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Feeding ecology of juvenile rockfishes off Oregon and Washington: insights into life history patterns based on stomach content and stable isotope analyses

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Abstract

We examined the feeding habits of pelagic juvenile rockfishes (*Sebastes* spp.) collected off Oregon and Washington during 2000, 2002, and 2006 using a combination of stomach content and stable isotope analyses. Species were identified using genetic techniques and the predominant species collected in all years were darkblotched (*S. crameri*), canary (*S. pinniger*), yellowtail (*S. flavidus*), and widow (*S. entomelas*) rockfishes. Analysis of stomach contents by numerical proportion revealed that darkblotched rockfish expressed a high degree of variability in their diets, while canary, yellowtail, and widow rockfishes had high dietary overlap, attributed to the common utilization of copepods and euphausiids. Less overlap in diets was observed among species when gravimetric proportions were examined. Multivariate analysis of stomach content data revealed significant differences in diet based on distance from shore where caught, fish size, and species. Nitrogen stable isotope analyses showed all rockfishes were feeding at about the same trophic level within each year; however there was a 1.5% difference in δ^{15} N between years. Depleted (more negative) δ^{13} C values of rockfish were indicative of primary production from a more off-shore origin, with widow consistently expressing the lowest values between years. Comprehensively, these results advance our understanding of some of the important environmental factors that affect young-of-the-year rockfish during their critical pelagic phase.

Keywords: Feeding ecology, juvenile rockfishes, stomach analysis, carbon and nitrogen stable isotopes

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Introduction

Knowing the identities and sources of prey items is fundamental to understanding trophic relationships in aquatic ecosystems. This information is often difficult to obtain because of seasonal, spatial, and ontogenetic changes in fish diets. Most fish encounter a series of complex assemblages of prey (Ghan and Sprules 1993; McClaren and Avendano 1995) as they undergo habitat shifts that are often related to their life-stage. Furthermore, the occurrence and frequency of prey items in stomachs of fish at the time of their collection offers only a recent snapshot of the prey consumed. This diet characterization may be biased by 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 N and 14 N) and carbon (13 C and 12 C) has proven to be a useful tool for identifying trophic relationships within food webs (Peterson and Fry 1987), where the ratio of heavy to light isotopes (15 N) 14 N and 13 C/ 12 C) relative to that of a standard is quantified and denoted in units of per mil (36) as δ^{15} N and δ^{13} C respectively (Peterson and Fry 1987). 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, 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 done through δ^{15} N with an approximate enrichment of 3.4% in muscle tissue of consumers relative to their prey (Post 2002). Changes in δ^{13} C between trophic levels are less consistent, however relative differences between the δ^{13} C values of an organism and their available prey can reveal the source of carbon fixation in terms of benthic vs. pelagic (Vander Zanden and Rasmussen 1999) and near-shore vs. 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 United States, 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 >80 species that occur in the Northeast Pacific are exploited, and several are currently designated as over-fished (<25% of estimated un-fished biomass; NOAA Office of Sustainable Fisheries). 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 and 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; 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). 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). Juvenile pelagic rockfish catches have increased in recent sampling (Brodeur et al. 2003; unpub. data), and conditions for favorable recruitment may be improving for some depleted species during the present oceanographic regime. 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 over-fished, though darkblotched and widow are now classified as rebuilding.

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), and there remains a significant gap in feeding studies of juvenile rockfishes in the northern California Current ecosystem. In this study, stomach content analysis and stable isotope ratios were used to examine diets and trophic position of several juvenile rockfish species collected during pelagic research surveys over several years off Oregon and Washington.

Methods

Field collection and laboratory analysis

Pelagic juvenile rockfish were collected from cruises covering two geographic areas. The first set of samples was taken from the Northeast Pacific Global Ocean Ecosystems Dynamics (GLOBEC) surveys during June of 2000 and 2002 (Miller et al. 2010). 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′), all occurring during daylight hours (Fig. 1). The second set of samples was collected during the NOAA Northwest Fisheries Science Center's (NWFSC) July 2006 GLOBEC Predator Surveys, along two transects, one off Willapa Bay, Washington, and the other off the Columbia River (Fig. 1). These collections were made during nighttime hours in the upper 20 m of the water. At each station for all surveys, rockfish were collected using a Nordic-264 rope trawl (30 m wide by 18 m deep) towed for 30 minutes. Upon collection, all fish were immediately frozen (-20°C) and taken to the laboratory for identification and processing.

