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# Constancy and change in marine predator diets across a shift in oceanographic conditions in the Northern California Current

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**Abstract** Variable ocean conditions can greatly impact prey assemblages and predator foraging in marine ecosystems. Our goal was to better understand how a change in ocean conditions influenced dietary niche overlap among a suite of midtrophic-level predators. We examined the diets of three fishes and one seabird off central Oregon during two boreal summer upwelling periods with contrasting El Niño (2010) and La Niña (2011) conditions. We found greater niche specialization during El Niño and increased niche overlap during La Niña in both the nekton and micronekton diet components, especially in the larger, more offshore predators. However, only the two smaller, more nearshore predators exhibited interannual variation in diet composition. Concurrent trawl surveys confirmed that changes in components of predator diets reflected changes

in the prey community. Using multiple predators across diverse taxa and life histories provided a comprehensive understanding of food-web dynamics during changing ocean conditions.

## Introduction

Although ecological theory predicts that predators would have specialized foraging strategies to avoid direct competition with one another when food resources are limited (Schoener 1971; Greene 1986), many marine predators are generalists at the population level and take advantage of a wide variety of available prey resources (Closs et al. 1999; Link 2002). Depending on the level of interspecific versus intraspecific competition, a predator might exhibit generalist foraging behavior at the population scale driven by diet specialization at the individual level. Neither trophic niche nor diet specialization is constant through time, but rather responds to changes in prey abundance and levels

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of competition for resources (Steenhof and Kochert 1988; Holbrook and Schmitt 1989; James 1991; Hunsicker et al. 2011). For example, when an individual prey type has a particularly abundant year class, many predators can take advantage of this available food resource, thereby increasing, at least short-term (monthly to yearly) niche overlap (Smith et al. 1978; Schoener 1982). Studies of seabirds and marine mammals have found greater niche overlap among species when prey resources were more abundant and greater niche partitioning when food was scarce (Ainley and Boekelheide 1990; Tinker et al. 2008; Barger and Kitaysky 2012). Likewise, there are numerous examples in marine fish communities of similar shifts in niche overlap with seasonal and interannual changes in prey abundance (Thorman 1982; Brodeur and Pearcy 1992; Feyrer et al. 2003). Understanding the drivers of this variation can provide key insights into trends in productivity and allow managers to better anticipate effects of future environmental change on trophic interactions. While changes in niche overlap have been studied across seabird and marine fish species separately, none of the studies conducted in the California Current have examined both to determine whether shifts in niche overlap occur across diverse taxa.

Large numbers of mobile marine predators share the productive waters of the Northern California Current off Oregon (Batchelder et al. 2005; Block et al. 2011). This is especially true during the summer months when nesting seabirds and predatory fish migrate into the Northern California Current to take advantage of the seasonally abundant food resources, fueled by seasonal wind-driven upwelling (Ainley et al. 2005; Emmett et al. 2006). Although marine predators have large areas available for foraging activities, their prey are often patchily distributed due to physical processes which may aggregate grazers and planktivores (Mann and Lazier 2006; Ainley et al. 2009; Santora et al. 2011). Therefore, many middle and upper trophic-level taxa often exploit resources in the same core areas of enhanced prey availability, temporarily increasing niche overlap (Reese and Brodeur 2006; Ainley et al. 2009). Marine food-web studies in the Northern California Current have indeed found that despite indications of food limitation and predicted competition for limited food resources across predator species, niche partitioning is not constant through time. Instead, trophic interactions, diet, and niche overlap differ among years of varying environmental conditions in the marine bird community and across a wide variety of predatory fishes (Ainley and Boekelheide 1990; Brodeur and Pearcy 1992; Emmett et al. 2006; Miller and Brodeur 2007).

Gaining insight into predator niche overlap and conditions under which niche partitioning might occur is essential for understanding coastal marine ecosystem dynamics and informing ecosystem-based management. Effective

fisheries management requires a clearer understanding of the trophic relationships of commercially important fishes and their shifting interconnections with nontarget species such as seabirds and forage fishes to predict future population levels of ecologically and economically important stocks. Including diet variability in ecosystem modeling and ecosystem-based management efforts has led to more realistic models with ever-increasing relevance to managers (Field et al. 2006; Brand et al. 2007; Ruzicka et al. 2012).

In this study, we aimed to elucidate the trophic relationships and dietary overlap among a suite of marine predators in the Northern California Current during 2 years of contrasting environmental conditions. Adult black rockfish (*Sebastes melanops*), Chinook salmon (*Oncorhynchus tshawytscha*), and Pacific halibut (*Hippoglossus stenolepis*) were selected because historical data indicated dietary overlap, especially in their consumption of small, pelagic schooling fishes even though they represent a range of body sizes, foraging tactics, selectivity in their food habits and cross-shelf distribution (Brodeur and Pearcy 1992; Dufault et al. 2009). Furthermore, these species could be obtained with relative ease and low cost through collaborations with the local commercial and recreational fisheries. A piscivorous seabird, the common murre (*Uria aalge*), was included as an additional species known to consume forage fish to examine cross-taxa dietary overlap of middle to upper trophic-level consumers. Important prey for murre varies throughout their range, with birds in the Northern California Current relying on a variety of forage fishes during the breeding season (Parrish and Zador 2003; Schrimpf et al. 2012) that overlap with the diets of fish predators, including salmon and halibut (Roseneau and Byrd 1997; Mills et al. 2007). Concurrent trawl surveys within our study area, part of a larger coast-wide effort, provided data on the relative availability of select prey species.

Contrasting basin-scale oceanographic conditions during two consecutive years (2010 and 2011) provided an opportunity to characterize individual predator diet responses, and corresponding changes in dietary overlap among predators, to varying environmental conditions. Moderate El Niño conditions preceded sampling in 2010. Although there was an abrupt physical shift to La Niña conditions in June 2010, the biological conditions did not transition from El Niño conditions as rapidly (Bjorkstedt et al. 2011). A southern (warm water) copepod community, typical of El Niño conditions, dominated the region well through the summer months, despite some of the coldest water temperatures on record and anomalously strong summer upwelling before shifting toward a more boreal community later in the summer and early fall (Bjorkstedt et al. 2011). Southern copepods generally have smaller body sizes and lower lipid content, while larger body sizes

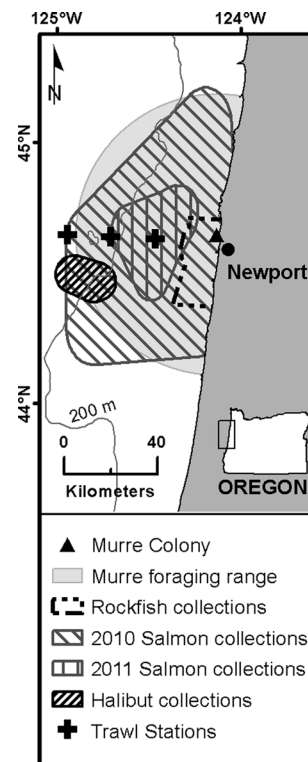
and higher lipid content are found in copepods typical of the boreal community, which in turn have major implications for energy acquisition of middle and upper trophic-level predators (Peterson et al. 2002). La Niña conditions persisted through the winter months between our sampling seasons and extended through the second summer of sampling in 2011. While the El Niño/La Niña conditions were not as strongly contrasting as some previous transitions (e.g., 1998/1999), this 2-year window provided an opportunity to examine short-term responses to a shift in environmental conditions.

