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A Feeding-Ecology-Based Approach to Evaluating Nursery Potential of Estuaries for Black Rockfish

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Abstract

Previous work suggests that Oregon estuaries function as nursery habitat and may play an important role in settlement of Black Rockfish *Sebastes melanops*. No research, however, has been conducted on juvenile Black Rockfish feeding ecology in estuarine habitats, which is necessary to evaluate habitat use and quality. We examined stomach contents and carbon and nitrogen stable isotope ratios for juvenile Black Rockfish collected from May to September in 2016 and 2017 at both anthropogenic (dock) and natural (eelgrass *Zostera marina*) habitats in Yaquina Bay, a marine-dominated estuary on the central Oregon coast. We found consumption of 94 different prey items, the majority of which are estuary derived, and benthic prey were most frequently consumed. In general, it appears that fish are feeding in the habitat in which they are caught, with marine-fouling prey being consumed in greater abundances at the dock habitat, whereas algae- or eelgrass-associated species were consumed in greater abundances at the eelgrass habitat. The increase in both $\delta^{15}N$ and $\delta^{13}C$ values in muscle tissue seasonally and the positive correlation with upwelling in 2016 suggests that upwelled, oceanic waters were the primary source of nutrients to Yaquina Bay in 2016. The high variability in $\delta^{15}N$ and general increase in $\delta^{13}C$ seasonally in 2017 suggests that oceanic waters were still present but may not have been the dominant nutrient source. Yaquina Bay appears to be an important foraging ground for juvenile Black Rockfish during summer months, providing a diversity of prey items, with special importance of benthic and eelgrass-associated prey. Our results support the hypothesis that estuaries can function as a nursery habitat for Black Rockfish, although additional data is needed to provide an absolute designation. Changes in benthic communities or available habitat may have negative effects on foraging ability, and thus nursery function, and should be considered during management decisions.

Identifying nursery and essential fish habitat is a critical process for the effective conservation and management of fish stocks (NMFS 2010). Most studies classify an area as a nursery if higher abundances of juveniles or faster growth rates are observed compared with other areas (Beck et al. 2001). This classification has recently been improved as a habitat where juveniles of a species contribute more, on average, to adult recruitment compared with other juvenile fish habitats for that species (Beck et al. 2001). This improved nursery definition moves beyond simple abundance estimates and emphasizes the importance of settled juveniles successfully reaching reproductive maturity to contribute to the stock. Under the Magnuson–Stevens Fishery Conservation Management Act, "essential fish habitat" means "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity" (NMFS 2010). Understanding how a fish uses a specific habitat contributes to the identification of nursery and essential fish habitat.

Due to their inherently high primary productivity, estuaries provide habitat for a diverse array of species (Beck et al. 2001). Although estuaries along the northeastern Pacific Ocean shore are smaller and fewer in number compared with those on the northwestern Atlantic Ocean shore (Hickey and Banas 2003), they have been found to be important nursery grounds for ecologically and economically important species of marine invertebrates and fish (Hughes et al. 2014). Northeastern Pacific Ocean estuaries, however, have experienced major habitat alterations due to human development, including dredging and construction of jetties and marine docks (OCMP 2016), many of which have replaced natural habitats, such as beds of eelgrass *Zostera marina* (Lewis and Henkel 2016). With major anthropogenic changes occurring in estuarine habitats, understanding the biological and environmental interactions of species is an essential step to understanding the function of estuarine habitats (Elliot et al. 2002; Lotze et al. 2006) and can subsequently help managers prioritize valuable habitats for protection.

A key biological interaction to assess estuarine function is feeding ecology, which provides insight into the prey resources and the source of nutrients provided by a specific habitat. An important feature for estuarine food webs in the northeastern Pacific Ocean is upwelling as it brings cool, saline, nutrient-rich water from the deep, which is then transported to nearshore waters via advection during wind relaxation and then into estuaries through tidal exchanges (Roegner et al. 2002; Miller and Shanks 2004). During years of strong upwelling off the Oregon coast, increased prey stability has been observed for pelagic nekton compared with years of reduced upwelling (Brodeur and Pearcy 1992). Additionally, river discharge is an important feature for estuarine food webs due to the transport of dissolved nutrients and terrestrial sediments into estuaries, but reductions in densities of pelagic zooplankton have been observed in years of extreme high-flow conditions in northeastern Pacific Ocean estuaries (Jones et al. 1990).

In spite of our current knowledge base, basic information is missing on the feeding ecology for the sensitive juvenile life stage of many species, especially habitat-specific information (Abrantes et al. 2015). When food is abundant, fish can store excess energy in the form of fat, but when food supplies are restricted those energy reserves must be utilized, thus decreasing condition and growth rate of the individual (Busacker et al. 1990). High growth rates and a larger size at age have been linked to food availability (Zenitani et al. 2007; Robert et al. 2009), consistent feeding success (Dower et al. 2009; Pepin et al. 2015), and consumption of more food (Pepin et al. 2015). Conversely, food limitation throughout the first year of life can contribute significantly to recruitment variability (Cowan et al. 2000) and lead to reduced growth rates and smaller sizes, resulting in increased overwintering

mortality (Miller and Kendall 2009). As estuarine zooplankton, invertebrate, and fish communities vary with habitat and substrate type (Hosack et al. 2006; França et al. 2009; Dalley et al. 2017), some habitats may be more important in terms of prey availability than others, and habitat-specific foraging should be considered when characterizing estuarine food webs.

Common methods used to describe feeding ecology include examining stomach contents directly and determining carbon and nitrogen stable isotope ratios ($^{12}C/^{13}C$, $^{14}N/^{15}N$) of fish muscle tissue (Bowen 1996; Layman et al. 2007). Stable isotopes are found to occur naturally in the environment, and their distribution reflects a history of physical and metabolic processes within the ecosystem, recording information about the origin of samples (Peterson and Fry 1987). Stable isotopes are a useful tool to complement and verify stomach content analysis and are used to reconstruct a longer-term perspective on diet as isotopic turnover rates for muscle tissue can reflect feeding behavior from the past several months, thereby providing insight into broader diet and feeding relationships of many organisms (Peterson and Fry 1987; Wells et al. 2008). Stable isotopes have been used in estuaries to examine the role of habitats as energy sources for fish (Vinagre et al. 2011; Stowell et al. 2019), the reliance on nutrients supplied from upwelling events (Carlier et al. 2015), the relative importance of fisheries food web support from benthic and pelagic production (Malek et al. 2016), and the effect of river flow in food web interactions (Vinagre et al. 2011). Stable isotopes have been successful in detecting changes in nutrient concentrations from upwelling events as increased carbon and nitrogen isotope ratios and values have been observed under upwelling conditions and periods of low river flow (Lee and Brown 2009; Vinagre et al. 2011; Carlier et al. 2015; Dyer et al. 2019).

Northeastern Pacific Ocean rockfishes *Sebastes* spp. are highly diverse, with around 96 documented species (Love et al. 2002), and have traditionally made up a large percentage of the U.S. West Coast groundfish fishery. Of particular importance to Oregon's recreational fisheries is Black Rockfish *S. melanops*. Although Black Rockfish generally settle in nearshore benthic habitats, defined here as those waters outside the mouth of an estuary to 3 nautical miles, the presence of juveniles has been documented in multiple habitat types in Oregon estuaries (Pearcy and Myers 1974; Bottom and Forsberg 1978; Appy and Collson 2000; Miller and Shanks 2005; Gallagher and Heppell 2010; Dauble et al. 2012; Lindsley 2016), with Oregon estuaries found to be essential fish habitat for juvenile Black Rockfish (Gallagher and Heppell 2010). This utilization and designation suggests that these estuaries function as a nursery area and may play an important role in the settlement and recruitment of Black Rockfish (Dauble et al. 2012; Lindsley 2016).

