Limnol. Oceanogr., 57(5), 2012, 1467–1478

doi:10.4319/lo.2012.57.5.1467

A comparative analysis of coastal and shelf-slope copepod communities in the northern California Current system: Synchronized response to large-scale forcing?

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Abstract

The synchrony between coastal and shelf-slope copepod communities was investigated in the northern California Current (NCC) system, a strong upwelling zone, using time series of zooplankton sampled from a nearshore station (9 km offshore, water depth 62 m) and a shelf-slope station (46 km offshore, water depth 297 m). Long-term trends and seasonal changes were constructed for the dissimilarity index (Euclidean distance) between the two stations and for the biomass of three different copepod assemblages at the two stations: cold neritic, southern, and warm neritic copepods. The dissimilarity between the community structures of the two stations showed little variation in the long-term trend, but exhibited a clear seasonal pattern. All three copepod assemblages showed similar long-term trends in relation to the large-scale forcing as indexed by the Pacific Decadal Oscillation at both stations, but variations in the long-term trend at the nearshore station were much higher than the offshore station. Most copepod groups exhibited regular seasonal patterns at both stations except southern copepods at the nearshore station. All three copepod assemblages exhibited more pronounced seasonal fluctuations at the nearshore station compared with the slope station, and this difference is likely driven by higher productivity nearshore fueled by nutrient-enriched upwelled water. Copepods in the inshore and offshore waters in the NCC ecosystem showed synchronized response to the large-scale variability in physical forcing and copepods in the coastal waters were more responsive to local perturbations than were those in the slope waters.

Large-scale climate variability has a clear effect on zooplankton communities and likely has substantial ecosystem consequences (Roemmich and McGowan 1995; Beaugrand et al. 2002; Richardson 2008). In the northern California Current (NCC) system, it is well-established that the zooplankton community structure is related to large-scale ocean and climate variability, such as El Niño (Keister and Peterson 2003) and the Pacific Decadal Oscillation (PDO; Hooff and Peterson 2006; Peterson 2009). When the PDO is persistently positive, there are more warm neritic and southern copepods and relatively fewer cold neritic copepods in shelf waters off Oregon; conversely, when the PDO is negative, there are more cold neritic copepods and few-to-none warm neritic and southern copepods. Both Bi et al. (2011*b*) and Keister et al. (2011) have shown that these PDO-related differences in copepod community composition are due to variations in transport of source waters that feed the NCC. These changes in zooplankton communities can have profound cascading effects on higher trophic levels (McGowan et al. 1998).

Understanding biophysical interactions at different alongshore and cross-shelf regions offers a unique opportunity to investigate how ecosystems respond to large-scale and local climate variability. Zooplankton in the entire California Current system from southern California to British Columbia exhibit a cohesive response to large climate events such as El Niño, although the zone most strongly affected extends from northern California to southern British Columbia (Mackas et al. 2006). Meanwhile, in the nearshore upwelling region, zonal variations in physical forcing and ecosystem structure are clear because of wind-driven coastal upwelling during the spring and summer months (Peterson et al. 1979; Smith et al. 2001; Huyer et al. 2007). The continental shelf waters in the NCC off Washington and Oregon are enriched during periods of upwelling as surface waters are moved offshore through Ekman transport and replaced with deeper waters high in nutrients. In comparison, offshore waters tend to have much lower concentrations of nutrients and less production. While Ekman pumping helps fertilize offshore surface waters (Rykaczewski and Checkley 2008) and a portion of the nutrients and phytoplankton found nearshore can be transported offshore (Keister et al. 2009; Yokomizo et al. 2010), a cross-shelf zonal gradient in nutrients and primary production is generally maintained. Cross-shelf zonal variations in copepod production (Peterson et al. 2002*a*) and community structure (Keister and Peterson 2003) are also observed, with typically higher secondary production nearshore relative to offshore. Variations in copepod species composition are also closely related to upwelling. Cold neritic copepod species dominate coastal waters during the summer upwelling season, while warm neritic and southern copepod species become relatively more abundant in coastal waters during the downwelling season (Hooff and Peterson 2006). Cross-shelf zonation is also important for species such as euphausiids, whose young life-history stages aggregate nearshore and benefit from higher phytoplankton standing stock relative to offshore regions (Gómez-Gutiérrez et al. 2005, 2007). Many other coastal invertebrate and fish species rely on cross-shelf transport and zonation to not only disperse their larvae and

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return them to nearshore regions for settlement (Shanks and Eckert 2005) but also to maintain their larvae in regions favorable for development and subsequent recruitment to the benthos as juveniles (Morgan et al. 2009).

One of the challenges of investigations designed to determine how ecosystems respond to basin-scale and local-scale variability is to separate the seasonal from the interannual variations. In the NCC, coastal upwelling varies interannually as a function of the strength and location of the North Pacific High pressure cell (Mass and Bond 1996; Bane et al. 2005). It also varies due to El Niño events (Huyer et al. 2002) and by the phase of the PDO (Chhak and Di Lorenzo 2007), with upwelling often stronger during negative phases and weaker during positive phases. Because of recent highly variable and strong climate signals (e.g., El Niño [1997–1998], two La Niña events [1999, 2008], and several sign changes of the PDO since 1998), upwelling has been particularly variable; including a 4-yr period of strong upwelling accompanied by cold ocean conditions and high productivity from 1999 to 2002 (Peterson and Schwing 2003), and reduced upwelling with warm ocean conditions in 2003–2004 followed by severely reduced biological productivity in 2005 (Kosro et al. 2006; Pierce et al. 2006).

To investigate how coastal (shelf) and slope copepod communities in the NCC respond to basin-scale forcing and to local-scale upwelling, we compare two time series of zooplankton samples collected along the Newport Hydrographic Line at Sta. NH05 (5 miles from shore = 9 km) and NH25 (25 miles from shore = 46 km). We hypothesized that the dissimilarities in the copepod species assemblages between NH05 (coastal waters) and NH25 (slope waters) are driven by cross-shelf transport related to seasonal upwelling. That is to say, during the upwelling season, cold neritic copepod species become abundant in coastal waters and offshore flows transport these species to slope waters; whereas during the downwelling season, onshore flows carry warm neritic and southern copepod species to coastal waters in the NCC. The interannual variations of copepod species groups at the two stations (NH05 and NH25) may be different depending on water mass affinities and source waters associated with the low-frequency climate variability as indexed by the PDO.

Methods

Study site—Zooplankton samples were collected twice monthly during daytime hours from 1998 to 2010 along the Newport Hydrographic Line (NH, Fig. 1) off Newport, Oregon at two stations located 9 km (NH05; 44.65°N, 124.18°W; water depth 62 m) and 46 km (NH25; 44.65°N, 124.67°W; water depth 297 m) from shore. Samples were collected with a 50-cm-diameter ring net fitted with 202-μm mesh, hauled vertically from 5 m off the bottom to the surface at NH05 and 100-m depth to the surface at NH25. A Tsurumi–Seiki flowmeter was attached to the mouth of the net to facilitate calculation of the volume of water filtered. In the lab, the net samples were diluted to 5–10 times the settled volume and all individuals were identified to species and developmental stage from two piston pipette 1-mL subsamples. All counts were standardized to the volume of water sampled. Biomass was calculated by multiplying the standardized abundance (no. per cubic meter) by the mean carbon weight of each species and stage from published length to weight relationships or from our measurements (Lamb and Peterson 2005).

