

## ***Feeding ecology of juvenile rockfishes off Oregon and Washington based on stomach content and stable isotope analyses***

The Faculty of Oregon State University has made this article openly available.  
Please share how this access benefits you. Your story matters.

<b>Citation</b>	Bosley, K. L., Miller, T. W., Brodeur, R. D., Bosley, K. M., Van Gaest, A., & Elz, A. (2014). Feeding ecology of juvenile rockfishes off Oregon and Washington based on stomach content and stable isotope analyses. <i>Marine Biology</i> , 161(10), 2381-2393. doi:10.1007/s00227-014-2513-8
<b>DOI</b>	10.1007/s00227-014-2513-8
<b>Publisher</b>	Springer
<b>Version</b>	Version of Record
<b>Terms of Use</b>	<a href="http://cdss.library.oregonstate.edu/sa-termsfuse">http://cdss.library.oregonstate.edu/sa-termsfuse</a>

# Feeding ecology of juvenile rockfishes off Oregon and Washington based on stomach content and stable isotope analyses

Keith L. Bosley · Todd W. Miller · Richard D. Brodeur ·  
Katelyn M. Bosley · Ahna Van Gaest · Anna Elz

Received: 13 September 2013 / Accepted: 30 July 2014 / Published online: 23 August 2014  
© Springer-Verlag Berlin Heidelberg (outside the USA) 2014

**Abstract** The feeding habits of pelagic, juvenile rockfishes (*Sebastes* spp.) collected off Oregon in 2002, and Oregon and Washington in 2006, were examined using stomach content and stable isotope analyses. Sampling occurred along a series of transects across the shelf between Crescent City, California (Lat. 41°54.0'), and Newport, Oregon (Lat. 44°39.0'), in 2002, and off Willapa Bay, Washington (Lat. 46°40.0'), and the Columbia River, Oregon (Lat. 46°10.0'), in 2006. Species composition varied both years with distance from shore, but the predominant species were darkblotched (*Sebastes crameri*), canary (*S. pinniger*), yellowtail (2006 only; *S. flavidus*), and widow (*S. entomelas*) rockfishes. Stomach content analysis revealed that darkblotched rockfish had highly variable diets, and canary, yellowtail, and widow rockfishes exhibited a high degree of overlap in 2006. Multivariate analysis showed significant differences in diet based on distance from shore where caught, fish size, and species. Stable isotope analysis indicated that all

species were feeding at about the same trophic level within each year, with a 1.5 ‰ difference in  $\delta^{15}\text{N}$  between years and regions. The difference in  $\delta^{15}\text{N}$  values may indicate a greater contribution of mesotrophic zooplankton such as euphausiids, hyperiid amphipods, and chaetognaths to fish diets in 2006. Depleted  $^{13}\text{C}$  values were indicative of diets based on primary production from a more offshore origin, suggesting that these rockfish had previously inhabited offshore waters. These results add to our understanding of some of the important environmental factors that affect young-of-the-year rockfishes during their pelagic phase.

## Introduction

Knowing the identities and sources of prey items is fundamental to understanding trophic relationships. In marine ecosystems, this information is often difficult to obtain because of seasonal, spatial, and ontogenetic changes in

Communicated by C. Harrod.

K. L. Bosley (✉)  
Fishery Resource Analysis and Monitoring Division, Northwest  
Fisheries Science Center, National Marine Fisheries Service,  
National Oceanic and Atmospheric Administration, 2032 SE  
OSU Drive, Newport, OR 97365, USA  
e-mail: keith.bosley@noaa.gov

T. W. Miller  
Fisheries Research Section, Division of Fish and Wildlife,  
Commonwealth of the Northern Mariana Islands, Lower Base,  
P.O. Box 10007, Saipan, MP 96950, USA

R. D. Brodeur  
Fish Ecology Division, Northwest Fisheries Science Center,  
National Marine Fisheries Service, National Oceanic  
and Atmospheric Administration, 2030 SE OSU Drive, Newport,  
OR 97365, USA

K. M. Bosley  
Department of Fisheries and Wildlife, Hatfield Marine Science  
Center, Oregon State University, Newport, OR 97365, USA

A. Van Gaest  
Environmental and Fisheries Sciences Division, Northwest  
Fisheries Science Center, National Marine Fisheries Service,  
National Oceanic and Atmospheric Administration, 2030 SE  
OSU Drive, Newport, OR 97365, USA

A. Elz  
Conservation Biology Division, Northwest Fisheries Science  
Center, National Marine Fisheries Service, National Oceanic  
and Atmospheric Administration, 2725 Montlake Boulevard East,  
Seattle, WA 98112, USA

fish diets. Most fish encounter a series of complex assemblages of prey (Perry and Neilson 1988; Ghan and Sprules 1993; McLaren and Avendano 1995) as they undergo habitat shifts that are often related to their life stages (Grover et al. 1998). Furthermore, the occurrence and frequency of prey items in stomachs of fish at the time of their collection offer only a recent snapshot of the prey consumed. This diet characterization may be biased by the differential digestibility of the prey and the environmental factors that affect digestion rate, along with small-scale patchiness of prey resources.

Stable isotope analysis of nitrogen ( $^{15}\text{N}$  and  $^{14}\text{N}$ ) and carbon ( $^{13}\text{C}$  and  $^{12}\text{C}$ ) has proven to be a useful tool for identifying trophic relationships within food webs (Fry 2006). Stable isotopes are naturally occurring tracers of recent mass and energy flow in a food web; thus, the analysis of stable isotopes in specific tissues of a consumer can substantially extend inferences about trophic relationships beyond those based solely on stomach contents. These extensions can include a time-integrated description of the diet (Hesslein et al. 1993), illumination of the sources of prey, and an ability to quantify the trophic position of, and the source of primary production for, an organism. Assessment of an organism's relative trophic level is mostly performed through  $\delta^{15}\text{N}$ . There is an approximate enrichment of 3.4 ‰ in muscle tissue of consumers relative to their prey (Post 2002), although the exact amount of enrichment may be more variable than that of carbon (McCutchan et al. 2003). Changes in  $\delta^{13}\text{C}$  among trophic levels are generally smaller than changes in  $\delta^{15}\text{N}$ , but relative differences between the  $\delta^{13}\text{C}$  values of an organism and its available prey can reveal the source of carbon fixation in terms of benthic versus pelagic (Vander Zanden and Rasmussen 1999) and near-shore versus offshore (Miller et al. 2008), with greater (less negative) values associated with near-shore habitats (Vander Zanden and Rasmussen 1999).

Along the west coast of the USA, a number of groundfish species have undergone dramatic declines in abundance in recent decades. Rockfishes (*Sebastes* spp.) are of particular interest because many of the species that occur in the Northeast Pacific (~36–45 species off Washington, Oregon, and northern California; Love et al. 2002) are exploited, and three are currently designated as overfished (<25 % of estimated pre-fishing biomass; PFMC 2014). Rockfishes are characterized by very high fecundity over a long adult life, with longevity exceeding 50 years in many species (Love et al. 2002). However, survival to maturity is extremely low, and strong year-classes are episodic for some species. An occasional, highly successful year-class will often become the primary component of the biomass for that species for many years (Ralston and Howard 1995; Ralston and Pearson 1997; MacCall et al. 1999).

Rockfish larvae and juveniles are pelagic for several months prior to settling to benthic habitats as subadults (Moser and Boehlert 1991). Recruitment success and subsequent year-class strength may be directly related to ocean conditions encountered during the pelagic stages on both broad and local spatial scales (Larson et al. 1994; Laidig 2010), although density effects may also occur at later stages (Zabel et al. 2011). During the pelagic phase, rockfish are affected by regime shifts, with cool oceanic conditions being most favorable for rockfish growth and survival (Butler et al. 2003; Smith and Moser 2003). Juvenile, pelagic, rockfish catches have increased in sampling over the past few years (Brodeur et al. 2003, 2011), and conditions for favorable recruitment may be improving during the present oceanographic regime for some depleted species. Of the eleven rockfish species identified so far from juveniles found in survey collections off Oregon, three species, darkblotched (*S. crameri*), canary (*S. pinniger*), and widow (*S. entomelas*) rockfish, have been declared overfished, though darkblotched is currently classified as rebuilding (biomass estimated to be between 25 and 40 % of unfished level), and widow is now classified as rebuilt (biomass estimated to be >40 % of unfished level; NOAA Fisheries, Office of Sustainable Fisheries, 2013 Status of U.S. Fisheries).