Although research has been conducted on juvenile benthic rockfish abundances in multiple Oregon estuaries (Dauble et al. 2012), to our knowledge no published studies have examined diet and stable isotopes of any juvenile rockfish species in Oregon estuaries. The majority of work conducted on juvenile rockfish feeding ecology has been in nearshore and offshore environments off the coast of California or Alaska (Carlson and Haight 1976; Hallacher and Roberts 1985; Singer 1985; Reilly et al. 1992; Rau et al. 2001; Miller and Brodeur 2007; Studebaker and Mulligan 2008, 2009; Boldt and Rooper 2009); the only studies performed in Oregon waters were in more offshore environments and on the pelagic life stage (Brodeur and Pearcy 1984; Bosley et al. 2014), although one agency report from 1977 examined the diet of unidentified benthic juvenile rockfish in Tillamook Bay estuary, Oregon (Forsberg et al. 1977). Juvenile rockfish are generally zooplanktivorous, with some species being generalists while others have a more restricted diet (Brodeur and Pearcy 1984; Singer 1985). Ontogenetic, habitat, spatial, temporal, and species-specific differences in diets have been observed for both pelagic and benthic juvenile rockfish (Carlson and Haight 1976; Brodeur and Pearcy 1984; Singer 1985; Boldt and Rooper 2009; Bosley et al. 2014). With large dietary variations, further investigation into feeding ecology of juvenile benthic rockfishes at multiple habitat types in Oregon estuaries is necessary to evaluate the role that these potential nursery areas play in foraging. To evaluate the role of Oregon estuaries for juvenile Black Rockfish feeding ecology during their benthic stage, we examined stomach contents and stable isotope values for individuals collected at both anthropogenic and natural habitats over 2 years in a marine-dominated estuary on the central Oregon coast.

METHODS

Sample collection and processing.— Juvenile Black Rockfish were sampled monthly in 2016 and 2017 on the low tide during the full and new moons in Yaquina Bay, Oregon. Sampling occurred once per month from October to March and twice per month from April to September. Fish were collected using a pair of unbaited, rectangular minnow traps, which are approximately 61×61 cm on the base and 46 cm tall, with a 1.27-cm-wide vertical opening and 0.64-cm mesh size. Weighted traps were placed at three anthropogenic (dock) and three natural (eelgrass) sites (Figure 1) and fished through two tidal cycles for approximately 24 h. Both dock and eelgrass habitats were sampled from April to September in 2016 and 2017, but high winter tides only allowed sampling at the dock habitat from October to March in 2016 and 2017. As the eelgrass sites could not be accessed from October to March and only one juvenile Black Rockfish was collected at a dock habitat in April 2017, only samples from May to September for 2016 and 2017 were analyzed.

All species caught were counted, and rockfish species were euthanized and taken back to the laboratory for further processing. Each individual was measured for length (mm TL) and weight (0.01 g) and the caudal fin was clipped for genetic analysis before being frozen for storage. Genetic analysis was used for species identification as juvenile rockfish are generally difficult to visually identify to species. Fin clips were sent to the Molecular Ecology and Genetic Analysis Lab at the National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center in Santa Cruz, California, for species identification.

Environmental conditions.— Temperature, salinity, freshwater discharge, and the Coastal Upwelling Transport Index data were gathered to examine the environmental conditions of Yaquina Bay during 2016 and 2017 and to determine if these impacted juvenile rockfish feeding ecology. Temperature (°C) and salinity (‰) were discretely measured when traps were set and retrieved for each sampling event using a YSI-85 multimeter. Two tributaries, Yaquina River and Elk Creek, contribute freshwater inflow almost equally into Yaquina Bay (State Water Resources Board 1965). The U.S. Geological Survey and the State of Oregon Water Resources Department only gauges the Yaquina River at a station 51 km upstream from the mouth of the estuary near Chitwood, Oregon (station 1430600). Discharge data (mean daily flow; m^3/s) from station 1430600 were gathered from the State of Oregon Water Resources Department (https://www.oregon.gov/owrd) for 2016 and 2017.

The metric to evaluate upwelling intensity along the northeastern Pacific Ocean shore is traditionally the Bakun Upwelling Index, but this index does not provide a complete picture of coastal upwelling as it does not capture (1) wind stress curl-driven upwelling associated with along wind gradients, (2) the contribution of the cross-shore geostrophic flow, or (3) the quality of upwelled waters (Jacox et al. 2018). Two new upwelling indices have been developed with technological advances to address the shortcomings of the Bakun Upwelling Index by relying on the Regional Ocean Modeling System with four-dimensional variational data assimilation (Jacox et al. 2018). The Coastal Upwelling Transport Index provides improved estimates of upwelling intensity and accounts for cross-shore geostrophic flow; the Biologically Effective Upwelling Transport Index provides estimates of the amount of nitrate being upwelled and can offer insight into the quality of upwelled waters (Jacox et al. 2018). The Coastal Upwelling Transport Index was the chosen metric to evaluate marine influence on Yaquina Bay. Daily values of the Coastal Upwelling Transport Index (m^2/s) at 45°N were gathered from the National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center, Environmental Research Division (https://oceanview.pfeg.noaa.gov/products/upwelling/cutibeuti).
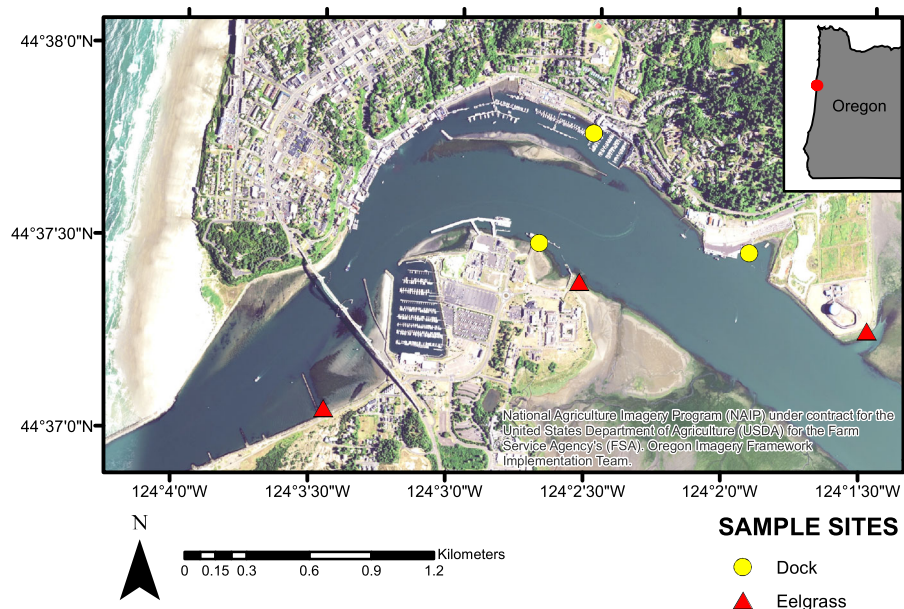
FIGURE 1. Map of the three dock and three eelgrass habitat sites in Yaquina Bay, Oregon, where juvenile Black Rockfish were collected.

Stable isotopes.— A subset of juvenile Black Rockfish muscle tissues was subject to stable isotope analysis ($n =$ 264; Table 1). To determine the sample size needed for each group, 38 samples from June 2016 and 60 samples from July 2016, comprised of both dock and eelgrass habitats, were analyzed to determine at what sample size the variance stabilized (leveled off). Fish from June and July of 2016 were chosen as these were the 2 months with large enough sample sizes from both habitat types. The variance began to stabilize around a sample size of 10 for both carbon ($\sigma = 0.22$) and nitrogen ($\sigma = 0.03$); therefore, a minimum of 10 samples per habitat per month in each year were analyzed. The only time a minimum sample size could not be achieved was at the dock habitat in May 2017 and at the eelgrass habitat in September in both 2016 and 2017 as less than 10 fish were collected (Table 1).

Epaxial muscle tissue was taken from the left side of each juvenile Black Rockfish selected for analysis. Tissues were dried at 60°C for 24 h in a drying oven and then homogenized using an agate mortar and pestle. Tissues were prepared per the sample preparation guidelines supplied by the Oregon State University Stable Isotope Laboratory, where samples were sent for analysis. Samples were analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) with an EA/DeltaPlus continuous-flow isotope ratio mass spectrometer. Carbon isotope data were calibrated using the international standard USGS40 (glutamic acid 40, $\delta^{13}C$ $= -26.389‰$ versus Vienna Pee Dee Belemnite) and the internal laboratory standard SUL Sucrose ($\delta^{13}C$ $= -11.85‰$ versus Vienna Pee Dee Belemnite). Carbon ($\delta^{13}C$) was not corrected for lipid as lipid content was

TABLE 1. Number of muscle tissue samples and stomachs per year, by month and habitat type (dock or eelgrass), used in the stable isotope and diet analyses of juvenile Black Rockfish collected in Yaquina Bay, Oregon.

