

## Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community

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### Abstract

To better delineate the relative contribution of shelf and slope production to the northern California Current (NCC) pelagic community, we examined the cross-shelf distribution of  $\delta^{13}\text{C}$  in 19 species of nekton, three species of *Cancer* decapod larvae, five gelatinous zooplankton, two dominant euphausiid species (*Thysanoessa spinifera* and *Euphausia pacifica*), calanoid copepods (*Acartia* sp. and *Pseudocalanus* sp.), and particulate organic matter (POM). Results showed  $^{13}\text{C}$  enrichment from nearshore shelf sites relative to offshore slope sites at all trophic levels. For POM, a significant trend in  $\delta^{13}\text{C}$  with log chlorophyll *a* (Chl *a*) was observed, with high Chl *a* values associated with shelf primary production. Copepods, gelatinous zooplankton, and nekton showed a significant linear decrease in  $\delta^{13}\text{C}$  with distance offshore. Nekton and gelatinous zooplankton associated with very nearshore shelf waters (<10 km distance offshore) had the highest  $\delta^{13}\text{C}$  values, whereas those off the slope (>20 km offshore) were more depleted in  $^{13}\text{C}$ . A comparison of results from nonparametric analysis of the pelagic community data to environmental variables also showed variables associated with the shelf and oceanic waters, with distance offshore, sea surface temperature (10 m in depth), and bottom depth being significant. Because pelagic systems are highly dynamic in space and time, our study indicated that  $\delta^{13}\text{C}$  could be used as an indicator of relative nearshore and offshore production across multiple trophic levels, even in active upwelling ecosystems such as the NCC.

Continental shelf and oceanic pelagic ecosystems are typically associated with marked differences in primary production (Thomas and Strub 2001) and community composition (Brodeur et al. 2005). However, these ecosystems are also connected through cross-shelf advective currents (Mackas and Coyle 2005) and active movement by larger organisms (Beamish et al. 2005). Delineating these systems and measuring their potential connectivity is problematic because of the dynamics of a fluid environment, organism mobility, and constraints on sampling a

large marine ecosystem. Cross-shelf advective processes of coastal upwelling have been the focus of recent investigations, in part because of the potential for hydrographic processes to link coastal and offshore basin ecosystems (McFarlane and McKinnell 2005). They are also studied because of the inherent links between changes in climate and atmospheric forcing and upwelling frequency and intensity. However, the extent to which shelf and oceanic ecosystems are connected at various trophic levels is not well understood.

The northern California Current (NCC) ecosystem extends from approximately central Vancouver Island (British Columbia, Canada) to northern California. Between May and September the coastal shelf is characterized as having a shelf band (water depth of <150 m) of high production and an extensive area of relatively low production offshore (>150 m) (Lentz 1992). Differences between the two environments are also associated with species-specific assemblages of birds (Veit et al. 1996), fish (Brodeur et al. 2005), and zooplankton (Cross and Small 1967; Peterson et al. 1979). These systems therefore represent distinct habitats for transitory species, habitats that may overlap through hydrographic processes such as coastal upwelling and cross-shelf advection of primary and secondary production and through active movement by nekton of higher trophic levels. As a result, the varying

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degrees by which species reside in a particular habitat are difficult to determine solely through distribution data, and it is difficult to reveal the relative dependence of these species on shelf vs. oceanic production.

Alternatively, stable isotopes of carbon and nitrogen have been used as biological tracers to measure the affinity of an organism to certain habitats as well as its movement across ecosystems (Peterson and Fry 1987). For carbon, differences in  $\delta^{13}\text{C}$  occur primarily at primary production, with small increases with increasing trophic level (0.4‰; Post 2002). Nitrogen stable isotopes are more problematic in this regard, because differences in  $\delta^{15}\text{N}$  can occur at the level of primary production (Waser et al. 1998) and with increasing trophic level (approximately 3.4‰; Post 2002) as well as diet (e.g., amount of protein; McCutchan et al. 2003). Therefore, because  $\delta^{13}\text{C}$  fractionates primarily at the level of primary production and changes little with increasing trophic level, it is often a more effective tracer of an organism's food source and affinity to certain habitats with differing types of primary production. Within marine ecosystems,  $\delta^{13}\text{C}$  has been shown to differentiate between benthic and pelagic-derived production (Davenport and Bax 2002) and between nearshore and offshore productivity (Kline 1999; Perry et al. 1999), with nearshore and benthic systems being more enriched in  $\delta^{13}\text{C}$ . However, the degree to which this difference is conveyed to higher trophic levels is not well known. Because differences in carbon isotopes between nearshore and offshore lower trophic levels exist and change little with trophic level,  $\delta^{13}\text{C}$  may be a useful tool for delineating shelf and oceanic food webs of large marine ecosystems.

In this study we investigated the use of  $\delta^{13}\text{C}$  as a biological indicator of relative shelf and oceanic production in the NCC pelagic ecosystem. Given known differences between shelf and oceanic primary production, we hypothesized that this should be expressed as differences in  $\delta^{13}\text{C}$  and thus should be transferred to higher trophic levels. To test this, we examined the distribution of  $\delta^{13}\text{C}$  in organisms and nekton community structure relative to cross-shelf differences in primary production and abiotic environmental factors indicative of shelf and oceanic waters.

## Materials and methods

Samples of nekton and most zooplankton for this study were collected from Northeast Pacific Global Ocean Ecosystems Dynamics (GLOBEC) cruises during May/June (29 May–18 June) and July/August (29 July–18 August) in 2002. Sampling occurred along a series of transects across the shelf between Crescent City, California (41°54.0'N), and Newport, Oregon (44°39.0'N) (Fig. 1). At each station various zooplankton and nekton species were collected using a Nordic 264 rope trawl (30 m wide by 18 m deep) and a surface neuston net (1-m<sup>2</sup> mouth, 335- $\mu\text{m}$  mesh). Some zooplankton collections for decapod larvae and copepods were made from June and September 2002 cruises just to the north of our study region. Particulate organic matter (POM) samples were collected using a

Niskin bottle sampled at 3 m in depth. Niskin samples were prefiltered through a 64- $\mu\text{m}$  sieve to remove copepod eggs and zooplankton and were then filtered through a 47-mm glass-fiber filter ( $\sim 0.7\ \mu\text{m}$ ) at  $<10\ \text{Pa}$ . All nekton, zooplankton, and POM samples were immediately frozen ( $-20^\circ\text{C}$ ) following collection at sea and were later taken to the laboratory for processing. At each sampling location chlorophyll *a* (Chl *a*) (3 m in depth) was measured, and depth-specific temperature and salinity (3 and 10 m in depth) were measured using a Seabird SBE 19 Seacat CTD profiler (Suchman and Brodeur 2005).

