

Abstract—In this study we analyzed the diets of 26 nekton species collected from two years (2000 and 2002) off Oregon and northern California to describe dominant nekton trophic groups of the northern California Current (NCC) pelagic ecosystem. We also examined interannual variation in the diets of three nekton species. Cluster analysis of predator diets resulted in nekton trophic groups based on the consumption of copepods, euphausiids, brachyuran larvae, larval-juvenile fishes, and adult nekton. However, many fish within trophic groups consumed prey from multiple trophic levels—euphausiids being the most widely consumed. Comparison of diets between years showed that most variation occurred with changes in the contribution of euphausiids and brachyuran larvae to nekton diets. The importance of euphausiids and other crustacean prey to nekton indicates that omnivory is an important characteristic of the NCC food web; however it may change during periods of lower or higher upwelling and ecosystem production.

Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem

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Eastern Pacific boundary upwelling zones, such as the California Current, are generally highly productive and support major fisheries, yet these ecosystems also exhibit substantial temporal fluctuations in primary and higher-level production (Francis and Hare, 1994; Carr, 2002; Chavez et al., 2003). This variation has been attributed to variability in abiotic forcing through relatively short-term (inter-annual) El Niño and La Niña events (Percy and Schoener, 1987), as well as long-term (decadal) environmental forcing (Francis and Hare, 1994; Mantua et al., 1997). This apparent link between abiotic forcing and the ecosystem has led to considerable discussion regarding energy flow through large marine ecosystems (Jackson et al., 2001). However, few studies have comprehensively examined multispecies trophic patterns within a system. Understanding trophic patterns and temporal changes between species across multiple trophic groups is essential in understanding energy transfer within a system and mechanisms behind ecosystem stability (Worm and Duffy, 2003).

The northern California Current (NCC) system encompasses the northern region of the California Current production zone (approximately 41–49° N) along the continental shelf and shelf break between northern

California and Washington. This system is a major upwelling region, where Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), jack mackerel (*Trachurus symmetricus*), market squid (*Loligo opalescens*), and Pacific hake (*Merluccius productus*) are the dominant nektonic species (Brodeur and Percy, 1986; Brodeur et al., 2005). Between April and September, strong but episodic coastal upwelling is the dominant hydrographic feature of the NCC. This upwelling provides cool nutrient-rich water to the euphotic zone across the shelf (Huyer, 1983), allowing for high levels of primary production (Hood et al., 1991). Inter-annual variation in coastal upwelling, particularly between El Niño and La Niña events, greatly influences primary production (Corwith and Wheeler, 2002) and higher trophic levels (Ainley et al., 1996). On an interdecadal scale, the California Current also experiences production regimes of 30 years or more, which have been linked to salmon survival (Mantua et al., 1997) and variation in NCC zooplankton biomass (McGowan et al., 1998).

The diets of multiple species within the NCC pelagic ecosystem have been examined in only a few studies, and these studies were mostly performed on single or a few closely related spe-

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cies (e.g., Brodeur and Pearcy, 1990; Robinson, 2000). During the 1980s, Brodeur et al. (1987) analyzed the diets from a diverse assemblage of pelagic nekton from the NCC, but since that time, the NCC system has exhibited major shifts in the abiotic environment and in community composition (Peterson and Schwing, 2003) and a concomitant change in nekton species composition (Emmett and Brodeur, 2000). Observed environmental shifts and changes in the NCC pelagic community are undoubtedly conveyed in-part through trophic interactions. Description of the NCC in the context of the current ocean environment and nekton community is therefore important in determining the mechanisms linking climate change and pelagic ecosystem response. In this study we analyzed the diets of 26 nekton species collected during two separate years (2000 and 2002) from coastal northern California to central Oregon, applied cluster analysis to diet data to delineate trophic groups based on dominant prey taxa, and compared the importance of these prey between the two years for several species.

Materials and methods

Field collections

Nekton were collected for diet analyses from Northeast Pacific Global Ocean Ecosystems Dynamics (GLOBEC) cruises during 29 May–18 June and 29 July–12 August 2000, and 29 May–18 June and 31 July–19 August 2002. Sampling occurred along nine transects across the shelf between Crescent City, CA (41°54'N), and Newport, OR (44°39'N) (for station locations see Brodeur et al. [2004] and Reese and Brodeur [2006]), during daylight hours. At each station, nekton were collected with a Nordic-264 (Nor'Eastern Trawl Systems, Bainbridge Island, WA) rope trawl (30 m wide × 18 m deep) that was towed for 30 minutes. Up to 30 individuals per species were collected per tow for diet analysis. Nekton were immediately frozen on ship (−20°C) after removal from the net and then processed at a later date in the laboratory.

Laboratory analysis

Laboratory processing of nekton involved measurement of individuals and extraction of stomachs for diet analysis. Lengths of fish and squid were measured (±1.0 mm) for either fork length, standard length, or dorsal mantle length. Stomachs were extracted and immediately placed in 10% buffered formalin for 10 days, rinsed with tap water, and transferred to 70% ethanol. Diet analyses were performed by assessing fullness, digestive condition, and identification and quantification of prey taxa in each stomach. Fullness was assessed on a scale of 0–5, with 0 being empty and 5 being distended. Condition of individual digested prey was assessed by using a 0–4 scale, with 0 being unrecognizable and 4 being fresh. Prey taxa were identified to the lowest possible taxon, enumerated, and wet weighed (±0.1 mg) after excess

water was removed with blotting paper. When individual prey items were too numerous to enumerate, individual weights were estimated by obtaining the damp weight of a known number of animals and regressing this number on the total weight of the prey. For Pacific sardine, diets comprised large amounts of phytoplankton mixed with small zooplankton and euphausiid eggs that required a subsampling method for diet analysis (Emmett et al., 2005). Chinook salmon (*Oncorhynchus tshawytscha*) were divided into subyearlings, yearlings, and adults, and coho salmon (*O. kisutch*) were separated into yearlings and adults (Brodeur et al., 2004).