Year	Month	Muscle tissues		Stomachs	
		Dock	Eelgrass	Dock	Eelgrass
2016	May	10	10	14	20
	Jun	10	28	15	68
	Jul	30	30	18	25
	Aug	10	14	8	25
	Sep	10	7	26	6
2017	May	8	10	9	4
	Jun	10	10	15	19
	Jul	10	11	15	11
	Aug	10	10	10	3
	Sep	23	3	17	3

consistently low (C:N < 3.5; Post et al. 2007). Nitrogen isotope data were calibrated daily using the international standards USGS40 ($\delta^{15}N = -4.52‰$ versus air) and IAEA-N2 (ammonium sulfate, $\delta^{15}N = +20.3‰$ versus air).

Final isotopic ratios are reported relative to the internal and international standards, calculated as follows:

$$\delta_{sample}() = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1{,}000,$$

where R represents the ratio of heavy to light isotope. Additionally, one juvenile Black Rockfish sample was

chosen as an interassay control and was run in every batch to assess instrument precision. The SE and CV ($100 \times$ SD/mean) of the personal standard for $\delta^{13}C$ were 0.01 and 0.24%, respectively, and the SE and CV for $\delta^{15}N$ was 0.02 and 0.44%, respectively; thus, the machine was considered stable over time.

Two separate ANOVAs were fit with type III sum of squares, one for $\delta^{13}C$ and one for $\delta^{15}N$, to evaluate the influence of habitat, month, and year on isotopic ratios. Linear regressions were first performed to see if fish length was correlated to $\delta^{13}C$ and $\delta^{15}N$. Size was not correlated to $\delta^{15}N$ ($P > 0.05$; $R^2 = 0.01$) but was positively correlated to $\delta^{13}C$ ($P < 0.0001$; $R^2 = 0.39$). To correct for length of fish for $\delta^{13}C$ values, residuals from the linear regression ($\delta^{13}C \sim TL$) were used as the dependent variable in the carbon ANOVA. Pairwise comparisons using Tukey's honestly significant difference were conducted using the estimated marginal means (also called least-squares means) from the "emmeans" version 1.3.3 R package (Lenth 2019). Significance was set at $P < 0.05$. Diagnostic plots of models were examined visually, and both met the assumptions of normality and homogeneity of variance.

Additionally, Spearman's rank correlation coefficients were calculated to test for associations between $\delta^{13}C$ and $\delta^{15}N$ values and upwelling and discharge. Temperature and salinity were not evaluated for associations as they covaried with upwelling and discharge, and the interest was to look at broader environmental drivers. Monthly averages of $\delta^{13}C$ and $\delta^{15}N$ were compared with the average value of the upwelling index and discharge of the previous month. For example, the average $\delta^{13}C$ and $\delta^{15}N$ values for the month of May were compared against the Coastal Upwelling Transport Index and discharge values for the month of April. As $\delta^{13}C$ and $\delta^{15}N$ isotopic turnover times are unknown for juvenile rockfish muscle tissue, a 1-month lag was chosen to reflect an average turnover time for muscle tissue of a juvenile fish, which can generally express a change in environment or diet within days, weeks, or months (Vander Zanden and Hulshof 1998; Bosley et al. 2002; Sweeting et al. 2005; Buchheister and Latour 2010).

Stomach contents.— All juvenile Black Rockfish stomachs collected from May to September were examined, except for June and July 2016 and June 2017 where a random subset was chosen due to the large catch during these months (see Figure 2A), resulting in a total of 331 stomachs used for analysis (Table 1). Stomachs were removed, placed in 10% formalin for a minimum of 48 h, and transferred to 70% ethanol solution until examination. During examination, stomach contents were removed, identified and sorted to the lowest taxonomic level possible, and counted. Juvenile Black Rockfish were placed in five size-classes based on total length: individuals between 30–49, 50–59, 60–69, 70–79, and ≥80 mm. Only three juvenile

Black Rockfish collected were between 30–39 mm and thus were combined with those between 40–49 mm to form the 30–49-mm group, and only three juvenile Black Rockfish were ≥90 mm and thus were combined with those between 80–89 mm to form the ≥80 mm group. The 10-mm bins were chosen to achieve a balance between an even distribution of sample sizes among size-classes and having enough groups, but not too many, to evaluate ontogenetic shifts in diet.

The quantification of stomach contents was accomplished by two methods: (1) percent frequency of occurrence (%FO) and (2) percent composition by number (%N). Percent by weight or volume were not chosen for analyses as many of the prey items were too small to weigh and results would have been biased when only parts of an organism were present. For analyses, contents were first sorted into 12 major prey categories (amphipod, polychaete, barnacle, bivalve, copepod, crab, crustacean, cumacean, fish, mysid, shrimp, zooplankton) and then were further subdivided into lower taxonomic levels among all major prey categories (Table 2). Many stomachs contained unclassifiable material, defined as material that does not included any bones, hard parts, or recognizable features for further classification into one of the prey categories. Unclassifiable material was excluded from %N and %FO analyses because an accurate count could not be obtained and thus numerical contribution could not be determined; other excluded categories for analyses were prey items that occurred in <5% of the sample units, which included cladocerans, Diptera pupae, and nematodes or items that were thought to be incidentally eaten, which included sand, sticks, and wood pieces.

A habitat association (benthic or pelagic) was assigned to each prey item found in the diets of juvenile Black Rockfish based upon Carlton (2007) and Hiebert et al. (2016). Habitat associations could not be determined for unidentified copepods, crustaceans, and fishes, but unidentified amphipods, cumaceans, and shrimps were assumed to be benthic (Supplementary Table S.1 provided separately online). Percent composition by number (%N) was then summed for each identifiable prey item to examine the contribution of benthic- and pelagic-associated prey to the diet. Presence of each prey item in Yaquina Bay was also noted from a literature search (Supplementary Table S.1).

Abundance data were $\log(x + 1)$ transformed to account for zeros in prey categories and to downweigh highly abundant prey species. Bray–Curtis coefficients were used to construct a resemblance matrix to assess similarity between abundance proportions of prey items for individuals. A permutational analysis of variance (PERMANOVA) was used to test for significant differences ($P < 0.05$) in prey abundances between size-classes, months,
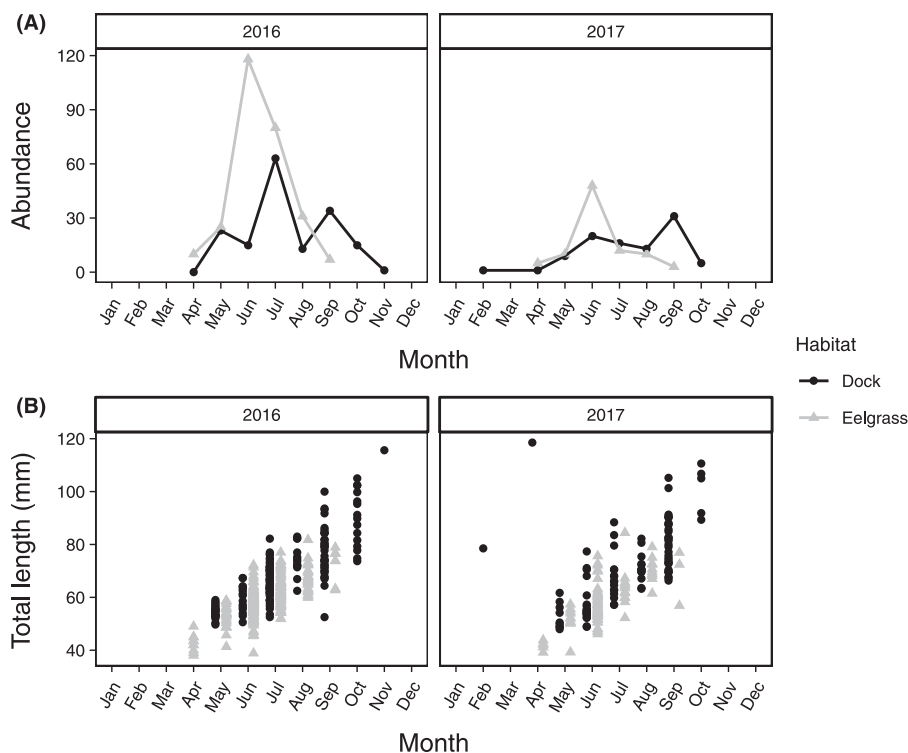
FIGURE 2. Graphs of **(A)** abundance and **(B)** total length (mm) of the 619 juvenile Black Rockfish collected at dock and eelgrass habitats in Yaquina Bay during 2016 and 2017.

years, and habitats. Statistical analyses to examine differences in diet were run with the PRIMER version 7 PERMANOVA+ statistical package (Anderson et al. 2008; Clarke and Gorley 2015).