**Laboratory**—Laboratory processing of nekton and zooplankton involved identification, measurement, and extraction of tissue for stable isotope analysis. Dorsal or lateral muscle tissue was extracted from nekton and larval and juvenile fishes, whereas the whole body was used for zooplankton. For POM, samples were first acid-treated to remove inorganic carbon by fumigating the POM filter with 12 molar HCl for 24 h. All samples were dried in a drying oven for 24 h at  $60^\circ\text{C}$ . After drying, all samples were pulverized using a mortar and pestle, weighed, and sent to one of two labs to measure stable isotope ratios. Most samples were analyzed at the National Marine Fisheries Service Northwest Fisheries Science Center (Seattle, Washington) isotope laboratory using a Costech ECS 4010 elemental analyzer coupled to a Thermo Electron Delta Plus stable isotope ratio mass spectrometer. Precision for the isotope analysis was  $<\pm 0.3$  for  $\delta^{15}\text{N}$  and  $<\pm 0.2$  for  $\delta^{13}\text{C}$ . Nitrogen and carbon values were referenced to air and Vienna Pee Dee Belemnite, respectively. Remaining samples were analyzed at the National Aeronautics and Space Administration Ames Research Center (Moffett Field, California) using a Carlo Erba 1108 elemental analyzer coupled to a Finnigan Mat, Delta Plus mass spectrometer. Instrument precision for carbon and nitrogen were  $\pm 0.08$  and  $\pm 0.25$ , respectively.

Stable isotopes are measured as the ratio of the heavy ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) to the lighter ( $^{12}\text{C}$  and  $^{14}\text{N}$ ) isotope of an element using the following equation:

$$\delta X = \left(1 - \left(R_{\text{sample}}/R_{\text{standard}}\right)\right) \times 10^3 \quad (1)$$

where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$  and  $R$  is the ratio of the heavy to the light isotope (Peterson and Fry 1987). After analyses, carbon isotopes were lipid-adjusted ( $\delta^{13}\text{C}'$ ) using an equation devised by McConnaughey and McRoy (1979). This was performed because lipids can influence carbon isotope ratios by retaining the lighter carbon isotope ( $\text{C}^{12}$ ) over the heavier ( $\text{C}^{13}$ ) (McConnaughey and McRoy 1979). Stable carbon isotopes can also be influenced by trophic-level enrichment (Rau et al. 1983), with an average of 0.4‰ enrichment per trophic level (Post 2002). To correct for this we applied the following equation by Kline (1999) to normalize for trophic level differences:

$$\delta^{13}\text{C}'_{\text{TL}} = \delta^{13}\text{C}' - \varepsilon_{\text{C}}/\varepsilon_{\text{N}}(\delta^{15}\text{N}_{\text{sample}} - \delta^{15}\text{N}_{\text{reference}}) \quad (2)$$

where  $\delta^{13}\text{C}'_{\text{TL}}$  is the trophic level of normalized  $\delta^{13}\text{C}'$  (lipid-adjusted  $\delta^{13}\text{C}$ ) based on the  $\delta^{15}\text{N}$  of the sample relative to a reference  $\delta^{15}\text{N}$  and where  $\varepsilon_{\text{C}}$  and  $\varepsilon_{\text{N}}$  represent the trophic

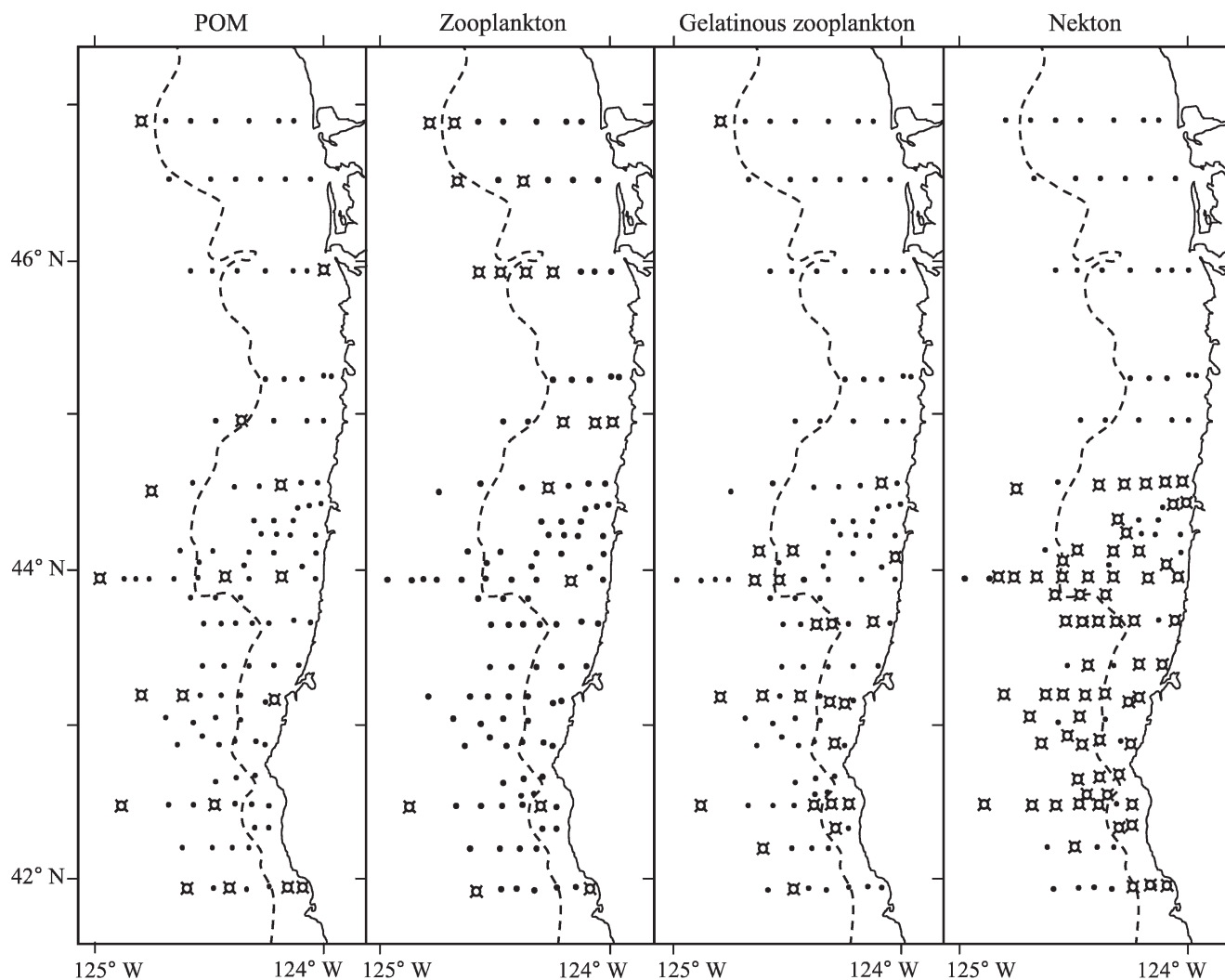


Fig. 1. Map of study region within shelf and slope waters of the northern California Current ecosystem. Open points denote sample sites where stable isotopes were measured for each taxa. Cross points denote other sample sites, where Nordic trawls sampled for nekton and gelatinous zooplankton densities. Dashed line is the 150-m isobath delineating the shelf break.

fractionation of carbon and nitrogen, respectively. For our study we used the overall average copepod  $\delta^{15}\text{N}$  (10.01‰) as the reference trophic level and fractionation factors ( $\epsilon$ ) of 1.0 for  $\epsilon_{\text{C}}$  and 3.4 for  $\epsilon_{\text{N}}$  as the amount of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  enrichment per trophic level (Kline 1999). Copepods were used as the reference level because as grazers they provide the most consistent link between POM and higher trophic levels.