Data analysis

Trophic relationships of nekton were examined by using agglomerative hierarchical cluster analysis (AHCA) to form cluster dendrograms. The percent wet weight contribution of prey to predator diets were arranged in a simple predator (row) × prey (column) matrix. For AHCA we used the Sørensen (Bray-Curtis) distance measure and Ward's linkage method. Trophic groups from cluster analysis were established by choosing a cutoff level with biological meaning while maintaining a reasonable level (at least 40%) of information explained in the cluster dendrogram. The significance of trophic groups was examined using a multiresponse permutation procedure (MRPP), which tests for the null hypothesis of no difference between groups. MRPP gauges within and between group differences using an A-statistic that ranges between 0 and 1, with 0 being no agreement within a group and 1 being complete agreement. All AHCA and MRPP analyses were performed with PC-ORD software (version 4, MjM Software, Gleneden Beach, OR).

Before nonparametric analyses of diets, certain modifications to the data were performed. Nekton species that were found in <5% of the tows within a cruise were excluded from analyses, although these species were retained in the general description of diets. This level of exclusion was somewhat arbitrary; however exclusion of nekton species that were found in 5–10% of tows would have removed many predator species from analyses. Prey taxa modifications involved removal of rare species and aggregation of certain groups. Larval-juvenile fishes, hyperiid amphipods, brachyuran and decapod larvae, and adult fish prey were combined into higher taxonomic categories and life history stages. This arrangement was required to retain important species groups for multivariate analyses. Adjustments for all data involved the removal of rare prey that were only present in ≤10% of the nekton diets (rows) in the main matrix. Removal of rarer species reduced noise in the data and allowed for comparisons of important prey between nekton predators.

Trophic relationships were also analyzed by calculating the degree of diet similarity between nekton species pairs by using Schoener's similarity index (Schoener, 1974), modified as a percent similarity index (PSI) of the diets of paired nekton:

$$PSI = \left[1 - 0.5 \sum_{i=1}^n |p_{ik} - p_{jk}| \right] \times 100, \quad (1)$$

where p = the proportion of biomass (wet weight) of the k th prey species consumed by predator species i and j .

Diet overlap values $\geq 60\%$ were considered biologically significant (Wallace and Ramsay, 1983). As in the AHCA, prey items of unidentified material, and fish and crustacean tissue, were eliminated from the calculation of PSI.

Diets (percent wet weight of major prey taxa) from selected species were compared with respect to interannual differences. Comparisons between 2000 and 2002 were limited to species and life history stages of nekton that were found in $\geq 5\%$ of the total number of hauls within a cruise, which left only yearling and adult chinook and coho salmon, and juvenile steelhead trout (*O. mykiss*). Comparisons between years were undertaken by visual inspection of plotted diet data.

Results

Trophic groups

A total of 3161 stomachs from 26 species of marine nekton were analyzed for diet composition from the June and August 2000 and 2002 cruises. A species-specific summary of number of stomachs analyzed, nekton percent frequency of occurrence, nekton size (mean and standard deviation), and mean stomach fullness and condition are presented in Table 1. A more detailed description of specific prey species consumed by nonsalmonids can be found in Miller (2006). Results from cluster analysis and MRPP showed major trophic groups for both years based on nekton diet (percent wet weight) of the following general prey groups: adult fish, larval-juvenile fish, euphausiids (*Thysanoessa spinifera* and *Euphausia pacifica*), decapod larvae, copepods, and other mixed zooplankton groups (predominantly hyperiid amphipods, gelatinous zooplankton, and phytoplankton). For 2000 and 2002, five significant trophic groups (2000 MRPP, A statistic=0.37, $P < 0.001$; 2002 MRPP, A statistic=0.31, $P < 0.001$) were observed at the cutoff level of 60% and 52% information remaining, respectively (Fig. 1).

From AHCA of nekton diets for the year 2000, trophic group A (blue shark [*Prionace glauca*] and adult coho salmon, Figs. 1 and 2) had diets that consisted (62% and 80%, respectively) of adult Osteichthyes (Clupeidae and unidentifiable fish tissue), and to a lesser extent of larval-juvenile Osteichthyes (for adult coho salmon) and euphausiids (for blue shark). Trophic group B (juvenile and adult salmon) had diets comprising $>90\%$ larval-juvenile fish and adult euphausiids for each age class. Of the euphausiids consumed, *T. spinifera* contributed the highest proportion by wet weight to salmonid diets. Trophic group C (jack mackerel, Pacific saury [*Cololabis saira*], and Pacific sardine) had diets of 86%, 93%, and

90% euphausiids, respectively; most euphausiids consumed by this group were identified as *E. pacifica*. Trophic group D (market squid and surf smelt [*Hypomesus pretiosus*]) had the most diverse diet of all nekton: mixed species of crustacean zooplankton (brachyuran larvae, euphausiids, hyperiid amphipods) accounted for most of the diet by wet weight. Trophic group E (Pacific herring [*Clupea pallasii*], whitebait smelt [*Allosmerus elongates*], and juvenile sablefish [*Anoplopoma fimbria*]), consumed euphausiids that contributed 77%, 96%, and 97% to the wet weight of their diets, respectively. Except for *E. pacifica*, which was consumed most by juvenile steelhead trout, *T. spinifera* was the dominant euphausiid species consumed by nekton within this group. The remaining nekton not included in the cluster analysis generally consumed a mix of crustacean zooplankton or crustacean zooplankton and larval-juvenile Osteichthyes (Fig. 2).