Therefore, we hypothesized that predator diets would differ between years and there would be greater niche specialization among predators under “poor” El Niño foraging conditions when opportunistic predators are forced to show more specialized foraging to find alternative prey (Ainley and Boekelheide 1990; Brodeur and Pearcy 1992; Barger and Kitaysky 2012). In contrast, we expected higher concordance among predatory fish and seabird diets in years of higher prey abundance whereby predator populations could concurrently take advantage of strong year classes of key prey (Brodeur and Pearcy 1992; Barger and Kitaysky 2012). This would be expected under La Niña conditions that often favor recruitment of winter-spawning forage fishes and are associated with enhanced energy transfer to higher trophic levels. Within these broad hypotheses, we expected that those predators with more spatial overlap in their foraging locations and more overlap in prey size ranges might exhibit stronger changes in niche overlap between the 2 years of our study.

## Methods

### Sample collection: trawl surveys

Midwater trawls were used to sample micronekton, including juvenile fishes and many invertebrate taxa, monthly from June to August of 2010 and 2011 along a cross-shelf transect off Yaquina Head, Newport, Oregon (44.65°N). Trawling was conducted at stations 27, 46, and 64 km offshore (Fig. 1) during each month. A Nordic 264-rope trawl was towed for 15–30 min with the head-rope at a target depth of 30 m. The effective fishing mouth of the Nordic 264-rope trawl was 12 m high and 28 m wide (336 m<sup>2</sup>), with a 6.1-m long, 3-mm stretched knotless web liner in the cod end. All trawls were conducted at night. The catches were frozen at sea and later thawed and sorted in the laboratory. Species densities were calculated by multiplying the towed distance (as determined by a flowmeter) by the mouth opening of the net. For additional details on the collection methodology, see Phillips et al. (2007).



**Fig. 1** Map of study area showing foraging range of murres and general collection areas for fishes. Trawl survey stations (*plus sign*), the Yaquina Head murre colony site (*triangle*), and the town of Newport (*circle*). The 200-m continental shelf break isobath is shown

### Focal predator species

Chinook salmon, a medium-to-large-bodied predator (maximum total length 1.5 m, Froese and Pauly 2013), actively pursues patchily distributed prey and relies heavily on schooling pelagic micronekton, especially clupeids and euphausiids during its ocean residence (Healey 1991). The Pacific halibut is a medium-to-large (maximum total length 2.58 m, Froese and Pauly 2013), highly mobile, opportunistic generalist that preys on midwater gadids such as hake and pollock, smaller flatfishes, small pelagic fishes, and a wide variety of benthic invertebrates (Best and St-Pierre 1986; Yang and Nelson 1999). Black rockfish are a medium-bodied (maximum total length 0.63 m, Froese and Pauly 2013), schooling pelagic rockfish associated with nearshore rocky reef habitats and known to prey on small schooling fishes and zooplankton (Steiner 1978).

### Sample collection: fish diets

Fish diets were obtained through collaborative sampling with commercial and recreational fishermen operating from Newport, Oregon. Chinook salmon, black rockfish, and Pacific halibut stomach samples were collected from May

1 to August 31 of 2010 and 2011. Commercial fishermen collected and returned whole stomachs of Chinook salmon and recorded the approximate weight, length, date, and catch location. Whole stomachs of black rockfish, Pacific halibut, and some Chinook salmon were collected at port from recreational fishermen. Fish length and an exact catch location or fishing area (within ~5 km) were recorded. Chinook salmon stomachs were collected at 1–2-week intervals. Black rockfish stomachs were collected on 2–5 days per week, and Pacific halibut stomachs were obtained during 3-day all-depth recreational fishing openings during May, June, and August in both years. Fishing effort for all three fish predators occurred within approximately 60 km of Newport (Fig. 1).

Stomach contents were identified to the lowest taxonomic level possible and enumerated. Once sorted, prey items were set on blotting paper briefly to remove excess water and then a damp mass was taken. With the exception of black rockfish samples from May to July of 2010, we took a length measurement from a subsample of each prey type. When soft tissue was too digested to identify, hard parts such as bones and otoliths were used to identify the prey species using a photographic reference collection, the Northwest Fisheries Science Center (NWFSC) Bone Identification Reference Database (J. Zamon, National Oceanic and Atmospheric Administration, NWFSC, Hammond, OR, unpublished data). Prey that were digested and identified only to a higher taxonomic level (i.e., fish or crustacean) were excluded from statistical analyses.

#### Sample collection: avian diets

Common murre chick-rearing diets were obtained observationally using digital photographs of chick feeding events (Larson and Craig 2006) at the Yaquina Head breeding colony located at Newport, Oregon. We used a Canon EOS T2i digital SLR camera with a 50-mm lens attached to a Swarovski 20–60 × 80 mm STM spotting scope. The photographer was 95–105 m from the birds holding fish. Photographs were taken of adult murrets returning to the colony with a single prey item between the hours of 0630–1800, 2–5 days per week during the chick-rearing period, 27 June–9 August 2010 and 2011. Photographs were examined, and prey were identified to the lowest taxonomic level possible. Although the exact foraging locations of adult murrets could not be ascertained, breeding murrets are central place foragers with known foraging distances ( $\leq$ ~60 km) and diving depths ( $\leq$ ~150 m) (Ainley et al. 1996; Hatch et al. 2000; Oedekoven et al. 2001; Hedd et al. 2009) that overlap the geographic (Fig. 1) and depth habitats of the fish predators in this study. Several prey species with similar appearance were difficult to identify in murre diet samples, and thus, prey were combined into more

general taxonomic groups to allow comparison between fish and bird predators (Supplemental materials, table S1). It is possible that our sampling method precluded detecting very small prey, but observations at another colony in the Northern California Current found similar prey size ranges (Schrimpf et al. 2012). Only prey species identified to the family level or lower were retained for analysis.

#### Data screening and transformation

The chick-feeding strategy of common murrets precludes the possibility of any chick-feeding event containing more than one prey species, whereas a fish predator stomach might contain a large number of species, including invertebrates. Although murrets may occasionally deliver small invertebrates such as euphausiids to chicks (Ainley et al. 1996), we were unable to detect such prey because of observers' distance (~100 m) from the colony. Given these two different data collection methods, we aggregated the data using different methods to allow for comparisons among the diets of all predators, fish predators only, and between the 2 years of the study within a single predator's diet. The diets of fish and avian predators were compared using only the nektonic (teleost and cephalopod) components of the diet (nekton prey dataset), while the fish predators were compared using the entire diet (complete dataset). We compared the diets of single predators between the 2 sampling years using the complete dataset for fish predators and nekton prey dataset for the murrets.