**Data analyses**—Several methods were used to compare shelf and oceanic differences in  $^{13}\text{C}$  and to relate any differences observed to biotic and abiotic factors. For POM and copepods, backwards regression methods (using Mallows's  $C_p$  criterion for elimination of variables; S-PLUS version 6.2, Mathsoft) were used to determine the linear dependence of  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}'$  for copepods) on independent variables sea surface temperature and salinity (3 and 10 m in depth), bottom depth (m), distance offshore (km), Chl *a*, and vertical gradients in temperature, salinity, and density. Vertical gradients were calculated by the difference in

values at 3- and 15-m depths, divided by the depth difference of the two points (12 m); higher values denoted a greater difference between the two depths, indicating higher stratification. General comparisons between shelf and oceanic collections were performed collectively for the two sampling periods using a Student's *t*-test for differences in the means ( $\alpha = 0.05$ ). Shelf and oceanic samples were defined as those collected in waters with bottom depths of <150 m and >150 m, respectively, following Lentz's (1992) delineation of shelf and slope (oceanic) waters of the NCC ecosystem. The definition by Lentz (1992) was based on the spatial distribution of mixed layer depth across the shelf, with nearshore of the 150-m bathymetric contour having a greater mixed layer depth.

Analysis of nekton and gelatinous zooplankton was performed using the same regression methods applied to POM and copepods. However, for nekton and gelatinous zooplankton, we examined the relationship of mean  $\delta^{13}\text{C}'_{\text{TL}}$  for each species relative to their distribution across the shelf

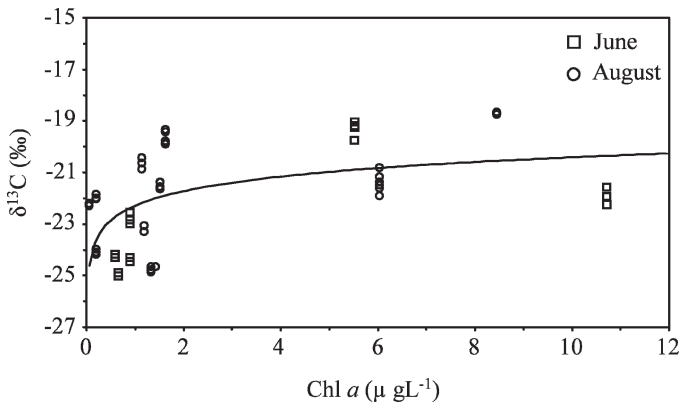


Fig. 2. Relationship of  $\delta^{13}\text{C}$  of POM and Chl *a* from waters nearshore and offshore of the 150-m isobath between northern California and Washington. Line represents the regression  $\delta^{13}\text{C} = 0.82\log(\text{Chl } a) - 22.3$  ( $r^2 = 0.31$ ,  $p = 0.005$ ).

based on densities derived from the volume of water filtered through the net by the number of individuals within a species (number of individuals  $\text{m}^{-3}$ ). The backwards regression model therefore examined the linear dependence of species  $\delta^{13}\text{C}'_{\text{TL}}$  to their distribution related to environmental variables.

To examine nekton and gelatinous zooplankton community structure in relation to environmental variables used in the regression analyses of  $\delta^{13}\text{C}'_{\text{TL}}$  and species distributions, we first applied agglomerative hierarchical cluster analysis (AHCA; relative Sørensen distance and flexible beta,  $\beta = -0.25$  linkage function) to the sample (row) by species (column) matrix to form cluster groups based on species distribution. Species cluster groups were established by choosing a cutoff level with biological meaning while maintaining a reasonable level (at least 50%) of information explained in the cluster dendrogram. The significance of trophic cluster groups was examined using a multiresponse permutation procedure (MRPP), which tests for the null hypothesis of no difference between groups. Ordination of sample units in species space was performed on the same matrix in examined AHCA using nonmetric multidimensional scaling (NMS), with an environmental matrix of sample (row) by environmental variables (columns), with cluster groups included in the environmental matrix as a factor. Prior to analyses, rare species that were in <10% of the rows (stations) were removed and species were transformed [ $\log(x + 1)$ ] to reduce column skewness and coefficient of variation. All nonparametric analyses were performed using PC-ORD (Version 4, MjM Software). The matrix was then applied to NMS to ordinate sample units in species space and to compare cluster groups to environmental variables. Environmental variables (the same as those used in the regression analyses) and cluster groups were included in NMS analyses by forming a second environmental matrix containing the same station (rows) but having the columns as environmental variables and a cluster group variable. The NMS analyses then examined the relationship of species distributions and the environmental variables most closely related to the distribution.

## Results

**POM and zooplankton**—Results from stepwise backwards linear regression of POM  $\delta^{13}\text{C}$  to environmental variables showed a significant positive correlation with only  $\log(\text{Chl } a)$  remaining ( $p = 0.005$ ) (Fig. 2), explaining 33% of variation observed. A significant difference was also observed when comparing  $\delta^{13}\text{C}$  values from POMs collected nearshore and offshore of the 150-m isobath (Student's *t*-test;  $p < 0.0001$ ; Fig. 1), with nearshore  $\delta^{13}\text{C}$  on average 2.47‰ higher than POMs from offshore, oceanic sites (Table 1). The minimum and maximum  $\delta^{13}\text{C}$  values associated with corresponding minimum and maximum Chl *a* were  $-22.0\text{‰}$  and  $-19.2\text{‰}$ , respectively.

Stepwise regression of copepod  $\delta^{13}\text{C}'$  as a function of environmental variables resulted in distance offshore being the only significant variable ( $p = 0.003$ ), explaining 18% of the variation observed (Fig. 3). General comparison of copepods collected on the shelf (<150 m in depth) to those collected off the slope in oceanic waters (>150 m) were significantly enriched in  $\delta^{13}\text{C}'$  (Student's *t*-test,  $p = 0.01$ ); mean  $\delta^{13}\text{C}'$  values of shelf and oceanic copepod samples were  $-16.4\text{‰}$  and  $-17.4\text{‰}$ , respectively. Extending this comparison between copepods collected well within the shelf (<5 km offshore) and well offshore of the slope (>60 km offshore) showed a notable difference in  $\delta^{13}\text{C}'$  between the shelf (mean  $\delta^{13}\text{C}' = -16.6\text{‰} \pm 0.3\text{‰}$ ;  $n = 9$ ) and oceanic (mean  $\delta^{13}\text{C}' = -19.6\text{‰} \pm 1.1\text{‰}$ ;  $n = 2$ ) (Fig. 3) waters; however, limited sample size did not allow for statistical analysis.