RESULTS

A total of 619 juvenile Black Rockfish were collected from Yaquina Bay in 2016 and 2017, with 359 from eelgrass habitat and 260 from dock habitat. Out of the 619 juveniles, 581 individuals were collected from the months of May to September. Juveniles (age 0) were present in the estuary from April until October or November for both years, but there were a greater number of individuals collected in 2016, especially in June and July (Figure 2A). Sizes ranged from 38 to 84 mm TL at the eelgrass habitat and from 48 to 118 mm TL at the dock habitat. The full-year size range was captured at the dock habitat as sampling occurred in all months; however, sampling at the eelgrass habitat did not occur from October to March, so the full-year size range is unknown for the eelgrass habitat. Total length of individuals increased during the year, and in general there were even size distributions between habitat types (Figure 2B). The one individual caught in February 2017 (78.5 mm) and the largest individual caught in April 2017 (118 mm) likely overwintered in the estuary. Settlement from the larval pelagic stage to the benthic juvenile stage for Black Rockfish has previously been found to occur from May to July at 30–40 mm long (Love et al. 2002); therefore, these fish likely settled in the estuary the previous year based on their large size for the month in which collected.

Environmental Conditions

Temperature during sampling was highly variable across months for 2016 and 2017 (Figure 3A). In general, temperature increased from January to July in both 2016 and 2017 and was on average greater in 2017 than 2016 from May to August (Figure 3A). Salinity showed similar patterns for both 2016 and 2017, with low values during winter and early spring months (January to April) and increasing values during late spring and summer months (May to September; Figure 3B). Salinity values were greater in 2016 compared with 2017 from the months of May to September (Figure 3B).

Upwelling values generally increased from May to August and began to decline in September during 2016, whereas values increased from May to July and began to decline in August during 2017 (Figure 3C). Upwelling was greater from April to June in 2016 than in 2017 (Figure 3C), with the larger value in April suggesting upwelling began sooner in 2016. Discharge generally decreased from February to September for both 2016 and 2017 (Figure 3D). Higher average mean daily flow rates were observed

TABLE 2. The number and frequency of occurrence (%FO) of prey items found in the diet of juvenile Black Rockfish at dock ($n = 162$) and eelgrass ($n = 189$) habitats in Yaquina Bay. In the first column, bold items represent the 12 prey categories used in analyses. Prey items under "Other prey" were excluded from analyses. The sample sizes listed here are before exclusion of the "Other prey" category and those items thought to be incidentally eaten (i.e., sand, sticks, and wood pieces).

Prey item	Count		%FO	
	Dock	Eelgrass	Dock	Eelgrass
Amphipod				
Unidentified amphipod (order Amphipoda)	80	82	22.8	25.4
Allorchestes angusta	2		1.2	
Americhelidium sp.		2		1.1
Family Ampithoidae				
Ampithoidae	2		0.6	
Ampithoe spp.	1	4	0.6	1.6
Ampithoe lacertosa	1	3	0.6	1.6
Ampithoe valida	3	1	1.9	0.5
Atylus tridens	38	17	8.6	1.6
Caprella spp.	27	9	6.2	4.2
Caprella anomala	1	2	0.6	1.1
Caprella drepanochir	3	2	1.9	1.1
Family Corophiidae	30	10	10.5	5.3
Americorophium spp.	5		1.2	
Americorophium brevis	21	2	7.4	1.1
Monocorophium spp.	5	5	3.1	2.1
Monocorophium acherusicum	18	14	4.3	5.3
Monocorophium californianum	5	3	1.2	1.6
Superfamily Calliopioidea				
Calliopius sp.	2	1	1.2	0.5
Paracalliopiella sp.		1		0.5
Pontogeneia spp.	2	14	1.2	3.7
Superfamily Gammaroidea				
Gammaroidea	3	27	1.9	8.5
Anisogammarus pugettensis	11	78	6.2	19.0
Eogammarus confervicolus	1	10	0.6	1.6
Gnathopleustes sp.	3	1	1.2	0.5
Grandidierella japonica	1	10	0.6	3.2
Superfamily Haustorioidea				
Eobrolgus spinosus	15	1	1.2	0.5
Eohaustorius sp. (likely *E. estuaris*)	1		0.6	
Family Ischyroceridae	2	9	0.6	3.2
Jassa spp.	6	1	3.1	0.5
Hyperiid amphipods	33		2.5	
Megamoera sp.	3	3	0.6	1.6
Protohyale frequens		1		0.5
Barnacle				
Barnacle (infraclass Cirripedia)	10	2	5.6	1.1
Barnacle cyprid	28	43	11.1	11.6
Barnacle nauplii	1		0.6	
Bivalve				
Bivalve (class Bivalvia) shell	14		7.4	
Bivalve egg/larvae	2	2	1.2	0.5

TABLE 2. Continued.

Prey item	Count		%FO	
	Dock	Eelgrass	Dock	Eelgrass
Copepod				
Subclass Copepoda	8	36	1.2	5.8
Order Calanoida				
Unidentified calanoid	139	481	13.0	16.9
Acartia longiremis	14	37	0.6	0.5
Epilabidocera sp.		1		0.5
Eurytemora sp.		5		1.1
Calanus spp.		8		0.5
Mertridia sp.		15		0.5
Order Cyclopoida				
Unidentified cyclopoid	25	36	5.6	6.9
Ditrichocorycaeus anglicus		2		0.5
Triconia spp.	1	8	0.6	3.7
Order Harpacticoida				
Unidentified harpacticoid	89	833	22.8	47.6
Family Miraciidae		1		0.5
Family Peltidiidae		1		0.5
Thalestris longimana		1		0.5
Zaus spp.	1	19	0.6	6.9
Crab				
Crab megalope				
Infraorder Brachyura	60	12	11.1	3.7
Metacarcinus magister	18	1	3.7	0.5
Family Paguridae	43	5	5.6	2.6
Family Porcellanidae	4		1.2	
Family Pinnotheridae	20	9	6.8	3.2
Crab zoea				
Family Porcellanidae	190	30	14.2	5.3
Pachycheles sp.				
Petrolisthes sp.				
Family Pinnotheridae	22	5	6.8	2.6
Crustacean				
Unidentified crustacean	9	10	4.3	3.7
Argulus sp.		1		0.5
Family Euphausiidae		1		0.5
Order Isopoda	1	1	0.6	0.5
Suborder Asellota		1		0.5
Gnorimosphaeroma spp.	4		2.5	
Pentidotea sp.		1		0.5
Order Tanaidacea	1	6	0.6	2.6
Cumacean				
Unidentified cumacean (order Cumacea)	37	11	4.3	3.2
Cumella vulgaris	15	36	6.8	12.7
Family Diastylidae	3	3	1.9	1.6
Mesolamprops dillonensis		3		1.6
Nippoleucon hinumensis	1	2	0.6	1.1
Fish				
Unidentified fishes	12	9	5.6	4.8

TABLE 2. Continued.

Prey item	Count		%FO	
	Dock	Eelgrass	Dock	Eelgrass
Family Gadidae		1		0.5
Family Pleuronectidae	1		0.6	
Mysid				
Order Mysida	109	177	13.0	11.1
Polychaete				
Class Polychaeta	11	24	6.2	4.8
Shrimp				
Caridean shrimp	19	32	8	7.9
Shrimp zoea	95	9	10.5	2.6
Neotrypaea californiensis	3		0.6	
N. californiensis zoea	6		0.6	
Family Crangonidae				
Crangon spp.	9	6	4.9	3.2
Crangon franciscorum	2		1.2	
Crangon nigricauda	4	7	2.5	3.7
Lissocrangon stylis		1		0.5
Genus *Heptacarpus*				
Heptacarpus spp.	6	1	3.7	0.5
Heptacarpus sitchensis		1		0.5
Zooplankton				
Unidentified zooplankton	6	23	3.7	1.6
Ascidian larvae	3		1.2	
Other prey				
Superorder Cladocera				
Evadne or *Pseuoevadne* spp.	1		0.6	
Class Insecta				
Order Diptera (pupae)	1		0.6	
Phylum Nematoda	41	37	17.3	14.3

in 2017, especially from February through May (Figure 3D), implying a greater freshwater influence which was also corroborated by lower salinity values in in 2017 compared with 2016 (Figure 3B).