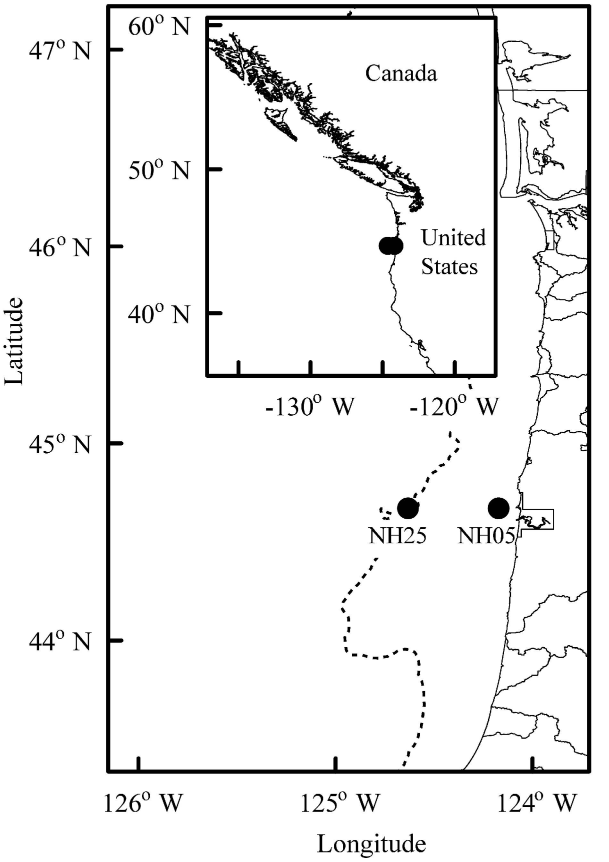

Fig. 1. The Newport Hydrographic (NH) Line stations NH05 and NH25 used in this study. Dotted line indicates the 200-m isobath.

Copepod species were classified into different ecological groups based on water mass affinities (Hooff and Peterson 2006). In the present study, we focused on three different groups that are good indicators of water mass and of the source water masses that feed the NCC: the cold neritic copepods, southern copepods, and warm neritic copepods. Cold neritic copepods included *Acartia hudsonica, A. longiremis, Calanus marshallae, Centropages abdominalis, Epilabidocera amphitrites, Pseudocalanus mimus,* and *Tortanus discaudatus.* Southern copepods included *A. danae, Calanus pacificus, Calocalanus* spp. (2 species), *Candacia bipinnata, Clausocalanus* spp. (5 species), *Eucalanus hyalinus, Euchirella rostrata, Mesocalanus tenuicornis, Pleuromamma abdominalis, Rhincalanus nasutus,* and *Sapphirina* sp. Warm neritic copepods included *A. tonsa, Corycaeus anglicus, Ctenocalanus vanus,* and *Paracalanus parvus.* The cold neritic species are characteristic of shelf waters off Oregon, Washington, Vancouver Island, and the Gulf of Alaska as well as the Bering Sea, whereas the southern species are characteristic of oceanic waters of the NCC (Mackas et al. 2001; Hooff and Peterson 2006), and the warm neritic species are characteristic of the coastal southern California Current (Barnett and Jahn 1987).

Temperature profiles were measured at each station with a Seabird model 19 conductivity–temperature–depth sensor to within a few meters of the bottom. Satellite-derived chlorophyll *a* (Chl *a*) concentrations are available from the West Coast Regional Node of the National Oceanic and Atmospheric Administration Coast Watch program website (http://coastwatch.pfeg.noaa.gov/). Monthly Chl *a* concentration from the Sea viewing Wide Field of view Sensor (SeaWiFS) onboard the OrbView-2 satellite from 1998 until October 2006, and from the Moderate Resolution Imaging Spectroradiometer (MODIS) after October 2006 were used to extract Chl *a* concentration along the NH Line, nearshore to ~ 150 km offshore. SeaWiFS data and MODIS data were processed and compiled into monthly composites of ocean Chl *a* concentration at 0.04° (~ 4 km) and 0.05° (~ 5 km) spatial resolution respectively. Time-series plots were constructed to show the seasonal and interannual variation in Chl *a* concentration along the NH Line. We recognized that data from MODIS and SeaWiFS cannot be compared as a time series and there is no simple correction coefficient that can be applied. Therefore, we only used the data to illustrate zonal variations.

The PDO is defined as the leading principle component of sea-surface temperature anomalies in the North Pacific and characterizes basin-scale forcing and low-frequency climate patterns of the NCC ecosystem (Mantua et al. 1997). Monthly values of the PDO were obtained from http://jisao.washington.edu/pdo. Daily values of upwelling strength for our study region (45°N, 125°W) were obtained from http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA and were averaged into monthly values to match the other data sets.

Data analysis—The dissimilarity between the entire copepod community at the two stations (NH05 and NH25) was calculated using the Euclidean distance measure (Deleeuw and Pruzansky 1978). In the present study, the Euclidean distance (Eq. 1) was computed between each species only for pairs of samples collected at both stations (NH05 and NH25) on the same day. From 1998 to 2010, NH05 was sampled 461 times, and NH25 was sampled 200 times. Euclidean distance was calculated for 170 paired samples.

$$\text{Euclidean Distance} = \sqrt{\sum_{i=1}^{n} (x_{1,i} - x_{2,i})^2} \qquad (1)$$

where $x_{1,i}$ and $x_{2,i}$ are the biomass (mg C m^{-3}) for species *i*at NH05 and NH25, respectively, and *n* is the number of species. Smaller Euclidean distance values indicate that copepod communities found at NH05 and NH25 on a given sampling day are more closely related, and vice versa.

To examine how the entire copepod community and the different copepod species assemblages respond to basin-scale and local forcing at NH05 and NH25, we performed time-series analysis to detect the overall trend and seasonality at each station. The principal of univariate time-series models are nothing more than regression models in which the explanatory variables are functions of time and the parameters are time-varying (Harvey and Shephard 1993). The simple univariate time-series models are based on a decomposition of the series into a number of components including a local trend, a deterministic seasonal component, and error terms (Eq. 2),

$$\begin{aligned} y_t &= T_t + S_t + v_t \\ T_t &= \phi T_{t-1} + w_{t1} \end{aligned} \qquad (2)$$

where T_t is the trend, S_t is the seasonal component, ϕ is the auto-correlation coefficient for T_t, $v_t \sim$ N(0, 1), $w_t \sim$ N(0, 1) independent of v_t, and N(0, 1) is a standard normal distribution. The coefficients were estimated using the Kalman Filter algorithm in Matrix Laboratory (MATLAB, Peng and Aston 2011). The local trend (T_t) is autocorrelated (i.e., the trend at time t + 1 is a function of the trend at time t, and the seasonal component (S_t) is modeled by the trigonometric seasonal model (a combination of sine and cosine functions with a seasonal period of 12 months; Harvey 1989). This allows for an estimate of long-term trends and seasonal components: long-term trends should be relatively smooth and the seasonal component should remain similar among years because the trigonometric seasonal model uses a combination of sine and cosine functions to model the recurrent patterns in the data set. Note that the long-term trend and seasonal component estimated from the model indicate the changes in biomass rather than the absolute values. R^2 is calculated to examine the portion of variance explained by the long-term trend and seasonal components.