There was a similar trend in 2002 nekton diets based on the consumption of adult and larval-juvenile Osteichthyes, euphausiids, and brachyuran larvae (Figs. 1 and 3). As in 2000, blue shark and adult coho salmon (trophic group A, Figs. 1 and 3) diets consisted mainly of adult Osteichthyes (81% and 30%, respectively); blue shark diets consisted secondarily of osteichthye tissue (16%), and adult coho salmon diet consisted secondarily of brachyuran larvae (69% of which were Dungeness crab [*Cancer magister*] megalopae). Pacific hake and adult chinook salmon, also in this group, consumed adult Osteichthyes (predominantly Clupeidae), larval-juvenile Osteichthyes (chinook salmon only), euphausiids (Pacific hake only), and brachyuran larvae (adult chinook and coho salmon). Trophic group B (Fig. 1) consisted of jack mackerel, northern anchovy, Pacific herring, juvenile sablefish, and whitebait smelt, whose diets consisted mostly of euphausiids (predominantly *T. spinifera*) and various other zooplankton and larval-juvenile Osteichthyes (Fig. 3). Juvenile chinook, coho, and chum salmon (*O. keta*), and juvenile steelhead trout formed a trophic group (C, Fig. 1), where larval-juvenile Osteichthyes represented $>50\%$ of wet weight of diet for all species (Fig. 3). Euphausiids were important in only juvenile steelhead trout (35%). Trophic group D (Fig. 1) consisted of market squid, surf smelt, spiny dogfish (*Squalus acanthias*), and Pacific sand lance (*Ammodytes hexapterus*) which consumed a mix of crustacean zooplankton (euphausiids, brachyuran larvae, hyperiids) and in the case of spiny dogfish, gelatinous zooplankton. Pacific sardine, juvenile widow rockfish (*Sebastes entomelas*), and Pacific saury clustered into a group (trophic group E, Fig. 1) that had mixed zooplankton diets of copepods, euphausiid eggs, and euphausiids. The remaining nekton not included in the cluster analysis were juvenile rockfish (*Sebastes* spp.) species and juvenile lingcod (*Ophiodon elongatus*). Juvenile lingcod diets consisted mostly of large copepods (68%, *Calanus* spp.), and larval-juvenile Osteichthyes (30%). Juvenile rockfish consumed a combination of euphausiids, copepods, hyperiid amphipods, and gelatinous zooplankton or material (Fig. 3).

Table 1

Summary of nekton species analyzed for stomach contents from June and August 2000 and 2002 GLOBEC cruises in the northern California Current ecosystem. Percent frequency of occurrence (FO) of individual species is the occurrence of a species from 163 and 212 net tows in 2000 and 2002, respectively. Length denotes fork length with the exception of *Loligo opalescens*, which was measured in dorsal mantle length, and *Prionace glauca*, *Merluccius productus*, and *Squalus acanthias* measured in total length. Standard deviation of length is denoted as SD.

Nekton taxa	2000				2002			
	n	FO (%)	Length (mm)		n	FO (%)	Length (mm)	
			Mean	SD			Mean	SD
Market squid (<i>Loligo opalescens</i>)	38	4.8	72	17	178	5.8	84	25
Blue shark (<i>Prionace glauca</i>)	9	6.3	1331	136	13	3.3	1607	234
Spiny dogfish (<i>Squalus acanthias</i>)				128	6.3	263	34	
Northern anchovy (<i>Engraulis mordax</i>)	4	2.5	152	6	177	12.7	157	16
Pacific herring (<i>Clupea pallasii</i>)	134	8.3	146	11	152	5.8	192	24
Pacific sardine (<i>Sardinops sagax</i>)	160	13.4	221	27	108	4.1	198	24
Surf smelt (<i>Hypomesus pretiosus</i>)				87	2.5	137	11	
Whitebait smelt (<i>Allosmerus elongatus</i>)	89	4.2	100	9	69	2.0	109	7
Chinook salmon (subyearling)								
(<i>Oncorhynchus tshawytscha</i>)	56	3.8	137	14	29	15.3	283	29
(yearling)	100	18.1	225	30	100	22.4	281	33
(adult)	32	12.6	378	43	100	24.3	378	108
Coho salmon (yearling) (<i>O. kisutch</i>)	84	19.7	261	48	38	25.0	25	182
(juvenile)				148	10.6	114	11	
(adult)	13	7.1	594	71	56	8.7	9	514
Chum salmon (juvenile) (<i>O. keta</i>)	147	10.6	113	11				
Cutthroat trout (adult) (<i>O. clarki</i>)	4	2.2	297	19	7	5.9	321	28
Steelhead trout (juvenile) (<i>O. mykiss</i>)	55	13.4	284	29	15	5.5	268	30
(adult)	1	1	430					
Pacific hake (<i>Merluccius productus</i>)				72	1.9	252	51	
Pacific saury (<i>Cololabis saira</i>)	40	5.1	157	22	140	5.8	214	38
Bank rockfish (juvenile) (<i>Sebastes rufus</i>)				9	1.0	84	25	
Canary rockfish (juvenile) (<i>S. pinniger</i>)				16	2.9	27	3	
Darkblotched rockfish (juvenile) (<i>S. crameri</i>)	7	1.2	47	4	11	2.9	29	2
Yellowtail rockfish (juvenile) (<i>S. flavidus</i>)	26	2.4	49	4				
Rockfish (juvenile) (<i>Sebastes</i> spp.)	4	1.2	48	2	19	2.9	37	7
Widow rockfish (juvenile) (<i>Sebastes entomelas</i>)				41	4.8	53	4	
Lingcod (juvenile) (<i>Ophiodon elongatus</i>)	10	4.8	74	4	1	1.0	64	
Sablefish (<i>Anoplopoma fimbria</i>)	6	2.5	157	22	15	5.0	181	9
Jack mackerel (<i>Trachurus symmetricus</i>)	74	11.4	497	75	242	13.1	505	54
Pacific mackerel (<i>Scomber japonicus</i>)	24	1.3	325	19				
Pacific sand lance (juvenile)				73	5.8	57	5	
(<i>Ammodytes hexapterus</i>)								
Total	1117				2044			