Other zooplankton species collected were euphausiids, *Cancer* spp. larvae, and gelatinous zooplankton; however, small sample numbers precluded robust statistical testing in relation to environmental variables. The euphausiid species *E. pacifica* and *T. spinifera* were collected together only during the August cruise at one station, with *T. spinifera* being significantly more enriched in  $^{13}\text{C}$  (Student's *t*-test;  $p = 0.01$ ; mean difference in  $\delta^{13}\text{C}'_{\text{TL}} = 1.45\text{‰}$ ). Analysis of three species of *Cancer* spp. megalopae, *Cancer magister*, *Cancer antennarius/gracilis*, and *Cancer oregonensis/productus*, showed no significant differences in  $\delta^{13}\text{C}'_{\text{TL}}$  among the three species (analysis of variance, Tukey honestly significantly different test;  $p > 0.05$ ).

**Nekton and gelatinous zooplankton**—Nekton and gelatinous zooplankton species showed a broad range of  $\delta^{13}\text{C}'_{\text{TL}}$  values that were associated with the shelf and oceanic waters of the NCC ecosystem. Backwards multiple regression of  $\delta^{13}\text{C}'_{\text{TL}}$  values in relation to environmental variables resulted in only distance offshore being marginally nonsignificant ( $p = 0.057$ ) and the only variable retained in the model. The model was only able to explain 13% of the variation observed; however, when the nekton species of adult coho and chum salmon, subyearling chinook salmon, and northern anchovy were excluded from the regression as a result of their migratory behavior, distance offshore was highly significant ( $p < 0.0001$ ), explaining 37% of the variation observed (Fig. 4).

The distribution of nekton and gelatinous plankton plotted with distance offshore and their carbon isotope

Table 1. Summary of  $\delta^{13}C'_{TL}$  (after lipid and trophic level correction) of each species or taxonomic group collected during June and August 2002 cruises. Values for particulate organic matter (POM) are not adjusted for lipid or trophic level adjusted; Copepoda values are after lipid adjustment ( $=\delta^{13}C'$ ). Species are adults unless noted in parentheses as megalopa larvae (l), juvenile (j), and subyearling (sy) and yearling (y).

Taxa	n	Mean $\delta^{13}C'_{TL}$ *
<b>POM</b>		
Shelf (depth < 150 m)	29	-20.51(0.37)
Slope (depth > 150 m)	39	-23.09(0.36)
<b>Zooplankton</b>		
Copepoda (shelf, depth < 150 m)	26	-16.59(0.29)
Copepoda (slope/oceanic, depth > 150 m)	19	-17.20(0.43)
<i>Thysanoessa spinifera</i>	6	-15.77(0.50)
<i>Euphausia pacifica</i>	10	-17.22(0.36)
<i>Cancer oregonensis/productus</i> (l)	20	-18.64(0.27)
<i>Cancer magister</i> (l)	14	-18.47(0.44)
<i>Cancer antennarius/gracilis</i> (l)	11	-18.22(0.65)
<b>Gelatinous zooplankton</b>		
<i>Aequorea victoria</i>	33	-16.79(0.44)
<i>Aurelia aurita</i>	15	-16.97(0.82)
<i>Beroe</i>	9	-18.54(0.19)
<i>Chrysaora fuscescens</i>	23	-14.87(0.15)
<i>Phacellophora camtschatica</i>	11	-16.86(0.62)
<b>Nekton</b>		
Market squid, <i>Loligo opalescens</i>	15	-16.31(0.11)
Spiny dogfish, <i>Squalus acanthias</i>	9	-18.01(0.12)
Blue shark, <i>Prionace glauca</i>	9	-19.2(0.18)
Coho salmon, <i>Oncorhynchus kisutch</i>	8	-20.21(0.13)
Chum salmon, <i>Oncorhynchus keta</i>	2	-20.06(0.31)
Chinook salmon (sy), <i>Oncorhynchus tshawytscha</i>	7	-18.88(0.73)
Chinook salmon (y)	30	-17.48(0.25)
Chinook salmon	47	-17.43(0.12)
Cutthroat trout, <i>Oncorhynchus clarki</i>	8	-18.73(0.19)
Steelhead trout (j), <i>Oncorhynchus mykiss</i>	4	-17.29(0.47)
Pacific sand lance (j), <i>Ammodytes hexapterus</i>	22	-17.47(0.20)
Surf smelt, <i>Hypomesus pretiosus</i>	6	-17.1(0.10)
Whitebait smelt, <i>Allosmerus elongatus</i>	12	-17.51(0.07)
Northern anchovy, <i>Engraulis mordax</i>	1	-17.08
Pacific sardine, <i>Sardinops sagax</i>	25	-17.95(0.17)
Pacific herring, <i>Clupea pallasii</i>	39	-16.88(0.09)
Jack mackerel, <i>Trachurus symmetricus</i>	8	-16.58(0.12)
Pacific hake, <i>Merluccius productus</i>	6	-16.92(0.11)
Rockfish (pelagic, [j]), <i>Sebastes</i> spp.	24	-21.17(0.21)
Pacific saury, <i>Cololabis saira</i>	11	-18.51(0.23)

\* SE, standard error.

values showed that Pacific herring, whitebait smelt, and surf smelt, including gelatinous zooplankton *Chrysaora* and *Aequorea*, had the highest  $\delta^{13}C'_{TL}$  values and were more strongly associated with being nearshore (<10 km). Nekton of blue shark, rex sole larvae, Pacific saury, cutthroat trout, jack mackerel, and gelatinous species *Beroe* had  $\delta^{13}C'_{TL}$  values below -18‰ and were associated with distances offshore of >20 km.

Results from AHCA of species by their distribution indicated two significant cluster groups from June (MRPP;

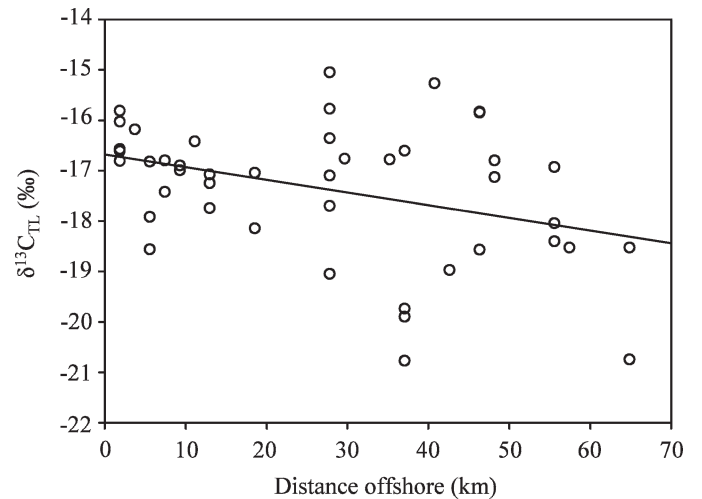


Fig. 3. Regression of  $\delta^{13}C'$  values of copepods and distance offshore collected from shelf and slope waters of the northern California Current ecosystem. Line represents the regression  $\delta^{13}C' = -0.025(\text{distance offshore}) - 16.64$  ( $r^2 = 0.18$ ,  $p = 0.003$ ).