We applied the univariate time-series model to the Euclidean distance measure of the entire copepod community and the biomass of cold neritic copepods, southern copepods, and warm neritic copepods at stations NH05 and NH25. Zooplankton samples were collected less frequently during the winter season than other seasons due to weather and vessel size (R/V *Elakha,* 16.5 m total length), so biomass data were binned (averaged) by month to avoid bias caused by sampling frequency. This also generated an equal sampling interval for time-series analysis and for matching with other parameters, such as the PDO (monthly values).

To examine how the entire copepod community and how the different copepod species assemblages respond to ocean conditions at the two stations, regression analyses were performed. We first tested the relationship between the dissimilarities in the community composition between the two stations measured by Euclidean distance vs. the PDO and monthly averaged upwelling. To test the hypothesis that long-term trends (interannual variation) are driven by basin-scale forcing as indexed by the PDO, we examined the relationships between the PDO and the long-term trends estimated from the univariate time-series models for the dissimilarities in the copepod community composition and for each of the different copepod species assemblages at the two stations. Finally, to test the hypothesis that upwelling was responsible for the seasonal patterns (within-year variation), the relationships between monthly averaged upwelling and the seasonal patterns estimated from the univariate time-series models were examined for the dissimilarities in the copepod community composition and for each of the different copepod species assemblages at the two stations.

Results

Oceanographic conditions and changes in copepod communities—During the period of study, the PDO alternated between a warm phase (1997–1998), a negative cold phase (1999–2002), a positive warm phase (2003–2007), and finally, a generally negative phase from 2008 to 2010 (Fig. 2a). The initial warm phase was during a strong El Niño (Jun 1997–Jun 1998) and the latter negative phase was interrupted by a moderate El Niño event from summer 2009 until spring 2010. The surface temperature at both stations showed strong seasonal changes. Surface temperature at NH25 was higher in the summer and lower in the winter, although the pattern was less clear and more variable at NH05 (Fig. 2b, c). Surface temperature at NH25 tended to be higher than NH05 in the summer from 2003 to 2009. Chl *a* concentrations at NH25 were positively correlated with NH05 (coefficient = 0.51, $R^2 = 0.43$, $p < 0.01$).

Copepod biomass showed both strong seasonal and interannual variation at both stations (Fig. 2d) with higher biomass in the summer and lower biomass in the winter. At NH05, copepod biomass ranged from 0.6 mg C m^{-3} to 94.5 mg C m^{-3} with a mean of 14.23 ± 12.53 (mean ± 1 SD) mg C m^{-3}. At NH25, copepod biomass ranged from 0.3 mg C m^{-3} to 34.8 mg C m^{-3} with a mean of 6.30 ± 5.08 mg C m^{-3}. During the summer upwelling season, zooplankton biomass at NH25 was 51% ± 40% of the biomass at NH05, whereas during the winter downwelling season, copepod biomass at NH25 was 75% ± 51% of the biomass at NH05. The biomass of cold neritic copepods, southern copepods, and warm neritic copepods at NH25 were all positively correlated with the corresponding assemblages at NH05 (cold neritic: coefficient = 0.56, $R^2 = 0.45$, $p < 0.01$; southern: coefficient = 0.81, $R^2 = 0.29$, $p < 0.01$; warm neritic: coefficient = 0.33, $R^2 = 0.27$, $p < 0.01$).

Dissimilarities in copepod communities between NH05 and NH25 showed strong seasonal changes (Fig. 3a); they tended to be higher (9.50 ± 7.01) in the summer when upwelling prevailed and lower (3.46 ± 3.12) in the winter when downwelling prevailed (Fig. 3b). Dissimilarity was particularly strong in the year 2000, strong in 2006–2010, weaker in 2001–2004, but very low during the warm year of 2005. The seasonal changes in dissimilarities were also coincidental with the seasonal fluctuations in Chl *a* concentrations, with higher dissimilarities occurring during peaks in Chl *a* concentrations (Fig. 3c).

When the dissimilarity index was decomposed into long-term and seasonal trends using the univariate time-series model (Fig. 4), the dissimilarity index showed little long-term variation (Fig. 4a; generally < 1); however, the long-term trend showed a negative correlation with the PDO (Table 1). The seasonal changes were the predominant pattern (Fig. 4b), which was highly correlated with upwelling (Table 1) and generally peaked during the upwelling season (Fig. 4b). Overall, the long-term and seasonal trend combined explained 40% of the variation in Euclidean distance (Table 1).

Interannual variation and seasonal changes of copepod species assemblages at NH05 and NH25—Cold neritic copepods were the dominant assemblage for both NH05 and NH25, with higher biomass at NH05 (Table 2). When the time series of cold neritic copepods at NH05 was decomposed into long-term and seasonal trends, the biomass of cold neritic copepods showed a relatively clear pattern in the long-term trend: low in 1998, high 1999–2000, decline 2001–2005, followed by an increase in 2006–2008, and then a decline (Fig. 5a). The seasonal changes of the cold neritic copepods were also clear: high biomass during the upwelling season and low biomass during the downwelling season (Fig. 5b). The biomass of cold neritic copepods at NH25 showed similar trends compared with NH05. However, the magnitude of variation in the long-term trend at NH25 was much smaller than at NH05 (Fig. 5c). The seasonal changes at NH25 were also clear, but the variation was much less than at NH05 (Fig. 5d). The long-term trend at both stations was negatively correlated with the PDO (Table 1). That is to say, when the PDO was in the positive (warm) phase, the biomass of cold neritic copepods declined at both stations. The seasonal changes of cold neritic copepods at NH05 and NH25 were positively correlated with upwelling (Table 1). Overall, the long-term and seasonal trend combined explained 72% of the variation at NH05 and 43% of the variation at NH25 (Table 1).

The biomass of southern copepods was relatively low at both NH05 and NH25 (Table 2). When the time series of southern copepods at NH05 was decomposed into long-term and seasonal trends, the biomass of southern copepods showed a clear pattern in the long-term trend: high in 1998, low 1999–2004, high in 2005, low 2006–2008, and an increase in 2009–2010 (Fig. 6a). The seasonal changes of the southern copepods were not consistent among years, but in general were high during the downwelling season and low during the upwelling season, except in 2009 and 2010, when the seasonal trend peaked during the early upwelling season and then declined quickly (Fig. 6b). The biomass of southern copepods at NH25 showed similar trends compared with NH05. However, the magnitude of variation in the long-term trend at NH25, particularly in 1998, was much smaller than at NH05 (Fig. 6c). The seasonal changes at NH25 were clear and more consistent compared with NH05 in that the abundance increased during the downwelling season and declined during the upwelling season (Fig. 6d). The long-term trend in biomass was weakly positively correlated with the PDO at both stations, and there was no relationship between the seasonal changes of southern copepods at either station with upwelling (Table 1). Overall, the long-term and seasonal trend combined explained 88% of the

