neutral biodiversity anomalies, alongshore transport was predominantly equatorward for nearly 18 months. During Phase III a shift in alongshore transport patterns (from equatorward to poleward) and a change toward anomalously high biodiversity levels occurred. This suggests that increased biodiversity during the summer of 2002, and thereafter, may be related to a shift toward anomalously high poleward transport along the Oregon coast.

A relationship between transport and species richness is suggested in Fig. 7, a plot of species richness versus water density at 50-m depth. A strong and significant relationship was observed between water density and species richness (seasonally averaged for the months Dec–Jan–Feb, Mar–Apr–May, etc.) with richness highest when low-density water is present (relatively warm and fresh as seen during El Niño events and during winter months) and lowest when water density was highest (cold and salty water as seen during the summer upwelling season). Thus the end points of the diversity continuum are associated with two different water types: (1) cold and salty water associated with coastal upwelling and southward flows out of the subarctic North Pacific, and (2) warm fresh waters associated with seasonal downwelling and northerly, onshore, or both flows whose origins are waters from either the south or offshore of Oregon.

To evaluate which physical processes may be most related to patterns of species richness, we compared biodiversity anomalies and environmental variables for all months during the 1996–2004 time period. The strongest pairwise regressions for species richness were observed with SST at the 46050 NOAA Weather Buoy (correlation coefficient $R = 0.47$, $p < 0.001$), the MEI ($R = 0.36$, $p < 0.001$), and the PDO ($R = 0.36$, $p < 0.001$) (Table 3). Visually, it appears that changes in the biodiversity indices lag PDO and MEI time series by several months (Fig. 6). Based on the assumption that basin-wide indices (i.e., PDO and MEI) could have a lagged response on ecological processes on the Oregon coast (particularly the equatorial forcing measured by the MEI), post-hoc comparisons revealed that 3- and 5-month lags in climatological indices resulted in much improved correlation coefficients. Richness showed strong correlations with a 3-month PDO lag ($R = 0.53$, $p < 0.001$) and a 3-month MEI lag ($R = 0.66$, p
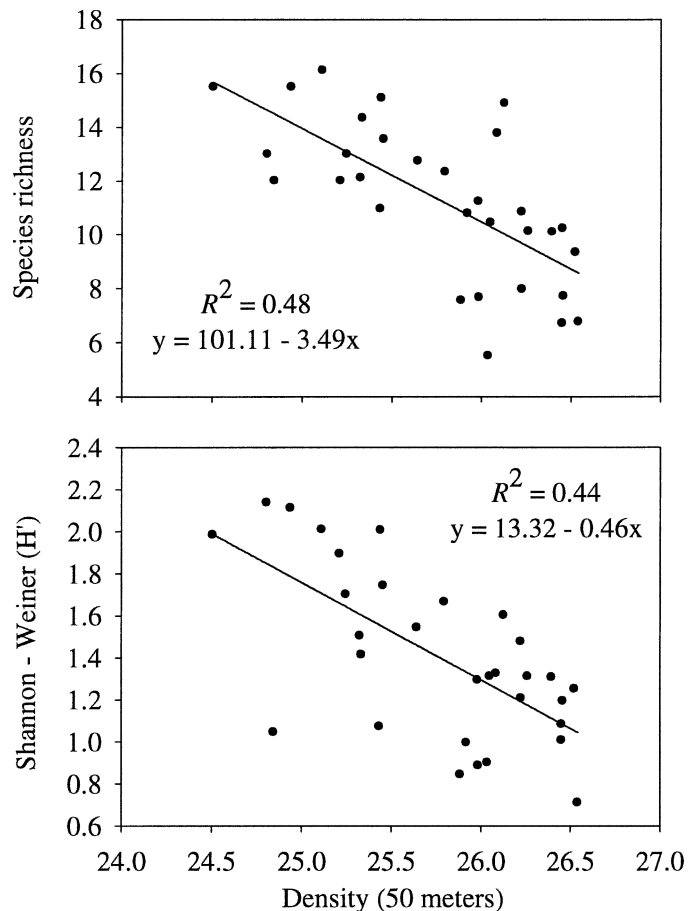

Fig. 7. Linear regression of biodiversity indices (S and H′) and NH05 water density at 50-m depth (1997–2004). Each data point represents three month seasonal averages (Dec–Jan–Feb, Mar–Apr–May, etc.)