$A = 0.4$ ,  $p \ll 0.001$ ) and August (MRPP;  $A = 0.6$ ,  $p \ll 0.001$ ) (Fig. 5); the cutoff level during both periods was <12% information remaining. The biological significance of these groups was confirmed in NMS from June and August, with the two groups from both periods divided along a shelf and oceanic gradient related to environmental variables (Fig. 6). The June NMS resulted in a three-dimensional solution explaining 81% of the variation between original and ordination space (stress = 16.3), with axes 2 and 3 explaining 37% and 22% of the variation, respectively. Of the environmental variables examined, only distance offshore and bottom depth were significant ( $r^2 = 0.35$  and  $0.25$ , respectively) along axis 2 (Fig. 6). Nekton most associated with the slope community generally coincided with lower  $\delta^{13}C'_{TL}$  values, with the exception of Pacific sand lance. For August, NMS resulted in a three-dimensional solution explaining 86% of the variation (stress = 14.1), with axes 2 and 3 explaining 35% and 29% of the variation, respectively. Environmental variables sea surface temperature (at 10-m depth) and distance offshore were significant ( $r^2 = 0.37$  and  $0.26$ , respectively) along axis 2 (Fig. 6). The two cluster groups within the joint plot showed separation along axis 2 with the two environmental variables of increasing distance offshore and temperature at 10 m. Shelf and slope species from the NMS expressed high and low  $\delta^{13}C'_{TL}$  values, respectively, associated with the shelf to slope gradients in distance offshore and sea surface temperature at 10-m depth.

## Discussion

Our study revealed a general shelf to slope trend in decreasing  $\delta^{13}C'_{TL}$  within multiple trophic levels of the pelagic community, providing a relative measure of a species shelf or oceanic base production in the food web. Differences in  $\delta^{13}C$  across multiple trophic groups were associated with cross-shelf changes in Chl *a* (for POM) and increased distance offshore (copepods, gelatinous zooplankton, and

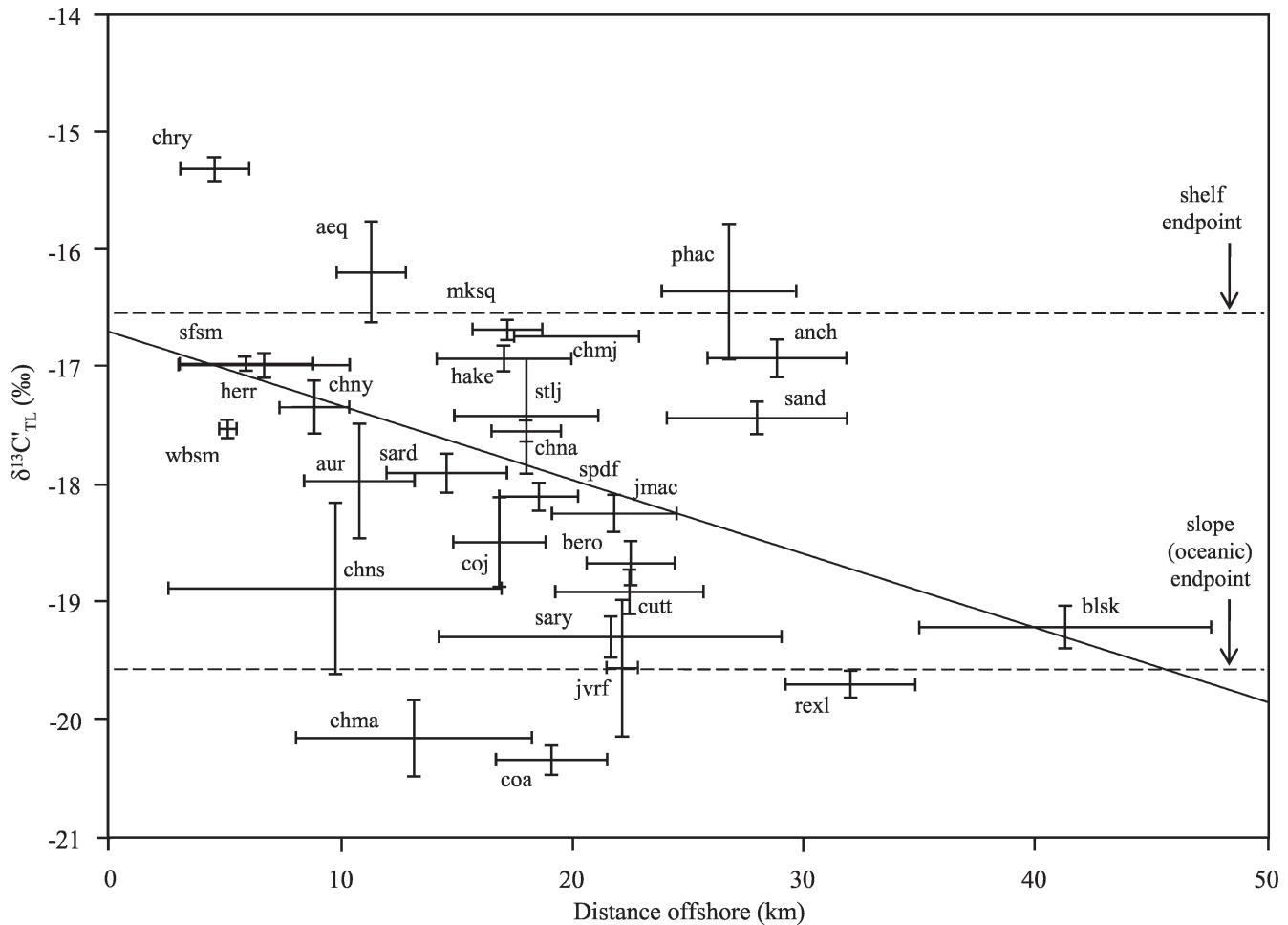


Fig. 4. Mean (error bars denote standard error [SE]) of  $\delta^{13}\text{C}_{\text{TL}}$  and distance offshore (km) of nekton and gelatinous zooplankton collected during June and August 2002 off northern California and Oregon. Line represents the regression  $\delta^{13}\text{C} = -0.053(\text{distance offshore}) - 16.9$  ( $r^2 = 0.13$ ,  $p = 0.057$ ). Dashed lines denote shelf and slope (oceanic)  $\delta^{13}\text{C}$  end member values based on copepods analyzed from  $<5\text{-km}$  ( $\delta^{13}\text{C} = -16.6\text{‰}$ ) and  $>60\text{-km}$  ( $\delta^{13}\text{C} = -19.6\text{‰}$ ) distance offshore, respectively. Point labels denote the following nekton species: blue shark (blsk), subyearling chinook salmon (chns), yearling chinook salmon (chny), adult chinook salmon (chna), juvenile chum salmon (chmj), adult chum salmon (chma), juvenile coho salmon (coj), adult coho salmon (coa), cutthroat trout (cutt), northern anchovy (anch), jack mackerel (jmac), market squid (mksq), Pacific hake (hake), Pacific herring (herr), juvenile Pacific sand lance (sand), Pacific sardine (sard), Pacific saury (sary), larval rex sole (rexl), juvenile rockfish (jvrf), spiny dogfish (spdf), juvenile steelhead trout (stlj), surf smelt (sfs), and whitebait smelt (wbsm). Gelatinous zooplankton within the plot are abbreviated as follows: *Aequorea victoria* (aeq), *Aurelia aurita* (aur), *Beroe* sp. (bero), *Chrysaora fuscescens* (chry), and *Phacellophora camtschatica* (phac).