We combined prey count data into ecologically relevant taxonomic categories for analysis; ten prey categories were used for the nekton dataset including all predators, and fourteen prey categories were used in the complete dataset to compare diets of fish predators (Supplemental materials, table S1). Combining prey into more general taxonomic categories alleviated concerns about the potential of missing rare species because of relatively low sample sizes for some predators.

We used percent number of prey consumed for statistical analysis for several reasons. We used an observational approach to determine murre diets and were unable to obtain measurements of prey biomass. Therefore, number of prey consumed was the only metric common across all predators. We examined diet composition based on both biomass and number consumed for predators where these metrics could be calculated (Supplemental Materials, figs. S2, S3, S4). Overall, results based on biomass were similar to those based on number consumed except for salmon, whose diet was a mix of invertebrates, which were highly numerous but of low mass, and fish prey, which were observed in lower numbers but had much higher mass per prey item.

For each level of multivariate analysis (all predators combined, fish predators only, and between year



comparison of single predators), prey groups which occurred in  $\leq 5$  % of the sample units were omitted, following the recommendations of McCune and Grace (2002). Omitting rare species allows for better detection of overall community structure by reducing the noise in the dataset without sacrificing much information (McCune and Grace 2002). We summed the counts of prey species in each stomach or bill load collected during each week and then divided by total count across all prey categories such that each value in the matrix ranged from zero to 1 (% number consumed). We then transformed these data using the arcsine square root transformation to reduce skewness and kurtosis, as appropriate for proportional data (McCune and Grace 2002). No outliers were detected using Sørensen distance, but we observed that sample units with the greatest distances were samples composed of only a single stomach. We felt that these samples may not be comparable to weeks in which many stomachs were collected and so we chose to exclude all instances of sample units composed of only a single stomach. Thus, two samples were excluded from the complete dataset analysis and two from the nekton only analysis.

#### Statistical analysis

We employed a multivariate ordination technique, non-metric multidimensional scaling (nMDS, Kruskal 1964; Mather 1976), to reduce the dimensionality of the prey data and allow for a visual representation of prey community structure among the different predator diets. Each ordination figure shown was conducted as a separate analysis. The points in ordination figures represent sample units and are plotted in prey category space. We applied a rigid rotation (Varimax), of the ordination such that the first axis represented the greatest portion of the variance, and that the second axis represented the second greatest portion of the variance (Mather 1976). We evaluated the dimensionality of ordinations using a scree plot of real data in relation to randomized data and by the evaluation of stress versus dimensionality of randomized Monte Carlo simulations. The stability of the ordination was evaluated using the final instability of the two-dimensional solutions against the  $10^{-4}$  value recommended by McCune and Grace (2002). Sørensen (Bray–Curtis) distance was used for all ordinations, and we employed a random starting configuration with 50 runs using real data, with up to 200 iterations per run, except for the 2011 nekton dataset for which we conducted 500 runs using real data, and up to 500 iterations per run. We evaluated the usefulness of the ordination in describing patterns in the original data by examining the stress, and conducting post hoc regressions of the distances between sample units in the ordination against distances between sample units in the original diet data. The

post hoc regression of distances between sample units in the ordination versus the original diet dataset provided a measure of variance (i.e., an  $R^2$  value) in the original diet data explained by the ordination. We also conducted post hoc correlations between nMDS scores and mean predator and prey lengths to help inform our interpretation of the ordinations. In the case of murre, we were unable to measure individuals in our study. But birds exhibit determinate growth; therefore, we used a length of 405 mm drawn from the literature (Ainley et al. 2002).

We used nonparametric, multi-response permutation procedure (MRPP) to test the null hypothesis of no significant difference in percent number of prey consumed among predators and years (Mielke and Berry 2001). We compared each individual predator's diet between years (i.e., black rockfish diets in 2010 vs. black rockfish diets in 2011). As separate analyses, we compared fish predators' diets for each year (i.e., black rockfish vs. Chinook salmon vs. Pacific halibut diets in 2010), and the nekton components of all predators diets in each year (i.e., black rockfish vs. Chinook salmon vs. common murre vs. Pacific halibut in 2010). For the multipredator comparisons, we conducted global MRPP tests as well as pairwise tests between individual predators. For all MRPP analyses, we used Sørensen distance to compare the similarity of sample units within a priori groups to the similarity of sample units across groups. MRPP assesses within- and between-group differences with a chance-corrected within-group agreement ( $A$ -value) which ranges from  $-1$  to  $1$ . An  $A$ -value of zero signifies that the agreement of sample units within a group is equal to that which would be expected by chance, while positive or negative  $A$ -values, respectively, indicate greater or lesser similarity within a group than among groups than would be expected by chance. In ecological studies, it is common to have  $A$ -values of  $<0.1$  that are significant and values of  $0.3$  or greater are considered high (McCune and Mefford 2011).

We conducted indicator species analysis on several different levels of our data to identify prey categories that may have driven differences in the diets between years (interannual variation in single predator's diets) and among predator species (dietary overlap of fish predators and dietary overlap of nekton component of all predators) (Dufrene and Legendre 1997). Indicator values (IVs) can assist in identifying prey categories that are important for a single group, but less important for other groups in the analysis. IVs are the product of the relative number consumed and relative frequency of a prey category within a group. Therefore, IVs capture both the exclusivity and constancy of a prey category within a group. Examples of groups we examined included a study year for a single predator's diet and an individual predator's diet when examining multiple predator diets in a single year. An IV can range from  $0$  to

100, with 100 indicating that the prey category was found in every sample for that predator and not found in any other predator's diet. The significance of the IV for each prey category was tested using 4999 Monte Carlo simulations. All multivariate statistical analyses were conducted using PC-ORD v. 6.0 (McCune and Mefford 2011) and the vegan package v. 2.0-7 in R v. 2.14.1 (Okansen et al. 2013; R Development Core Team 2013).

## Results

### Interannual differences in trawl survey catches

We observed order of magnitude differences in the density of some prey species between the 2 years, suggesting that the prey community available to predators changed during the course of our study. Juvenile rockfishes and shrimp were one to two orders of magnitude more abundant in the trawl surveys in 2010 than 2011 ( $943.8 \times 10^6 \text{ m}^{-3}$  vs.  $90.4 \times 10^6 \text{ m}^{-3}$ , Table 1). Shrimp densities were nearly two orders of magnitude greater in 2010 than in 2011 ( $166.1 \times 10^6 \text{ m}^{-3}$  vs.  $2.5 \times 10^6 \text{ m}^{-3}$ , Table 1). In contrast, krill, a pelagic pteropod, cancrid crab larvae, and other crab larvae were substantially less abundant in 2010 compared with 2011. In 2010, krill were a third the density observed in 2011, while cancrid crab larvae and *Limacina helicina* were an order of magnitude less abundant (Table 1). The difference in density of other crab larvae was also striking, as this prey category was not observed in 2010 but found at densities of  $466.1 \times 10^6 \text{ m}^{-3}$  in 2011.