Percent similarity of diets between nekton species varied by year (Tables 2 and 3). During 2000 (Table 2), highest similarity values were found between yearling chinook and yearling coho salmon (94%), yearling and adult chinook salmon (88%), and yearling coho salmon and adult chinook salmon (88%). Trophic groups B (yearling and adult chinook salmon and yearling coho salmon) and C (jack mackerel, Pacific saury, and Pacific sardine) had the highest similarities in diet (mean 90% and 58%, respectively). For trophic group B, larval-

juvenile Osteichthyes and adult euphausiids together accounted for over 80% of the total percent similarity in diets among the three nekton, and larval-juvenile Osteichthyes accounted for 60% of the overlap. Other nekton that had significant (>60%) percent similarity in diets (Table 2) were 1) jack mackerel and juvenile steelhead trout and 2) juvenile steelhead trout and Pacific herring; and the similarities were primarily due to euphausiids, or to species that fed on euphausiids and other mixed zooplankton, or in the case of adult coho

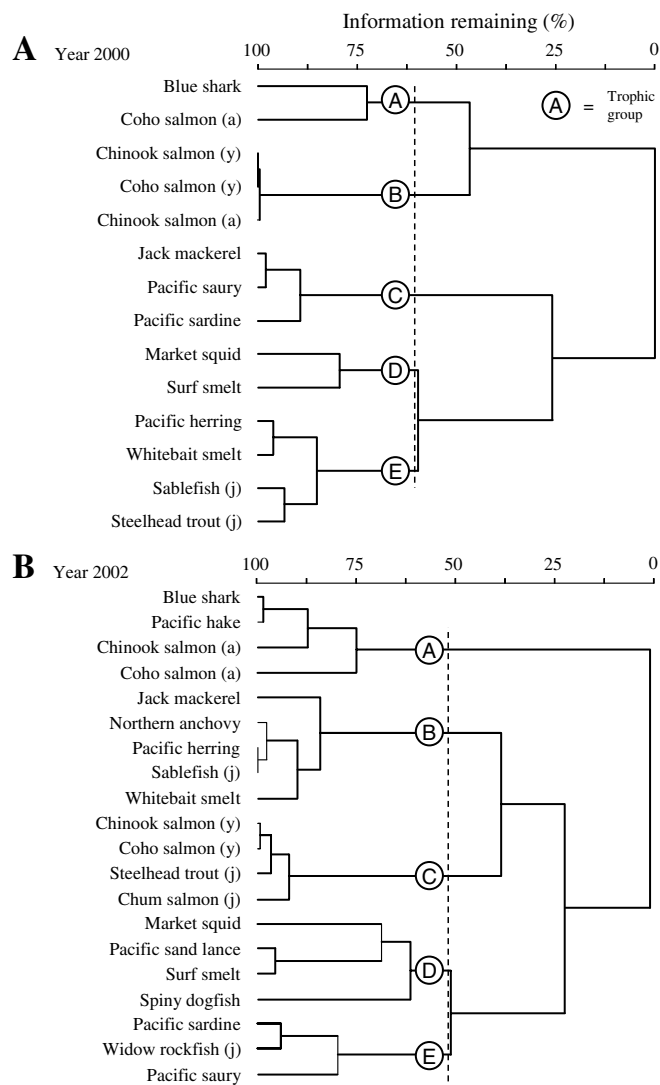


Figure 1

Dendrograms of nekton based on diet (percent wet weight contribution of prey) as determined by agglomerative hierarchical cluster analysis of nekton collected from the northern California Current during June and August 2000 and 2002 GLOBEC (GLOBAL ocean ECosystems dynamics) cruises. Dashed line denotes the level (percent information remaining) at which trophic groups were established in the dendrogram. The percent information remaining is a function of the amount of information lost at each step of hierarchical cluster analysis. Scientific names of the species in the order they appear in the figure (from top to bottom) are the following: blue shark (*Prionace glauca*), coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), jack mackerel (*Trachurus symmetricus*), Pacific saury (*Cololabis saira*), Pacific sardine (*Sardinops sagax*), market squid (*Loligo opalescens*), surf smelt (*Hypomesus pretiosus*), Pacific herring (*Clupea pallasii*), whitebait smelt (*Allosmerus elongatus*), sablefish (*Anoplopoma fimbria*), steelhead trout (*O. mykiss*), Pacific hake (*Merluccius productus*), northern anchovy (*Engraulis mordax*), chum salmon (*O. keta*), Pacific sand lance (*Ammodytes hexapterus*), spiny dogfish (*Squalus acanthias*), and widow rockfish (*Sebastes entomelas*). Life history stages of nekton are shown in parentheses: j = juvenile, y = yearling, and a = adult; nekton and prey with no indication of life history stage are adult.

salmon and blue shark, to adult Osteichthyes (Fig. 2).