nekton). Other studies have examined nearshore to offshore differences in  $\delta^{13}\text{C}$  in nekton, but not to the extent of the trophic levels observed here. Sydesman et al. (1997) observed that slope-oriented species of small fishes, zooplankton, and birds had more negative  $\delta^{13}\text{C}$  values, and they deduced that nearshore to offshore differences in  $\delta^{13}\text{C}$  existed off northern California. Davenport and Bax (2002) observed no significant nearshore vs. offshore difference in fish across the southeast Australian shelf and attributed differences in  $\delta^{13}\text{C}$  between benthic and pelagic production. Sherwood and Rose (2005) also observed very little difference between fish collected nearshore and offshore from the Newfoundland–Labrador shelf food web. The relative distinction between nearshore and offshore species at higher trophic levels within the NCC system is probably due to the more structured shelf and slope waters from upwelling (Lentz 1992) and to our

focus on more pelagic species. Other systems, such as the Georges Bank (Fry 1988) and Scotian Shelf (Mills et al. 1984) systems, have displayed little or no apparent  $\delta^{13}\text{C}$  differentiation between nearshore and more offshore species. This may be due in part to their relatively shallow, well-mixed waters, which allow for more benthic–pelagic coupling to occur, and the absence of strong coastal upwelling that forms fronts and, thus, structure for pelagic ecosystems. Our study was limited to the horizontal distribution in  $\delta^{13}\text{C}_{\text{TL}}$  of the dominant pelagic species at various trophic levels in the NCC, and we did not examine many of the benthic and epibenthic species that likely interact with the pelagic environment (e.g., pandalid shrimp, flatfishes, and adult rockfishes). Additional study using  $\delta^{13}\text{C}$  of benthic vs. pelagic organisms would further clarify the degree of benthic–pelagic coupling in this system.

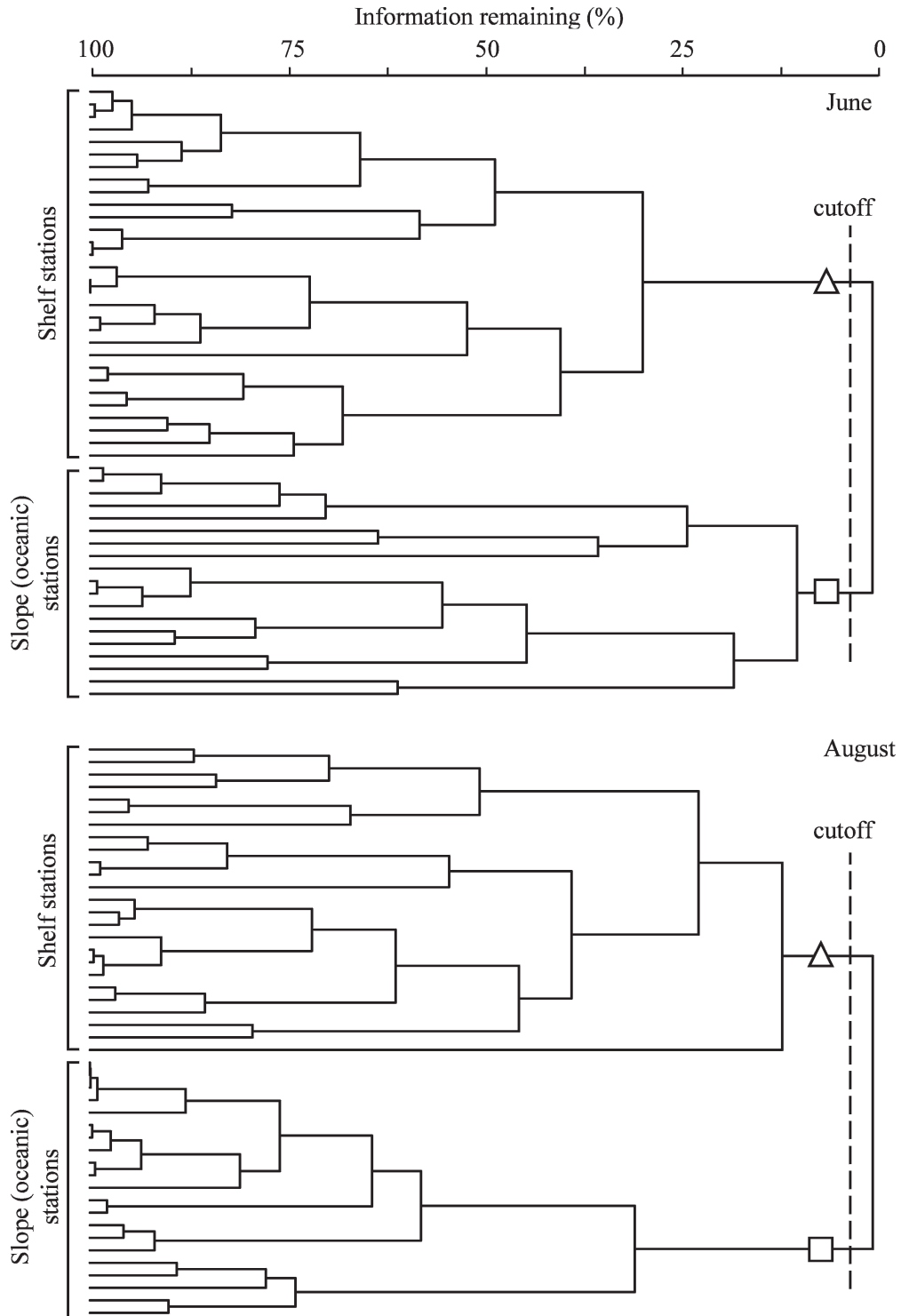


Fig. 5. Dendrograms from agglomerative hierarchical cluster analysis (relative Sørensen, distance measure; flexible beta linkage function) of sample units (stations) and nekton and gelatinous zooplankton species composition. Sampling occurred during June and August 2002 from the northern California Current ecosystem. Vertical dashed lines denote the cutoff levels for cluster groups (squares and triangles). Percent information remaining is the amount of information left at each node.