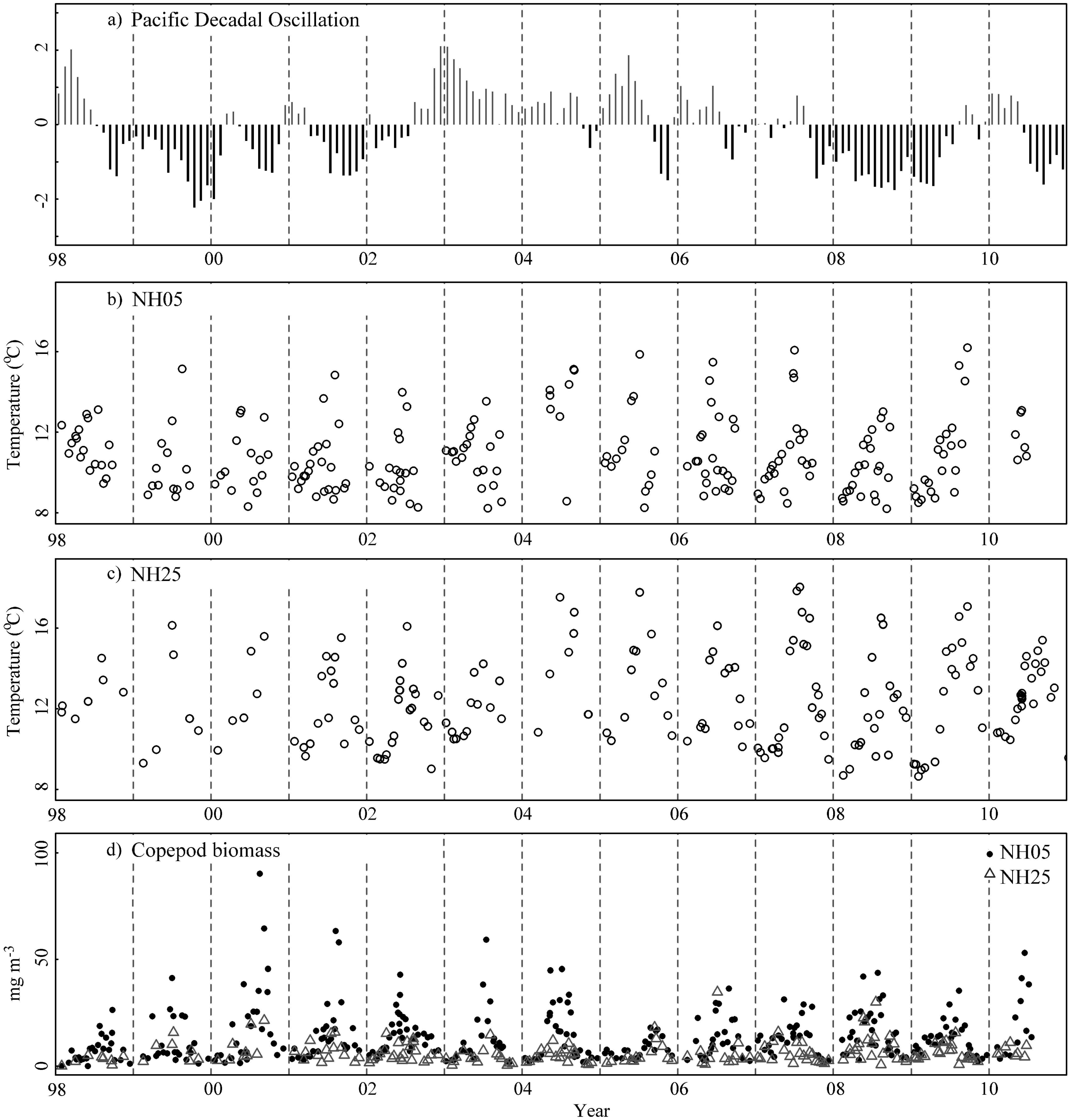

Fig. 2. (a) The Pacific Decadal Oscillation (PDO) from 1998 to 2010; (b) Surface temperature (1 m) at NH05; (c) Surface temperature (1 m) at NH25; (d) Copepod biomass at NH05 (circles) and NH25 (squares).

variation at NH05 and 51% of the variation at NH25 (Table 1).

The biomass of warm neritic copepods was relatively low at both NH05 and NH25 (Table 2). When the time series of warm neritic copepods at NH05 was decomposed into long-term and seasonal trends, the biomass was relatively high in 2004–2005, 2007, and 2010 (Fig. 7a). The seasonal changes of the warm neritic copepods were clear: their abundance started to increase during the late upwelling season and then gradually declined during the downwelling season (Fig. 7b). The biomass of warm neritic copepods at NH25 showed similar trends compared with NH05, but the magnitude of variation in the long-term trend was much smaller at NH25 compared with NH05 (Fig. 7c). The

