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Characterization of Trophic Niches for a Rockfish Assemblage (*Sebastes* spp.) in Southeast Alaska †

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Abstract: We characterized the trophic relationships of 10 cooccurring species of rockfish from southeast Alaska. We used $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis to compare the position, size, and overlap of trophic niches for the rockfish assemblage. All rockfish occupied a similar area in isospace and mean values. Rockfish varied by approximately 2‰ in $\delta^{13}C$ and approximately 3‰ in $\delta^{15}N$. While both pelagic and demersal rockfish varied similarly in range of $\delta^{15}N$, pelagic rockfish varied in $\delta^{13}C$ while the mean position based on $\delta^{13}C$ of demersal rockfish was the same among species. Our niche overlap analysis showed that rockfish varied from 29% to 178% niche overlap among species. Pelagic rockfish species generally had higher trophic niche overlap than demersal rockfish. Our results show some differences in trophic niche position, and size among rockfish, especially when comparing pelagic and demersal rockfish as groups. The differences in the position, size, and overlap of the trophic niche of these rockfish suggest that there is some level of differentiation among rockfish species.

Keywords: niche differentiation; food web; carbon; nitrogen; stable isotopes

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1. Introduction

Food webs characterize trophic interactions and are important to understand ecological network structure and their evolutionary implications [1]. Classic ecological theory asserts that the number of species in ecological networks are limited by the similarities among cooccurring competitors [2]. Thus, studying closely related species that occupy comparable trophic dimensions can provide insight into how they coexist. For example, closely related species may require similar environmental conditions therefore explaining their cooccurrence. Yet, these same similarities may be the driver of competitive interactions that may limit their coexistence [2,3]. Development of quantitative tools in stable isotope ecology now makes it possible to easily compare trophic niche position, size, and overlap among species [4–6]. However, there are only a handful of published studies that have used these tools to quantify trophic relationships among a few closely related competitors [7–12], none of which cover cooccurring species of rockfish (*Sebastes* spp.).

Rockfish are a diverse genus of marine fishes consisting of 102 currently described species that are predominantly distributed along the west coast of North America [13]. While there is a substantial amount of diversity among rockfish in terms of species and life histories, many exhibit similar morphologies and habitat use [13]. Therefore, rockfish are a closely related group that are well suited for trophic characterization but so far have been poorly studied. Stable isotope techniques have been applied only a few times to this group, with most of the studies only including one to three cooccurring species [14–18]. One study did document the trophic relationships of 16 rockfish species in Prince William

Sound, Alaska [19]. However, this particular study had small sample sizes and included little comparison beyond mean isotope values among species.

To characterize the trophic relationships of this group of fish, we studied 10 congeneric species of rockfish from a cooccurring assemblage. The primary objective of our study was to characterize the trophic niche in terms of position, size, and overlap within the rockfish assemblage using $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis. Our secondary objective was to observe if the niche position, size, and overlap of this rockfish assemblage followed general patterns consistent with coexistence theory.

2. Methods

Our study area consisted of the marine environment within 15 km of 56°59′9.82″ N 134°9′3.35″ W. We collected fish samples (n = 846) during June to August from 2013–2018. We used hook and line sampling techniques to collect fish. All fish were caught at a depth no greater than 100 m. We identified each fish to species and measured for total length to the nearest mm. Rockfish species were considered as either pelagic or demersal based on their ecology. We sampled approximately 1–2 cm^3 of tissue from the dorsal epaxial muscle. We froze samples at −20 °C in the field and were transported frozen to Brigham Young University where they were stored at −80 °C before being used for stable isotope analysis.

Stable isotopes samples were prepared using standard techniques [20].Samples were prepared for stable isotope analysis by being oven-dried at 60 °C for at least 48 h. Once desiccated, samples were ground to a homogeneous powder using a mortar and pestle then encapsulated in a 4mm × 6 mm tin capsule. Samples weighed between 0.6–1.2 mg. Samples were shipped to the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University (Flagstaff, AZ, USA) for stable isotope analysis.

Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$) were expressed in permil (‰) using delta notation [21]. We used the package Stable Isotope Bayesian Ellipses in R (SIBER) to model the trophic niche for each species in our study [22,23]. We calculated and plotted standard ellipses which are the bivariate equivalent of univariate standard deviations [4]. The standard ellipses were used as a representation of each species' trophic niche in iso-space. For comparison in niche size and overlap, we calculated standard ellipse area (SEA) and standard ellipse area corrected for small sample size (SEA_c) measured in $‰^2$ for each rockfish species. We then performed a pairwise comparison of percent SEA overlap to calculate the percent of their niche that is shared among species. We did this by calculating the sum of all pairwise percent overlaps among Rockfish to be used as a "crowdedness" metric [24]. For example, a species with no niche overlap would have a crowdedness score of 0% while a complete niche overlap of three additional species would result in a crowdedness score of 300% for the target species.

3. Results

A comparison of mean isotopic ratios shows that the rockfish assemblage varied in approximately 2‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$ (Figure 1). *Sebastes variabilis* and *S. ciliatus* were more deplete in $\delta^{15}N$ and $\delta^{13}C$ than other rockfish species while *S. ruberrimus* was more enriched in $\delta^{15}N$. The demersal rockfish were equally enriched in $\delta^{13}C$ and only appear differentiated by $\delta^{15}N$.

The standard ellipse area varied from 0.36$‰^2$ to 1.3$‰^{2.}$ (Table 1, Figure 2). *Sebastes brevispinis* had the largest SEA which was about 3.5 times larger than the smallest SEA of *S. caurinus*. Standard ellipse areas corrected for a small sample size yielded slightly larger ellipses than the basic SEA.

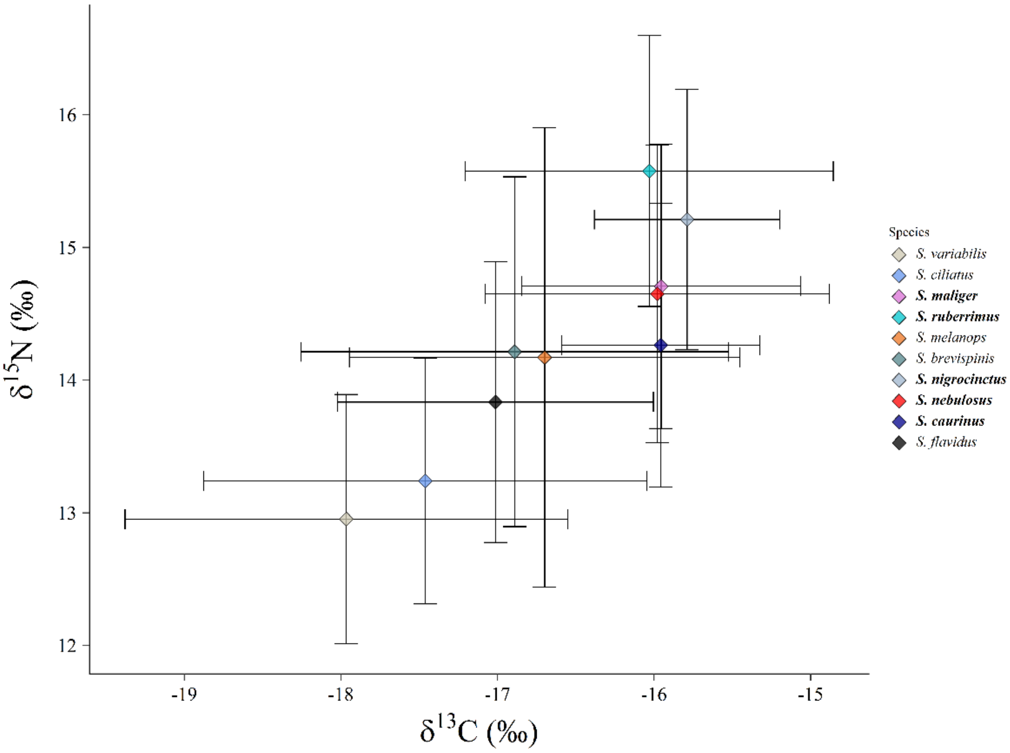

Figure 1. Mean isotopic δ values and 95% confidence intervals for ten rockfish species from southeast Alaska. Bolded species are demersal and nonbolded are pelagic.