< 0.001). The most significant pairwise correlations for Shannon diversity were achieved with the 3-month lags of both MEI ($R = 0.62$, $p < 0.001$) and PDO ($R = 0.53$, $p < 0.001$), as well as SST ($R = 0.44$, $p < 0.001$).

To further explore mechanisms which may have a season-specific influence on copepod biodiversity, we investigated correlations for summer (May–Sep) and winter (Nov–Mar) months individually (Table 3). This approach revealed a stronger relationship between biodiversity and many physical variables during the summer months, particularly the MEI and temperature at 50-m water depth. Temperature at 50 m was significantly correlated with both richness ($R = 0.53$, $p < 0.01$) and Shannon diversity ($R = 0.57$, $p < 0.001$). Species richness showed a much stronger correlation with the MEI 5-month lag ($R = 0.87$, $p < 0.001$) as compared to Shannon diversity ($R = 0.61$, $p < 0.001$). For winter-specific regressions, no pairwise comparisons revealed improved correlations, and contrary to the summer season, there is no evidence for a lagged response between diversity and either of the basin-wide climatological indices.

Multiple regression analyses resulted in best-fit models that explain approximately 50% of the variation in biodiversity for all months combined (Table 4). Patterns

Table 3. Pairwise linear regression parameters (1996–2004) for monthly anomalies and season-specific monthly averaged values of biodiversity (species richness and Shannon–Weiner diversity index) compared to a variety of physical, meteorological, and climatological variables.

Species richness (S) versus	All months					May–Sep					Nov–Mar				
	df	F ratio	Corr. coeff.	R^2	p value	df	F ratio	Corr. coeff.	R^2	p value	df	F ratio	Corr. coeff.	R^2	p value
SST–buoy 46050	70	19.42	0.47	0.22	**	33	5.76	0.39	0.15		23	2.51	0.31	0.10	
10-m Temperature–NH05	83	6.44	0.27	0.07		36	2.04	0.23	0.05		30	5.01	0.38	0.14	
50-m Temperature–NH05	83	5.16	0.24	0.06		36	13.92	0.59	0.28	*	30	2.21	0.26	0.07	
Thermal gradient (10–50 m)	83	0.06	0.03	<0.01		36	0.04	−0.03	0.001		30	0.86	0.15	0.02	
Sea surface height (HMSC)	96	6.48	0.25	0.06		43	2.06	0.21	0.05		34	2.72	0.27	0.07	
V wind (buoy 46050)	96	0.40	0.06	<0.01		52	0.50	0.09	<0.01		43	0.09	0.05	<0.01	
Ekman transport (buoy 46050)	96	1.22	0.11	0.01		43	0.64	0.12	0.02		34	0.05	0.04	<0.01	
45°N upwelling index	96	0.10	−0.03	<0.01		43	0.55	0.11	0.01		35	0.14	0.06	<0.01	
NH10 alongshore pseudodisplacement	68	0.80	0.10	0.01		30	1.59	0.22	0.05		25	0.02	0.03	<0.01	
PDO	96	13.66	0.35	0.12	**	43	1.59	0.19	0.04		35	13.83	0.53	0.28	*
PDO–3 month lag	96	37.45	0.53	0.28	**	43	20.00	0.56	0.32	**	35	4.59	0.34	0.12	
MEI	96	13.76	0.35	0.13	**	43	2.93	0.25	0.06		35	10.34	0.48	0.23	*
MEI–3 month lag	96	70.54	0.65	0.42	**	43	107.40	0.85	0.71	**	35	10.62	0.48	0.23	*
MEI–5 month lag	96	76.66	0.67	0.44	**	43	134.89	0.87	0.76	**	35	13.87	0.53	0.28	*
Shannon diversity (H′) versus															
SST–buoy 46050	70	16.32	0.43	0.19	**	33	4.32	0.34	0.12		23	0.45	0.14	0.02	
10-m Temperature–NH05	83	9.73	0.32	0.10	*	36	4.23	0.32	0.11		30	1.39	0.21	0.04	
50-m Temperature–NH05	83	4.09	0.22	0.05		36	17.25	0.57	0.32	**	30	0.86	0.17	0.03	
Thermal gradient (10–50 m)	83	1.11	0.11	0.01		36	0.67	0.12	0.01		30	0.51	0.12	0.01	
Sea surface height (HMSC)	96	7.33	0.27	0.07	*	43	4.51	0.31	0.10		34	1.95	0.23	0.05	
V wind (buoy 46050)	96	0.69	0.09	<0.01		52	0.96	0.13	0.01		43	0.15	0.06	<0.01	
Ekman transport (buoy 46050)	96	2.71	0.17	0.02		43	1.98	0.21	0.04		34	0.13	0.06	<0.01	
45°N upwelling index	96	1.06	−0.11	0.01		43	0.01	0.02	<0.01		35	0.89	0.16	0.03	
NH10 alongshore pseudodisplacement	68	0.31	0.06	<0.01		30	0.22	0.08	<0.01		25	0.11	0.07	<0.01	
PDO	96	17.24	0.39	0.15	**	43	3.10	0.26	0.07		35	14.03	0.54	0.29	*
PDO–3 month lag	96	36.91	0.53	0.28	**	43	11.07	0.45	0.21	*	35	11.47	0.50	0.25	*
MEI	96	25.96	0.46	0.21	**	43	4.88	0.32	0.10		35	16.64	0.57	0.32	**
MEI–3 month lag	96	59.04	0.62	0.38	**	43	41.55	0.70	0.49	**	35	15.35	0.55	0.31	**
MEI–5 month lag	96	50.21	0.61	0.37	**	43	25.08	0.61	0.37	**	35	17.94	0.58	0.34	**