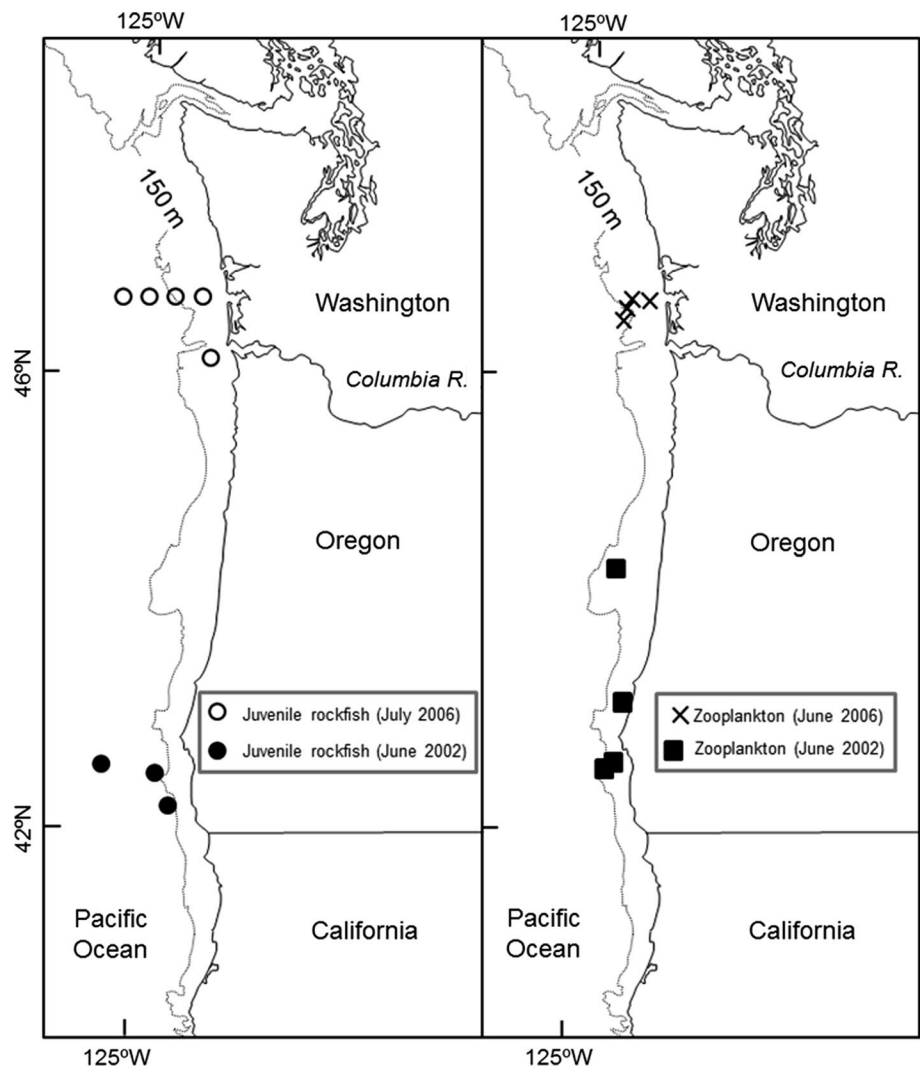
Improving our understanding of the pelagic ecology and survival of these species may lend insight as to what conditions lead to good year-classes that will help rebuild and sustain the populations. Most of what is known about the feeding habits of rockfishes during their early-life pelagic phase comes from studies off California (Reilly et al. 1992; Rau et al. 2001), and there remains a significant gap in feeding studies of juvenile rockfishes in the Northern California Current Ecosystem. Our objective was to add to what is known by using stomach content analysis and stable isotope ratios to examine diets and trophic position of several juvenile rockfish species, using fish from two different pelagic research surveys done off Oregon and Washington. Our specific goal was to look for similarities or differences in diets (dietary overlap) among species and determine whether intrinsic or extrinsic factors were correlated with them to achieve a better understanding of some of the conditions that may be favorable for rockfish year-class strength.

## Materials and methods

### Field collection and laboratory analysis

Pelagic, juvenile rockfish were collected from two geographic areas during separate time periods. The first set of fish was from a Northeast Pacific Global Ocean Ecosystems

**Fig. 1** Sampling locations off Oregon and Washington for fish (left) and zooplankton (right) that were collected for this study; the depth contour shown is the 150 m isobath



Dynamics (GLOBEC) survey during June of 2002 that followed the methodologies as they were described in Miller et al. (2008, 2010). Sampling occurred along a series of transects across the shelf between Crescent City, California (Lat.  $41^{\circ}54.0'$ ), and Newport, Oregon (Lat.  $44^{\circ}39.0'$ ), during daylight hours (Fig. 1). The second set of collections was taken from the Predator Surveys, July 5–8, 2006, following the methodologies described in Emmett et al. (2006). Sampling occurred along two transects across the shelf, one off Willapa Bay, Washington (Lat.  $46^{\circ}40.0'$ ), and the other off the Columbia River, Oregon (Lat.  $46^{\circ}10.0'$ ; Fig. 1), during nighttime hours in the upper 20 m of the water column. At each station for all surveys, rockfishes were collected using a Nordic-264 rope trawl (30 m wide by 18 m deep) towed for 30 min. Upon collection, all fish were immediately frozen ( $-20^{\circ}\text{C}$ ) and taken to the laboratory for identification and processing.

Samples of some of the potential prey for the stable isotope portion of this study were also obtained. All samples

of prey items were collected using surface-neuston hauls ( $1\text{ m}^2$  mouth,  $335\ \mu\text{m}$  mesh). Zooplankton samples were collected by the same vessel that was collecting fish in 2002; they were collected by a separate vessel working in the same areas where fish were caught in 2006, but 1 month prior (June 3–7, 2006) to the time when the fish were collected (Fig. 1). Zooplankton were frozen at sea ( $-20^{\circ}\text{C}$ ) then sorted and identified to the lowest taxonomic level (species, when possible) at a laboratory on shore.

#### Genetic analysis

Samples collected in 2002 were identified solely using visual characters and meristics; no identifications were made using genetic techniques with fish from this group. The 2006 collection was identified with a combination of meristic and genetic information because of the high number of morphologically similar species (Kendall et al. 2007). Genomic DNA was isolated from ethanol-preserved

fin clips with Qiagen DNeasy 96 Tissue Kits. PCR amplification of the cytochrome-b (cyt-b) mtDNA region and the nuclear S7 ribosomal protein intron 2 was performed as outlined in Rocha-Olivares et al. (1999) and Chow and Hazama (1998). Sequencing was performed on an ABI 3100 using Applied Biosystems, BigDye version 3.1. Unknown larval specimens were compared with an in-house reference database of rockfish sequences to identify the unknowns to species. The nuclear S7 intron 2 sequence data were necessary to further distinguish between widow rockfish and blue rockfish (*S. mystinus*).

#### Stomach content analysis

Standard lengths (SL) of fish were measured ( $\pm 1.0$  mm), and then stomachs were extracted and immediately placed in 70 % ethanol. Diets were characterized by assessing fullness, digestive conditions, and identification and quantification of prey taxa in each stomach. Fullness was quantified based on a scale of 0–5, with 0 being empty, 4 full, and 5 distended. Digestive condition of individual prey items was assessed on a scale of 0–4, with 0 being unrecognizable and 4 being fresh. Prey was identified to lowest possible taxon, enumerated, and weighed ( $\pm 0.0001$  g).

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

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

where  $p$  is the proportion of biomass (wet weight and number) 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).

#### Stable isotope analysis

Prior to analysis, muscle tissue and prey samples were dried at 55 °C for at least 24 h in glass vials. The samples were ground and homogenized using a Wig-L-Bug™ (Dentsply Corp.) automated mortar and pestle with stainless steel vials and then loaded into tin capsules. Stable isotope analysis was carried out using a Costech elemental analyzer coupled to a Thermo Finnegan stable isotope ratio mass spectrometer in the continuous-flow mode, with ultrahigh-purity helium as the carrier gas.