In 2002, trophic group C containing yearling chinook and coho salmon, juvenile chum salmon, and steelhead trout had the highest overall mean percent similarity (63%); and the highest similarity (78%) was between yearling chinook and yearling coho salmon (Table 3). Most of the similarity in diet within this trophic group was due to larval-juvenile Osteichthyes (70% of total similarity). Trophic groups B and A had the next highest similarities in diet (mean 61% and 46%, respectively). Similarities in diet within these two groups were primarily attributed to euphausiids (that represented 68% of total similarity) for trophic group B, and adult Osteichthyes (that represented 58% of total similarity) for trophic group A. The remaining trophic groups D and E had percent similarities <30%.

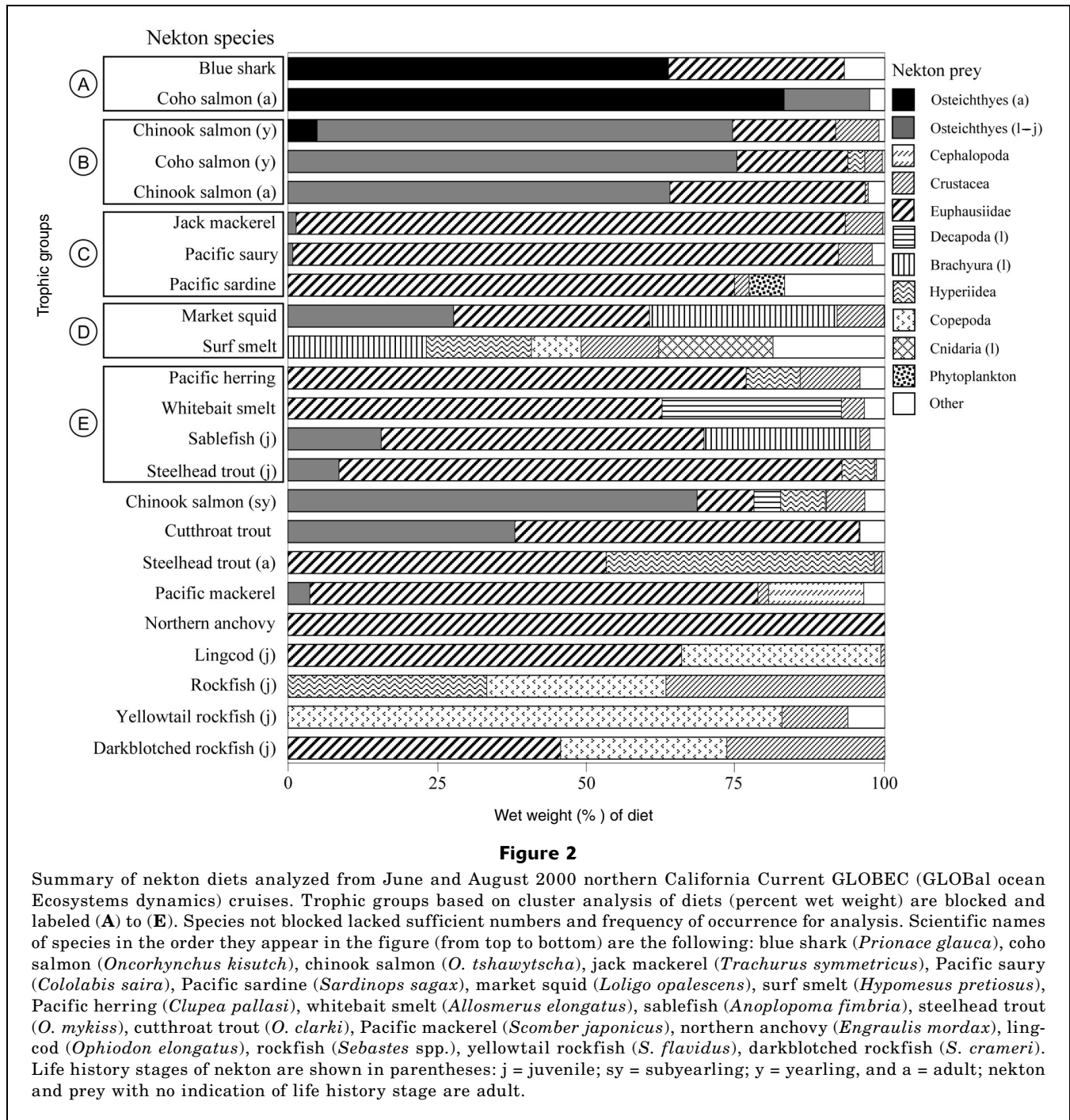
Interannual variation

Adult coho salmon and juvenile steelhead trout displayed the largest contrast in diet between 2000 and 2002. For adult coho salmon, adult and larval-juvenile Osteichthyes contributed >95% of the diet in 2000, and brachyuran larvae contributed approximately 50% of the diet in 2002 (Fig. 4). Steelhead trout had a greater proportion of its diet from euphausiids (84%) in 2000, whereas larval-juvenile Osteichthyes were more important in 2002 (57%). The remaining nekton displayed relatively similar diets between years, although differences were observed in the contribution of euphausiids and brachyuran larvae. Yearling coho and chinook salmon showed that larval-juvenile fishes contributed >70% of their diet for both years. Euphausiids contributed more to diets of both species during 2000 ($\geq 18\%$) compared to 2002 (>5%), whereas in 2002 brachyuran larvae were more prominent in the diets (Fig. 4). The trend of higher proportions of euphausiids in diets in 2000 and of brachyuran larvae in 2002 was also observed in adult coho and chinook salmon.