Stable Isotopes

Values for δ^{13}C ranged from $-20.83‰$ to $-15.98‰$. The month $\times$ habitat, month $\times$ year, and habitat $\times$ year interaction terms were significant contributors to the variation in juvenile Black Rockfish δ^{13}C values (ANOVA: $P < 0.05$; Table 3). Overall, δ^{13}C values increased from May to September in 2016 at both habitats and in 2017 at the eelgrass habitat, but values for each month were more negative in 2017 than 2016 (Figure 4A). In 2016, δ^{13}C values differed between dock and eelgrass habitats (ANOVA: $P < 0.05$), with a greater value observed at the eelgrass habitat than at the dock habitat. Results of δ^{13}C pairwise comparisons for the month $\times$ year, month $\times$ habitat, and habitat $\times$ year interaction terms can be found in

Supplementary Tables S.2, S.3, and S.4, respectively. Carbon (δ^{13}C) values were positively, but not significantly, correlated to the previous months upwelling index value for both 2016 and 2017 (Spearman's rank correlation: $\rho = 0.7$, $P = 0.23$ and $\rho = 0.6$, $P = 0.35$, respectively; Supplementary Figure S.1A available separately online). Carbon (δ^{13}C) values were negatively correlated to the previous month's discharge value for both 2016 and 2017 ($\rho = -1$, $P = 0.01$ and $\rho = -0.9$, $P = 0.08$, respectively; Supplementary Figure S.1B), with less variability observed in 2016.

Values for δ^{15}N ranged from $10.99‰$ to $14.27‰$. Month and the month $\times$ year interaction were significant contributors to the variation in juvenile Black Rockfish δ^{15}N values (ANOVA: $P < 0.05$; Table 3). In general, δ^{15}N values in 2016 increased from May to September at both habitats, while a decrease in δ^{15}N values was observed in 2017 from June to August at the dock habitat and June to September at the eelgrass habitat (Figure 4B).
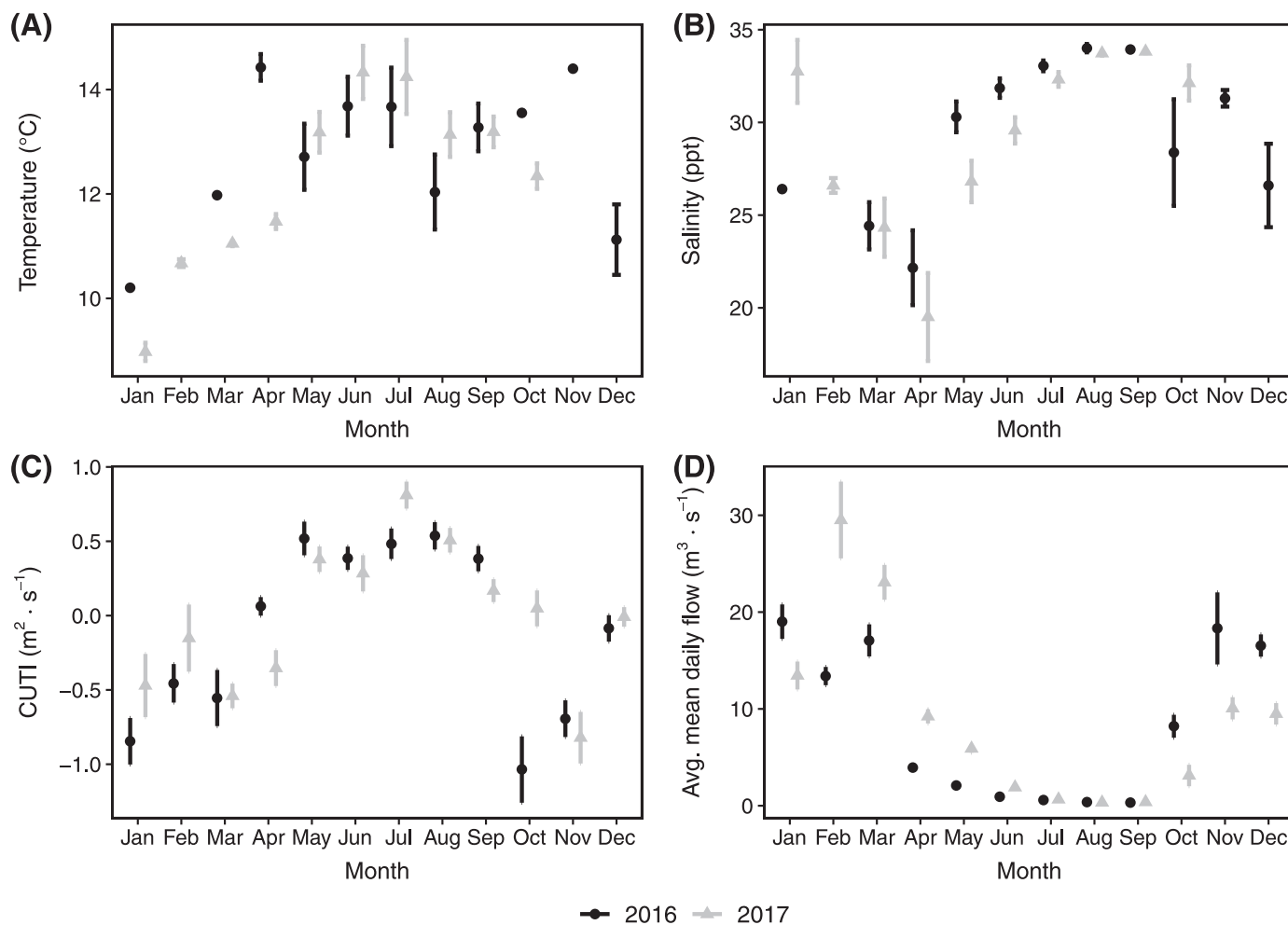
FIGURE 3. Average monthly values for **(A)** temperature (°C), **(B)** salinity (‰), **(C)** Coastal Upwelling Transport Index (CUTI; m^2/s) at 45°N, 125°W, and **(D)** discharge (mean daily flow; m^3/s) for the Yaquina River at station 1430600 near Chitwood, Oregon, for 2016 and 2017. Errors bars represent ±1 SE.

Nitrogen ($\delta^{15}N$) values for 2016 were also less variable in 2016 compared with $\delta^{15}N$ values in 2017. Results of $\delta^{15}N$ pairwise comparisons for the month × year interaction term can be found in Supplementary Table S.5. A positive, but not significant, correlation was found between $\delta^{15}N$ values and the previous months upwelling index value for 2016 (Spearman's rank correlation: $\rho = 0.6$, $P = 0.35$) but were not correlated for 2017 ($\rho = 0.1$, $P = 0.95$; Supplementary Figure S.2A). Similar to $\delta^{13}C$, $\delta^{15}N$ values were negatively correlated to the previous month's discharge value for 2016 ($\rho = -0.9$, $P = 0.08$) but were not correlated for 2017 ($\rho = -0.1$, $P = 0.95$; Supplementary Figure S.2B).

Stomach Contents

A total of 489 stomachs were analyzed for diet, with 451 of those being from individuals collected from May to September in 2016 and 2017. Out of the 451 samples, 20

stomachs were truly empty (4.4%; eelgrass: $n = 9$; dock: $n = 11$), 3 were damaged from extraction, and 77 contained only unidentifiable material. After taking out prey categories that occurred in <5% of the sample units and those thought to be eaten incidentally (see Methods), 331 stomachs were used in analyses (Table 1).