The stable isotope ratios were reported as  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , where the ratio of heavy-to-light isotopes ( $^{15}\text{N}/^{14}\text{N}$  and  $^{13}\text{C}/^{12}\text{C}$ ) relative to that of a standard is quantified and denoted in units of per mil (‰) (for more details see

Peterson and Fry 1987). In-house standards were L-histidine and aspartic acid, with instrument error (SD) of  $\pm 0.3$  ‰ for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Lipids are depleted in  $^{13}\text{C}$  relative to other biochemical fractions (DeNiro and Epstein 1977, 1978; Tieszen et al. 1983), which can cause variation attributed to lipid level alone. To correct for this,  $\delta^{13}\text{C}$  values for all fish and invertebrate samples were lipid-corrected using the following equation by Post et al. (2007) for aquatic organisms:

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N} \quad (2)$$

where  $\delta^{13}\text{C}_{\text{normalized}}$  and  $\delta^{13}\text{C}_{\text{untreated}}$  are the lipid-corrected and uncorrected  $\delta^{13}\text{C}$  values, respectively.

We calculated hypothetical stable isotope values for the different rockfish using the measured stable isotope values of prey along with their relative abundance (% weight) in the diet of each rockfish species, coupled with average trophic enrichment factors (TEFs) of 3.4 ‰ for  $\delta^{15}\text{N}$  and 0.5 ‰ for  $\delta^{13}\text{C}$  (Post 2002). Prey items for which stable isotope values were not available were excluded, and the remaining ones were relativized so that they combined to make up 100 % of the diet of each species by weight. Although we did not have measured isotopic values for all of the prey items that were identified in their diets (Appendix), the values we had comprised 76–82 % of the total 2002 diets and 73–98 % of the total 2006 diets.

#### Multivariate analysis

##### Data structure

Multivariate analysis was done with the goal of determining whether the diets of pelagic juvenile rockfish are associated with factors such as fish species or size, or the location where captured (distance from shore). All multivariate analyses of stomach content data were based on percent of total weight to avoid bias caused by either a large number of small-prey items or a small number of large-prey items. Non-empty stomachs from four species (darkblotched, canary, widow, and yellowtail [*S. flavidus*] rockfish) were used in the analysis. Because samples were collected at different years and locations, 2002 and 2006 data were analyzed separately to eliminate bias that may be introduced from a prey species being present in only one of the groups. Prey items that appeared in five or more individual fish were deemed to be common prey items and were included, while prey items that appeared in less than five individual fish were deemed to be rare and were excluded. The species matrix for 2002 data was comprised of 67 sample units with 11 major prey items (Amphipods, Appendicularians, Chaetognaths, Cirripedes, Copepods, other Crustaceans, Decapods, Euphausiids, Euphausiid eggs, Euphausiid larvae, and unidentified material). The species matrix for



2006 data was comprised of 83 sample units and 7 major prey items (Amphipods, Copepods, other Crustaceans, Euphausiids, Euphausiid eggs, Euphausiid larvae, and unidentified material). Elements in the matrix consisted of the percent of total weight for each prey type found in an individual rockfish stomach. Secondary trait matrices for each group contained attributes associated with each sample unit in the main matrix, such as distance from shore (binned at 10-km intervals), fish length (binned at 10-mm intervals), and species. Additional matrices were created for the fish from 2006 that had carbon and nitrogen stable isotope data available (although tissue was collected from every fish, not all of them were analyzed) to see whether they were associated with diets. The isotope species matrix was comprised of 68 sample units and 6 major prey items, with the same elements as described above (except for Euphausiid larvae). The secondary matrix included nitrogen and carbon stable isotope ratios, as well as the other trait information described above. Finally, all of the analyses described below were done with the food item “unidentified material” both included and excluded. There was no difference in the results of the analyses when it was excluded so it was included in the results reported below.

#### Data analysis

Prior to the analyses, an arcsine-square-root transformation was done on each main matrix to reduce the influence of extremes and improve normality (Sokal and Rohlf 1995, McCune and Grace 2002). All analyses were undertaken with the statistical software package R (R core development team). Multi-response permutation procedure (MRPP) was conducted on both 2002 and 2006 data to test the within-group heterogeneity for groups defined by distance from shore, fish length, and species. A Bray–Curtis distance measure was used to calculate the distance matrix for all MRPP tests. Indicator species analysis (ISA) was also performed to determine which prey items were most strongly associated with groups defined by distance from shore, fish length, and species for each sample period. An ordination of diet-composition data from 2006 fish that also had isotope values available was conducted with nonmetric multidimensional scaling (NMS), using a Bray–Curtis distance measure. A joint plot of sample-unit trait variables was used to examine correlations between isotopic values and distance from shore with the ordination axes.

#### Results

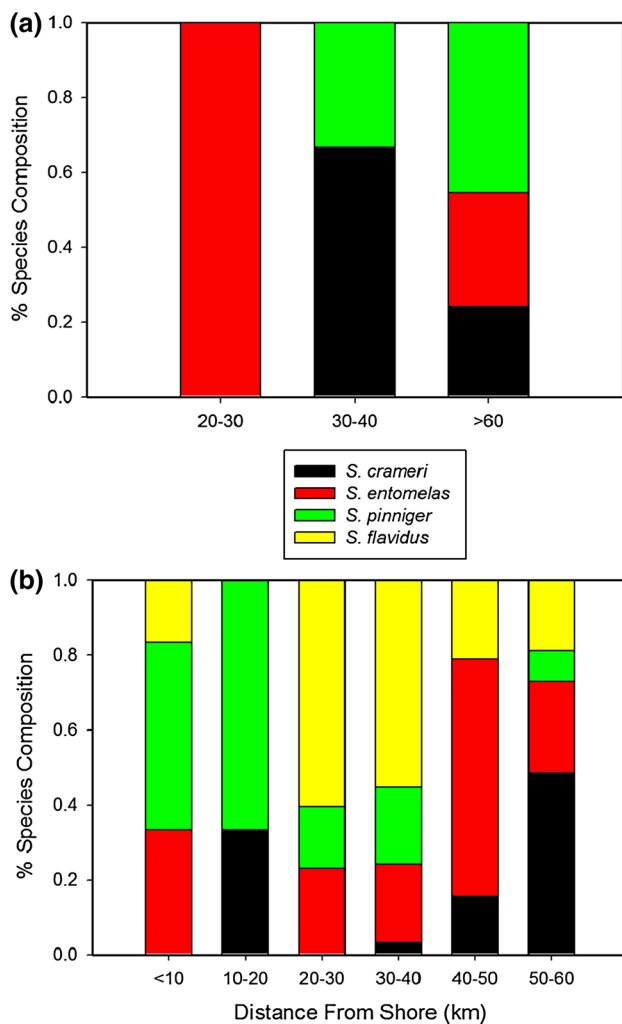
A total of 93 pelagic juvenile rockfishes were collected in 2002. Three species dominated the catch, consisting of canary, darkblotched, and widow rockfishes. Included in the

total, but not used in this study, were 17 fish that could not be positively identified and 9 bank rockfish (*S. rufus*), leaving 67 fish from 2002, all of which were included in subsequent analyses. A total of 237 juvenile rockfishes were collected in 2006, and canary, darkblotched, yellowtail, and widow were the dominant species (86 could not be positively identified). Of the 151 that were identified from 2006, genetic analysis either confirmed the visual identification of, or identified outright, a total of 75 fish comprising 10 different rockfish species; a total of seven different species were originally identified using visual characteristics. While a total of 139 fish were collected in 2006 from the four dominant species (see counts below), only fish with non-empty stomachs ( $N = 83$ ) were included in subsequent analyses.

Between sample years, species composition varied with distance from shore (Fig. 2a, b). In 2002, widow rockfish made up all of the nearshore catch. At an intermediate distance darkblotched rockfish predominated. Canary rockfish were more abundant at the most offshore stations, but both darkblotched rockfish and widow rockfish were there as well (Fig. 2a). In 2006, canary rockfish was the predominant species inshore, and widow rockfish and yellowtail rockfish made up more than 75 % of the species composition at the mid-distance stations. Darkblotched rockfish were found mostly offshore (Fig. 2b).