Discussion

Trophic groups

Diet analysis of 26 nekton species of the northern California Current ecosystem



revealed general trophic groups that primarily consumed adult Osteichthyes, larval-juvenile Osteichthyes, euphausiids, mixed zooplankton, and copepods; however, in each trophic group omnivory was expressed and actually predominated in some nekton trophic groups. The importance of omnivory in the higher trophic group of blue shark and adult coho salmon indicated that the typical mid-trophic level taxa, such as anchovy and Pacific sardine, were sometimes bypassed for direct feeding on

large zooplankton, in particular adult euphausiids. Previous studies from the NCC system have also shown that blue shark (Brodeur et al., 1987; Harvey, 1989), adult coho (Brodeur et al., 1987), and adult chinook (Hunt et al., 1999) salmon feed on adult nekton and euphausiids. With the exception of Pacific hake, top-down trophic pressure from fish may be less influential in the NCC because top nekton predators are not as abundant in this system as nekton prey such as euphausiids (Ressler

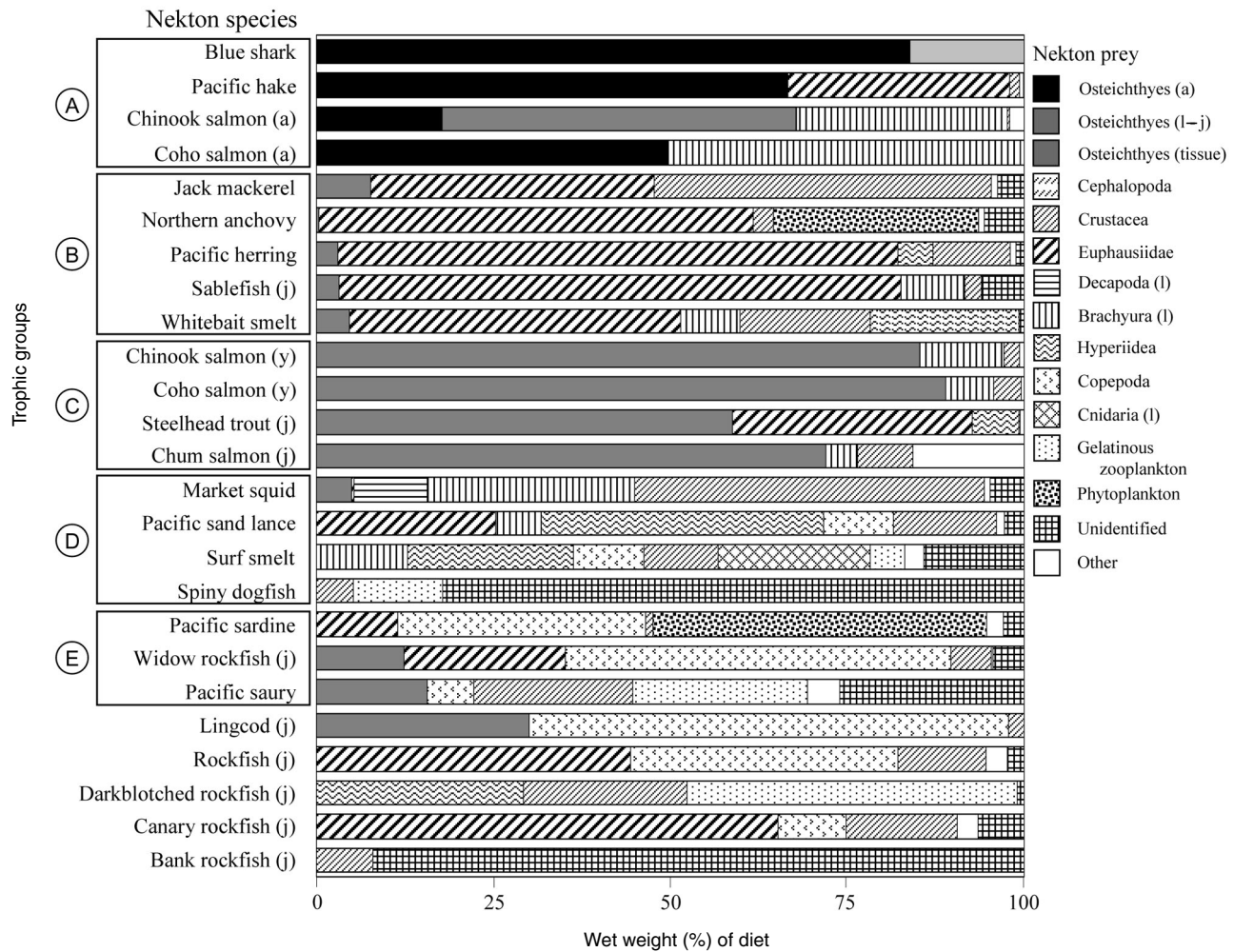


Figure 3

Summary of nekton diets analyzed from June and August 2002 northern California Current GLOBEC (GLOBAL ocean ECosystems dynamics) cruises. Trophic groups based on cluster analysis of diets (percent wet weight) are blocked and labeled (A) to (E). Species not blocked lacked sufficient numbers and frequency of occurrence for analysis. Scientific names of species in the order they appear in the figure are the following: blue shark (*Prionace glauca*), Pacific hake (*Merluccius productus*), chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), jack mackerel (*Trachurus symmetricus*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), sablefish (*Anoplopoma fimbria*), whitebait smelt (*Allosmerus elongatus*), steelhead trout (*O. mykiss*), chum salmon (*O. keta*), market squid (*Loligo opalescens*), Pacific sand lance (*Ammodytes hexapterus*), surf smelt (*Hypomesus pretiosus*), spiny dogfish (*Squalus acanthias*), Pacific sardine (*Sardinops sagax*), widow rockfish (*Sebastes entomelas*), Pacific saury (*Cololabis saira*), lingcod (*Ophiodon elongatus*), rockfish (*Sebastes* sp.), darkblotched rockfish (*S. crameri*), canary rockfish (*S. pinniger*), and bank rockfish (*S. rufus*). Life history stages of nekton are shown in parentheses: j = juvenile, y = yearling, and a = adult; nekton and prey with no indication of life history stage are adult.

