National Marine
Fisheries Service
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Fishery Bulletin
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Comparing the localized feeding ecology of black sea bass (*Centropristis striata*) at natural and artificial reefs: gut content and stable isotope analyses

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Abstract—Black sea bass (*Centropristis striata*) feed on epibenthic prey, particularly decapods, and become more piscivorous as they grow larger, a trend that has energetic consequences for growth. In the coming decades, construction of wind energy systems will expose black sea bass to a large-scale manipulation of continental shelf habitats in the northeastern United States. In this study, we tested the effects of habitat type (natural versus artificial reef habitats) on size, age, growth, diet, and trophic dynamics of black sea bass, using 407 specimens collected with rod-and-reel gear near Ocean City, Maryland, in 2016 and 2018. No significant differences in fish length, age, size at age, or diet are attributable to habitat. The stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) in samples of 3 tissue types (liver, muscle, and mucus) vary significantly by habitat except for $\delta^{15}N$ values in mucus samples. Across tissue type, $\delta^{13}C$ values are higher for fish at artificial habitats, indicating more littoral than pelagic feeding. We conclude that, although both types of reef habitats are ecologically equivalent as a source of growth and diet for black sea bass, the differences in stable isotope signatures indicate functional differences in system energy flow that should be investigated further in this and other marine species that will be affected by offshore wind energy development.

Manuscript submitted 14 May 2024.
Manuscript accepted 29 November 2024.
Fish. Bull. 123:58–70 (2025).
Online publication date: 27 January 2025.
doi: 10.7755/FB.123.1.5

In the coming decades, black sea bass (*Centropristis striata*) will be exposed to a large-scale manipulation of the ecosystem of the U.S. continental shelf, with construction of wind energy systems that will significantly increase the proportion of structured habitats along the coasts of Maryland and New England (Kimmell and Stalenhoef, 2011; Methratta et al., 2020). The black sea bass is a reef-oriented fish species (Steimle et al., 1999; Steimle and Zetlin, 2000; Fabrizio et al., 2013, 2014), and it may or may not benefit from more structured habitats in this region, which overlaps with the distribution of its northern stock. Some researchers have examined effects of habitat on abundance of black sea bass. Malek et al. (2014) stated that black sea bass are sensitive to physical changes in the seafloor, such as those caused by structural development. Schweitzer and Stevens (2019) reported an increase in abundance of black sea bass in areas where colorful sea whips (*Leptogorgia virgulata*) were located on the seafloor. Although the intent of our study was not to determine whether environmental disturbances associated with the construction of offshore wind structures could affect black sea bass, offshore wind structures can serve as artificial reefs, and therefore habitats, for these fish given the physical characteristics of such structures. In this study, we investigated the effects of habitat type (natural versus artificial reef structures) on the demographics (size, age, and size at age) and feeding history (gut contents and stable isotope composition) of black sea bass to test the hypothesis that type of reef habitat does not affect these aspects of the biology and ecology of this species.

Sampling occurred offshore of Maryland, near Ocean City, from coastal waters in spring and summer to near the continental shelf edge in the fall and winter (Moser and Shepherd, 2009; Fabrizio et al., 2014). During the period of this study, May–November, black sea bass associate with hard-bottom structures, henceforth referred to as *reefs*, with high rugosity at depths <28 m (Fabrizio et al., 2013). Black sea bass are protogynous hermaphrodites, reaching a maximum size of about 45 cm in standard length (2.3 kg) and longevity of >10 years (Lavenda, 1949; Wenner et al., 1986; Provost et al., 2017).

Black sea bass have a broad benthic diet, with some degree of dietary specialization on decapod crab species (particularly *Cancer* spp.), but the diet also includes a variety of other invertebrates and small fish species (Smith and Link, 2010). Byron and Link (2010) found ontogenetic diet shifts in black sea bass from mostly polychaetes and arthropods to fish, when the black sea bass are between 9 and 14 cm in total length (TL). However, considering that black sea bass prefer reef habitats, and even have exhibited fidelity to their selected habitats on an annual basis (Moser and Shepherd, 2009; Fabrizio et al., 2013; Secor et al., 2019), our focus was on the effect of reef habitat substrates, whether artificial or natural. In other studies, habitat of black sea bass has been related to feeding dynamics (Steimle and Ogren, 1982; Sedberry, 1988; Lindquist et al., 1994; Steimle and Figley, 1996), but no study has involved characterization of life history, feeding, and stable isotope signatures as they relate to habitat. For example, if habitat type affects prey type and growth, changes in available habitat could affect the productivity of a fishery that targets black sea bass, and effects on fishery productivity may be dynamic and widespread at the large scale of wind energy development planned in this region (Methratta et al., 2020).