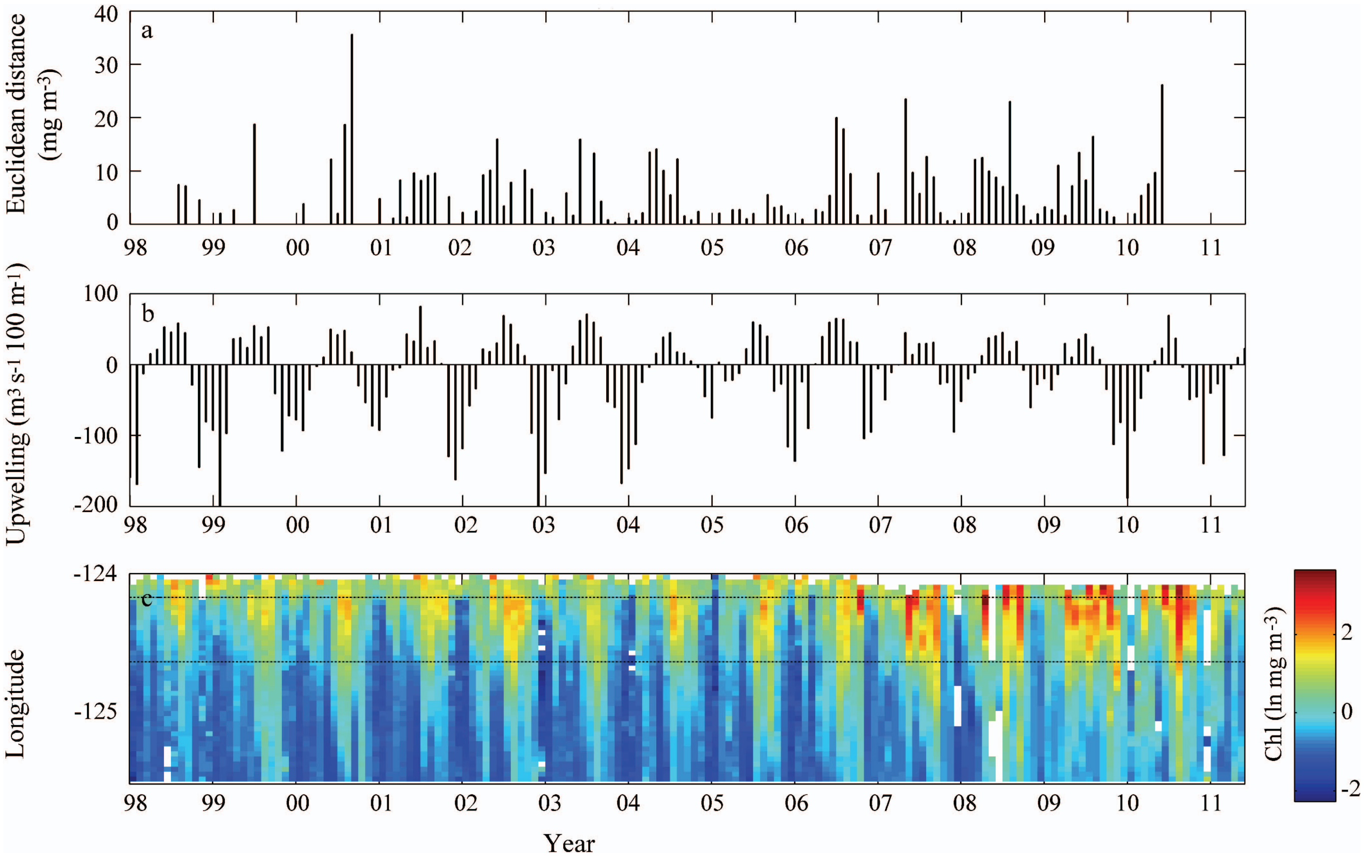

Fig. 3. (a) Euclidean distances between the copepod communities at NH05 and NH25; (b) Monthly upwelling index where positive values indicate upwelling and negative values indicate downwelling; (c) Chl *a* concentrations (ln mg Chl *a* m^{-3}) along the Newport Hydrographic Line. Data are from SeaWiFS from 1998 to October 2006 and from MODIS after October 2006. Dashed horizontal lines show the location of the two sampling stations.

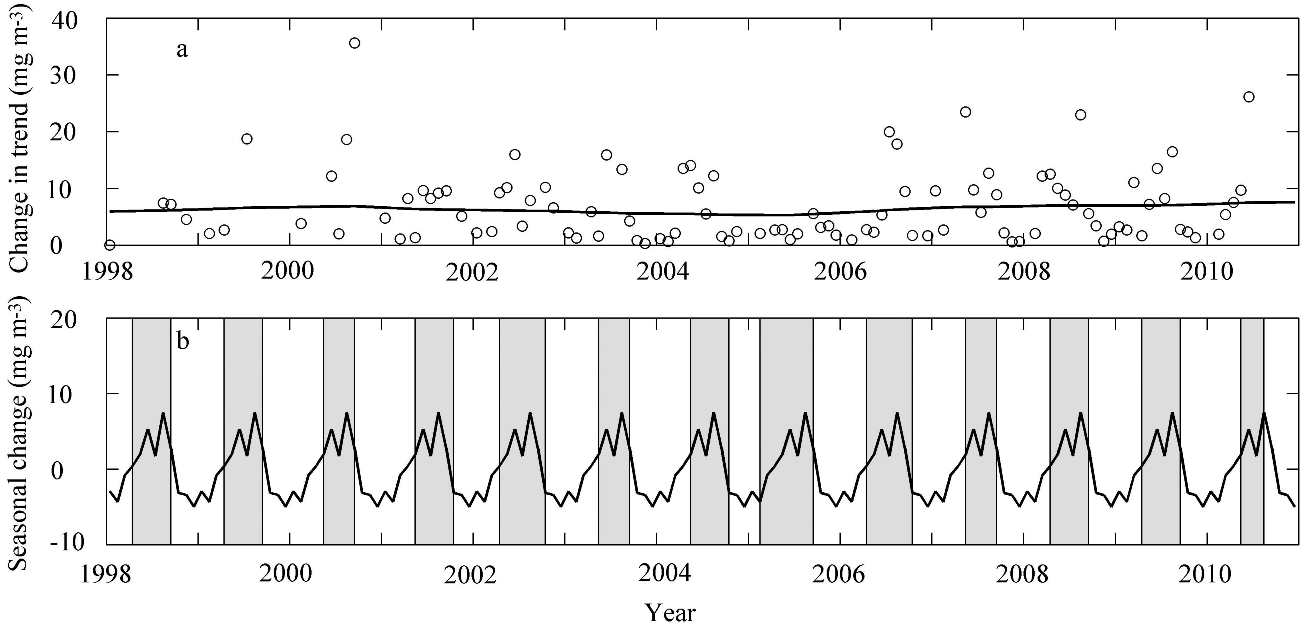

Fig. 4. Results from time-series analysis of the Euclidean distance: (a) Estimated long-term trend (solid line) and the dissimilarity between the copepod communities at NH05 and NH25 as indexed by the Euclidean distance (open circles); (b) Seasonal changes for the dissimilarity between the copepod communities at NH05 and NH25 with shaded areas indicating the upwelling season.

Table 1. Summary of linear regression models to examine (1) changes in the long-term trend and the PDO, (2) seasonal changes and the upwelling index (UI), and (3) the observed values and the predicted values (i.e., the sum of the predicted changes in trend and the predicted seasonal changes).

Group	Station	Response	Predictor	Model	R^2	p
Euclidean distance		Long-term trend	PDO	$y=6.27-0.33\times x$	0.23	<0.01
		Season	UI	$y=5.01\times e^{0.01\times x}-5$	0.63	<0.01
		Predicted	Observed	$y=-0.27+1.04\times x$	0.40	<0.01
Cold neritic copepods	NH05	Long-term trend	PDO	$y=9.55-1.87\times x$	0.24	<0.01
		Season	UI	$y=10.21\times e^{0.01\times x}-10$	0.57	<0.01
		Predicted	Observed	$y=-2.14+1.20\times x$	0.72	<0.01
	NH25	Long-term trend	PDO	$y=3.72-0.45\times x$	0.28	<0.01
		Season	UI	$y=5.04\times e^{0.01\times x}-5$	0.54	<0.01
		Predicted	Observed	$y=-0.38+1.09\times x$	0.43	<0.01
Southern copepods	NH05	Long-term trend	PDO	$y=0.60+0.19\times x$	0.06	0.01
		Season	UI	$y=-0.03-0.01\times x$	0.03	0.07
		Predicted	Observed	$y=-0.12+1.21\times x$	0.88	<0.01
	NH25	Long-term trend	PDO	$y=0.39+0.10\times x$	0.17	<0.01
		Season	UI	$y=-0.01-0.01\times x$	0.02	0.10
		Predicted	Observed	$y=-0.10+1.27\times x$	0.51	<0.01
Warm neritic copepods	NH05	Long-term trend	PDO	$y=0.64+0.26\times x$	0.16	<0.01
		Season	UI	$y=-0.01-0.01\times x$	0.05	0.03
		Predicted	Observed	$y=-0.08+1.13\times x$	0.77	<0.01
	NH25	Long-term trend	PDO	$y=0.31+0.10\times x$	0.32	<0.01
		Season	UI	$y=0.02+0.01\times x$	0.14	0.01
		Predicted	Observed	$y=-0.09+1.27\times x$	0.41	<0.01

seasonal changes at NH25 were also consistent with NH05, with abundance increasing during the late upwelling season and declining during the downwelling season (Fig. 7d). The long-term trend of warm neritic copepods was positively correlated with the PDO and the seasonal changes of warm neritic copepods were weakly correlated with upwelling at both stations (Table 1). Overall, the long-term and seasonal trend combined explained 77% of the variation at NH05 and 41% of the variation at NH25 (Table 1).