et al., 2005). Pacific hake likely represent the largest predatory biomass off the west coast of North America (Methot and Dorn, 1995). They feed on adult nekton (Brodeur et al., 1987; Emmett and Krutzikowsky, in press) but also extensively on euphausiids (Brodeur et al., 1987; Tanasichuk, 2002) and give evidence that as omnivores they may not impose direct and intensive trophic pressures upon adjacent trophic species in this

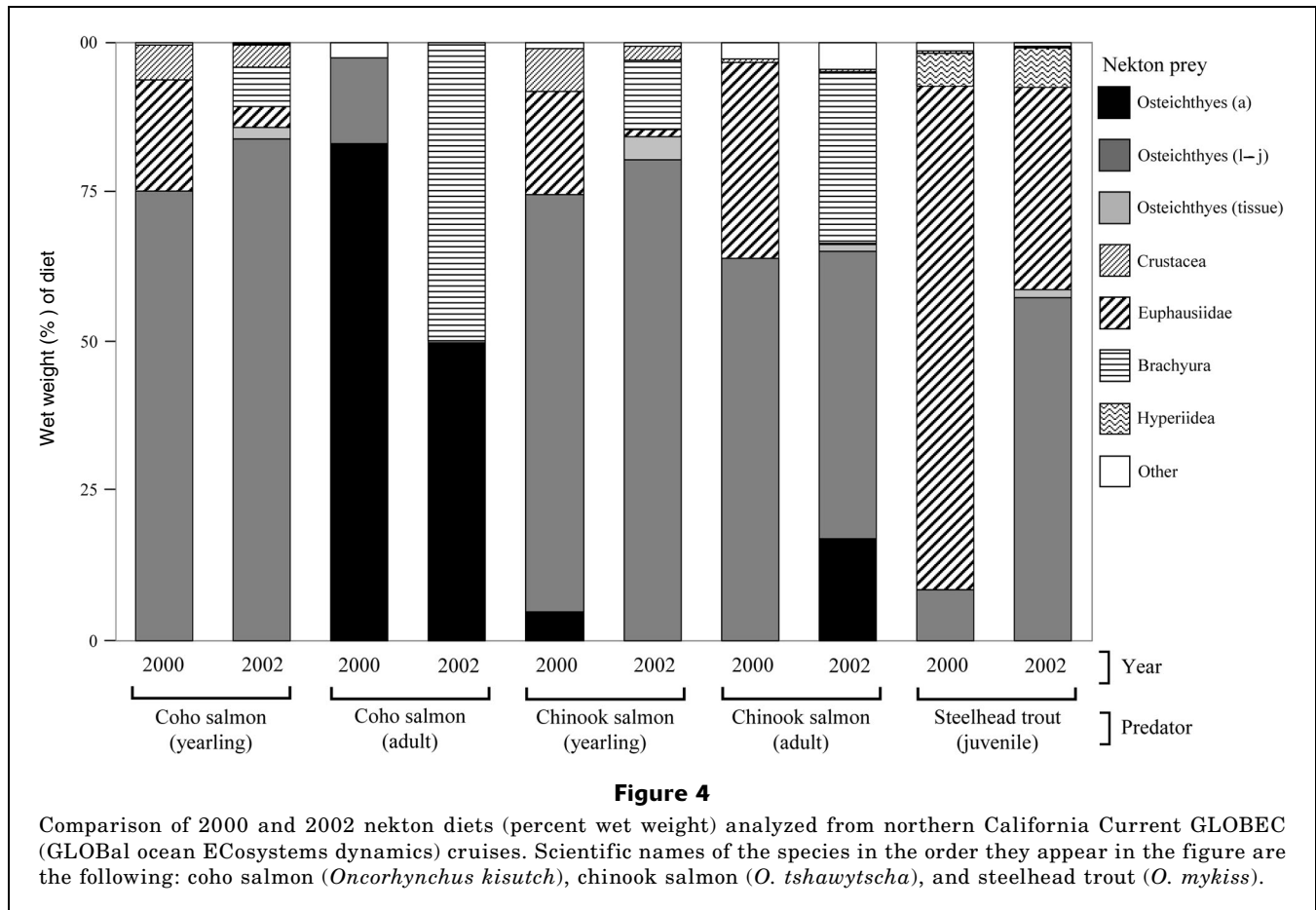
upwelling ecosystem, as would be implied by the classical theory of top-down control.

Euphausiids were also observed as important prey of many middle-trophic-level nekton species. Three trophic groups were evident at this trophic level: 1) a group of species that consumed predominantly larval-juvenile fish and to a lesser degree euphausiids, 2) a group of species that consumed mostly euphausiids, and 3) a group of

Table 3

Percent similarity index (PSI) of diets of nekton species collected from the northern California Current during June and August 2002 GLOBEC cruises. Trophic groups were derived from agglomerative hierarchical cluster analysis (AHCA) of percent wet weight of diet. Blocked PSI values denote within-trophic group comparisons. PSI values >60% are shown in bold. Life history stages of nekton are shown in parentheses and represent juvenile (j), yearling (y), and adult (a); nekton with no indication of life history stage are adult.