Feeding history has been inferred from values of δ^{13}C and δ^{15}N, both measures of stable isotope composition, in the tissues of fish (Araújo et al., 2007; Becker et al., 2007; Bauchinger and McWilliams, 2009), but in our study, we employed a tissue source that is relatively novel for black sea bass. For 2 commonly used sources, muscle and liver tissues, isotopic turnover occurs over months and weeks, respectively. In mucus, a tissue that can be collected in a way that is not lethal, turnover times for stable isotope signatures apparently are quite variable.

Church et al. (2009) noted the utility of using external mucus to determine short-term (30–36 d) turnover in δ^{13}C and δ^{15}N values in juvenile steelhead trout (*Oncorhynchus mykiss*) but recommended sampling multiple tissues, and Maruyama et al. (2017) reported a much longer turnover (200 d) for these signatures in mucus samples of 5-year-old Japanese catfish (*Silurus asotus*). Results from a study by Ibarz et al. (2019) support the notion that food ingestion affects mucus exudation in gilthead bream (*Sparus aurata*) in short time intervals (≤24 h). Ibarz et al. (2019) found some enrichment at 12 h but did not find a significant difference at 24 h, suggesting that mucus sampling could be useful for examining "the effects of environmental challenges." Winter et al. (2019) suggested that epidermal mucus collected from live common carp (*Cyprinus carpio*) can replace the use of dorsal muscle for readings of stable isotope composition, on the basis of results from diet-switching lab experiments, but they cautioned that differences in tissue turnover rates are dependent on diet and need to be considered if used in field research. However, the reliability of mucus in tracking uptake of stable isotopes in wild fish has been quantified in few studies, and none, to our knowledge, have included testing mucus as a tissue fraction for readings of stable isotope signatures in black sea bass.

Sampling black sea bass at artificial and natural reefs offshore of Maryland over 2 years, we examined if habitat type was associated 1) with specific length, age, or size-at-age traits determined with otolith-based ages, 2) with snapshots of diets inferred from whole gut content analysis and compared to broad-scale diet data for the region, and 3) with feeding history inferred from analysis of stable isotope composition as sourced from fish liver, muscle, and mucus tissues and compared to isotopic values of common prey organisms in the region. We considered whether the 2 types of reef habitats were equivalent in terms of attracting and supporting black sea bass and what any differences might indicate about the biology and ecology of black sea bass on a continental shelf where wind energy systems may be developed.

Methods and materials

Field sampling

Black sea bass were collected through rod-and-reel angling at natural and artificial reef habitats off the coast of Maryland, near Ocean City (Fig. 1), from May through November 2016 and from May through August 2018. Angling occurred during daylight hours, by using squid (*Loligo* spp.) as bait. All fish were immediately euthanized upon retrieval. Natural hard-bottom reef habitats consisted mostly of substrates of cobble and shell with a few soft corals, whereas artificial reef habitats were mostly shipwrecks and other metal structures. The locations and more detailed descriptions of the sampling sites appear in Supplementary Table 1.

Additional stomach content data were provided from black sea bass examined at sea, after capture from New Jersey to North Carolina during bottom-trawl surveys conducted by the NOAA Northeast Fisheries Science Center (Politis et al.[1]). These comparative data were available for fish caught during spring (March–May) and fall (September–November) in 2000–2016 at latitudes between 35°N and 40°N (Fig. 1). Black sea bass were measured for size (in TL), and sex was determined macroscopically. Stomach

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[1] Politis, P. J., J. K. Galbraith, P. Kostovick, and R. W. Brown. 2014. Northeast Fisheries Science Center bottom trawl survey protocols for the NOAA Ship *Henry B. Bigelow*. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 14-06, 138 p. [Available from website.]