Table 1. Standard ellipse area (SEA) and standard ellipse area corrected for small sample size (SEAc) expressed in ‰² for ten rockfish species from southeast Alaska. Bolded species are demersal and nonbolded are pelagic.

Species	SEA	SEAc
S. brevispinis	1.303	1.362
S. caurinus	0.3634	0.4371
S. ciliatus	0.9634	0.9699
S. flavidus	0.7285	0.7487
S. maliger	0.7397	0.7445
S. melanops	0.8205	0.8951
S. nebulosus	0.4059	0.4397
S. nigrocinctus	0.4288	0.4386
S. ruberrimus	0.958	0.9658
S. variabilis	1.009	1.017

Our pairwise niche overlap analysis showed the highest niche overlap was observed for *S. brevispinis* and *S. melanops* having 168% and 178% overlap respectively (Table 2, Figure 2). *Sebastes ruberrimus* had the lowest niche overlap (Figure 2, Table 2). Most pelagic rockfish had a percent niche overlap above 100% except for *S. variabilis* which had 55% of its niche overlap with other species. Demersal rockfish had generally lower niche overlap with *S. maliger* being the only demersal species sharing more than 100% of its trophic niche with other rockfish (Table 2).

Table 2. Pairwise niche overlap among ten rockfish species from southeast Alaska. Bold numbers represent total percent SEA overlap with all other Rockfish species. Bolded species are demersal and nonbolded are pelagic.

	S. brevispinis	***S. caurinus***	*S. ciliatus*	*S. flavidus*	***S. maliger***	*S. melanops*	***S. nebulosus***	***S. nigrocinctus***	*S. ruberrimus*	*S. variabilis*
S. brevispinis	**168**									
S. caurinus	4	**49**								
S. ciliatus	10	0	**105**							
S. flavidus	60	0	25	**140**						
S. maliger	11	25	0	0	**114**					
S. melanops	71	7	17	53	18	**178**				
S. nebulosus	12	13	0	1	36	10	**83**			
S. nigrocinctus	0	0	0	0	19	0	11	**53**		
S. ruberrimus	0	0	0	0	5	1	0	23	**29**	
S. variabilis	0	0	53	1	0	1	0	0	0	**55**