Discussion

Synchronization between the coastal and shelf-slope waters—The northern California Current (NCC) system is an upwelling-dominated region. However, active upwelling off the coasts of Washington and northern Oregon is restricted to a narrow coastal band (about 10–25 km wide; Huyer 1983). Huyer et al. (2007) provided a thorough review on the hydrographic conditions of our study region, the Newport Hydrographic Line. The inshore station (NH05) is located within the active upwelling cell, a region where upwelling water comes to the sea surface; whereas the slope station (NH25) is outside the region of active upwelling, but is influenced by upwelling through cross-shelf Ekman transport. Variations in copepod community structure at the NH05 station has been well-documented in terms of relationships to the PDO, upwelling, and both cross-shelf and alongshore transport (Peterson et al. 2002*b;* Peterson 2009; Bi et al. 2011*b*). However, copepod communities at NH25, within the transitional zone between upwelling-dominated coastal waters and offshore oceanic waters, have not been investigated until now.

Copepod species composition at NH25 and NH05, as indicated by Euclidean distance, did not show an obvious long-term trend. However, differences in the copepod community structure between the two stations appeared to be driven largely by seasonal upwelling. At the start of upwelling (April) there was a peak of Chl *a* inshore (Fig. 3a) and the copepod biomass at NH05 increased (Fig. 2d), causing a spike in the Euclidean distance. Meanwhile, the increase of Chl *a* and the copepod biomass at NH25 typically happened later in the summer because the upwelling cell is only 5–25 km, so the increased production did not immediately make it out to NH25. In the autumn, the downwelling affects the entire shelf and the

Table 2. Summary statistics for different copepod species assemblages at NH05 and NH25. SD represents standard deviation.

Groups	Station	Range (mg C m^{-3})	Mean biomass (mg C m^{-3}; mean±1 SD)	Percentage of the total biomass (%; mean±1 SD)
Cold neritic copepods	NH05	0–66.78	11.01±10.49	72.76±26.00
	NH25	0.05–33.62	4.13±4.95	56.18±28.72
Southern copepods	NH05	0–9.45	0.56±0.29	7.69±12.37
	NH25	0–2.92	0.08±0.12	8.76±1.01
Warm neritic copepods	NH05	0–3.90	0.60±0.82	9.24±13.00
	NH25	0–3.58	0.18±0.47	6.74±7.36

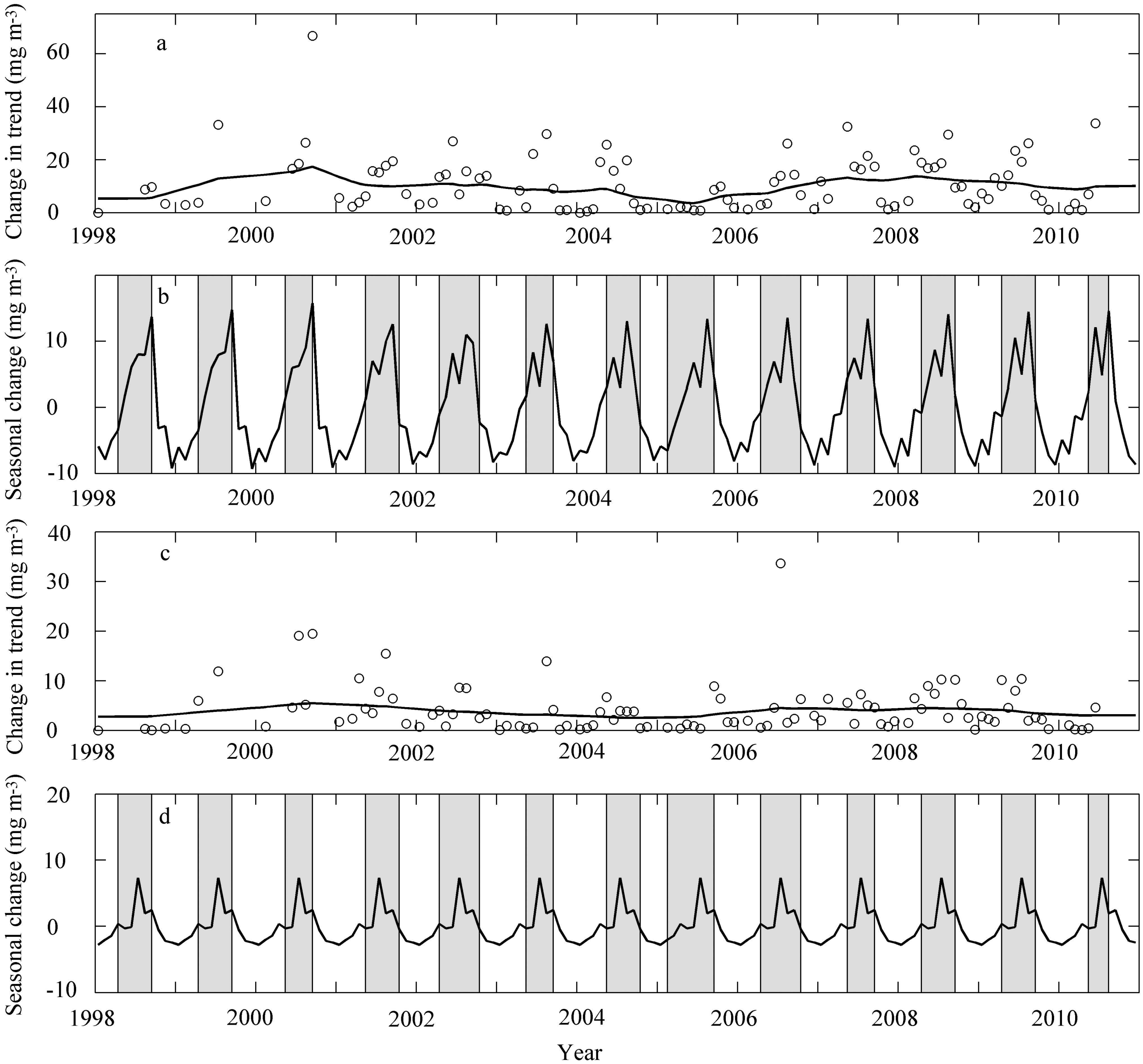

Fig. 5. Results from time-series analysis of the biomass (mg C m^{-3}) of cold neritic copepods: (a) Long-term trends at NH05; (b) Seasonal changes at NH05 with shaded areas indicating the upwelling season; (c) Long-term trends at NH25; (d) Seasonal changes at NH25 with shaded areas indicating upwelling season.

southern copepod assemblages are transported all the way across the entire shelf and community structure become homogenous, which results in little difference in the community structure as measured by Euclidean distance.

Copepod species assemblages—Zooplankton are by definition drifters; thus, different copepod assemblages are typically associated with different water masses or water types. Such affinities make copepods an ideal candidate for examination of the origin of water masses that supply the NCC (Hooff and Peterson 2006). Moreover, grouping copepods based on their affinities with different water types is an effective way to investigate how different biophysical processes influence zooplankton. Analysis at the community level summarizes the data well, but it is perhaps of greater interest to extract information on individual species and then examine the corresponding processes that may affect the seasonal and interannual variations in their density. However, at the species level, this can be a daunting task because the inherent variability makes statistical analysis difficult. Grouping copepod species based on their affinities with different water types can effectively reduce the amount of variability while preserving the information pertaining to different biophysical processes.