$*p<0.01; **p<0.001.$

of species richness were best explained by MEI (3-month lag), SST, and thermal gradient anomalies ($R^2 = 0.59$, $p < 0.001$). For summer months, MEI (3-month lag), 50-m temperature, and SSH explain 80% of the variability in species richness values. For winter observations of Shannon diversity, MEI (no lag), SSH, and alongshore transport revealed the most significant relationship ($R^2 = 0.49$, $p < 0.001$). In all cases, a majority of the explanatory power comes from the relationship between biodiversity and the MEI (and to a lesser extent, PDO), suggesting that the observed interannual patterns, including the recent increases, are more associated with regional or basin-wide changes in ocean processes than variations in the dynamics associated with local wind forcing.

Discussion

Seasonal variations in biomass and biodiversity are a common feature in the Oregon upwelling zone and can be explained by seasonal changes in coastal circulation patterns. High copepod biomass is accompanied by low biodiversity and vice versa, with changes following a seasonal pattern of low diversity in summer and high diversity in winter. The cause of these seasonal patterns is clearly related to changes in wind-driven upwelling dynamics and the subsequent variation in the source waters feeding into the coastal zone off the Pacific Northwest. That is, during winter, the Davidson current flows north along the Oregon coast bringing to the Pacific Northwest a subtropical neritic fauna that is normally resident off California and has higher diversity because of its subtropical origins. Similarly, the same relationships between high diversity and low biomass hold for large El Niño events, such as observed in 1983 and 1997–98, because of anomalous northward transport associated with oceanic Kelvin waves that accompany such events (e.g., Lynn and Bograd 2002). Thus, the stronger the northward transport the greater the occurrence of anomalous southern species that appear off the coast of Oregon (Keister et al. 2005). Conversely, the summer upwelling season is typically

Table 4. Best-fit models based on multiple regression analyses (backward removal) exploring the relationship between copepod biodiversity (species richness [S] and Shannon–Weiner Diversity [H′]) and environmental covariates. Covariates include depth-specific temperature (SST, 10 mT and 50 mT), thermal gradient (T_gradient), sea-surface height (SSH), and alongshore pseudodisplacement (AS). Three- and five-month lagged indices of the MEI are represented by MEI(3) and MEI(5), respectively.

Best-fit model (1996–2004)	df	SS	MS	F	p	SE est.	Adj. R^2
All Months							
S = MEI(3) + SST + T_gradient						1.94	0.59
Regression	3	325.68	108.56	28.71	**		
Residual	56	211.79	3.78				
Total	59	537.46					
H′ = MEI(3) + 10 mT						0.30	0.46
Regression	2	4.78	2.39	26.33	**		
Residual	57	5.17	0.91				
Total	59	9.95					
Summer (May–Sep)							
S = MEI(5) + 50 mT + SSH						1.32	0.80
Regression	3	187.74	62.58	35.88	**		
Residual	22	40.12	1.74				
Total	25	227.85					
H′ = MEI(5) + SSH + T_gradient + 50 mT						0.21	0.64
Regression	4	2.18	0.55	12.29	**		
Residual	22	0.98	0.04				
Total	26	3.16					
Winter (Nov–Mar)							
S = PDO(no lag) + 10 mT						2.61	0.30
Regression	2	87.02	43.51	6.38	*		
Residual	23	156.93	6.82				
Total	25	243.95					
H′ = MEI(no lag) + SSH + AS						0.34	0.49
Regression	3	3.24	1.08	9.23	**		
Residual	22	2.57	0.12				
Total	25	5.81					

*$p<0.01$; **$p<0.001$.

characterized by transport from the north, wherein the copepod community off the Oregon coast is subarctic boreal neritic in origin.