### Interannual differences in individual predator diets

The number of adult Chinook salmon stomachs obtained with identifiable prey numbered 66 in 2010 and 29 in 2011. In 2010 and 2011, 23.2 and 14.7 %, respectively, of salmon stomachs were empty. We obtained 230 rockfish stomachs with identifiable prey in 2010 and 258 in 2011. In 2011, 13.7 % of rockfish stomachs were empty (empty rockfish stomachs were not enumerated in 2010). In 2010, 49.2 % of halibut stomachs collected were empty, leaving 62 halibut stomachs with identifiable prey. In 2011, 43.4 % of halibut stomachs were empty and 138 stomachs had identifiable prey. For murre diets, we were able to obtain diet information for 585 identifiable bill loads in 2010 and 304 in 2011. Sample sizes were low for halibut in 2010 and Chinook in 2011, and it is possible that some rare prey were not detected in our sampling. We examined rarefaction curves for the diet of each predator using the lowest taxonomic identification of prey items (Supplemental materials, figure S1). Curves for halibut in both years and Chinook in 2011 did not appear to approach an asymptote, which

suggested that our samples may not have been sufficient to characterize the full prey spectrum that these predators consume. Rarefaction curves for black rockfish diets more closely approached an asymptote in both years, suggesting that our sampling captured the diversity of rockfish prey adequately. There were weak but significant differences in percent numbers of portions of the prey community for rockfish, salmon, and halibut combined between the 2 years (MRPP,  $A = 0.027$ ,  $P = 0.016$ ) and for the nekton community of all predators combined between the 2 years (MRPP,  $A = 0.034$ ,  $P = 0.00017$ ). Therefore, some components of the prey consumed by multiple predators differed between years.

Rockfish diets (55 taxa) differed in prey consumed between 2010 and 2011 (MRPP,  $A = 0.0465$ ,  $P = 0.006$ ). In both years, black rockfish relied primarily on seasonally abundant larval invertebrates, such as cancrid crab megalopae, and juvenile and adult stages of pandalid shrimp and crangonid shrimp, as well as adult mysids. Black rockfish consumed twice as many mysids in 2010 than they did in 2011 (47.7 % in 2010 vs. 23.0 % in 2011, Table 1). In 2011, the proportion of crab larvae increased, with cancer and other crab larvae combined categories comprising 59.4 % of black rockfish diets, while in 2010, those two categories comprised only 37.1 % of the diet (Table 1). Pacific sand lance (*Ammodytes hexapterus*,  $IV = 48.7$ ,  $P = 0.002$ ,) was identified as key indicator prey for black rockfish 2010, while a pelagic pteropod (*L. helicina*,  $IV = 35.3$ ,  $P = 0.002$ ), krill ( $IV = 72.9$ ,  $P = 0.002$ , 98.4 % *Thysanoessa spinifera*), and other crab larvae ( $IV = 66.2$ ,  $P = 0.002$ , 48.3 % Paguridae, 27.7 % Grapsidae) were significant indicator prey categories for 2011.

Salmon diets (17 taxa) did not differ between years (MRPP,  $A = 0.024$ ,  $P = 0.168$ ) and we found no significant indicator prey species. Krill were very important prey in both years, comprising over half the diet (Table 1, 41.9 % *T. spinifera* and 58.1 % *Euphausia pacifica* in 2010, 36.9 % *T. spinifera* and 63.1 % *E. pacifica* in 2011). Cancrid crab megalopae and clupeids (85.3 % Pacific herring *Clupea pallasii*, 13.3 % Pacific sardine *Sardinops sagax*, and 1.3 % American shad *Alosa sapidissima*) were found in higher numbers in 2010 compared to 2011. While invertebrates dominated the diet numerically, clupeids and Pacific hake (*Merluccius productus*) formed an important contribution in terms of biomass in both years, as expected since salmon consumed a combination of small invertebrates and larger fish prey (Fig. S4).

Pacific halibut (37 taxa) did not differ between years (MRPP,  $A = -0.019$ ,  $P = 0.632$ ) and showed more exclusive piscivory than the other predatory fish species examined (>85 % fish; Table 1). Pacific hake was the most common prey, comprising nearly half the diet in both years. Demersal flatfishes were also important in halibut diets,

**Table 1** Predator diets and trawl survey observations summarized in broad taxonomic categories

	Black rockfish		Chinook salmon		Pacific halibut		Common murre		Trawl surveys	
	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011
	% Number consumed								Number × 106 m <sup>-3</sup> (SE)	
Small zooplankton (Amphipoda, Cumacea, Isopoda)	3.4	6.9	–	0.4	–	–	–	–	63.4 (12.6)	410.4 (126.9)
Krill (Euphausiidae)	0.3	2.8	50.7	54.6	–	–	–	–	84,505.0 (9,022.6)	215,371.4 (56,926.6)
Pelagic pteropod ( <i>Limacina helicina</i> )	–	3.2	–	–	–	–	–	–	87.6 (52.1)	796.0 (206.2)
Mysids (Mysidacea)	47.7	23.0	–	9.2	–	–	–	–	–	–
Cancer crabs ( <i>Cancer spp.</i> )	34.7	43.0	21.7	8.4	–	3.7	–	–	20.6 (4.3)	298.8 (11.6)
Other crab larvae (Porcellanidae, Paguridae, Diogenidae, Pinnotheridae, Grapsidae)	2.4	16.4	–	–	–	–	–	–	–	466.1 (45.4)
Shrimps (Caridea)	10.5	4.1	–	–	0.9	1.1	–	–	166.1 (77.9)	2.5 (0.3)
Squid and octopus (Cephalopoda)	<0.1	–	1.8	0.4	2.7	6.9	0.7	3.3	6.7 (1.8)	7.8 (17.4)
Herring, sardine, shad (Clupeidae)	<0.1	–	10.0	3.8	23.6	11.7	7.0	12.7	–	2.2 (0.2)
Salmon ( <i>Oncorhynchus spp.</i> )	–	–	–	–	–	–	0.2	2.0	–	–
Smelts (Osmeridae)	–	0.3	2.7	12.6	–	–	71.8	35.8	–	–
Hake and cods (Gadiformes)	–	<0.1	2.6	3.8	49.1	45.3	0.9	0.7	31.5 (2.2)	–
Rockfishes ( <i>Sebastes spp.</i> )	<0.1	0.1	6.2	3.4	4.55 <sup>b</sup>	9.9	12.7	1.0	943.8 (138.2)	90.4 (25.9)
Pacific sand lance ( <i>Ammodytes hexapterus</i> )	0.4	<0.1	2.1	1.3	–	–	2.7	16.3	–	–
Flatfishes (Pleuronectiformes)	0.2	<0.1	–	1.7	18.2	19.7	1.9	23.1	67.4 (7.2)	28.4 (2.1)
Other fishes (Cottidae, Liparidae, Hexagrammidae, Engraulidae, Agonidae, Chimaeridae, Petromyzontidae)	<0.1	0.2	2.1	0.4	0.9	1.8	2.2	5.2	296.0 (101.6)	83.2 (38.2)
<i>n</i>	230	258	62	28 <sup>a</sup>	62	138	585	304	12	14
Predator length (cm)	TL		FL		TL					
Minimum	28.6	24.3	66	68	72.4	66	–	–	–	–
Median	40.5	38.8	80	79	88.9	90	–	–	–	–
Maximum	60	50.2	97	98	147	128.5	–	–	–	–