Cold neritic copepods—Cold neritic copepods are the major (in terms of biomass) copepod group in the shelf and

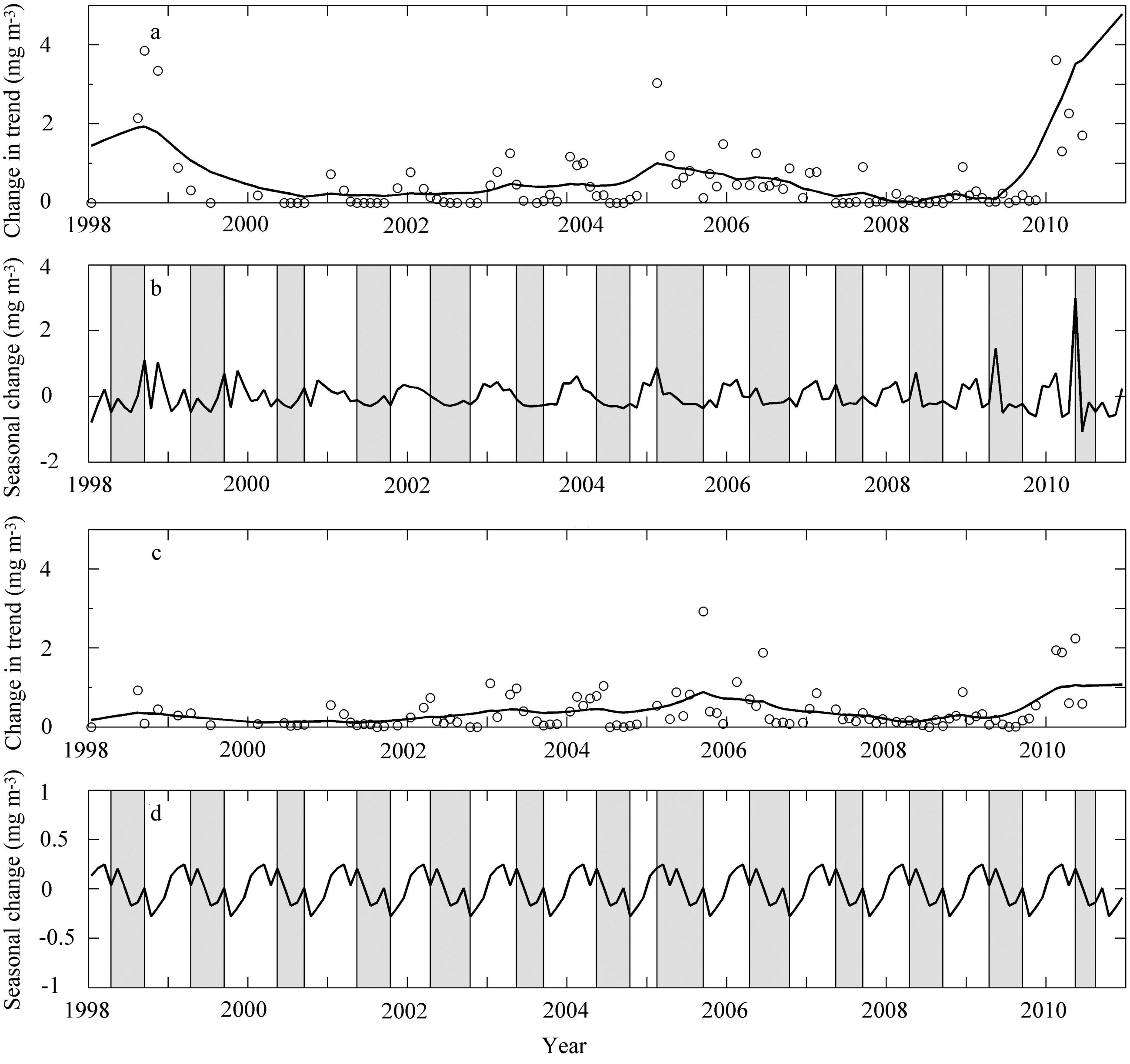

Fig. 6. Results from time-series analysis of the biomass (mg C m^{-3}) of southern copepods: (a) Long-term trends at NH05; (b) Seasonal changes at NH05 with shaded areas indicating the upwelling season; (c) Long-term trends at NH25; (d) Seasonal changes at NH25 with shaded areas indicating upwelling season.

slope waters of the NCC and they can serve as proxies for higher trophic-level food-chain processes (Peterson and Schwing 2003; Bi et al. 2011*a*). In coastal waters (NH05), when the PDO is negative, there is more advection of coastal subarctic water from the north; upwelling can be stronger, and productivity higher, resulting in a greater biomass of cold neritic copepods (Bi et al. 2011*b*). The present analysis shows that the long-term trends of cold neritic copepods at NH05 and NH25 were both consistent with the PDO (i.e., negative PDO led to more cold neritic copepods at both stations). Cold neritic copepods at both stations also showed a similar seasonal pattern that was closely associated with the seasonal upwelling and downwelling cycle. A difference between the coastal and shelf-slope stations is that the variations at NH25, including the long-term and seasonal trends, were less than half of the variations at NH05. The difference in the magnitude of both the long-term trend and the seasonal cycle could be attributed to higher secondary production due to far higher phytoplankton concentration at the coastal station. This suggests that the physical and biological dynamics at the two stations are similar during the negative phase of the PDO and that, at such times, the connectivity between shelf and slope waters is high. Thus, with respect to the cold neritic copepods, the two stations are synchronous in their response to both upwelling and the sign of the PDO, and thus showed similar long-term trends in biomass.