Our efforts to explain copepod biodiversity measures at interannual scales in terms of local forcing dynamics (i.e., local winds, Ekman transport, and Bakun upwelling index) did not yield strong relationships, but instead, these analyses suggest a greater influence of remote basin scale forcing. The same result has been found from analysis of hydrographic data from the California Cooperative Oceanic Fisheries Investigations program for the time period 1949–2000. Di Lorenzo et al. (2005) showed that the temperature signals in the California current were coherent with indices of large-scale climate variability (the PDO). Moreover, the temperature signal in the California current is controlled by net-surface heat flux forcing over the entire northeastern Pacific. Locally the temperature anomalies are maintained by southward advection of northeast Pacific waters that redistribute the large-scale heat input.

Our demonstration of biological response to basin scale forcing is supported by results of ordinary and multiple regressions shown in Tables 3 and 4: the strongest correlations were between biodiversity and climatological indices (PDO and MEI) rather than local winds. Although

correspondence with the PDO is relatively strong, there are multiple periods during 1996–2004 when the PDO is out of phase with biodiversity anomalies (Fig. 6). The lack of strong correlation with the PDO appears to be related to neutral biodiversity values during 1996 and 2001–2002 relative to the value of the PDO. The MEI, which is representative of equatorial forcing and (presumably) teleconnection to the northeast Pacific, provided a stronger climatological signal for modeling copepod biodiversity response.

The response of biodiversity to both of these climatological indices demonstrates a considerable lag in some cases, from 1 to 7 months. However, the lag varied among years and season, thereby complicating any standardized adjustment for regression analyses. For example, the pronounced shift in biodiversity in November 1999 lagged the change in sign of the PDO and MEI by 4 months, whereas the shift to high diversity in October 2003 lagged the PDO by 3 months but the MEI by 7 months. Generally, the lag of biodiversity response to basin-wide forcing was substantially less during winter months than during summer months (Tables 3, 4).

Regardless of slightly variable lag times, shifts in biodiversity anomaly signals are clearly associated with

large-scale climate events: (1) the 1997–1998 El Niño event, (2) the 1999–2002 cool period associated with negative PDO and MEI values, and (3) the warm period of 2002–2005 associated with positive values of the PDO and MEI. A variety of coast-wide observations during the 1999–2002 time period suggested that the transition in the PDO from positive values (which dominated from 1977–1998) to negative values (initiated in August 1998) may have represented a new long-term (decadal) shift in northeast Pacific Ocean conditions (Peterson and Schwing 2003; Bond et al. 2003). Contrary to these expectations, the PDO and MEI changed sign again after only 4 years (in autumn of 2002). Copepod biodiversity began to increase in November 2002 and continued to exhibit anomalously high values through the summer 2005 (Figs. 3, 6A,B; W. Peterson pers. obs.). Thus the short duration of the recent 4-year cool period that was then followed by a 3-year warm period (and the accompanying changes in biodiversity and biomass) calls into question the status of long-term changes in Northern California Current (NCC) productivity and the applicability of the decadal-scale regime shift model (*sensu* Mantua et al. 1997).

The change from anomalously low biodiversity (in 1999) to neutral levels of biodiversity during 2001–2002 (*see Phase II*, Fig. 4) appears to have been facilitated by an anomalous subarctic hydrographic influence (Freeland et al. 2003; Huyer et al. 2003), particularly apparent in the increased summertime occurrence of taxa with cold-water affinities (Fig. 5B). The increased frequency of occurrence and abundance of *M. pusillus, S. minor*, and *T. discaudatus* (Table 1, Fig. 6B), indicators of subarctic waters, support earlier reports documenting anomalous subarctic influence on the bottom waters of the NCC coast during the 2002 time period (Freeland et al. 2003; Huyer et al. 2003). Earlier studies from Ocean station "P" in the Gulf of Alaska (50°N, 145°W) document a predominantly deep (>200 m) distribution of *M. pusillus* (Marlowe and Miller 1975). Therefore, anomalously high abundance of these subarctic taxa on the Oregon shelf may be indicative of buoyancy driven deep-water intrusion from the subarctic.