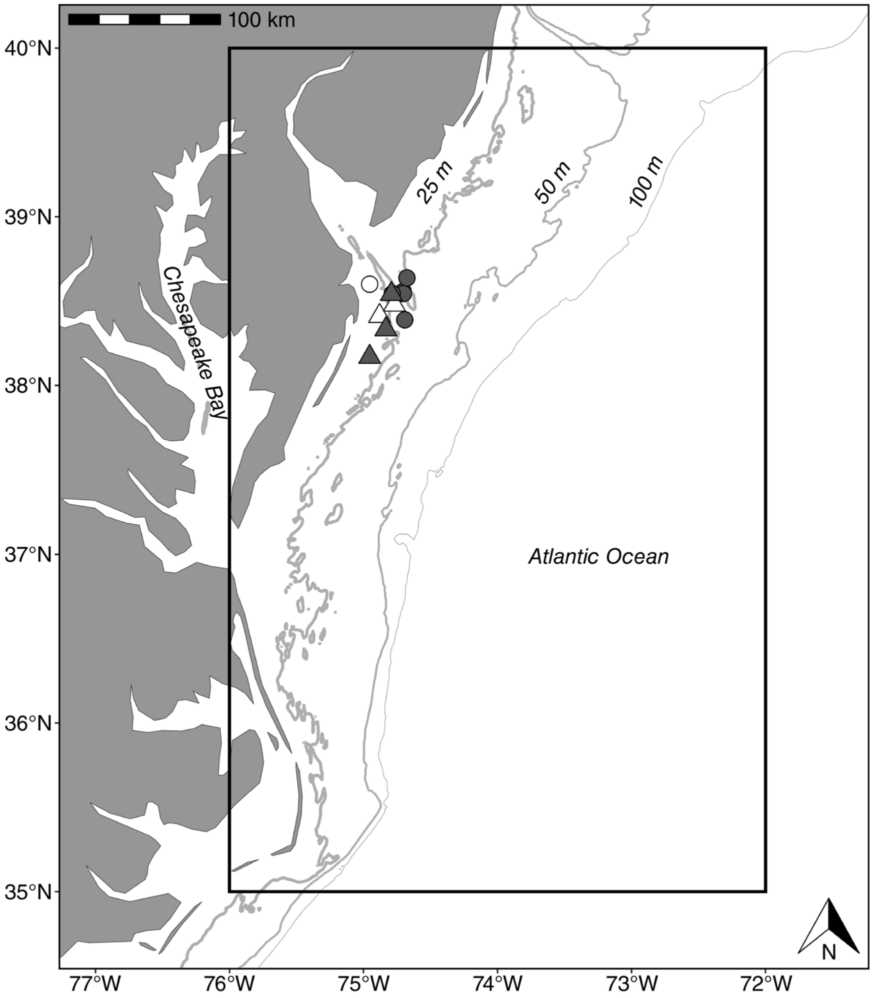

Figure 1

Map of sampling sites at natural (gray symbols) and artificial (white symbols) reefs near Ocean City, Maryland, where black sea bass (*Centropristis striata*) were collected through rod-and-reel angling during May–November 2016 (circles) and May–August 2018 (triangles). The bounding box indicates the area where additional black sea bass were caught in NOAA bottom-trawl surveys during spring and fall in 2000–2016. The gray lines represent the 25-m, 50-m, and 100-m isobaths.

contents were identified macroscopically and recorded to the lowest possible taxonomic level (Smith and Link, 2010). The methods of measurement and of stomach content and sex determination were consistent for fish sampled in bottom-trawl surveys and for the fish caught during the rod-and-reel angling of this study.

To compare stable isotope composition, δ^{13}C and δ^{15}N values, for samples of potential prey items to those for fish tissues, whole organisms representative of potential prey species were fished in the fall of 2018 in both natural and artificial reefs, by using a small-mesh otter trawl to sample benthic organisms from flat-bottom habitats adjacent (<1 km) to the sites sampled in 2018. Specimens of the known species collected during tows of the trawl were retained.

Fish and tissue processing

Upon capture by angling, fish were immediately placed in individual plastic freezer bags to prevent mucus contamination and immersed in ice. Samples were subsequently frozen at −27°C (−80°F) as recommended for minimal effect on δ^{13}C and δ^{15}N values in contrast to other methods (Bosley and Wainright, 1999; Kaehler and Pakhomov, 2001). In the laboratory, fish were measured for TL (to the nearest 1 cm) and weighed (to the nearest 1 g), and sex was determined by the examination of gonad tissues. Fish that were not clearly identifiable as male or female after dissection were categorized as either transitional or unknown.