Predator diets shown as percent number consumed (%), which is the count of the individuals in a prey category divided by the total number of individual in a predator's diet in a single year. Trawl survey data shown as number per 106 m<sup>3</sup> towed, with standard errors shown in parentheses. Dash signifies not observed. Sample size (*n*) refers to stomachs containing identifiable prey, identifiable murre bill loads, or tows

<sup>a</sup> One outlier sample was excluded from these unstandardized data, but was retained in the statistical analyses

<sup>b</sup> Pacific halibut consumed rockfish with a mean length of 216 mm, while smaller rockfish with a mean length ranging from 44 to 80 mm were found in other predator diets

along with more pelagic clupeids (54.2 % Pacific herring, 38.9 % Pacific sardine, 1.7 % American shad, and 5 % unidentified clupeid). The proportion of clupeids in halibut diets was higher in 2010 compared to 2011 (23.6 % vs. 11.7 %).

The diets of common murre (12 taxa) contained prey generally found close to shore, including smelts and flatfishes (Pleuronectiformes), as well as more widely ranging schooling coastal pelagic species such as Pacific sand lance (juveniles), Pacific herring, Pacific sardines, and northern anchovies (*Engraulis mordax*; Table 1). Common murre diets differed between 2010 and 2011 (MRPP,  $A = 0.175$ ,  $P = 0.0007$ ). Clupeids and smelts were important prey in both years, but smelts were consumed in much higher

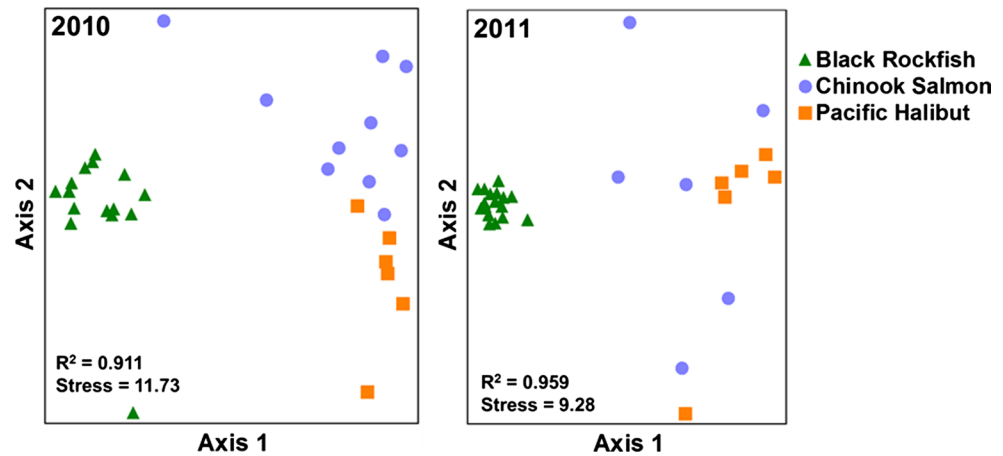
proportions in 2010 compared with 2011 (2010: 71.79 % vs. 2011: 35.83 %, Table 1). Smelts were identified as a significant indicator prey in 2010 (IV = 61.9,  $P = 0.007$ , whereas Pacific sand lance (IV = 72.5,  $P = 0.003$ ) flatfishes (IV = 79.1,  $P = 0.001$ ) and other fishes (IV = 63.1,  $P = 0.049$ ) were identified as significant indicator prey for 2011. Although juvenile rockfishes were not a significant indicator (IV = 62.1,  $P = 0.105$ ), they were found in higher proportions in 2010 than 2011.

#### Dietary overlap of fishes

Post hoc regressions of two-dimensional nMDS ordinations of fish predator diets in 2010 and 2011 showed that the



**Fig. 2** Nonmetric multidimensional scaling ordinations of percent number of prey consumed for fish predators in 2010 and 2011. The ordination for 2010 was conducted separately from the ordination for 2011. Each point represents the diet for a single predator collected during a single calendar week. All identifiable prey were included in these analyses. The coordinates of some sample units in these ordinations are the same, such that they are not visibly separated



ordinations explained 91.1 and 95.9 % of the variance in the original diet data, respectively. The final stress of these two ordinations (2010 = 11.73; 2011 = 9.28) suggested that they provided meaningful representation of the original data (Clarke 1993; McCune and Grace 2002). These ordinations revealed similar general patterns, but some differences were observed in dietary overlap between the 2 years (Fig. 2). Because of the varimax rotation, axis 1 captured the majority amount of the variance in the original diet matrix (2010:  $R^2 = 0.663$ ; 2011:  $R^2 = 0.777$ ), whereas axis 2 accounted for a relatively small portion of the variance (2010:  $R^2 = 0.249$ ; 2011:  $R^2 = 0.182$ ). In both years, axis 1 was strongly positively correlated with both predator length (2010:  $R = 0.811$ ; 2011:  $R = 0.975$ ) and prey length (2010:  $R = 0.805$ ; 2011:  $R = 0.800$ ). As expected, these two variables were also strongly correlated with one another (2010:  $R = 0.743$ ; 2011:  $R = 0.890$ ). Positions of prey species centroids (not shown) also support this interpretation that axis 1 appeared to capture a gradient in prey sizes from smaller, micronektonic prey to larger nektonic prey. Axis 2 was also correlated with prey length and predator length, although the correlations differed between the 2 years. In 2010, axis 2 was weakly negatively correlated with predator length ( $R = -0.155$ ) and more strongly negatively correlated with prey length ( $R = -0.523$ ). In 2011, axis 2 was weakly positively correlated with predator length ( $R = 0.280$ ) and not correlated with prey length ( $R < 0.001$ ). Black rockfish diet samples ordinated low on axis 1 and near the midpoint of axis 2 in both years, but were more tightly clustered in 2011. Salmon and halibut diets overlapped more in multivariate space in 2011 compared to 2010, consistent with our initial hypothesis of greater dietary overlap during La Niña conditions in 2011.