Samples of potential prey for the stable isotope portion of this study were obtained from other vessels but the collections were made around the same time and location that the juvenile rockfish were being collected for this study (Miller et al. 2008, 2010; Fig. 1). Prey items were collected using surface neuston hauls (1-m² mouth, 335-µm mesh). Bulk zooplankton samples were taken from five hauls at locations in close proximity to one another (Fig. 1) and were frozen at sea (-20°C); samples were subsequently brought to the laboratory where they were sorted and identified to the lowest taxonomic level.

Genetic analysis

Tentative identifications of rockfishes were initially made in the laboratory using visual characteristics, but because of the high number of morphologically similar species occurring in the area, many fish were too difficult to identify strictly from visual or meristic characteristics alone (Kendall et al. 2007). Therefore, a fin clip from each individual was stored in pure ethanol and sent to a genetics laboratory to validate species identity.

Genomic DNA was isolated from ethanol-preserved fins with DNeasy 96 Tissue Kits (QIAGEN) using a BioRobot 8000 (QIAGEN) according to the manufacturer's instructions. DNA was quantified using fluorometry and diluted to 5-10 ng ml⁻¹ for polymerase chain reaction (PCR) amplifications. PCR amplification of the Cytochrome-b (cyt-b) mtDNA region (~750, bp) and the nuclear S7 ribosomal protein intron 2 were performed with previously published primers as outlined in Rocha-Olivares et al. (1999) and Chow and Hazama (1998), respectively. Purification of 40µl PCR products was carried out using Millipore's Multiscreen HT 96-well filtration plates. Sequences were generated by automated sequencing on an ABI 3100 following termination of PCR reactions with Applied Biosystems, BigDye ver. 3.1 and Clean-SEQ purification. All sequencing reactions were performed in both directions for each set of primers. Multiple DNA sequences were aligned with Sequencher 4.5 (Genecodes Corp). Phylogenetic analysis was performed on cyt-b mtDNA sequence information with MEGA2 ver. 2.1 (Kumar et al. 2001) to group unknown larval specimens with known rockfish sequences based on 1000 bootstrap replicates. Alignments of nuclear S7 intron 2 sequence data were used to distinguish between widow rockfish and blue rockfish (*S. mystinus*).

Stomach content analysis

A total of 283 rockfish stomachs were examined, 126 from the 2000/2002 collections and 157 from the 2006 collections. Standard lengths (SL) of fish were measured (±1.0 mm), and then stomachs were extracted and immediately placed in 70% ethanol. Diet analysis was performed by assessing fullness, digestive condition, and identification and quantification of prey taxa in each stomach. Fullness was assessed by applying a scale of 0-5, with 0 being empty, 4 full, and 5 distended. Digestive condition of individual prey was assessed using a 0-4 scale, with 0 being unrecognizable and 4 being fresh. Prey taxa were identified to lowest possible taxon, enumerated, and weighed (±0.0001g).

Trophic relationships were also analyzed by calculating the degree of diet similarity between nekton species pairs by using a percent similarity index (PSI) between the diets of paired rockfishes. 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 ultra-high-purity helium as the carrier gas.

The stable-isotope ratios were reported as $\delta^{15}N$ and $\delta^{13}C$, with units of per mil (‰) difference relative to standards. Lipids are depleted in ^{13}C relative to other biochemical fractions (DeNiro and Epstein 1978, Tieszen *et al.* 1983), which can cause variation attributed to lipid level alone. To correct for this, $\delta^{13}C$ values for all fish and invertebrate samples were lipid-normalized using a commonly-used series of equations developed by McConnaughey and McRoy (1979).