Trophic group	Nekton species	<i>Prionace glauca</i>	<i>Merluccius productus</i>	<i>Oncorhynchus tshawytscha</i> (a)	<i>O. kisutch</i> (a)	<i>Trachurus symmetricus</i>	<i>Bregalis mordax</i>	<i>Clupea pallasi</i>	<i>Anoplopoma fimbria</i> (j)	<i>Allosmerus elongatus</i>	<i>O. tshawytscha</i> (y)	<i>O. kisutch</i> (y)	<i>O. mykiss</i> (y)	<i>O. keta</i> (j)	<i>Loligo opalescens</i>	<i>Ammodytes hexapterus</i>	<i>Hypomesus pretiosus</i>	<i>Squalus acanthias</i>	<i>Sardinops sagax</i>	<i>Sebastes entomelas</i> (j)	<i>Cololabis saira</i>	
A	<i>Prionace glauca</i>	X																				
	<i>Merluccius productus</i>	67	X																			
	<i>Oncorhynchus tshawytscha</i> (a)	41	62	X																		
	<i>O. kisutch</i> (a)	30	33	41	X																	
B	<i>Trachurus symmetricus</i>	1	26	27	8	X																
	<i>Engraulis mordax</i>	0	30	31	2	33	X															
	<i>Clupea pallasi</i>	1	33	34	6	49	63	X														
	<i>Anoplopoma fimbria</i> (j)	0	32	34	10	39	61	76	X													
	<i>Allosmerus elongatus</i>	0	26	33	6	28	43	62	58	X												
	<i>O. tshawytscha</i> (y)	0	41	35	5	38	24	40	28	34	X											
C	<i>O. kisutch</i> (y)	1	27	78	27	37	34	44	38	28	78	X										
	<i>O. mykiss</i> (j)	0	31	53	5	39	38	49	40	36	54	74	X									
	<i>O. keta</i> (j)	0	4	34	4	15	9	19	9	19	71	57	45	X								
	<i>Loligo opalescens</i>	1	5	7	2	7	4	8	4	13	8	7	3	9	X							
D	<i>Ammodytes hexapterus</i>	0	14	19	5	12	33	44	30	38	19	27	21	10	6	X						
	<i>Hypomesus pretiosus</i>	0	7	14	6	13	13	29	10	24	15	19	11	21	15	50	X					
	<i>Squalus acanthias</i>	0	4	8	1	8	7	9	6	8	7	11	6	7	3	3	8	X				
	<i>Sardinops sagax</i>	0	10	16	4	14	51	26	12	16	16	17	15	14	5	26	21	8	X			
E	<i>Sebastes entomelas</i> (j)	0	3	19	2	13	11	17	9	13	19	18	18	21	3	17	18	4	49	X		
	<i>Cololabis saira</i>	0	3	16	6	16	11	17	10	15	13	19	16	18	3	15	18	5	17	23	X	



Feeding by many nekton directly on phytophagous euphausiids results in more direct food webs and fewer trophic levels, and concomitant increases in food-web efficiency. Observations by Brodeur and Pearcy (1992) and by the authors of the present study thus indicate that trophic characteristics of the NCC system may have periods of high production when euphausiids are consumed across many trophic levels. Additional research of trophic relationships between dominant nekton and zooplankton within the NCC at varying levels of production would further clarify whether this pattern is an important characteristic of this ecosystem.

Interannual variation

Limited interannual variation in diets was observed; only juvenile steelhead trout and adult coho salmon expressed major differences between 2000 and 2002. Other nekton, particularly yearling coho and chinook salmon, showed relatively little variation in diet; only euphausiids and brachyuran larvae (which represent a small portion of nekton diet in general) varied most between the two years. Whether this variability was an artifact of sampling is uncertain; however, it is interesting to note that the higher prevalence of euphausiids in the 2000 diets and the higher prevalence of brachyuran

larvae in 2002 diets indicated that variation between the two years may have been a result of the relative abundance of these prey. Other studies from the NCC have also indicated high temporal variation in zooplankton (Mackas et al., 2001, 2004) and in the diets of Pacific hake (Emmett and Krutzikowsky, in press) and juvenile salmonids (Brodeur and Pearcy, 1990). Although both 2000 and 2002 were years of high upwelling and high production, substantial interannual variability in the hydrographic environment was observed. During the summer of 2002, an intrusion of cold, nutrient-rich, subarctic bottom water resided on the Oregon shelf, resulting in high phytoplankton production in surface waters and in hypoxic conditions near the bottom (Thomas et al., 2003; Wheeler et al., 2003). Although it is possible that this nutrient-rich water may have influenced the prey field available to the different predators, no discernible effect on their diet was observed in our study.

The temporal variability in nekton diets reveals an important characteristic of the NCC system in that this variability reflects the duration of trophic interactions between predator and prey in relation to population-scale parameters. If variability in the time scale of trophic links is short compared to nekton population dynamics, then more short-lived species (such as market squid) or those exhibiting a critical ontogenetic

shift (such as juvenile salmonids) will be more influenced by interannual variability in the availability and quality of prey. Species exhibiting extensive feeding migrations through the NCC system, such as Pacific hake and Pacific sardine, may be less influenced by localized prey limitation because critical feeding for recruitment success can occur in other regions with different physical and biological parameters.

Interannual and interdecadal comparisons of species distribution and community structure of pelagic nekton have demonstrated that the northern California Current ecosystem can vary between months and years (Brodeur et al., 2005). As fishery management shifts away from single-species towards multispecies or ecosystem-based fishery management (Pikitch et al., 2004), detailed information on the trophic interactions within this pelagic ecosystem as presented here will become indispensable for development of management plans and ecosystem models. Further analysis of the relationships between major nekton and their prey is warranted to elucidate differences in trophic relationships between major upwelling regions, especially those that are influenced by strong climatic variability.

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