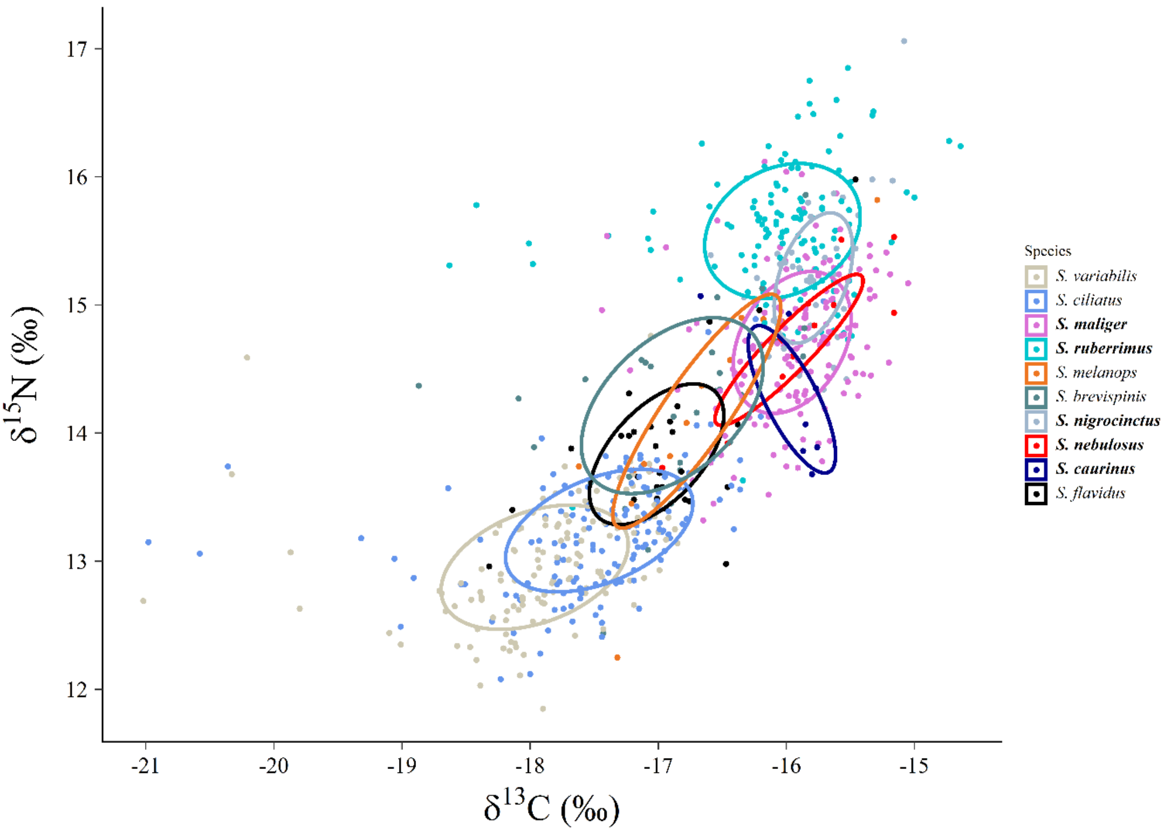

Figure 2. Standard ellipse plot for ten rockfish species from southeast Alaska. Bolded species are demersal and nonbolded are pelagic.

4. Discussion

In this paper we characterized ten trophic niches of a cooccurring rockfish assemblage. Our findings on niche position appear to be in line with one other rockfish community that has been studies in the north pacific suggesting some uniformity in one dimension of rockfish trophic structure [19]. Our results show that this rockfish assemblage appears to have an iso-space trend with more pelagic fish depleted and more demersal species being more enriched in $\delta^{13}C$. Demersal rockfish were not differentiated in $\delta^{13}C$ among species. The $\delta^{13}C$ values of these fish reside about −16‰ with completely overlapping 95% confidence intervals suggesting no significant difference in $\delta^{13}C$ (Figure 1). This suggests that demersal rockfish share the same source of carbon fixation, though studies are needed that mixing models to confirm the source carbon for this group. As for the pelagic rockfish, there appears to be a wider distribution in carbon uptake than the demersal rockfish (Figure 1) while also varying between 1.3–1.4‰ in isotopic means for $\delta^{15}N$. These general findings are of note in that both feeding groups of fish were caught within the same geographic location but at different depths within the water column, thus there appears to be differentiation in diets between these groups.

In addition to this trophic niche characterization, this rockfish assemblage reflects other highly diverse congeneric groups of fishes in niche overlap [9,12,25] in that there is a mixture of high niche overlap (pelagic rockfish) and little to no niche overlap (demersal rockfish; Table 2). One interesting observation of note is between *S. maliger* and *S. nebulosus* and how these fish may be partitioning their niches. The isotopic means of these two fish are nearly identical (Figure 1) but when plotted as ellipses we see that these to fish show some level of niche partitioning, especially in regards to their niche orientation and size (Table 1, Figure 2). Specifically, the ellipse of *S. nebulosus* appears to have higher eccentricity than *S. maliger*. Thus, while mean isotopic position appeared identical, it seems that there are differences in resource use between these species.

Rockfish assemblages provides a landscape for exploring niche theory and community assembly in diverse communities. This is in part due to the high levels of speciation, co-occurring congenerics, and low movement leading to diverse rockfish assemblages in small areas [26]. In highly diverse fish communities, multiple theories have been proposed including lottery model and niche partitioning model to explain coexistence [27–30]. When looking at rockfish evolution, it appears that speciation within rockfish is tied to utilization of the water column rather than barriers to migration [31]. Due to variation in water column use, the morphologies of these species have been shaped to differentially utilize available resources [26]. Our findings reflect both of these ideas in that we see both a demersal and pelagic divergence in how the community is structured and some level of niche partitioning in terms of niche position, size, and overlap (Figures 1 and 2, Tables 1 and 2). Though our study was not designed specifically to answer these questions of niche theory, we indicate that rockfish can be used as a model group for testing niche theory and warrant further investigation.

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Informed Consent Statement:

Data Availability Statement: The data is available from the authors upon reasonable request.

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