Data analysis

All multivariate analyses that used stomach content data were conducted using the percent of total weight data. This was done to avoid any bias that could result from having a large number of small prey items or a small number of large prey items. Composition of rockfish diets was analyzed separately for 2000/2002 and 2006, using fish from the four species of interest (darkblotched, canary, widow, and yellowtail rockfish *S. flavidus*) with non-empty stomachs. This produced a main species matrix for the percent of total weight for each prey type found in an individual rockfish stomach. Secondary matrices for both years contained trait information associated with each sample unit in the main matrix. Trait variables included distance from shore (binned at 10-km intervals), fish length (binned at 10-mm intervals), and species. Additional matrices were constructed to examine how isotope ratios correlated with rockfish diet from the 2006 samples. The secondary matrix included nitrogen and carbon stable-isotope ratios for fish collected in 2006, as well as the grouping variables listed above. Prior to the analysis, an arcsine square root transformation was done on each main matrix to reduce the influence of extremes and improve normality (McCune and Medford 2006).

All analyses were preformed with the statistical software package PC-ORD 5.0 (McCune and Medford 2006). Multi-response Permutation Procedure (MRPP) was conducted on both 2000/2002 and 2006 data to test the within-group heterogeneity for groups defined by distance from shore, fish length, and species. A Sorenson 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 the 2006 isotope data was conducted with Nonmetric Multidimensional Scaling (NMS) using a Sorensen distance measure in PC-ORD (McCune and Medford 2006). A joint plot of sample unit trait variables was used to examine correlations between isotopic signatures and distance from shore with the ordination axes.

Results

A total of 237 juvenile rockfish were collected in 2006. Of these, 86 could not be positively identified visually or through genetic analysis. Of the 157 that were identified, genetic analysis either confirmed the visual identification of, or identified outright, a total of 75 fish comprising 10 different rockfish species. Four species comprised the bulk of what was caught: darkblotched, yellowtail, canary and widow rockfish. A total of 104 fish from 2000/2002 were looked at in this study (21 fish could not be positively identified visually or through genetic analysis). The same four species were predominant in 2000 (yellowtail) and 2002 (darkblotched, canary and widow).

Species composition varied with distance from shore between sample years (Figs. 2A, 2B). In 2000/2002, widow rockfish made up 80% of the nearshore catch, with yellowtail rockfish making up the other 20%. At the intermediate distance, yellowtail and darkblotched rockfish predominated, while canary rockfish was found primarily at the most offshore stations, along with darkblotched and widow (Fig. 2A). In 2006, canary was the predominant species inshore, while widow and yellowtail made up over 75% of the species composition at the mid-distance stations. Darkblotched rockfish were found

mostly offshore (Fig. 2B). For all years combined, canary rockfish were smaller in size than yellowtail and widow rockfish, while darkblotched rockfish spanned the size range.

Percent diet composition for each species by time period is shown in Figure 3. Pair-wise comparisons of diet showed darkblotched rockfish had significantly different diets by weight and number (Table 1) from all other species in both years. Darkblotched rockfish tended to eat lower numbers of larger prey (euphausiid adults and furcilia, gelatinous zooplankton, amphipods), whereas canary, widow, and yellowtail rockfish tended to eat high numbers of smaller prey (copepods, euphausiid furcilia and eggs)(Fig. 3). Percent Similarity Index (PSI) values were calculated for the diets using both percent number and percent weight (Table 1). PSI values for % number indicated that the diets of canary, yellowtail and widow all had a significant degree of overlap (i.e., PSI > 60). PSI values for % weight indicated that only the diets of widow and canary had a significant degree of overlap.

MRPP indicated significant differences in diet among species, length bins, and distance offshore (Table 2). This was true in both sampling time periods. Based on the findings of the MRPP, indicator species analyses (ISA) were run to determine what was driving the differences. ISA 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 (Fig. 3). In 2006, darkblotched rockfish diets were strongly associated with adult euphausiids, mostly *Euphausia pacifica* and *Thysanoessa spinifera*, and yellowtail rockfish diets were strongly associated with copepods (Fig. 3). Proximity to shore was also a factor affecting diets in 2000/2002 and 2006. Fish caught closer to shore (between 20 and 30 km) were associated with euphausiid eggs in 2002 and copepods in 2006. Fish caught farthest from shore (>60 km) were associated with chaetognaths and euphausiid larvae in 2002 and "other" (unidentifiable material) in 2006 (Table 3). Finally, in 2000/2002, fish in the 21-30 mm size range were associated with euphausiid larvae, and fish in the 31-40 mm size range were associated with copepods (Table 3).