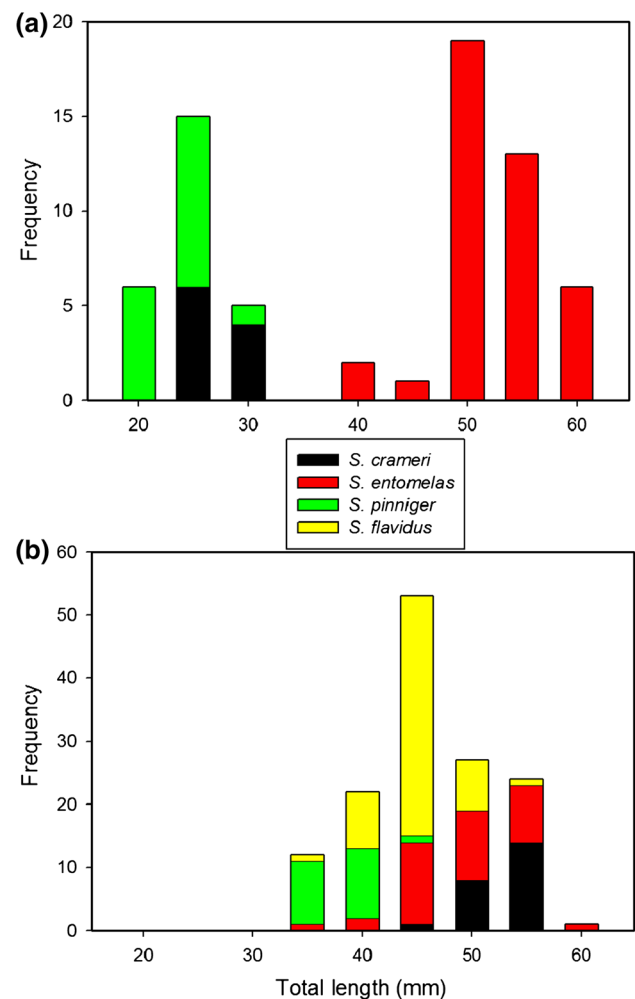
Total length (mm) varied among species. In 2002 and 2006, canary rockfish were mostly smaller than the other species (Fig. 3). Darkblotched rockfish were smaller in size in 2002 than they were in 2006; widow were the largest fish in 2002 but spanned the size range in 2006, while yellowtail rockfish was predominantly in the middle of the size ranges in 2006 (Fig. 3). In 2002, the mean size of canary rockfish was 25.9 mm ( $\pm 3.2$  SD,  $N = 16$ ); widow rockfish was 53.9 mm ( $\pm 4.1$ ,  $N = 41$ ), and darkblotched rockfish was 29.2 mm ( $\pm 1.9$ ,  $N = 10$ ). In 2006, the mean sizes were 39.6 mm ( $\pm 3.1$ ,  $N = 22$ ), 51.1 mm ( $\pm 5.1$ ,  $N = 37$ ), and 54.7 mm ( $\pm 3.1$ ,  $N = 23$ ), respectively, and yellowtail rockfish was 47.0 mm ( $\pm 3.2$ ,  $N = 57$ ).

A breakdown of diets by percent weight and number for each rockfish species is listed in “Appendix.” Darkblotched rockfish tended to eat lower numbers of larger prey (2002: gelatinous zooplankton and amphipods; 2006: euphausiid adults), whereas canary, widow, and yellowtail rockfishes tended to eat high numbers of smaller prey (copepods, euphausiid furcilia, and eggs). Percent similarity indices (PSI) were calculated for diets based on both percent number and percent weight (Table 1). There was no significant overlap in diets (i.e.,  $PSI > 60$ ) by either percent number or weight in 2002. In 2006, PSI for percent number indicated that the diets of canary, yellowtail, and widow rockfishes had significant overlap; PSI values based on percent weight indicated that the diets of widow and canary rockfishes had a significant degree of overlap (Table 1).



**Fig. 2** Species composition binned by station location at 10-km intervals for 2002 (a) and 2006 (b); there were no stations <20 km or 40–50 km offshore in 2002, and >60 km in 2006

MRPP indicated significant differences in diet among species, length bins, and distances offshore (Table 2) for both groups. In 2002, diets from fish collected at different distances offshore showed the greatest amount of separation. The greatest difference in 2006 was seen among species; however, diets also differed by distance offshore, but with a lesser degree of separation than what was observed in 2002. Based on these findings, indicator species analyses (ISA) were run to determine the source of these differences. ISA results suggested that different rockfish species were strongly associated with specific food items (Table 3). In 2002, ISA indicated that canary rockfish were strongly associated with larval euphausiids and darkblotched rockfish were associated with amphipods, decapods, and euphausiid eggs. In 2006, darkblotched rockfish diets were strongly associated with adult euphausiids, mostly *Euphausia pacifica*, and yellowtail rockfish diets were strongly



**Fig. 3** Length-frequency distributions of the predominant rockfish species collected in 2002 (a) and 2006 (b)

associated with copepods (Table 3). Proximity to shore was also a factor affecting diets in both years. Fish caught closer to shore (between 20 and 30 km) were associated with copepods in 2002 and 2006. In 2002, amphipods and gelatinous material were associated with fish caught between 30 and 40 km offshore (Table 3). Finally, in 2002, fish in the 31–40-mm-size range were associated with gelatinous material, while fish in the 41–50-mm-size range were strongly associated with copepods in 2006 (Table 3).

Results from stable isotope analysis showed little difference in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  between rockfish species in 2006, whereas in 2002, there was greater interspecies variation (Fig. 4a, b), particularly with respect to  $\delta^{13}\text{C}$  values. Mean  $\delta^{15}\text{N}$  values of the 2006 rockfish were approximately 1.5 ‰ enriched compared to the values of rockfish from 2002 (Fig. 4a, b), and 2002 rockfish  $\delta^{13}\text{C}$  values varied by almost 2 ‰ (darkblotched rockfish  $\sim -19$  ‰ vs. widow rockfish  $\sim -21$  ‰). Mean values of potential prey, *E. pacifica*, showed a similar pattern, with euphausiids from 2006

**Table 1** PSI for diets by % weight (below the diagonal) and % number (above the diagonal)

2002	<i>S. crameri</i>	<i>S. pinniger</i>	<i>S. entomelas</i>	
<i>S. crameri</i>	–	28.3	43.0	
<i>S. pinniger</i>	33.6	–	2.6	
<i>S. entomelas</i>	3.7	25.0	–	
2006	<i>S. crameri</i>	<i>S. pinniger</i>	<i>S. entomelas</i>	<i>S. flavidus</i>
<i>S. crameri</i>	–	17.5	17.4	15.7
<i>S. pinniger</i>	30.0	–	<b>62.1</b>	<b>84.6</b>
<i>S. entomelas</i>	44.4	<b>71.8</b>	–	<b>76.4</b>
<i>S. flavidus</i>	5.1	55.1	56.0	–

A PSI value >60 represents significant dietary overlap (in bold)

**Table 2** Results obtained from multi-response permutation procedure (MRPP) analysis for differences in rockfish diets by species, total length (TL, mm), and distance (km) from shore

	MRPP	
	A	p
2002		
Species	0.082	0.001
Total length	0.053	0.01
Distance	0.131	0.001
2006		
Species	0.148	0.001
Total length	0.057	0.001
Distance	0.102	0.001

“A” values represent the chance-corrected, within-group agreement statistic. A higher value of “A” suggests less overlap in diet composition among groups

being enriched around 1 ‰ in  $\delta^{15}\text{N}$  and depleted slightly in  $\delta^{13}\text{C}$ . Hyperiid amphipods had similar  $\delta^{15}\text{N}$  values between years but were depleted by almost 2 ‰ in 2002 relative to 2006. One additional potential prey item from 2002 and 2006, *T. spinifera*, had nearly identical  $\delta^{15}\text{N}$  values and varied only slightly (<1 ‰) in  $\delta^{13}\text{C}$  between years. The rest of the potential prey were from 2006 and ranged from 8 ‰ (*E. pacifica* developmental stages) to almost 12 ‰ (chaetognaths) in  $\delta^{15}\text{N}$  values and from –16 ‰ (gelatinous zooplankton) to just under –18 ‰ (*E. pacifica*) in  $\delta^{13}\text{C}$  values (Fig. 4b). The hypothetical  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values show what the fish might have looked like had they been feeding on and equilibrated to the prey items for which we had stable isotope values (Fig. 4a, b).