The increased abundance of warm-water taxa during winter 2000–2001 and 2001–2002 (Fig. 4) was likely the result of anomalous westerlies (Bond et al. 2003) advecting offshore surface waters on to the Oregon shelf. This suggests that increased biodiversity of copepod taxa may be the result of a greater influence of transition zone waters on the Oregon shelf, much like ecological changes observed in the North Sea in response to source water variability (Russel 1939; Cushing and Dickson 1976; Reid et al. 2001).

The overall increase toward high copepod biodiversity levels in the NCC since late 2002 (Phase III, Fig. 6), however, appears to be the result of another shift in ocean transport dynamics. In particular, the presence of *A. tonsa* and *C. anglicus* during the summer seasons of 2003 and 2004 (Fig. 5A), and which continued through summer 2005, (W. Peterson pers. obs.) suggests a particularly strong presence of warm neritic source waters from the south. Elevated biodiversity levels observed off Newport during the 2002–2005 time period correspond with an increased proportion of warm-water taxa and a longer duration of

their winter-time occurrence into the summer months (Fig. 4). As such, these species-specific taxonomic data provide important clues regarding biological response to climate and source water changes in the NCC.

The northeast Pacific has undergone extreme interannual variability over the past decade, frustrating efforts to forecast fisheries and ecosystem response to climate change. Mantua (2004) argues that even in instances when local fisheries data and large-scale climate indices reveal a strong statistical relationship, the correlation rarely provides a clear indication of the critical biophysical processes that are responsible for the observed variability. Instead, he suggests that upscaling local biophysically relevant parameters to larger-scale climatic patterns may provide a more fruitful approach toward understanding mechanistic relationships and ecological predictability. Plankton community response indicators, such as copepod biodiversity off the Oregon coast, may provide an example of such a parameter that represents an ecologically relevant link between large-scale hydroclimate patterns and system response at higher trophic levels (Peterson and Schwing 2003; Wooster and Zhang 2004). That is, during periods of negative PDO, cool temperatures, and low copepod biodiversity, the dominant copepod species off Oregon are subarctic neritic in origin: *C. marshallae, P. mimus, C. abdominalis*, and *A. longiremis*. The first two species are relatively large, characterized as being lipid-rich, and thus have greater per capita bioenergetic content. On the other hand, subtropical neritic and warm-water transition zone species (such as *Paracalanus parvus, Clausocalanus* spp., *Ctenocalanus vanus*, and *A. tonsa*) are smaller than the subarctic species and have lower lipid reserves (e.g., Benson and Lee 1975). Thus, extended periods of low biodiversity are associated with relatively large copepods that contain higher per capita bioenergetic value as compared to high biodiversity periods when the copepods are smaller but with lower per capita bioenergetic value. Differences in lipid and bioenergetic content of copepods under cold versus warm water conditions could impact the efficiency with which energy is transferred to higher trophic levels. Specifically, lipid content can significantly influence overwinter survival of marine fishes such as salmon during a critical life-history phase (Trudel et al. 2005) and therefore may represent an important bottom-up regulation link between climate and salmon abundance (Beamish and Mahnken, 2001).

In conclusion, widespread evidence supports the idea that plankton community composition may be an important harbinger of change in marine systems (Beaugrand et al. 2000; 2002; Hays et al. 2005). Ecologically integrative parameters such as biodiversity may, in fact, provide a more sensitive indication of changing ocean conditions and transport variability than physical measures (Taylor et al. 2002). Following the lead of Beaugrand et al. (2002), we believe that changes in biodiversity and community structure reflect adjustments of pelagic ecosystems to large-scale climate-driven modifications in water mass distributions. They attribute the recent distributional shifts in the North Atlantic to a combination of warming of the North Atlantic as well as a change in circulation caused by

the North Atlantic Oscillation. Our biodiversity time series supports the idea that fluctuations in copepod community structure are the result of changes in the source waters influencing the northern California current, rather than suggesting any change in latitudinal ranges of species. Moreover, our observations suggest that local meteorological and hydrographic measures alone are not sufficient for describing ecosystem variability in the NCC. The same conclusion was reached by Di Lorenzo et al. (2005) through analysis of water mass structure in the California current. Our results also highlight the importance of ecologically integrative measures (i.e., biodiversity and sentinel species) because these types of data seem to provide early detection of biological response to climate-driven changes in coastal ecosystems.

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