A total of 94 prey items were found in the stomachs of juvenile Black Rockfish (Table 2), the majority of which are identified inhabitants of Yaquina Bay (Supplementary Table S.1). A complete inventory of the benthic and pelagic zooplankton present in Yaquina Bay is difficult, so it is possible that all of the prey species consumed by juvenile Black Rockfish inhabit Yaquina Bay. The most abundant identifiable species within each large prey category were *Anisogammarus pugettensis* (amphipod prey category), barnacle cyprid (barnacle prey category), unidentified harpacticoids (copepod prey category), order Tanaidacea (crustacean prey category), family Porcellanidae zoea (crab

TABLE 3. Results of the individual analysis of variance (ANOVA) model testing for the effects of habitat (dock and eelgrass), month (May, June, July, August, and September), and year (2016 and 2017) on juvenile Black Rockfish δ^{13}C (carbon) and δ^{15}N (nitrogen) values. The δ^{13}C model was corrected for fish total length.

Isotope ratio	Source	Sum of squares	df	F-value	Pr($>F$)
δ^{13}C	Habitat	1.02	1	3.179	0.076
	Month	13.014	4	10.142	<0.001
	Year	38.611	1	120.359	<0.001
	Habitat × month	3.598	4	2.804	0.026
	Habitat × year	3.179	1	9.909	0.002
	Month × year	10.886	4	8.484	<0.001
	Habitat × month × year	2.511	4	1.957	0.102
	Residuals	78.274	244		
δ^{15}N	Habitat	0.381	1	3.447	0.065
	Month	4.187	4	9.484	<0.001
	Year	0.053	1	0.476	0.491
	Habitat × month	0.645	4	1.461	0.215
	Habitat × year	0.004	1	0.035	0.851
	Month × year	7.253	4	16.427	<0.001
	Habitat × month × year	0.613	4	1.387	0.2390
	Residuals	26.933	244		

prey category), *Cumella vulgaris* (cumacean prey category), and zoea and juvenile shrimp (shrimp prey category). Overall, harpacticoid and calanoid copepods, mysid, Porcellanidae zoea, and unidentified amphipods were the most abundantly consumed prey and made up 60% of the total numerical abundance. Additionally, harpacticoid and calanoid copepods, unidentified amphipods, the amphipod *A. pugettensis* and mysids were the most frequently consumed prey (Table 2). General diversity was similar between habitats, with 73 and 76 prey items consumed at dock and eelgrass habitats, respectively. Species-specific amphipod consumption, however, varied between habitats; superfamily Gammaroidea (i.e., *A. pugettensis* and *Eogammarus confervicolus*), *Grandidierella japonica*, and *Pontogeneia* spp. were consumed in greater abundances at the eelgrass habitat, whereas *Atylus tridens*, family Corophiidae, superfamily Haustorioidea, and hyperiid amphipods (which were absent from eelgrass) were consumed in greater abundances at the dock habitat (Table 2).

Diet based on numerical abundances varied among size-classes of juvenile Black Rockfish, months within habitats, and months within years (PERMANOVA: $P <$ 0.05; Table 4). Prey item abundances differed among all juvenile Black Rockfish size-classes (PERMANOVA: $P <$ 0.05) except between fish 50–59 mm and 60–69 mm, between fish 60–69 mm and ≥ 80 mm, and between fish 70–79 mm and ≥ 80 mm (Supplementary Table S.6). As juvenile Black Rockfish size increased, consumption of copepods decreased and consumption of amphipods and crabs increased (Figure 5A). In every month, more

copepods were consumed at eelgrass habitat than at the dock habitat, whereas more crabs, shrimps, and amphipods were consumed at the dock habitat (Figure 5B). Although diet statistically differed among months within years, there were no striking patterns, except a large number of mysids were consumed in July 2017 (Figure 5C). Similar numerical abundances for each category across months, however, are observed for 2016 compared with 2017 (Figure 5C). Results of pairwise comparisons for the habitat × month and the year × month interaction terms can be found in Supplementary Tables S.7 and S.8, respectively.

Benthic prey was consumed more frequently and in greater numerical abundances than pelagic prey for all size-classes of juvenile Black Rockfish, habitats, months, and years (Table 5). The only exceptions were that a slightly greater numerical abundance of pelagic prey was consumed by the largest individuals (≥80 mm) and individuals collected in May and September (Table 5).

DISCUSSION

Here we document the most detailed description of juvenile Black Rockfish prey consumption that has been performed in any system to date, allowing for a deeper understanding of habitat use in regard to foraging for the early life stages of Black Rockfish. We found that juveniles consumed a wide diversity of prey items, the majority of which are estuarine in nature, implying that juvenile Black Rockfish forage within the estuary during summer
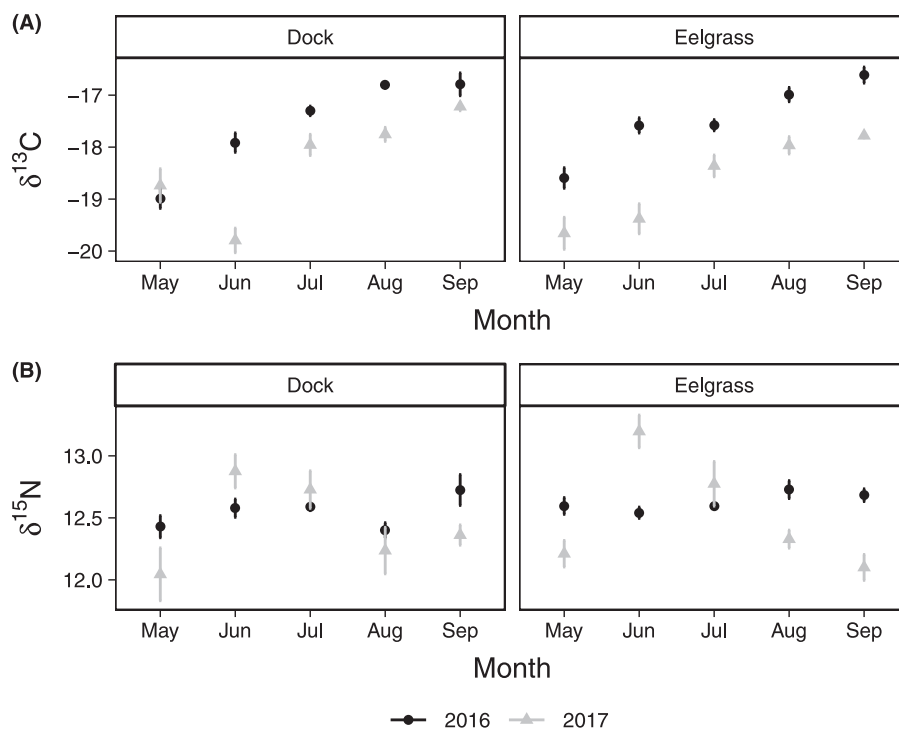
FIGURE 4. **(A)** Carbon (δ^{13}C) and **(B)** nitrogen (δ^{15}N) values of juvenile Black Rockfish muscle tissue for 2016 and 2017 across months from dock and eelgrass habitats. Errors bars represent ±1 SE.

TABLE 4. Permutational ANOVA (PERMANOVA) model testing the effects of juvenile Black Rockfish size-class (30–49, 50–59, 60–69, 70–79, and ≥80 mm TL), habitat (dock and eelgrass), month (May, June, July, August, and September), and year (2016 and 2017) on the diet of juvenile Black Rockfish based on numerical abundance.

Source and total	df	Sum of squares	Mean square	Pseudo-F	P (permutation)	Unique permutations
Size-class	4	30,696	7,674	2.812	0.0001	9,919
Habitat	1	10,524	10,524	3.856	0.0013	9,953
Month	4	28,059	7,014.8	2.570	0.0002	9,890
Year	1	6,372.5	6,372.5	2.335	0.0316	9,954
Habitat × month	4	17,798	4,449.6	1.630	0.0316	9,906
Habitat × year	1	2,822.4	2,822.4	1.034	0.4069	9,948
Month × year	4	26,843	6,710.8	2.459	0.0001	9,897
Habitat × month × year	4	9,704.7	2,426.2	0.889	0.6059	9,893
Residual	307	8.38×10^5	2,729.4			
Total	330	1.01×10^6				

months. One possible reason for the continual use of estuarine habitats from April to October for juvenile Black Rockfish may be due to the availability of diverse prey, leading to increased foraging opportunities. The continual use of estuarine habitats during the first year of life and the availability of diverse prey supports the hypothesis that marine-dominated estuaries on the Oregon coast can function as a nursery habitat for Black Rockfish, although additional data like growth and the contribution of

estuaries to adult populations are still needed to provide an absolute designation (Beck et al. 2001).