Nonmetric multidimensional scaling (NMS) ordination of diet-composition data from the 2006 fish for which isotope values were available resulted in a two-dimensional solution with a final stress of 0.134 after 20 iterations. The first two axes were highly significant and explained 94 %

**Table 3** Results from indicator species analysis (ISA) showing specific prey items that were associated with the variables that were tested in both sample groups

Year	Variable	Prey item	Indicator value	p value
Species				
2002	Canary	Euphausiid larvae	43.3	0.004
	Darkblotched	Amphipods	21.3	0.028
		Decapods	19.3	0.032
		Euphausiid eggs	34.9	0.027
2006	Darkblotched	Euphausiids	66.8	<0.001
	Yellowtail	Copepods	37.4	<0.001
Distance (km)				
2002	20–29	Copepods	69.0	<0.001
	30–39	Amphipods	48.3	0.007
		Gelatinous material	50.0	0.031
2006	20–29	Copepods	32.4	0.011
Length (mm)				
2002	31–40	Gelatinous material	33.3	0.043
2006	41–50	Copepods	44.1	0.001

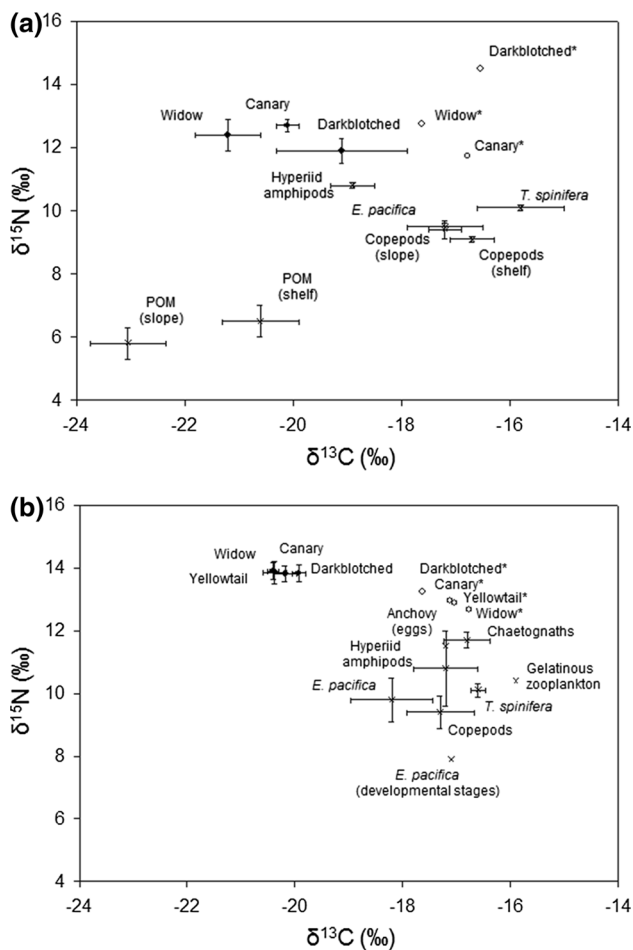
The indicator value represents how strongly a prey item is associated with a pre-defined group (e.g., species, distance, or length); only significant values are reported

of the variance in the data. Distance from shore was highly correlated with axis 1 ( $r = 0.926$ ,  $p = 0.001$ ), and  $\delta^{13}\text{C}$  was correlated with axis 2 ( $r = -0.997$ ,  $p = 0.031$ ) (Fig. 5). Correlation coefficients were weak for  $\delta^{15}\text{N}$ , suggesting no significant trend relative to rockfish diets (Fig. 5).

## Discussion

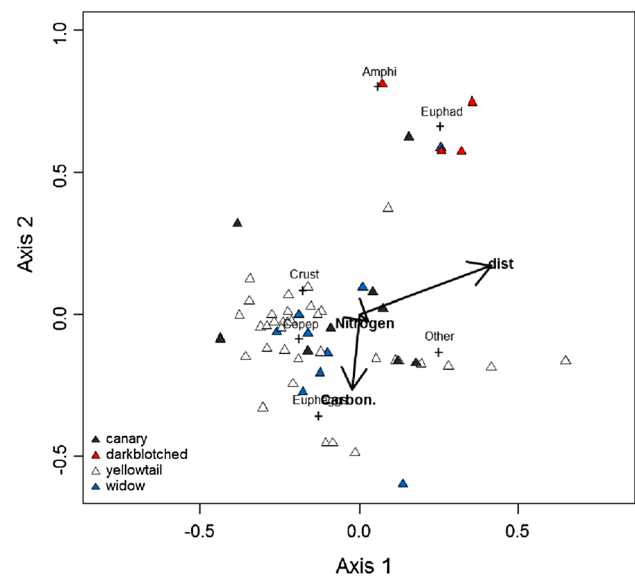
These findings add to what has been done previously to look at the diet and trophic position of juvenile rockfish in the California Current Ecosystem. Our primary goal





**Fig. 4** Mean  $\delta^{13}\text{C}$  versus  $\delta^{15}\text{N}$  values ( $\pm 1$  SD) for rockfish and prey items from 2002 (a) and 2006 (b); rockfish are denoted by *filled circles*, estimated rockfish  $\delta^{13}\text{C}$  versus  $\delta^{15}\text{N}$  values based on their diets and the isotopic composition of prey are denoted by *open circles* and *asterisk*, and zooplankton by an *X*

was to use stomach content and stable isotope analyses to look for similarities or differences in diets (dietary overlap) among species and to determine some of the factors that were correlated with them. Our results showed a varying degree of interspecific dietary overlap within and between years. There was much less overlap in 2002 than there was in 2006, and the differences in mean stable isotope values between species showed this as well (more aggregated values in 2006). Though the actual items comprising the diets varied somewhat between years, the diets of darkblotched rockfish were significantly different from those of the other most abundant rockfish species in both years (i.e., no overlap). In a prior study of the trophic ecology of pelagic juvenile rockfishes (Reilly et al. 1992), a high degree of dietary overlap was observed among species within a year which was greater than the amount of overlap that was observed for a given species between years. Year-to-year variation in the diets of the different rockfish species was



**Fig. 5** NMS ordination of juvenile rockfish diets (% weight of stomach contents) from 2006 with *different symbols* representing each rockfish species. *Axes 1* and *2* represents 94 % of the variance cumulatively; *crosses (+)* represent prey-type scores in the ordination space (amphipods, copepods, crustaceans, euphausiids, euphausiids eggs, and other); *vectors* show the correlation between environmental variables (distance from shore, carbon [ $\delta^{13}\text{C}$ ], and nitrogen [ $\delta^{15}\text{N}$ ]) and the ordination axes

generally greater than within-year variation among the species (Reilly et al. 1992). While we observed variation in diets for each species between years as well, we also saw a greater degree of dietary overlap in 1 year/geographic location (2006/N. Oregon and S. Washington) than we did in another (2002/S. Oregon). We also found the diet of one rockfish species (darkblotched) to be consistently different than all of the others over both years and in two distinct geographic areas. The differences between Reilly et al. (1992) and our study could stem, at least in part, from the more narrow geographic range of sampling locations along the central California coast used in the earlier study. However, all of the fish that were collected for this study, similar to Reilly et al. (1992), were from roughly the same time of the year (early summer), so the degree of dietary overlap between rockfish species whose juveniles are present during other times of the year may be different than what was observed in both of these studies.

We are uncertain as to the period when year-class formation occurs in these juvenile rockfishes but studies from California (Ralston and Howard 1995; Laidig et al. 2007) suggest that the late-larval or early juvenile period may be critical in setting year-class strength. Thus, high diet overlap at this critical period of time could result in slow growth and increased mortality due to predation, assuming that prey resources are limiting. Results from coast-wide surveys over multiple years (2004–2009) indicated that 2006

was an anomalous year in terms of juvenile rockfish abundance (lowest of the time series for three species included in our study), and their distribution was shifted to the north (Ralston and Stewart 2013). These authors attribute these changes to unusual wind patterns and decreased productivity due to late upwelling in 2006.

Juvenile rockfish in 2006 were difficult to distinguish isotopically, showing smaller differences between carbon and nitrogen values than their potential prey. This could simply mean that their diets were not isotopically variable. It is also possible that the differences observed among the diets of darkblotched and the other three species were from a relatively recent shift in diet, perhaps on the order of days to a week, since juvenile fish exhibit a rapid response in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  when diet changes (Bosley et al. 2002, Witting et al. 2004). For example, darkblotched rockfish could have switched from feeding on copepods, which the other three species were also feeding on, to euphausiids, but the switch was recent enough that it was not apparent yet in the isotopic composition of their tissue. The turnover rates of these rockfish species would need to be known in order to say this with certainty. The slight difference in sampling times (June vs. July) between zooplankton (potential prey) and fish must also be considered when interpreting the stable isotope results for 2006; the isotopic composition of the prey the fish were feeding on in early July could have been different from what we measured a month earlier. Nonetheless, the estimated isotopic values were substantially shifted to more enriched (i.e., nearshore) C values compared to the actual values measured in the rockfish (Fig. 4a, b), suggesting that they were not in isotopic equilibrium with the local prey resources.