Results from $\delta^{15}N$ and $\delta^{13}C$ analysis showed little difference between rockfish species in 2006, with 2002 showing considerably more inter-species variation (Fig. 4). Mean $\delta^{15}N$ values of the 2006

rockfish were approximately 1.5‰ enriched compared to the group mean of rockfish from 2002 (Fig. 4), but the 2002 rockfish were enriched slightly in mean δ^{13} C values. Mean values of potential prey, *E. pacifica*, similarly showed this pattern, with 2006 being enriched around 1‰ in 15 N and depleted slightly in 13 C. One other potential prey item from both time periods, *T. spinifera*, had nearly identical δ^{15} N values, and varied only slightly (<1‰) in δ^{13} C. The rest of the potential prey were from 2006, and ranged from 8‰ (*E. pacifica* developmental stages) to almost 12‰ (chaetognaths) in δ^{15} N values, and from -16‰ (gelatinous zooplankton) to just under -18‰ (*E. pacifica*) in δ^{13} C values (Fig. 4).

Nonmetric multidimensional scaling (NMS) ordination of 2006 diet composition data resulted in a 2-dimensional solution after 500 iterations. The first two axes were highly significant (p = 0.004) and explained 91.4% of the variance in the data. Distance from shore was correlated with axis 1 (r = -0.56) (Fig. 5). Correlation coefficients were weak for both carbon and nitrogen signatures suggesting no significant trend in isotope values relative to rockfish diet.

Discussion

In one of the only previous studies of diet variation and overlap between pelagic juvenile rockfishes (Reilly et al. 1992), a high degree of dietary overlap was observed among species within a year, and it was greater than the amount of overlap that was observed for a given species between years. There was generally less overlap in the 2000/2002 sampling period than there was 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 collected at both times.

Juvenile rockfish were difficult to distinguish isotopically in 2006, showing much less spread between carbon or nitrogen values than that of their potential prey. This finding suggests that the differences observed between the diets of darkblotched and the other three species were from a relatively recent shift in diet, on the order of days to a week, based on the presumption of a rapid response in δ^{13} C and δ^{15} N with changes in diet, as occurs with juveniles of other species of fish (Bosley et al. 2002). The

mean δ^{15} N values of the 2006 rockfish were ~1.5% greater than rockfish from 2002. The mean δ^{15} N values for potential prey that were available from 2002 were also ~1.5‰ lower than those from 2006, possibly reflecting a spatial difference between the different sampling locations as well. 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), with February – July 2002 showing a strong negative PDO cool phase (mean = -0.34) and from January – July 2006 in a warm positive phase (mean = +0.57). Both time periods cover the time frame at which juvenile rockfish would have grown from a very early stage to when they were collected for stable isotope analysis, and therefore differences in their $\delta^{15}N$ and $\delta^{13}C$ may have been caused by a difference in available prey. Major shifts in zooplankton taxa of 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. 2001). Higher δ^{13} C values during 2002 furthermore suggest that greater coastal upwelling during the cool phase in the PDO would have increased ¹³C-enriched diatom production, and that upwelling may have made this production more available to the offshore food web. These results should be examined further with respect to comparing food web structure between warm and cool-phases of the PDO in this productive ecosystem. Juvenile rockfish may be ideal indicators of this shift because of their very high growth rates and subsequent turnover times, but also because they are an important component as prey in the California Current food web (Brodeur and Pearcy 1992; Miller and Brodeur 2007).