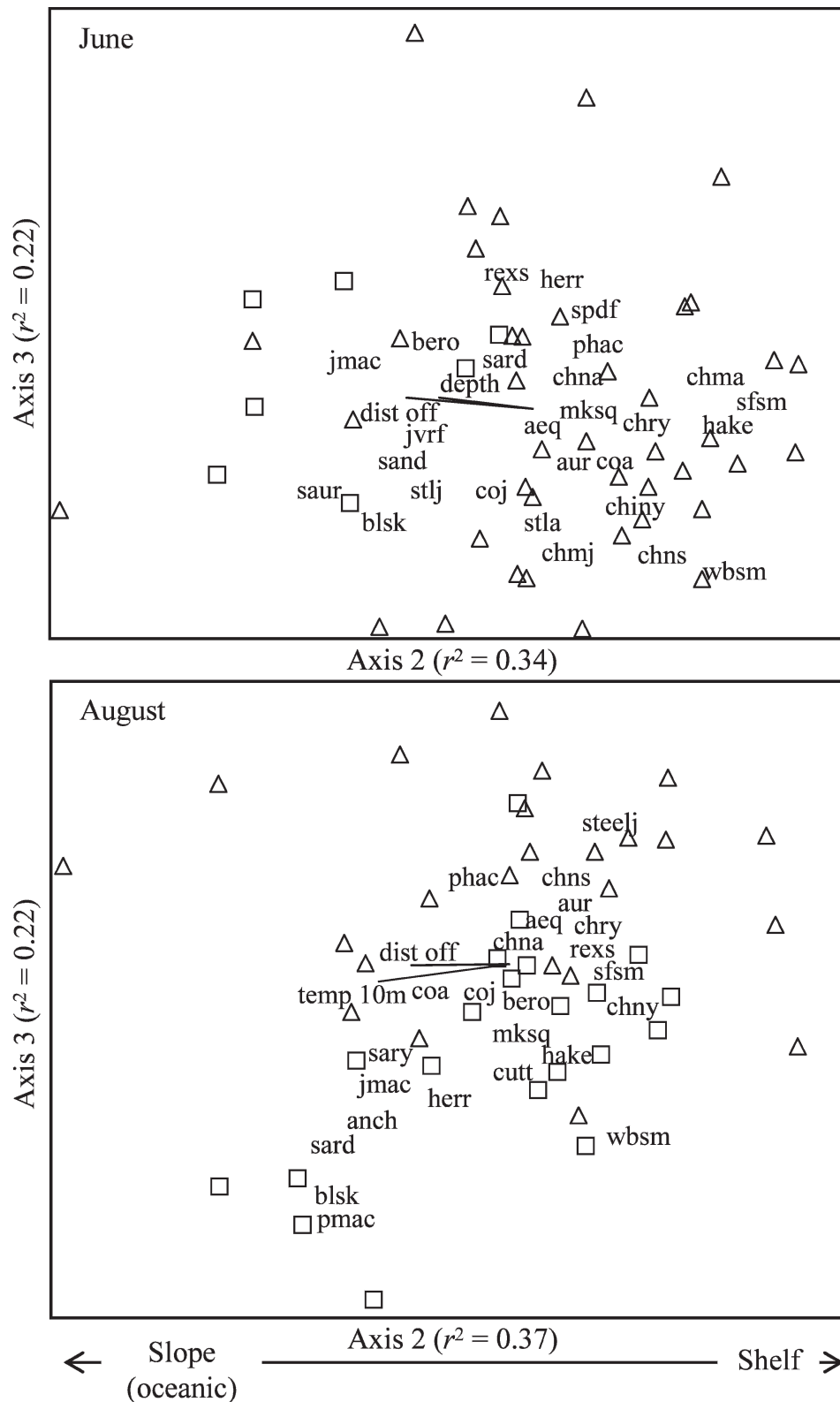


Fig. 6. Nonmetric multidimensional scaling (NMS) ordination of nekton and gelatinous zooplankton in sample unit space from June (stress = 16.3) and August (stress = 14.1) 2002 collections of the northern California Current ecosystem. Sample units are indicated by boxes and triangles representing shelf and slope (oceanic) cluster groups based on agglomerative hierarchical cluster analysis (Fig. 5) of species distributions in sample unit space. Significant environmental variables ( $r^2 > 0.25$ ) are denoted by the following: distance offshore (dist off), bottom depth (depth), and temperature at 10-m depth (temp 10 m). Nekton species within the plot are abbreviated as follows: Pacific sardine (sard), Pacific herring (herr), northern anchovy (anch), jack mackerel (jmac), Pacific mackerel (pmac), surf smelt

The correlation of POM  $\delta^{13}\text{C}$  to log Chl *a* indicated the likely source of the  $\delta^{13}\text{C}$  pattern observed across the shelf and slope in copepods, other zooplankton, and nekton. Analysis of Chl *a* and  $\delta^{13}\text{C}$  showed a relationship of increasing  $\delta^{13}\text{C}$  and log(Chl *a*) (Fig. 2); values of  $>5.0 \mu\text{g L}^{-1}$  were typically associated with elevated  $\delta^{13}\text{C}$  values of  $-20.3\text{‰} \pm 0.4\text{‰}$ , whereas values of  $<3.0 \mu\text{g L}^{-1}$  had a mean of  $-22.8\text{‰} \pm 0.5\text{‰}$ . Within the same area and time of our study, Sherr et al. (2005) observed a higher fraction of diatoms nearshore of the upwelling front associated with Chl *a* measures of  $>5 \mu\text{g L}^{-1}$ , with smaller phytoplankton ( $<5\text{-}\mu\text{m}$  coccoid cyanobacteria and eukaryotic phytoplankton) being more abundant in samples offshore of the front. The mechanisms behind this difference in carbon fractionation ( $\epsilon_p$ ) from phytoplankton are not understood and are likely due to a complex of various factors, including growth rate (Rau et al. 1997) and the ability of diatoms to store  $[\text{CO}_2]_{\text{aq}}$  (Woodworth et al. 2004).

The ranges of  $\delta^{13}\text{C}$  in our POM samples were within the range observed in marine POM from other studies ( $-23\text{‰}$  to  $-18.5\text{‰}$  at  $45^\circ\text{N}$  [Hofmann et al. 2000] and  $-23\text{‰}$  to  $-21\text{‰}$  off Oregon [Bosley et al. 2004]). Lower (more negative)  $\delta^{13}\text{C}$  values from this range, however, appear too depleted to account for the  $\delta^{13}\text{C}$  values observed in higher trophic levels. After correcting for trophic level  $^{13}\text{C}$  enrichment, most zooplankton and nekton remained  $\sim 2\text{--}3\text{‰}$  enriched relative to POM (Table 1), which remains too enriched to account for any residual trophic level differences. Possible reasons for this result are (1) the fractionation correction factor ( $\delta^{13}\text{C}'_{\text{TL}}$ ) underestimated trophic fractionation in  $\delta^{13}\text{C}$  for consumers; (2) spatial and temporal limitations in sampling resulted in a failure to obtain the most  $^{13}\text{C}$ -enriched nearshore signatures of base production; (3) POM samples were not representative of selective utilization of base production by primary consumers; and/or (4) a more benthic source of food was being utilized.

The fractionation correction factor most likely did not account for much of the difference because after initial corrections, most species remained as much as  $3\text{‰}$  from base production, well beyond the generally accepted  $0.4\text{‰}$  (Post 2002) enrichment per trophic level. Our POM samples may have missed the nearshore shelf signature of primary production. However, based on Chl *a* vs.  $\delta^{13}\text{C}$  of POM samples, increased diatoms in our samples failed to enrich samples beyond approximately  $-18.7\text{‰}$ , indicating that we probably obtained the full range of  $\delta^{13}\text{C}$  from POM samples (Fig. 2). POM samples may not have been a true representation of the specific phytoplankton groups being utilized by primary consumers and, thus, may not have offered a true estimation of the carbon available to

higher trophic levels. In our study, nearshore POM samples likely contained a higher fraction of diatoms, although the sample would have also been diluted by some proportion of nonphotosynthetic material (del Giorgio and France 1996). Finally, the enrichment of certain species may be due to utilization of more benthic-oriented prey that typically have higher  $\delta^{13}\text{C}$  values (McConnaughey and McRoy 1979). Market squid, Pacific herring, northern anchovy, surf smelt, and most of the gelatinous zooplankton (excluding *Beroe*) had  $\delta^{13}\text{C}'_{\text{TL}}$  values that measured well above what would be predicted based on  $\delta^{13}\text{C}$  of nearshore POM. However, it is unlikely that their signatures were derived from a benthic source, because these species (mainly Pacific herring, northern anchovy, and surf smelt) are obligate zooplanktivores (Brodeur and Pearcy 1992), feeding on zooplankton that consume more surface-oriented primary and secondary production. It is more likely that the discrepancies between POM and higher trophic levels were due to the selective feeding on phytoplankton by copepods and other primary consumers and that our POM samples obtained the signature from utilized and nonutilized material.