The  $\delta^{15}\text{N}$  values of rockfish and other organisms appear to have a less-pronounced shelf-slope gradient, especially as seen between shelf and slope copepod baselines (Fig. 4a), and the inclusion of other prey between the 2 years provided additional insight into the trophic differences between 2002 and 2006. The most notable difference was in the higher  $\delta^{15}\text{N}$  values of all juvenile rockfish from 2006. In a 10-year study off Vancouver Island (48.2° N), El-Sabaawi et al. (2012) found substantial interannual differences in  $\delta^{15}\text{N}$  values of zooplankton with 2006 being about 2 ‰ higher than 2002, similar to the differences we observed between the rockfish and potential prey values. Assuming a  $\delta^{15}\text{N}$  trophic enrichment factor of 3.4 ‰ (Post 2002), juvenile rockfish from 2002 showed  $\delta^{15}\text{N}$  values of approximately 1 trophic level (TL) above copepods, whereas rockfish from 2006 were 1.3 TLs above copepods and approximately 1 TL above hyperiid amphipods and euphausiids. Although higher  $\delta^{15}\text{N}$  values may be attributed to the relative importance of more upwelled relative to fixed nitrogen, the  $\delta^{15}\text{N}$  of juvenile rockfish is too high to be from an N-fixed source. Thus, in 2006 zooplankton

prey of euphausiids, hyperiid amphipods, chaetognaths, and other similar mesotrophic zooplankton may have more directly contributed to juvenile rockfish growth and survival. The utility of such prey as an important resource for juvenile rockfish is also supported by their contribution to the diets in this study (Table 3; Appendix).

It is also possible to infer some important information beyond what the rockfish may have been feeding on from the carbon stable isotope data. It is interesting to note that the early months of these years were markedly different in the sign phase of the Pacific Decadal Oscillation (PDO, Mantua et al. 1997). February–July 2002 was characterized by a strong negative PDO cool phase (mean =  $-0.34$ ), whereas January–July 2006 exhibited a warm positive phase (mean =  $+0.57$ ). Both periods cover the time during which juvenile rockfish grew from a very early larval stage to the juvenile stage (when they were collected for stable isotope analysis). Differences in  $\delta^{13}\text{C}$  may have been caused by a difference in available prey under different PDO phases. Major shifts in zooplankton taxa such as copepods and chaetognaths have been shown to occur with warm/cool changes in the PDO off Oregon and the southern region of Vancouver, British Columbia (Mackas et al. 2004; Peterson 2009). The higher (less negative)  $\delta^{13}\text{C}$  values of darkblotched rockfish in 2002 further suggest that greater coastal upwelling during the cool phase in the PDO increased  $^{13}\text{C}$ -enriched diatom production and that upwelling may have made this production more available to the offshore food web. Similarly, bulk zooplankton  $\delta^{13}\text{C}$  values off central Vancouver Island were about 1 ‰ higher offshore than on the shelf and approximately 2 ‰ higher in 2002 than 2006 (El-Sabaawi et al. 2012).

However, other physical processes that are spatially and temporally more restricted than upwelling, such as the Columbia River plume and nearshore hypoxia (Checkley and Barth 2009), may also alter stable isotope ratios in coastal systems (Strauss et al. 2012). Thus, the stable isotopic composition of juvenile rockfish may be useful indicators that they occupied oceanographically different habitats (Hobson 1999; McMahon et al. 2013). In addition, a prior study by Rau et al. (2003) off the central California coast found that the  $\delta^{15}\text{N}$  values of one species of calanoid copepod (*Calanus pacificus*) and two species of chaetognaths (*Sagitta bierii* and *S. eumeritica*) were not associated with changes in PDO when looked at over a 50-year timespan. Rau et al. (2003) also found a significant inverse relationship between  $\delta^{15}\text{N}$  values and PDO for another calanoid copepod (*Eucalanus californicus*) over the same time frame. In contrast, the  $\delta^{15}\text{N}$  values of both rockfish and *E. pacifica* in our study (Fig. 4a, b) were lower during a negative PDO (2002) and higher during a positive PDO (2006). Our results are confounded by utilizing samples taken from two geographic areas, so while they may be useful for further examining differences in food

web structure between warm and cool phases of the PDO in this productive ecosystem, we acknowledge that limited inferences can be made from them.

The mean  $\delta^{13}\text{C}$  values of rockfishes from both time periods are indicative of carbon coming from an offshore source, which is depleted in  $^{13}\text{C}$  relative to primary production occurring closer to shore (Perry et al. 1999; Miller et al. 2008; Kline 2010). The addition of nearshore and offshore mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of particulate organic matter (POM) from Miller et al. (2008, 2010) clearly shows a nearshore–offshore depletion in  $^{13}\text{C}$ , with most rockfish positioned more toward the offshore value. Following this, if trophic fractionation factors for  $\delta^{13}\text{C}$  that are consistent with the literature (Post 2002) are assumed, then the  $^{13}\text{C}$ -enriched prey collected on the shelf in this study probably did not contribute to the isotopic values of these rockfishes. Furthermore, the rate at which muscle tissue responds isotopically to a change in diet for juvenile fish (in estuaries) has been shown to be fairly rapid, on the order of days to a week (e.g., Herzka and Holt 2000; Bosley et al. 2002; Witting et al. 2004). If rates are similar for marine fishes, it would suggest that the fish from both study areas had either recently inhabited offshore regions and then moved or were transported onto the shelf, or alternatively preyed on offshore prey that had been advected onto the shelf. Although both of these scenarios are possible, the former is supported by the capture of very high densities of late-larval and juvenile rockfishes far off the shelf along the Oregon and California coasts in some years (Auth 2009; Brodeur unpubl data). Previous studies on these species off Oregon and California show that the larvae are generally located offshore, and there is a progression onshore with later stages until they settle to their demersal habitat (Laroche and Richardson 1979, 1981; Richardson and Laroche 1979; Larson et al. 1994). Pelagic juvenile rockfishes (including some of the species we examined) have been shown to possess the ability to swim against the prevailing current speeds which would allow them to move onshore even during periods of offshore flow (Kashef et al. 2014). The results of this study indicate that the juvenile rockfish we collected were likely inhabiting offshore waters some time prior to capture, deriving some of their sustenance from prey found there, based on their isotopic signatures, and were subsequently advected or actively migrated onto the shelf where we sampled them. As juvenile rockfishes are prey for a number of important shelf species (Brodeur and Percy 1992; Miller and Brodeur 2007; Daly et al. 2009), the offshore consumption of rockfish by these species represents a potentially important cross-shelf transport of oceanic carbon to the shelf, with important ecological implications for shelf production. Similar offshore trophic subsidies are seen in the northern Gulf of Alaska, where transport is onshore much of the year (Kline 1999, 2010; Mackas and Coyle 2005).

## Conclusion

This study represents the first comprehensive examination of the feeding habits of juvenile rockfishes off Oregon and Washington and provides valuable information on the degree of dietary overlap for several species, as well as spatial and temporal differences in diet among species. Although the actual items comprising the diets varied somewhat between years, the diets of darkblotched rockfish were significantly different from those of the other abundant rockfish species. There was significant variation in the feeding ecology of rockfish on localized spatial scales, with distance from shore, fish size, and species all being influential determinants of diet. Though diets consisted of items found in the waters where they were captured, their stable isotopic compositions reflected diets of an offshore origin, suggesting these rockfish were recent arrivals to the sampling area. Although co-occurring juvenile rockfish share a degree of dietary overlap in their early juvenile phase, differentiation of diets among species was already occurring, and fish size was a significant contributor to variation in diet.

**Acknowledgments** This study was funded through the NOAA Northwest Fisheries Science Center Internal Grants Program, U.S. Global Ocean Ecosystem Dynamics Northeast Pacific Program, and the Bonneville Power Administration. Comments from Chris Harvey, Aimee Keller, Chris Harrod, and two anonymous reviewers improved the manuscript considerably, as did edits from Karen Bosley. We also wish to thank Chris Harvey and Phil Levin for invaluable assistance obtaining funding, and R. Emmett, J. Fisher, T. Sandell, S. Pool, and P. Bentley for help in sampling. Special thanks to M. Kubo, W. Reichert, and K. Turk for help with the stable isotope analysis.

**Ethical standard** These experiments comply with the current laws of the country in which they were performed.

## Appendix

Descriptions of juvenile pelagic rockfish diets as percent damp weight, percent total number  $N$  (in parentheses), and percent frequency of occurrence (F.O.) for fish collected in June 2002 and July 2006.