As juvenile Black Rockfish are found in multiple environments including estuaries and nearshore habitats, such as tide pools and kelp beds (Love et al. 2002; Studebaker et al. 2009), comparing what prey resources are consumed in these environments can offer insight into habitat use and ultimately habitat quality. Estuary-rearing juvenile Black Rockfish, those that spend their first year of life in
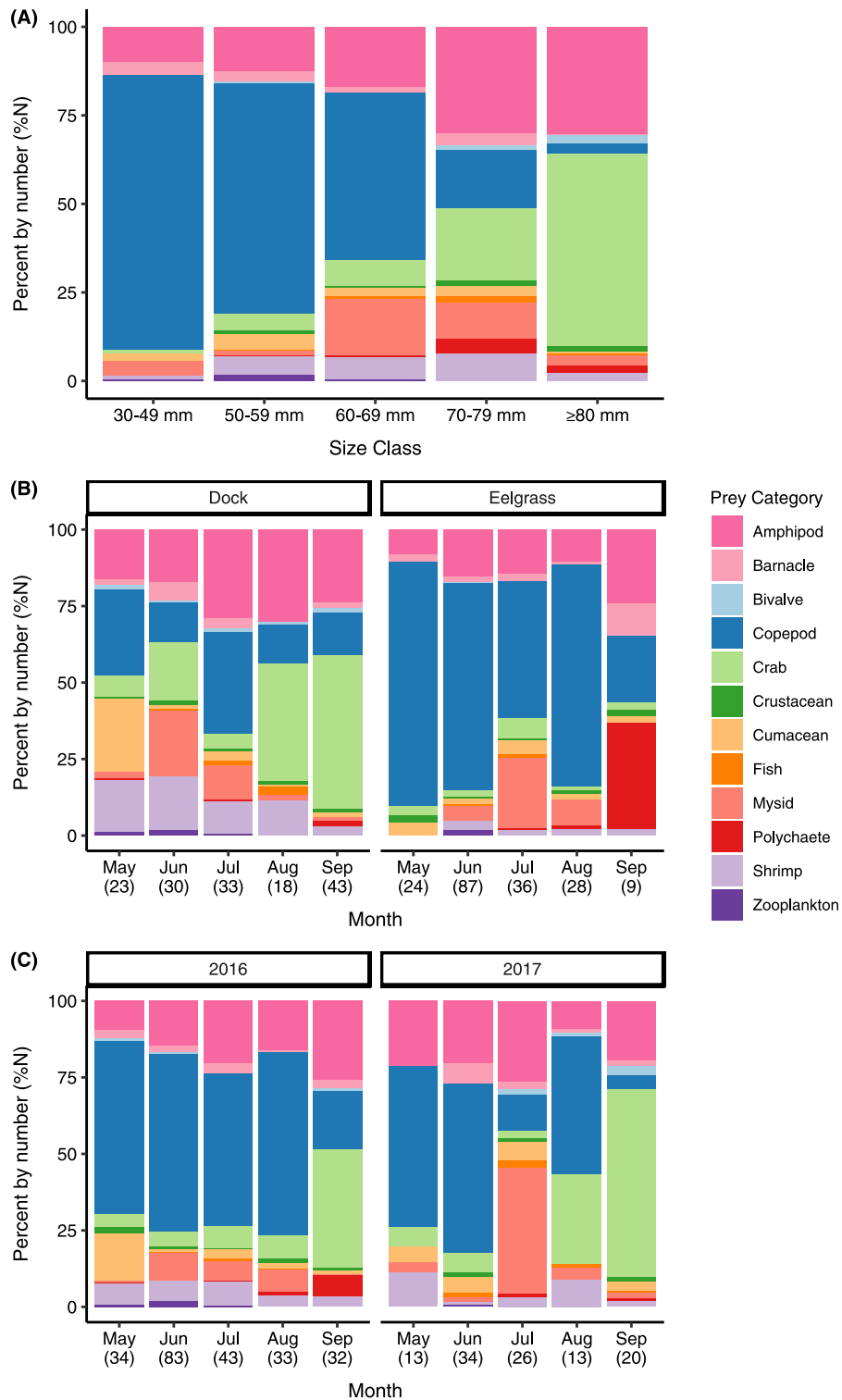
FIGURE 5. Percent by number (%N) of the 12 prey categories by **(A)** juvenile Black Rockfish size-class, **(B)** month at dock and eelgrass habitats, and **(C)** month in 2016 and 2017. The sample size for each group is listed in parentheses.

the estuary, appear to feed on similar benthic prey categories, such as gammarid amphipods and copepods (specifically harpacticoids), as the juveniles of rockfishes

in nearshore, benthic habitats (Forsberg et al. 1977; Studebaker and Mulligan 2008, 2009). Details of which species were in each prey category, however, were not

TABLE 5. Summary of percent by number (%N) and percent frequency of occurrence (%FO) of benthic- and pelagic-associated prey items in the diet of juvenile Black Rockfish of different size-classes, habitats, months, and years within Yaquina Bay, Oregon.

Factor	Group	%N Benthic	%N Pelagic	%FO Benthic	%FO Pelagic
Size-class	30–49 mm	57.5	33.7	93.8	50.0
	50–59 mm	70.1	27.8	89.5	47.6
	60–69 mm	54.6	43.7	95.4	51.4
	70–79 mm	75.9	21.4	88.9	39.7
	≥80 mm	40.7	58.4	90.0	65.0
Habitat	Dock	53.0	44.9	90.5	56.8
	Eelgrass	67.8	29.8	92.4	41.8
Month	May	47.2	48.5	85.4	58.3
	Jun	72.2	24.6	93.2	43.6
	Jul	69.3	28.7	92.8	47.8
	Aug	50.3	48.8	89.1	56.5
	Sep	45.3	54.1	94.2	44.2
Year	2016	61.4	36.3	92.9	46.0
	2017	65.3	32.2	88.7	53.8

provided in these studies and thus specific diet comparisons cannot be made. No study has compared feeding ecology of juvenile rockfish between estuarine and nearshore environments, and relatively few studies in general have examined this for other species. Studies examining benthic macrofauna in Oregon's nearshore environment have reported the presence of similar prey categories as was found in the stomachs of the estuarine juvenile Black Rockfish in the present study (i.e., *Crangon* spp., mysid, amphipod, cumacean, isopod) (Henkel et al. 2014; Henkel and Hellin 2015; Hemery et al. 2017); these studies, however, did not identify the specific species within these larger taxonomic prey categories, except *Crangon* spp. and mysid. The lack of studies providing species-specific accounts of zooplankton and benthic macrofaunal assemblages in Oregon's nearshore environments precludes direct comparison of estuarine and nearshore prey assemblages. Concurrent sampling of nearshore and estuarine juvenile rockfish is needed in order to directly compare feeding ecology and ultimately habitat quality between environments.

Conversely, different prey categories are consumed by juvenile rockfish in offshore pelagic habitats and nearshore kelp forests, with high consumption of euphausiids, copepods (specifically calanoid), crab zoea, and hyperiid amphipods (Singer 1985; Reilly et al. 1992; Miller and Brodeur 2007; Boldt and Rooper 2009; Bosley et al. 2014). The diet of individuals at the dock habitat in the present study more closely resembles that of offshore pelagic and kelp forest habitats, with increased consumption of pelagic

species (e.g., hyperiid amphipods). It should be noted that hyperiid amphipods have been found in plankton tows at a dock habitat in Yaquina Bay (B. D. Schwartzkopf and A. Harris, Oregon State University, unpublished data), so this prey item can be locally available; plankton tows were not conducted at eelgrass sites so the presence of hyperiid amphipods at this habitat cannot be stated. The dock sites were located in deeper water than the eelgrass sites, so it is possible that individuals at dock habitats feed throughout the water column due to the increased depth and vertical structure provided by the pilings, which can increase predation risk (Cermak 2002). If foraging throughout the water column at the dock habitat does increase vulnerability to predators, this strategy may not be as beneficial as foraging within eelgrass habitats, which are known to provide refuge from predators (Cowan et al. 2012).