A comparison of overlap among the three fish predators showed that there were significant differences between individual species' diets in each year (MRPP, 2010:  $A = 0.361$ ,  $P < 0.0001$ , 2011:  $A = 0.396$ ,  $P < 0.0001$ ). Pairwise comparisons of fish predator diets also revealed

**Table 2** Pairwise comparisons of fish predator diets in 2010 and 2011 using multi-response permutation procedure

	Chinook salmon	Pacific halibut
<i>2010</i>		
Black rockfish	<b>0.302</b>	<b>0.369</b>
Chinook salmon		0.150
<i>2011</i>		
Black rockfish	<b>0.306</b>	<b>0.431</b>
Chinook salmon		0.089

All comparisons showed significant ( $P < 0.05$ ) differences between predators. Strong differences ( $A > 0.3$ ) are highlighted in bold

significant differences between predators, although the differences were stronger ( $A > 0.3$ ) between rockfish and the other fish predators than between salmon and halibut (Table 2). Pairwise MRPP results also reinforced our visual interpretation of the ordinations, with an increase in dietary overlap between salmon and halibut in 2011 shown by a lower  $A$ -value compared to 2010 (Table 2).

Indicator prey categories for black rockfish were invertebrate prey, including *Cancer* spp., shrimps, mysids, other crab larvae, and small zooplankton (Table 3). Prey that indicated salmon diets were of intermediate and larger size, including krill in both years, and osmerids and clupeids in 2010. Larger, nektonic prey categories indicated halibut diets, particularly Gadiformes (100 % Pacific hake, when identifiable) during both years, and cephalopods, clupeids, and flatfishes in 2011.

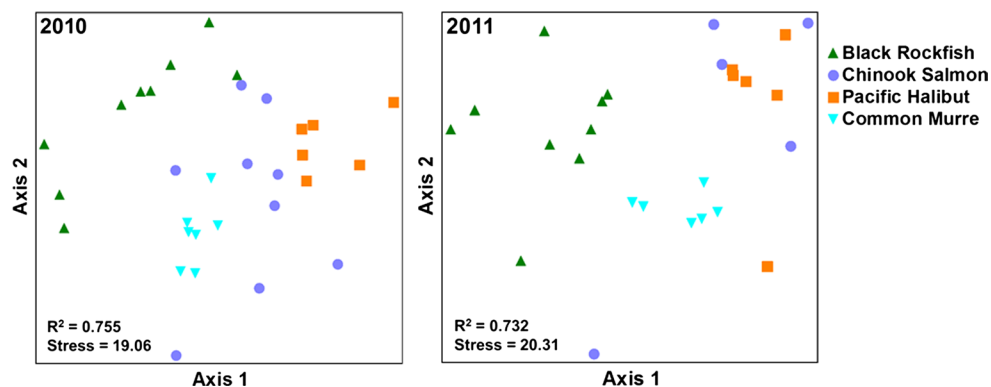
#### Dietary overlap of nekton component of all predators

Ordinations explained 75.5 and 73.2 % of the variance in the diets in 2010 and 2011, respectively, based on post hoc regressions of the distances between points in two-dimensional ordinations of nekton components from predator diets with the distances between points in the original

**Table 3** Indicator values (%) for each prey category in the 2010 and 2011 comparison of fish predator diets

Common name	2010			2011		
	Black rockfish	Chinook salmon	Pacific halibut	Black rockfish	Chinook salmon	Pacific halibut
Small zooplankton	<b>73</b>	0	0	<b>85</b>	2	0
Krill	3	<b>43</b>	0	25	<b>60</b>	0
Mysids	<b>87</b>	0	0	<b>86</b>	2	0
Cancerid crabs	<b>75</b>	8	0	<b>68</b>	7	4
Other crab larvae	7	0	0	<b>76</b>	0	0
Shrimps	<b>93</b>	0	1	<b>87</b>	0	4
Squids and octopus	0	10	14	0	2	<b>72</b>
Herring, sardine and shad	0	<b>56</b>	31	0	29	<b>47</b>
Smelts	0	<b>40</b>	0	1	29	0
Hake and cods	0	5	<b>86</b>	0	25	<b>52</b>
Rockfishes	8	21	24	2	12	37
Pacific sand lance	21	16	0	0	15	0
Flatfishes	4	0	27	2	14	<b>66</b>
Other fishes	5	0	11	<b>48</b>	0	11

Significant indicator values ( $P < 0.05$ ) are shown in bold



**Fig. 3** Nonmetric multidimensional scaling ordinations of percent number of prey consumed for all predators in 2010 and 2011. The ordination for 2010 was conducted separately from the ordination for 2011. Each point represents the diet of a single predator collected

during a single calendar week. Only teleost and cephalopod prey were included in the analyses. The coordinates of some sample units in these ordinations are the same, such that they are not visibly separated

matrices. Similar to the ordinations of fish predator diets, axis 1 captures a greater amount of the variance in the original diet matrix in both years (2010:  $R^2 = 0.44$ ; 2011:  $R^2 = 0.45$ ), whereas axis 2 accounts for a smaller portion of the variance (2010:  $R^2 = 0.31$ ; 2011:  $R^2 = 0.27$ ). Again, axis 1 appears to explain an increasing gradient in both predator and prey size. Axis 1 was strongly positively correlated with both predator length (2010:  $R = 0.684$ ; 2011:  $R = 0.672$ ) and prey length (2010:  $R = 0.820$ ; 2011:  $R = 0.792$ ). These two variables were also strongly correlated with one another (2010:  $R = 0.724$ ; 2011:  $R = 0.800$ ).

The relative positions of rockfish, salmon, and murre diets in nMDS ordinations of the nekton components

among predator diets for 2010 and 2011 were different (Fig. 3). Black rockfish diets cluster low on axis 1 in both years, but extend further along axis 1 in 2010 compared to 2011. There is also a linear pattern to the rockfish samples in 2010 that is not present in 2011. This linearity does not appear to be associated with any seasonal progression in nekton prey of rockfish nor differences in predator or prey size, but is more likely related to the larger number of samples that contained nekton prey in 2010 compared with 2011. Interestingly, halibut diets ordinate highest on axis 1 in 2010, but salmon diets are positioned similarly to halibut on axis 1 in 2011. There appears to be overlap in nekton consumed between these

**Table 4** Pairwise comparisons of all predator diets in 2010 and 2011 using multi-response permutation procedure

	Chinook salmon	Pacific halibut	Common murre
<i>2010</i>			
Black rockfish	0.161*	0.274*	0.287*
Chinook salmon		0.138*	0.162*
Halibut			<b>0.385*</b>
<i>2011</i>			
Black rockfish	0.141*	0.231*	0.251*
Chinook salmon		-0.011	0.128*
Halibut			0.289*

A-values designated with an \* indicate significant ( $P < 0.01$ ) differences between predators. Strong differences (A-values  $>0.3$ ) are highlighted in bold

two predators in both years, but greater overlap in 2011, similar to our results that included all dietary components. Common murre diets ordinate in an intermediate position between rockfish and other fish in both years, but with what appears to be more overlap with salmon in 2010.