### Canary rockfish (*Sebastes pinniger*)

Prey taxa	Percent wet weight (%)		F.O. (%)
	June 2002	July 2006	July 2006
Chaetognatha	2.9 (0.8)		–
Crustacea			
Copepoda	9.2 (24.1)	40.3 (87.2)	91.7
<i>Calanus</i> sp.	–	2.1 (1.0)	8.3
<i>Pseudocalanus</i> sp. (adult)	0.5 (1.2)	2.3 (1.2)	8.3

Prey taxa	Percent wet weight (%)		F.O. (%)
	June 2002	July 2006	July 2006
Amphipoda			
Hyperiidia	–	<0.1 (0.5)	8.3
Euphausiacea			
Furcilia	65.2 (73.5)	<0.1 (0.2)	8.3
Adult	–	10.7 (0.2)	8.3
Egg	–	<0.1 (9.4)	16.7
<i>Euphausia pacifica</i>	–	17.7 (0.2)	8.3
Material	15.7	9.6	33.3
Unidentified material	6.5 (0.4)	17.2	75.0

**Darkblotched rockfish (*Sebastes crameri*)**

Prey taxa	Percent wet weight (% N)		F.O. (%)
	June 2002	July 2006	July 2006
Chaetognatha	<0.1 (0.2)	–	–
Crustacea			
Cirripedia (cyprid larva)	<0.1 (0.2)	–	–
Copepoda	2.6 (42.5)	0.1 (13.5)	25.0
<i>Calanus</i> sp.	0.4 (0.5)	–	–
<i>Pseudocalanus</i> sp.	0.2 (3.6)	0.1 (8.7)	15.0
Amphipoda			
Hyperiidia	0.4 (0.8)	<0.1 (0.8)	5.0
<i>Vibilia australis</i>	28.8 (17.6)	–	–
<i>Themisto pacifica</i>	–	0.1 (13.5)	15.0
Decapoda (larva)	0.1 (0.4)	(0.8)	5.0
Brachyura			
<i>Cancer</i> sp. (meg.)	2.3 (0.2)	–	–
Euphausiacea			
Egg	0.5 (33.9)	<0.1 (1.6)	5.0
Calytopis	–	0.3 (0.8)	55.0
Furcilia	–	2.1 (5.6)	5.0
Adult	–	18.7 (14.3)	20.0
<i>Thysanoessa spinifera</i>	–	2.0 (1.6)	10.0
<i>Euphausia pacifica</i>	–	74.5 (38.1)	85.0
Mysidacea	–	0.7 (0.8)	5.0
Material	16.9 (0.2)	0.4	25.0
Gelatinous material	46.6 (0.2)	–	–
Unidentified material	1.0	1.0	50.0

**Widow rockfish (*Sebastes entomelas*)**

Prey taxa	Percent wet weight (% N)		F.O. (%)
	June 2002	July 2006	July 2006
Appendicularia	0.1 (0.1)	0.1 (0.1)	4.1
Chaetognatha	0.1 (<0.1)	–	–
Crustacea (larva)	0.2 (<0.1)	–	–
Copepoda	52.5 (54.6)	32.6 (50.5)	87.8
<i>Calanus</i> sp.	1.1 (0.1)	4.2 (2.1)	42.9
<i>Eucalanus</i> sp.	0.2 (0.1)	–	–

Prey taxa	Percent wet weight (% N)		F.O. (%)
	June 2002	July 2006	July 2006
<i>Epilabidocera</i> sp.	0.2 (<0.1)	–	–
<i>Epilabidocera longipedata</i>	–	<0.1 (<0.1)	2.0
<i>Epilabidocera amphitrites</i>	0.4 (0.1)	–	–
<i>Pseudocalanus</i> sp.	0.1 (0.1)	<0.1 (0.2)	2.0
Material	0.9 (–)	–	–
Amphipoda			
Hyperiidia	–	<0.1 (0.5)	28.6
<i>Hyperia medusarum</i>	<0.1 (<0.1)	<0.1 (0.1)	4.1
<i>Themisto pacifica</i>	0.2 (<0.1)	0.4 (0.7)	36.7
<i>Vibilia australis</i>	–	<0.1 (<0.1)	2.0
Decapoda			
Larva	0.2 (<0.1)	<0.1 (–)	2.0
Zoea			
Euphausiacea			
Egg	<0.1 (<0.1)	<0.1 (–)	2.0
Calytopis	5.7 (40.4)	6.9 (44.9)	51.0
Furcilia	11.6 (2.4)	2.5 (0.4)	20.4
Adult	1.6 (<0.1)	14.8 (0.1)	12.2
<i>Euphausia pacifica</i>			
Furcilia	0.3 (<0.1)	–	–
Adult	–	23.8 (0.2)	16.3
<i>Thysanoessa spinifera</i>			
Furcilia	1.0 (0.3)	0.9 (<0.1)	2.0
Adult	–	5.1 (<0.1)	6.1
Material	0.6	–	–
Material	4.2	3.8	51.0
Osteichthyes (larva)	12.4 (0.1)	–	–
Unidentified material	4.4	4.7	91.8

**Yellowtail rockfish (*Sebastes flavidus*)**

Prey taxa	Percent wet weight (% N)	F.O. (%)
	July 2006	July 2006
Copepoda		
Adult	72.4 (73.7)	100.0
<i>Calanus</i> sp. (adult)	6.8 (1.7)	62.5
<i>Calanus marshallii</i>	–	2.5
<i>Calanus pacificus</i>	0.5 (0.2)	5.0
<i>Pseudocalanus</i> sp.	<0.1 (0.4)	15.0
<i>Epilabidocera longipedata</i>	–	2.5
Amphipoda		
Hyperiidia	<0.1 (0.1)	10.0
<i>Themisto pacifica</i>	<0.1 (0.1)	12.5
Euphausiacea		
Egg	7.5 (23.8)	75.0
Calytopis	<0.1 (–)	2.5
<i>Euphausia pacifica</i>	3.6 (<0.1)	2.5
Material	3.8	52.5
Unidentified material	5.3	80.0