Copepods provided a more accurate indicator of the endpoints of source production, with shelf samples collected very near shore ( $<5$  km in distance from shore, mean  $\delta^{13}\text{C}' = -16.8$ ) and slope samples collected far offshore ( $>50$  km, mean  $\delta^{13}\text{C}' = -19.22$ ) capturing the range of most nekton species in the shelf to oceanic pelagic ecosystem (Fig. 4). The comparisons of copepod  $\delta^{13}\text{C}'$  from shelf and oceanic samples, as defined by the 150-m isobath, were significant ( $p = 0.01$ ), but there was considerable enrichment of oceanic copepod samples relative to oceanic-oriented nekton. During the months from May to August, the NCC exhibits very strong and persistent coastal upwelling, and the marginal difference between shelf and oceanic copepods, as delineated by the 150-m isobath, may have been due to offshore advection. The copepods measured for this study were primarily *Acartia* spp., which are small (prosome length  $\sim 0.7\text{--}1.0$  mm) and more prone to transport by advective currents (Morgan et al. 2003).

Stable isotope studies of aquatic systems often use copepods over POM samples as a reference for the food web (Vander Zanden and Rasmussen 2001), in part because they represent the true signature of base production utilized and thus are less prone to short-term (e.g., days) fluctuations in primary production. The  $\delta^{13}\text{C}'$  of copepods in our study provided a general correspondence of shelf and slope copepods to higher trophic levels (Fig. 4), but there was considerable overlap, which precludes its use as an effective end member of shelf and slope production. A more reasonable estimate of end member values for shelf

←

(sfsm), Pacific saury (sary), whitebait smelt (wbsm), Pacific hake (hake), juvenile rockfish (jvrf), Pacific sand lance (sand), larval rex sole (rexs), subyearling chinook salmon (chns), yearling chinook salmon (chny), adult chinook salmon (chna), juvenile coho salmon (coj), adult coho salmon (coa), juvenile chum salmon (chmj), adult chum salmon (chma), juvenile steelhead trout (steelj), cutthroat trout (cutt), spiny dogfish (spdf), blue shark (blsk), and market squid (mksq). Gelatinous zooplankton within the plot are abbreviated as follows: *Aequorea victoria* (aeq), *Aurelia aurita* (aur), *Beroe* sp. (bero), *Chrysaora fuscescens* (chry), and *Phacellophora camtschatica* (phac).

and oceanic production are likely copepods that were collected well within the shelf and well offshore of the slope, defined here as <5 km and >60 km offshore, respectively. Using this criterion, there was a greater separation of the  $\delta^{13}\text{C}'$  values that were more compatible with the cross-shelf distribution and  $\delta^{13}\text{C}'_{\text{TL}}$  values of higher trophic level nekton and gelatinous zooplankton (Fig. 4).

Distance offshore was the only significant variable in describing  $\delta^{13}\text{C}'_{\text{TL}}$  for nekton and gelatinous zooplankton, with very nearshore shelf species expressing high  $\delta^{13}\text{C}'_{\text{TL}}$  values relative to more oceanic species. Nekton and gelatinous zooplankton therefore expressed an approximate gradual (linear) relationship with distance offshore. Some species, as indicated by AHCA and NMS ordination of the community, showed strong associations with either oceanic or the very nearshore waters (Fig. 6), with many dispersed across the mid-shelf. The significance of the environmental variables distance offshore and bottom depth in June and temperature at 10-m depth and distance offshore in the NMS are all related to changes in the shelf to slope ecosystem. The significance of temperature at 10-m depth in August may have occurred as the result of a combination of increased upwelling prior to the August sampling and the decreased presence of the Columbia River plume, which bisects the shelf and oceanic waters of the NCC. High upwelling would have established a stronger temperature gradient across the shelf, and the attenuation of plume waters later in the summer would have decreased variability in surface temperature and salinity between shelf and oceanic waters.

Within the same general region of this study, Brodeur and Percy (1992) also observed strong spatial shifts in the NCC food web, with general divisions of very nearshore, mid-shelf, and slope species of nekton. Several nekton that added considerable variation to the  $\delta^{13}\text{C}'_{\text{TL}}$  regression here were most likely undergoing migrations at the time of this study (e.g., adult coho and chum salmon, subyearling chinook salmon, and northern anchovy). Adult coho and chum salmon and subyearling chinook salmon had very low  $\delta^{13}\text{C}'_{\text{TL}}$  values, which is in agreement with the low values they would have obtained from their recent oceanic (coho and chum) and freshwater (subyearling chinook salmon) existence. In contrast, northern anchovy displayed a more shelf signature but were distributed more off the slope, primarily as a result of summer spawning migrations from shelf to slope waters. The shelf to oceanic nekton community is therefore represented by species with strong affinities to the shelf or more slope, oceanic waters, by migratory species, and by those which utilize both the shelf and oceanic waters. Carbon stable isotopes can help better refine the spatial relationships, as observed here; however, it is also important to consider the biology and behavior of organisms to make sense of isotopic results.

In the regression analyses of  $\delta^{13}\text{C}$ , the environmental variable log Chl *a* was significant for POM, but distance offshore was significant for the other taxa. The closer relationship of POM  $\delta^{13}\text{C}$  to log Chl *a* likely occurred as a result of the high turnover rate of  $\delta^{13}\text{C}$  in phytoplankton relative to zooplankton and nekton and also because of

the influence of the phytoplankton community on Chl *a* (Sherr et al. 2005) and  $\delta^{13}\text{C}$  (Tortell et al. 2000). For copepods, the lower turnover rate in  $\delta^{13}\text{C}$  and coastal advection from upwelling (Morgan et al. 2003) likely resulted in copepods that were some distance from their original food source, based on which they exhibited much of their growth. Similarly, the significance of distance offshore for nekton and gelatinous zooplankton may have been due to the ability of nekton to swim against currents and to forage between water masses. The apparent nonsignificance in variables associated with shelf and oceanic water masses, such as temperature and salinity, may have been due to the convoluted shelf break (Fig. 1), latitudinal gradients in coastal upwelling (Morgan et al. 2003), and the presence of a large, warm, freshwater plume flowing southward from the Columbia River, which bisects coastal and offshore waters (Barnes et al. 1972). This complexity and the movements of pelagic organisms indicate the need to incorporate carbon stable isotope analyses to understand coastal advection processes in zooplankton and nekton.

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