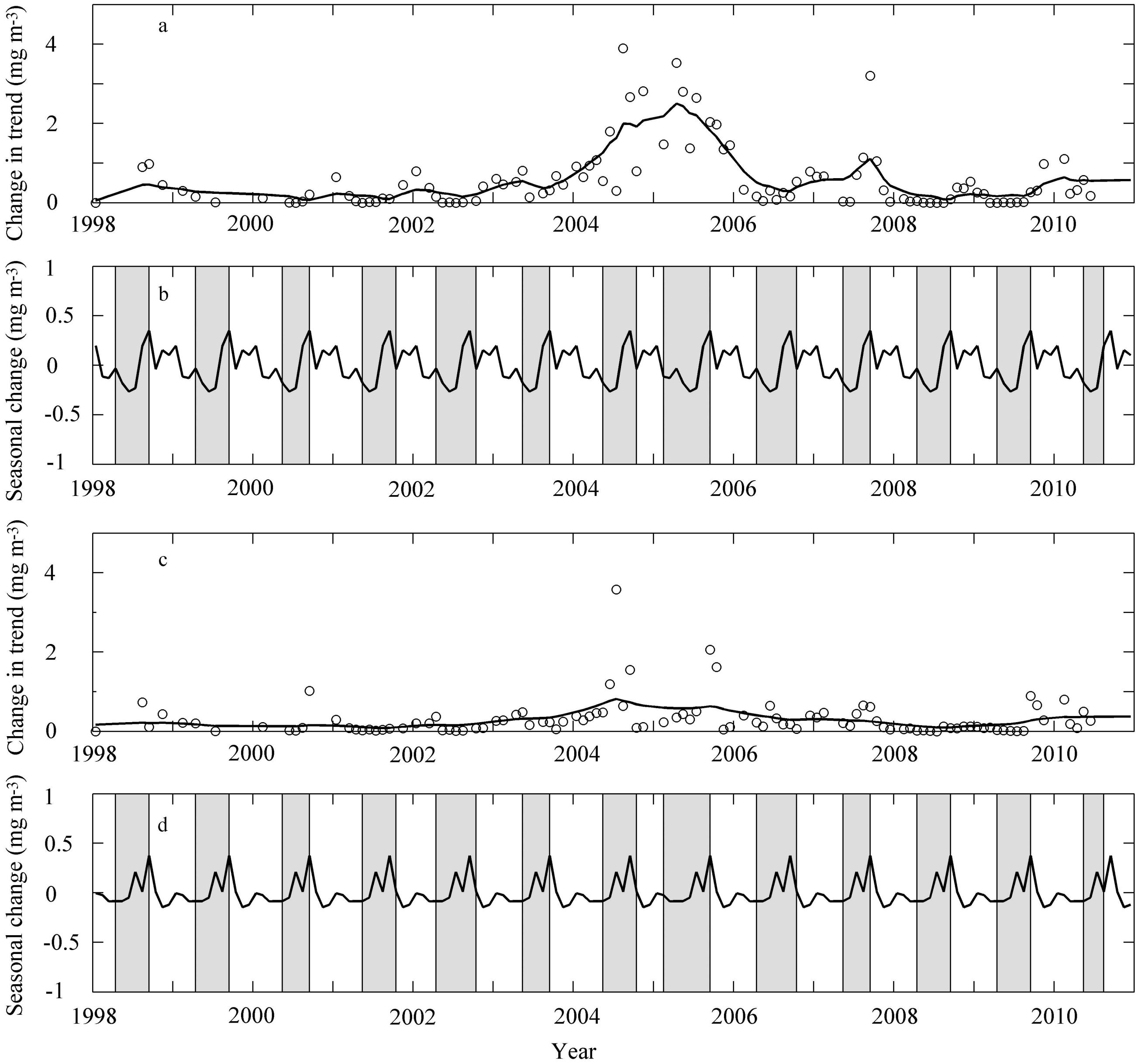

Fig. 7. Results from time-series analysis of the biomass (mg C m^{-3}) of warm neritic copepods: (a) Long-term trends at NH05; (b) Seasonal changes at NH05 with shaded areas indicating the upwelling season; (c) Long-term trends at NH25; (d) Seasonal changes at NH25 with shaded areas indicating upwelling season.

Southern copepods—Southern copepods tell a slightly different story. They are also good indicators of large-scale forcing in the NCC ecosystem (Peterson et al. 2002*b;* Di Lorenzo et al. 2008; Keister et al. 2011), but in an opposite manner from the cold neritic copepods. That is, when the PDO is positive, oceanic species increase in biomass by 5–10-fold; however, the response was different at the two stations: the magnitude of the long-term variation at NH05 was higher than NH25, and the seasonal pattern at NH05 was more variable than NH25. The variation in the long-term trend at NH05, although relatively weak, was generally consistent with the PDO: high in 1997–1998, 2005, and 2010 when the PDO was positive. These years were characterized by an El Niño event (1997–1998 and 2009–2010) and by anomalously warm ocean conditions due to delayed upwelling (in 2005, discussed below). On the other hand, the long-term trend in oceanic copepod biomass at NH25 was significantly correlated with the PDO, but not with coastal upwelling. One possible explanation for these patterns is that oceanic copepods only became conspicuous at NH05 and NH25 during periods of sustained downwelling (largely in summer) that occur when the PDO is in a positive phase, which helps explain the positive correlation of ocean copepod biomass at NH25 with the PDO. Lack of a correlation with NH05 may arise because onshore advection of oceanic waters during downwelling in summer is not sufficiently strong to displace (or replace) shelf waters nearshore with oceanic waters because this generally only occurs during winter. Even in winter, however, the warm neritic copepod community found on the shelf is different from the southern copepod community found at NH25. Furthermore, during summer, when the PDO is positive, differences between NH05 and NH25 likely become magnified because shelf waters continue to experience some productivity whereas NH25 does not. That is, regardless of the sign of the PDO or the strength of upwelling, shelf waters are inherently more productive than slope waters at any time, despite perturbations associated with El Niño events or years of relatively weak upwelling.

Warm neritic copepods—The long-term trend of warm neritic copepods was very different from the other two groups. The biomass of warm neritic copepods increased in 2004–2005 compared with previous years, which was coincidental with the 'El Niño-like' event in 2005 when the onset of the upwelling season occurred 5 weeks later than usual, and well-established upwelling with a cold surface signature did not occur until mid-July, an additional 7 weeks later (Pierce et al. 2006). Warm neritic copepods, such as *Acartia tonsa* and *Paracalanus parvus,* were very abundant in spring–summer 2005, which suggested that during the canonical upwelling season, they may benefit from a prolonged warm period (and lack of offshore transport) to establish a temporary local population. The variation in the long-term trend at the shelf-slope station was much weaker than the long-term trend at the nearshore station. This pattern likely occurred because warm neritic copepods found in offshore waters probably originated nearshore, and were transported offshore through cross-shelf advection. These species are adapted to a coastal environment and do not prosper in offshore waters where food concentration is reduced, despite similar temperatures.

In conclusion, the present study demonstrates that large-scale forcing has differential influences on the different copepod species assemblages. Nearshore coastal water appeared to be more responsive or sensitive to large-scale forcing. The shelf (NH05) and slope (NH25) stations were synchronous in their response to large-scale forcing when cold neritic copepods dominated during periods of strong upwelling and a negative PDO. During warm phases of the PDO, positive correlations with the PDO occurred with warm neritic copepods at NH05 and with warm neritic and southern copepods at NH25. This suggests that large-scale processes associated with the PDO are more apparent in offshore waters when the PDO is positive. Further, when the PDO is positive, slope waters likely become decoupled from coastal shelf waters because the inherent differences in productivity between the two regions are magnified when upwelling (and cross-shelf transport) is weak. In other words, regardless of the phase of the PDO, there is always enhanced productivity at NH05 relative to NH25 due to coastal upwelling nearshore; but, at NH25, upwelling effects are most prominent during years of strong upwelling (which generally are associated with negative PDO). The two stations are, thus, only coupled during these years. Further investigation into the different physical and biological processes among years with positive PDO could improve our understanding of the differential response to the large-scale forcing at the species level.

Acknowledgment

We thank many people who contributed greatly to the collection and processing of data: Leah Feinberg, Tracy Shaw, Jennifer Menkel, Hui Liu, Cheryl Morgan, Rian Hooff, and Karen Hunter. We would also like to thank the anonymous reviewers for their excellent suggestions. This synthesis work is supported by the Comparative Analysis of Marine Ecosystem Organization (CAMEO) program (NA09NMF4720182).

Data collection was funded by various sources including the National Oceanographic Partnership Program, the Office of Naval Research, U.S. Global Ocean Ecosystems Dynamics program, National Marine Fisheries Service Protected Species Stock Assessment Improvement Plan, and the Bonneville Power Administration. Some of the data processing was funded by the National Aeronautics and Space Administration grant NNX08AR40G.

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Associate editor: Michael R. Landry

Received: 07 November 2011
Accepted: 22 May 2012
Amended: 05 June 2012