## References

- Auth TD (2009) Importance of far-offshore sampling in evaluating the ichthyoplankton community in the northern California Current. *CalCOFI Rep* 50:107–117
- Bosley KL, Witting DA, Chambers RC, Wainright SC (2002) Estimating turnover rates of carbon and nitrogen in recently metamorphosed winter flounder, *Pseudopleuronectes americanus*, with stable isotopes. *Mar Ecol Prog Ser* 236:233–240
- Brodeur RD, Pearcy WG (1992) Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. *Mar Ecol Prog Ser* 84:101–119
- Brodeur RD, Pearcy WG, Ralston S (2003) Abundance and distribution patterns of nekton and micronekton in the Northern California Current Transition Zone. *J Oceanogr* 59:515–534
- Brodeur RD, Auth TD, Britt T, Daly EA, Litz MNC, Emmett RL (2011) Dynamics of larval and juvenile rockfish (*Sebastes* spp.) recruitment in coastal waters of the Northern California Current. *ICES CM* 2011/H:12
- Butler JL, Jacobson LD, Barnes JT, Moser HG (2003) Biology and population dynamics of cowcod (*Sebastes levis*) in the southern California Bight. *Fish Bull* 101:260–280
- Checkley DM, Barth JA (2009) Patterns and processes in the California Current System. *Prog Oceanogr* 83:49–64
- Chow S, Hazama K (1998) Universal PCR primers for S7 ribosomal protein gene introns in fish. *Mol Ecol* 7:1255–1256
- Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: important for marine survival? *Trans Am Fish Soc* 138:1420–1438
- DeNiro MJ, Epstein S (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* 197:261–263
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- El-Sabaawi RW, Trudel M, Mackas D, Dower JF, Mazumder A (2012) Interannual variability in bottom-up processes in the upstream range of the California Current system. *Prog Oceanogr* 106:16–27
- Emmett RL, Krutzikowsky GK, Bentley P (2006) Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. *Prog Oceanogr* 68:1–26
- Fry B (2006) *Stable isotope ecology*. Springer, New York
- Ghan D, Sprules WG (1993) Diet, prey selection, and growth of larval and juvenile burbot *Lota lota* (L.). *J Fish Biol* 42(1):47–64
- Grover JJ, Eggleston DB, Shenker JM (1998) Transition from pelagic to demersal phase in early juvenile Nassau grouper, *Epinephelus striatus*: pigmentation, squamation, and ontogeny of diet. *Bull Mar Sci* 62:97–113
- Herzka SZ, Holt GJ (2000) Changes in isotopic composition of red drum (*Sciaenops ocellatus*) larvae in response to dietary shifts: potential applications to settlement studies. *Can J Fish Aquat Sci* 57:137–147
- Hesslein RH, Hallard KA, Ramlal P (1993) Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by delta super 34S, delta super 13C, and delta super 15N. *Can J Fish Aquat Sci* 50(10):2071–2076
- Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314–326
- Kashef NS, Sogard SM, Fisher R, Largier JL (2014) Ontogeny of critical swimming speeds for larval and pelagic juvenile rockfishes (*Sebastes* spp., family Scorpaenidae). *Mar Ecol Prog Ser* 500:231–243
- Kendall AW Jr, Kondzela C, Li Z, Clausen D, Gharrett AJ (2007) Genetic and morphological identification of pelagic juvenile rockfish collected from the Gulf of Alaska. *NOAA Prof Pap NMFS* 9:1–26
- Kline TC Jr (1999) Temporal and spatial variability of 13C/12C and 15N/14N in pelagic biota of Prince William Sound, Alaska. *Can J Fish Aquat Sci* 56(Suppl 1):94–117
- Kline TC Jr (2010) Stable carbon and nitrogen isotope variation in the northern lampfish and *Neocalanus*, marine survival rates of pink salmon, and meso-scale eddies in the Gulf of Alaska. *Prog Oceanogr* 87:49–60
- Laidig TE (2010) Influence of ocean conditions on the timing of early life history events for blue rockfish (*Sebastes mystinus*) off California. *Fish Bull* 108:442–449
- Laidig TE, Chess JR, Howard DF (2007) Relationship between abundance of juvenile rockfishes (*Sebastes* spp.) and environmental variables documented off northern California and potential mechanisms for the covariation. *Fish Bull* 105(39):48
- Laroche WA, Richardson SL (1979) Development and occurrence of larvae and juveniles of the rockfishes *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. *Fish Bull* 77:901–924
- Laroche WA, Richardson SL (1981) Development of larvae and juveniles of the rockfishes *Sebastes entomelas* and *S. zacentrus* (family Scorpaenidae) and occurrence off Oregon, with notes on head spines of *S. mystinus*, *S. flavidus*, and *S. melanops*. *Fish Bull* 79:231–258
- Larson RJ, Lenarz WH, Ralston S (1994) The distribution of pelagic juvenile rockfish of the genus *Sebastes* in the upwelling region off central California. *CalCOFI Rep* 35:175–221
- Love MS, Yoklavich M, Thorsteinson L (2002) The rockfishes of the Northeast Pacific. The University of California Press, Berkeley
- MacCall AD, Ralston S, Pearson D, Williams E (1999) Status of the bocaccio off California in 1999 and outlook for the next millennium. In: Appendix to the status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000, Pacific Fisheries Management Council, 2130 SW Fifth Ave, Suite 224, Portland, OR 97201
- Mackas DL, Coyle KO (2005) Shelf-offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. *Deep-Sea Res II* 52:707–725
- Mackas DL, Peterson WT, Zamon JE (2004) Comparisons of interannual biomass anomalies of zooplankton communities along the continental margins of British Columbia and Oregon. *Deep-Sea Res II* 51:875–896
- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific decadal climate oscillation with impacts on salmon. *Bull Am Meteorol Soc* 78:1069–1079
- McCune B, Grace JB (2002) *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR
- McCutchan JH Jr, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390
- McLaren A, Avendano P (1995) Prey field and diet of larval cod on Western Bank, Scotian Shelf. *Can J Fish Aquat Sci* 52:448–463
- McMahon KW, Hamady LL, Thorrold SR (2013) A review of eco-geochemistry approaches to estimating movements of marine animals. *Limnol Oceanogr* 58:697–714
- Miller TW, Brodeur RD (2007) Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. *Fish Bull* 105:548–559
- Miller TW, Brodeur RD, Rau GH (2008) Carbon stable isotopes reveal relative contribution of shelf-slope production to the Northern California Current pelagic community. *Limnol Oceanogr* 53:1493–1503



- Miller TW, Brodeur RD, Rau GH, Omori K (2010) Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. *Mar Ecol Prog Ser* 420:15–26
- Moser HG, Boehlert GW (1991) Ecology of pelagic larvae and juveniles of the genus *Sebastes*. *Environ Biol Fish* 30:203–224
- Pacific Fishery Management Council (2014) Pacific Coast Groundfish Fishery Management Plan for the California, Oregon and Washington Groundfish Fishery. Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR 97220
- Perry RI, Neilson JD (1988) Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. *Mar Ecol Prog Ser* 49:199–214
- Perry RI, Thompson PA, Mackas DL, Harrison PJ, Yelland DR (1999) Stable carbon isotopes as pelagic food web tracers in adjacent shelf and slope regions off British Columbia, Canada. *Can J Fish Aquat Sci* 56:2477–2486
- Peterson WT (2009) Copepod species richness as an indicator of long term changes in the coastal ecosystem of the Northern California Current. *Calif Coop Ocean Fish Invest Rep* 50:73–81
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Ann Rev Ecol Syst* 18:293–320
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- Ralston S, Howard DF (1995) On the development of year-class strength and cohort variability in two northern California rockfishes. *Fish Bull* 93:710–720
- Ralston S, Pearson D (1997) Status of the widow rockfish stock in 1997. In: Appendix to the status of the Pacific Coast groundfish fishery through 1997 and recommended acceptable biological catches for 1998. Pacific Fisheries Management Council, 2130 SW Fifth Ave, Suite 224, Portland, OR 97201
- Ralston S, Stewart IJ (2013) Anomalous distributions of pelagic juvenile rockfish on the U.S. west coast in 2005 and 2006. *Calif Coop Ocean Fish Invest Rep* 54:155–166
- Rau GH, Ralston S, Southon JR, Chavez FP (2001) Upwelling and the condition and diet of juvenile rockfish: a study using  $^{14}\text{C}$ ,  $^{13}\text{C}$ , and  $^{15}\text{N}$  natural abundances. *Limnol Oceanogr* 46:1565–1570
- Rau GH, Ohman MD, Pierrot-Bults A (2003) Linking nitrogen dynamics to climate variability off central California: a 51 year record based on  $^{15}\text{N}/^{14}\text{N}$  in CalCOFI zooplankton. *Deep-Sea Res II* 50:2431–2447
- Reilly CA, Echeverria TW, Ralston S (1992) Interannual variation and overlap in the diets of pelagic juvenile rockfish (Genus, *Sebastes*) off central California. *Fish Bull* 90:505–515
- Richardson SL, Laroche WA (1979) Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family Scorpaenidae) off Oregon. *Fish Bull* 77:1–46
- Rocha-Olivares A, Kimbrell CA, Eitner BJ, Vetter RD (1999) Evolution of a mitochondrial cytochrome b gene sequence in the species-rich genus *Sebastes* (Teleostei, Scorpaenidae) and its utility in testing the monophyly of the subgenus *Sebastes*. *Mol Physiol Evol* 11:426–440
- Schoener TW (1974) Resource partitioning in ecological communities. *Science* 185:27–39
- Smith PE, Moser HG (2003) Long-term trends and variability in the larvae of Pacific sardine and associated fish species of the California Current region. *Deep-Sea Res* 50:2519–2536
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. W.H. Freeman & Co., New York
- Strauss J, Grossman EL, DiMarco SF (2012) Stable isotope characterization of hypoxia-susceptible waters on the Louisiana shelf: tracing freshwater discharge and benthic respiration. *Cont Shelf Res* 47:7–15
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for  $\delta^{13}\text{C}$  analysis of diet. *Oecologia* 57:32–37
- Vander Zanden JM, Rasmussen JB (1999) Primary consumer  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and the trophic position of aquatic consumers. *Ecology* 80:1395–1404
- Wallace H, Ramsay JS (1983) Reliability in measuring diet overlap. *Can J Fish Aquat Sci* 40:347–351
- Witting DA, Chambers RC, Bosley KL, Wainright SC (2004) Experimental evaluation of ontogenetic diet transitions in summer flounder, *Paralichthys dentatus*, using stable isotopes as diet tracers. *Can J Fish Aquat Sci* 61:2069–2084
- Zabel RW, Levin PS, Tolimieri N, Mantua NJ (2011) Interactions between climate and population density in the episodic recruitment of bocaccio, *Sebastes paucispinis*, a Pacific rockfish. *Fish Oceanogr* 20:294–304