All predators showed some degree of specialization in nekton prey species in both years when all predators were included in the analysis (MRPP, 2010:  $A = 0.293$ ,  $P < 0.0001$ , 2011:  $A = 0.262$ ,  $P < 0.0001$ ). Similar to the analysis of fish predators, pairwise comparisons of predators using the nekton dataset revealed changes in dietary overlap among predators between years. We found that the nekton components of salmon and halibut diets were significantly different in 2010, although the difference was not very strong (Table 4, A-value  $<0.3$ ). In 2011, however, we did not detect any significant difference between the nekton components of salmon and halibut diets, which reinforced changing overlap between years

for these predators as we observed in the nMDS ordination (Table 4, Fig. 3). We saw a slight increase in overlap in diets between Chinook salmon and common murre in 2011 (Table 4), which appears to conflict with the patterns described in the ordinations above. The anomalous Chinook sample that ordinated far from all other Chinook samples in 2011 may be contributing to this finding, as MRPP relies on measures of within-group differences as well as differences across groups. In contrast to the results from the analysis of fish predators where we found several strong differences in pairwise comparisons ( $A > 0.3$ ), the only strong difference in the nekton components of predator diets was found between halibut and murre in 2010.

A number of prey categories were associated with differences in the nekton components of predator diets (Table 5). Indicator taxa for black rockfish were smaller fish including Pacific sand lance in 2010 and larval sculpins (Cottidae) in 2011. Clupeids, often considered more schooling pelagic prey, indicated salmon diets in 2010. Gadiformes, primarily Pacific hake, indicated the halibut diets in both years. Common murre had the most indicator nekton categories in both years (Table 5). Smelts and squids and octopus were indicators in 2010. Smelts and cephalopods were indicators for murre diets again in 2011, along with Pacific sand lance, northern anchovy, and other fishes.

## Discussion

Our ability to understand food-web structure and function depends on understanding predator responses to both small and large perturbations as well as variability within a normal range (Wells et al. 2008). In our study, we expected to

**Table 5** Indicator values (%) for each prey category in the 2010 and 2011 comparison of all predator diets

Common name	2010				2011			
	Black rockfish	Chinook salmon	Pacific halibut	Common murre	Black rockfish	Chinook salmon	Pacific halibut	Common murre
Squids and octopus	0	0	0	<b>57</b>	0	0	0	<b>67</b>
Herring, sardine and shad	0	<b>45</b>	23	20	0	23	29	25
Smelts	0	10	0	<b>76</b>	2	9	0	<b>59</b>
Hake and cods	0	5	<b>80</b>	4	0	24	<b>50</b>	1
Rockfishes	26	10	10	20	12	8	8	20
Pacific sand lance	<b>54</b>	5	0	18	0	3	0	<b>75</b>
Flatfishes	6	0	15	18	9	11	35	24
Sculpins	12	0	0	12	<b>83</b>	0	0	3
Northern anchovy	2	14	0	20	0	5	0	<b>36</b>
Other fishes	3	0	16	3	1	0	16	<b>44</b>

Significant indicator values ( $P < 0.05$ ) are shown in bold

observe differences in diet composition and overlap among predators between the two sampling years of contrasting oceanographic conditions. We found only partial support for hypothesized differences between years, suggesting that differences in environmental conditions affecting prey assemblages were relatively subtle and did not impact predators uniformly. Similarly, some components of trawl catches showed marked increases during La Niña conditions (most invertebrate prey categories) while other prey sharply decreased (fish and squid prey categories). Some amount of diet specialization was observed in both years, but was more pronounced during El Niño conditions in 2010, as hypothesized. Where changes in niche overlap were confirmed, e.g., in Chinook salmon and halibut, they occurred in both the zooplankton and fish components of predator diets. This finding was somewhat surprising, considering the differences in both numerical and aggregative responses of micronektonic invertebrate species and nektonic vertebrate species (Mann and Lazier 2006).

Ocean conditions suspected to influence predator diets varied between our sampling years, yet it appears that the environmental perturbations were not severe enough to cause changes in all predator diets. The relationships between ocean conditions, prey abundance, and predator consumption are complex, but several important basin-scale, physical oceanographic indices that affect prey abundance in the California Current System showed shifts between our sampling years (Bjorkstedt et al. 2011). These shifts, however, did not occur in similar directions, thus precluding stronger, additive effects. Previous observations of high variability in predator diet overlap in the California Current were associated with extreme instances of El Niño and La Niña, and less so with more subtle environmental shifts (Ainley and Boekelheide 1990). The Multivariate El Niño/Southern Oscillation Index (MEI) and the Pacific Decadal Oscillation (PDO), both of which are associated with changes in biological productivity and community assemblages, tracked one another, although neither year was strongly anomalous (MEI: <http://www.esrl.noaa.gov/psd/enso/mei/>, PDO: <http://jisao.washington.edu/pdo/>). Both the MEI and PDO showed positive (warm, low productivity) anomalies during the early part of 2010, switching to negative anomalies (cool, high productivity) in May and June 2010 and remaining negative, consistent with a switch from a relatively weak to moderate El Niño to a strong La Niña event in 2011 (Bjorkstedt et al. 2011).

The North Pacific Gyre Oscillation (NPGO, Di Lorenzo et al. 2008), however, has not shown similar timing in transition and may have dampened the biological effects of changes in MEI and PDO between years. The NPGO tracks the strength of the gyre circulation in the North Pacific and is closely associated with the strength

of the California Current; positive NPGO values have been associated with a strengthening in gyre circulation and strength of the California Current and increased productivity throughout the California Current (<http://www.o3d.org/npgo/>; Bjorkstedt et al. 2011). Recent evidence links the NPGO and timing of the spring transition in the California Current, with profound effects on productivity during the summer months (Chenillat et al. 2012). There is some evidence to suggest that NPGO might have strong influences on some prey species but not others. Sydeman et al. (2013) found a strong relationship between NPGO and abundance of a neritic krill species *T. spinifera*, but no relationship with *E. pacifica*, a species which is generally found further from shore. In recent years, the NPGO may have had stronger influences on the California Current ecosystem than the PDO, and historical studies have recorded years that mimicked El Niño though they were not officially designated as such (Ainley and Boekelheide 1990; Di Lorenzo et al. 2008; Chenillat et al. 2012). Despite a switch from El Niño to La Niña conditions in 2010, NPGO remained positive throughout our study period. Hence, during generally low-productivity El Niño conditions in the California Current, there were confounding NPGO conditions that favored productivity. Despite arguably subtle and complex physical oceanographic differences between our 2 sampling years, we were still able to detect biological responses.