In general, it appears that fish are feeding in the habitat in which they are caught. Prey species that are more associated with hard surfaces and marine-fouling communities (e.g., the amphipods *Ampithoe valida*, family Caprellidae, family Corophiidae, and *Jassa* spp., as well as barnacles, Paguridae megalope, *Gnorimosphaeroma* spp., and ascidian larvae; Carlton 2007; Hiebert et al. 2016), were consumed in greater numbers by juvenile Black Rockfish caught at the dock habitat. Interestingly, at least five invasive aquatic species were consumed by juvenile Black Rockfish (*A. valida*, *Caprella drepanochir*, *Monocorophium acherusicum*, *Grandidierella japonica*, *Eobrolgus spinosus*; Fofonoff et al. 2018), all of which were consumed in greater numbers at the dock habitat, except *G. japonica*. Two other potential invasive species that may have been consumed but could not be definitively identified to species are *M. insidiosum* and *Jassa marmorata*. Conversely, algae- or eelgrass-associated species (e.g., the amphipods *A. pugettensis*, *E. confervicolus*, and *Pontogeneia* spp., as well as harpacticoid copepods, *Pentidotea resecata*, *Cumella vulgaris*, and *Crangon nigricauda*; Carlton 2007; Hiebert et al. 2016) were consumed in greater numbers at the eelgrass habitat. Higher densities of epibenthic invertebrates, harpacticoid copepods, and benthic invertebrates have been found in eelgrass habitats compared with mudflats in a northeastern Pacific Ocean estuary (Hosack et al. 2006).

Interestingly, the isopod *Pentidotea resecata* was found to make up a large percentage of epifauna on eelgrass in Yaquina Bay (Hayduk et al. 2019), yet only one *P. resecata* was found in the diet of juvenile Black Rockfish. Although juvenile rockfish are thought to be opportunistic feeders (Reilly et al. 1992; Studebaker and Mulligan 2008), juvenile Splitnose Rockfish *S. diploproa* were found to selectively avoid certain prey on drift vegetation habitat off Washington (Shaffer et al. 1995). Juvenile rockfish have been found to play a role in local invertebrate recruitment (Studebaker and Mulligan 2008), with

decreased numbers of barnacle cyprids found when juvenile rockfish abundances are high (Gaines and Roughgarden 1987). The green color of *P. resecata* against eelgrass blades could provide camouflage (Hiebert et al. 2016), or juvenile Black Rockfish may be prey selective. Juvenile Black Rockfish would potentially be an ecosystem driver if they are selecting against *P. resecata*, which could allow *P. resecata* population abundances to remain high.

Marine waters have been shown to be the dominant source of nutrients during the dry season (summer) in Yaquina Bay due to the ingress of upwelled waters into the bay during tidal exchanges (Lee and Brown 2009). Lower $\delta^{13}C$ values have been found for terrestrial carbon sources compared with that of marine carbon sources (Dunton et al. 2012; Whitney et al. 2018), with an increase in $\delta^{13}C$ values observed under upwelling conditions and periods of low river flow (Vinagre et al. 2011; Carlier et al. 2015; Dyer et al. 2019). Higher $\delta^{13}C$ values have been found for burrowing shrimp (ghost shrimp *Neotrypaea californiensis* and blue mud shrimp *Upogebia pugettensis*), their potential food items, and juvenile English Sole *Parophrys vetulus* collected at sites near the mouth of Yaquina Bay during summer compared with individuals collected at upriver sites, revealing a diet sourced from marine carbon (Bosley et al. 2017; Stowell et al. 2019).

When looking at the source of nutrients, an increase in the upwelling index seasonally correlated to an increase of juvenile Black Rockfish $\delta^{13}C$ values, suggesting that nearshore, marine waters became the dominant source of nutrients within the estuary as the summer progressed for both 2016 and 2017. Stronger upwelling that began sooner, in conjunction with reduced freshwater flow in 2016, likely contributed to the increased $\delta^{13}C$ values observed in 2016 compared with 2017, which indicates a greater proportion of marine-sourced carbon in 2016. Bosley et al. (2014) also found increased $\delta^{13}C$ values of juvenile Darkblotched Rockfish *S. crameri* during a year with greater coastal upwelling compared with a year with less. The increase in upwelling as summer progressed was likely the driving factor for the positive correlation between total length and $\delta^{13}C$ as the total length of juvenile Black Rockfish also increased from May to September.

An increase in marine-sourced carbon throughout the summer in Yaquina Bay has been correlated with an increase in the energetic condition of English Sole (Stowell et al. 2019). If this trend holds true for juvenile Black Rockfish, the prevalence of marine-sourced carbon during summer months may have positive effects on energetic condition, and years with greater upwelling may lead to individuals with greater energetic condition. A concurrent study examining the recent growth (last 30 d) of the juvenile Black Rockfish sampled in the present study supports this idea, with recent growth found to be highest in 2016 compared with 2017 (Schwartzkopf 2020).

The greater intensity and consistency of upwelling in 2016 likely contributed to the slight increase in $\delta^{15}N$ values and positive correlation to the upwelling index observed during this year. Marine organisms generally have higher $\delta^{15}N$ values relative to freshwater organisms (France 1995). Increased $\delta^{15}N$ values of green macroalgae in Yaquina Bay were found during the upwelling season, with macroalgae from sites located at the mouth of the estuary and upriver exhibiting indistinguishable isotopic compositions, implying that one nitrogen source is being utilized during the dry period (Lee and Brown 2009). Possible mixing of both fresh and marine waters in the present study due to higher discharge and delayed upwelling in 2017 could have contributed to the increased variability observed for juvenile Black Rockfish $\delta^{15}N$ values in this year.

The prey types consumed by juvenile Black Rockfish in the present study likely contributed to differences in stable isotope values as well, specifically $\delta^{15}N$. The influx of upwelled, nearshore waters was likely the dominant driver of $\delta^{13}C$ values rather than what prey were consumed as larger diet differences were observed between habitat types than between years. Nitrogen isotopes ratios vary between trophic levels (Fry 2006), but we found that $\delta^{15}N$ was not related to total length of juvenile Black Rockfish. Even though the consumption of copepods decreased and the consumption of crabs increased as juvenile Black Rockfish size increased, the species that made up the majority of the crab category consumed by large fish ($\geq 80\,mm$) were zoea of porcelain crabs (family Porcellanidae), which are of similar size and are in the same general trophic level as copepods (Miller et al. 2010), and may help explain the lack of a correlation between $\delta^{15}N$ and total length. Although previous studies have found ontogenetic shifts of juvenile rockfish to larger prey items (Boldt and Rooper 2009; Bosley et al. 2014), the larger prey items in these studies were still around the same trophic level (i.e., small copepods, large copepods, and euphausiids). The morphology of juvenile Black Rockfish, with a smaller head and mouth and longer gill rakers compared with other species like Copper Rockfish *S. caurinus* (Singer 1985), is a likely contributor to the consumption of similarly sized prey items as length increases.

Overall, juvenile Black Rockfish in Yaquina Bay, Oregon, feed on estuary-sourced prey, but the source of dietary carbon and nitrogen is from nearshore, marine waters. Yaquina Bay appears to be an important foraging ground for juvenile Black Rockfish, providing a wide diversity of prey items, with special importance of benthic and eelgrass-associated prey. Yaquina Bay has been considerably altered by human development, with recent construction of a new pier in 2010 that damaged benthic habitat and replaced eelgrass beds, although mitigation for this included creation of a transplanted eelgrass bed (Lewis and Henkel 2016;

OCMP 2016). Any future modification or alteration that decreases the amount of available benthic habitat or flow of marine waters into the bay could have deleterious effects on the prey resources to juvenile Black Rockfish. Other commercially and recreationally important species have been found to reside in Yaquina Bay during their early life, including other rockfishes, Cabezon *Scorpaenichthys marmoratus*, English Sole, Kelp Greenling *Hexagrammos decagrammus*, and Lingcod *Ophiodon elongatus* (Pearcy and Myers 1974; De Ben et al. 1990; Schwartzkopf et al. 2020). If these species exhibit similar foraging strategies as juvenile Black Rockfish, future modifications of benthic and eelgrass habitats could have unknown and extensive consequences for multiple important species and should be considered during management decisions.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.