The mean δ^{13} C values of rockfishes from both time periods are also indicative of carbon coming from a more offshore source, which is depleted in 13 C relative to primary production occurring closer to shore (Miller et al. 2008). If we assume trophic fractionation levels for δ^{13} C which are consistent with the literature, the potential prey collected on the shelf in our study showed carbon signatures that probably did not contribute to the isotopic signatures of these rockfishes. Furthermore, the rate at which muscle tissue responds isotopically to a change in diet for juvenile fish has been shown to be fairly rapid, on the order of days to a week (*e.g.* Bosley et al. 2002; Witting et al. 2004). This suggests that the fish we examined from both study areas had either recently inhabited offshore regions and then moved onto the

shelf, or alternatively preyed on offshore prey that had been advected onto the shelf. Although both 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 unpub. data). Previous studies on these species off Oregon and California show that the larvae are generally 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). Our results suggest that these juveniles were likely ones that had survived from offshore spawning and had been advected or had actively migrated onto the shelf. As juvenile rockfishes are fed upon by a number of important shelf species (Miller and Brodeur 2007; Daly et al. 2009), the offshore feeding 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 shoreward much of the year (Kline 1999, 2010).

Conclusions

This study represents the first comprehensive examination of the feeding habits of juvenile rockfishes off Oregon and Washington, by which we were able to gain valuable information about the degree of dietary overlap for several species, three of which have been classified as being over-fished. Although 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. 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 reflective of feeding 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. While co-occurring juvenile rockfish share a degree of dietary overlap in their early-juvenile phase, differentiation of diets between species was already occurring between some species, and fish size was a significant contributor to variation in diet.

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Table 1. The Percent Similarity Index (PSI) values for diets by % weight and % number (in parenthesis). A PSI value >60 represents significant dietary overlap (in bold).

2000/2002	<u>Darkblotched</u>	Canary	Yellowtail	Widow
Darkblotched	X			
Canary	19.7 (25.5)	X		
Yellowtail	12.7 (43.0)	20.2 (24.1)	X	
Widow	10.6 (44.2)	29.6 (26.7)	61.2 (55.3)	X

2006	Darkblotched	Canary	Yellowtail	Widow
Darkblotched	X			
Canary	30.0 (17.5)	X		
Yellowtail	5.1 (15.7)	55.1 (84.6)	X	
Widow	44.4 (17.4)	71.8 (62.1)	56.0 (76.4)	X

Table 2. Results obtained from multi-response permutation procedure (MRPP) analysis for differences in rockfish diets by species, TL and distance from shore. "A" values represent the chance-corrected, within-group agreement statistic.

	MRPP	
2000/2002	\mathbf{A}	р
Species	0.087	< 0.001
Length	0.059	< 0.001
Distance	0.116	< 0.001
2006	A	p
Species	0.166	< 0.001
Length	0.060	< 0.001
Distance	0.108	< 0.001

Table 3. Results from indicator species analysis showing specific prey items that were associated with a given rockfish species and distance from shore in both sample years. Only values that were found to be significant are reported.

Year	Species	Food Item	IV	<u>p</u>
2002	Canary	euphausiid larvae	43.0	< 0.001
2006	Darkblotched	euphausiids	66.8	< 0.001
	Yellowtail	copepods	37.4	< 0.001
	Distance (km)			
2002	20-29	euphausiid eggs	26.6	0.005
	60+	euphausiid larvae	57.6	< 0.001
		Chaetognath	10.6	0.040
2006	20-29	copepods	32.4	0.012
	60+	"other"	39.0	0.007
	Length (mm)			
2002	21-30	euphausiid larvae	27.9	0.035
	31-40	crustacean	37.6	0.034
2006	41-50	copepods	44.1	0.001

FIGURE LEGENDS

Figure 1 Sampling locations for this study.

Figure 2 Species composition binned by station location at 10 km intervals for 2000/2002 (A) and 2006 (B).

Figure 3 Diets of juvenile rockfishes for 2000/2002 (top) and 2006 (bottom) by percent of total weight of major prey categories.

Figure 4 Mean δ^{13} C v. δ^{15} N values (± 1 SE) for rockfish and prey items from 2000/2002 and 2006. Upper ovals enclose juvenile rockfish from each time period. The arrow on left indicates approximate enrichment on N equivalent to an increase in one trophic level.

Figure 5 NMS ordination of juvenile rockfish diets from 2006 with axes 1 and 2 representing 69.0% and 25.5% of the variance respectively. Crosses (+) represent prey type scores in the ordination space. Vectors shown have $r^2 > 0.20$.