While our diet observations cannot be used to directly infer relative abundance, changes in select components of predator diets corresponded with expected patterns of warm- and cold-water-associated species under the shift between El Niño and La Niña conditions and changes in prey density in trawl surveys. Common murre diets closely followed predicted changes, as taxa with cold water affinities such as Pacific sand lance increased in the diets under La Niña conditions. Similarly, a subarctic pelagic pteropod (*L. helicina*) was found in black rockfish diets and in much higher densities in trawl surveys during the cooler La Niña conditions. Juvenile *Sebastes* spp. were observed in higher numbers in Chinook, murre and to a limited extent black rockfish diets during El Niño compared to La Niña the following year, concurrent with anomalously high densities of juvenile rockfishes in both the trawl surveys examined here (Table 1) and larval/juvenile fish surveys off Oregon and Washington in 2010 (Brodeur et al. 2011; Auth, unpublished data). During warm, low upwelling, El Niño-like years, juvenile rockfishes normally found beyond the shelf break off Oregon appeared to be more abundant in coastal waters (Brodeur et al. 2011) and became more common in other predator diets in 2010 as well (Daly et al. 2013). But, the higher proportions of juvenile rockfish in predator diets did not impact overall dietary overlap or correspond directly to changes in density from trawl surveys. The

proportion of juvenile rockfish in predator diets was only 2.86–11.67 % higher while trawl surveys showed densities that were more than ten times higher in 2010 than 2011.

We did not detect differences in the diets of Chinook salmon and Pacific halibut between the 2 years when the diets of these species were examined on their own, but the possibility that these predators may show dietary changes under some circumstances should not be discounted. These predators have access to a broader range of available prey sizes and can seek favorable prey conditions through active searching over larger areas and depth ranges during foraging compared to the other two predators studied. These samples were also collected further offshore, and it is possible that the offshore prey community remained more constant during our study than the inshore prey community. Therefore, changes in salmon and halibut diets might signal when environmental conditions make large departures from average conditions with potentially greater ecological effects across the shelf, which we did not encounter during our short sampling period.

The results from salmon and halibut diets lent support to our initial hypotheses, as these two predators exhibited differences in niche overlap in nekton components of their diet between the 2 years of the study. Whereas these two predators' diets differed during 2010, the nekton components of their diets were indistinguishable from one another during favorable ocean conditions in 2011. These two predators forage in similar spatial domains near the shelf break and might simultaneously benefit from abundant pelagic, nektonic prey during favorable ocean conditions. However, the individual diets of these two predators did not differ significantly between years. It is possible that the smaller sample sizes collected and the importance of micronekton components of these two predators' diets, especially krill for Chinook salmon, made it difficult to detect interannual changes in the individual predator diet. Predators with relatively consistent diets from year to year may provide a useful way to track food-web variability that occurs at much longer (interannual and decadal) temporal scales, while predators whose diets respond on shorter time scales may reflect smaller, annual, and seasonal changes.

Although all predators were medium-to-large-bodied generalist predators, important differences may exist in their foraging flexibility under variable environmental conditions (Ainley et al. 2002; Dufault et al. 2009). The common murre and black rockfish, which had more constrained foraging ranges and smaller body sizes, had significant dietary differences between the 2 years of sampling. While they remained distinct from one another, niche overlap between murre and halibut diet also increased in 2011. Murres may have been foraging more broadly across the shelf in 2011, as indicated by increased Pacific sand lance in the diet which can occur

further offshore as juveniles (Miller and Brodeur 2007). Black rockfish are associated with rocky reef substrates, are relatively slow swimmers, and have limited home ranges (Parker et al. 2008; Hannah and Rankin 2011). Murres are central place foragers during the breeding season, remaining within 45–60 km of the breeding colony and typically diving to 20–40 m depth (max distance 135 km, max depth 152 m; Ainley and Boekelheide 1990; Hatch et al. 2000; Oedekoven et al. 2001; Hedd et al. 2009). It is possible that murres could be foraging much closer to shore in some years, further reducing their foraging area and making them more vulnerable to changes in the prey inshore community (Ainley and Boekelheide 1990). These morphological and life history constraints may reduce the area available to rockfishes and murres for finding prey, making them more vulnerable to changes in prey availability. Another possibility is that the inshore prey community changed more dramatically than the offshore community, although Phillips et al. (2009) found relative interannual stability in both the inshore and offshore micronekton communities in this region. Unfortunately, we cannot disentangle whether the inshore prey community changed or the foraging locations of these two predators changed but future research should seek to address the complex interplay of these factors.

We expected greater dietary overlap than we observed, as previous studies found that schooling fishes such as herring, smelts, flatfishes, and juvenile rockfishes were important prey for all the predators in our study (Steiner 1978; Brodeur and Percy 1992; Dufault et al. 2009). Differences between our findings and previous studies were especially pronounced for black rockfish. Steiner (1978) found that black rockfish diets during the summer months near Depoe Bay, Oregon, were dominated by smelts, flatfishes, rockfish, and mysids. Black rockfish, collected in a similar manner to our study in the late 1970s, were primarily consumers of nekton, whereas we observed that recent rockfish diets are dominated by micronektonic invertebrate prey. It remains unclear whether the differences between historic rockfish diets and current rockfish diets are related to long-term reorganization of the food web or just stronger short-term variability in predator diets than we observed during this study.

Predators integrate information about changes in the ecosystem over multiple trophic levels and may be sentinels of ecosystem shifts (Parsons et al. 2008; Durant et al. 2009; Bond et al. 2011). It is important to note that our study only examined responses to a single shift in oceanographic conditions. It is clear that longer time series are needed to gain a more complete understanding of ecosystem responses to environmental variation. Long-term changes in the marine food web are especially important to track and understand in light of predicted effects of continued commercial



harvest of marine predators, ocean acidification, and global climate change (Field et al. 2006; Ruzicka et al. 2012). The Northern California Current is also subject to moderately high cumulative human impacts (Halpern et al. 2009) and has a particular need for low-cost measures of ecosystem change. While caution in extrapolating estimates of prey abundance based on generalist predator diets is warranted (Asseburg et al. 2006), seabirds and other marine predator diets have been used to obtain both qualitative and quantitative information about ecosystem changes (Ainley and Boekelheide 1990; Frederiksen et al. 2007; Mills et al. 2007).

Overall, examining a suite of marine predator diets revealed a more nuanced and complex understanding of interannual shifts in the marine food web than any single predator studied in isolation. Studying predator diets is no substitute for traditional surveys of prey density, such as the trawl surveys included in our study. Rather, periodic monitoring of predator diets through collaborative fisheries research would augment current efforts to track prey for commercially and recreationally important predator species. Future studies examining predator diets and prey density in concert should further refine our understanding of how environmental changes propagate through the food web. Including predator diets in integrated ecosystem research could enhance our understanding of food-web dynamics and energy flow under varying oceanographic regimes and, thereby, aid in adaptive management of marine ecosystems.

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