Stomachs were initially placed in 10% formaldehyde for a minimum of 2 weeks and transferred to 70% ethanol for preservation until further sorting of prey items. Prey items were removed from stomachs of black sea bass, weighed to the nearest 0.01 g, and identified to the lowest possible taxonomic level.

Mucus, liver, and muscle samples were prepared for stable isotope analysis. Livers were removed, white muscle tissue was excised from an area directly above the pectoral fin, and both types of tissue samples were immediately frozen at −27°C. In 2018, a subsample of fish collected that year was selected to test mucus for stable isotope analysis with $\delta^{13}C$ and $\delta^{15}N$ values. Also in 2018, otoliths were collected from and used to age fish sampled in that year.

Age and growth

Otoliths (sagittae) were taken from fish, when possible, rinsed with fresh water to remove excess tissue, and stored dry in envelopes. Following techniques adapted from Penttila and Dery (1998), whole otoliths were placed in a black dish containing a solution of 5% dish soap, and whole annuli were counted by using reflected light and a dissecting microscope. A subset of paired ages of fish from a second reader were used for quality control, by following the guidance of McBride (2015) and by using the package ALKr (vers. 0.5.3.1; Loff et al., 2014), with code developed by Ogle (2016), in statistical software R, vers. 3.4.0 (R Core Team, 2017). Ages assigned to fish by using otoliths were compared between readers by using percentage of agreement and Chang's coefficient of variation (Chang, 1982), and bias was assessed by using Bowker's test (Bowker, 1948). Between-reader precision was good (percentage of agreement=80%, Chang's coefficient of variation=4.98%), and there was no significant bias between readers (Bowker's test: P=0.25). For each otolith, final monthly age was assigned as follows (Wuenschel et al.[2]):

$$A + M - (4 / 12), \tag{1}$$

where A = the number of annuli; and
M = the month of collection.

The fraction (4/12) is used to assume a spawning date in April.

Growth was examined by using a multinomial model of size at age in the R package FSA (vers. 0.818; Ogle et al., 2018) developed by Ogle (2016). Size-at-age relationships were not separated by sex because the black sea bass is a protogynous hermaphrodite (Hood et al., 1994). Instead, the covariate used to test if size at age differed was *habitat type*. To determine whether fish sizes at habitat were significantly different, we used several tests, including a Student's t-test, which can be used to determine whether the mean sizes of the population are different. A Kolmogorov–Smirnov test, a nonparametric test to compare 2 sample distributions, was also used to help compare age at length based on our samples.

Stomach analysis

A prey-specific index of relative importance (PSIRI), expressed as a percentage, was calculated as follows (Brown et al., 2012; Varela et al., 2017):

$$PSIRI = (\%FO_{\mathrm{i}} \times [\%PN_{\mathrm{i}} + \%PW_{\mathrm{i}}]) / 2, \tag{2}$$

where $\%FO_{\mathrm{i}}$ = (number of stomachs with prey item i / total number of non-empty stomachs)100;
$\%PN_{\mathrm{i}}$ = (number of prey item i / total number of prey items)100; and
$\%PW_{\mathrm{i}}$ = (weight of prey item i / total weight of all prey items)100.

The PSIRI was chosen because the values are additive in respect to taxonomic level, and that additive approach facilitates the comparison of prey composition of fish stomach contents between the habitat types (Brown et al., 2012). Chi-square tests of independence were used to determine if significant differences existed between diets of fish at artificial and natural habitats, with response variables of *habitat type*, *size*, or *sex*. The PSIRI was used to compare prey composition in stomach contents between fish collected for this study and those collected during NOAA bottom-trawl surveys. Fish were categorized as small (0–25 cm TL), medium (25–50 cm TL), and large (>50 cm TL) on the basis of sizes used in Byron and Link (2010). No large fish were sampled by using rod-and-reel gear.

Stable isotope analysis

Muscle and liver samples were dried for 48 h in an oven at 65°C, homogenized with a mortar and pestle, and enclosed in tin capsules before being shipped for analysis. Samples not sent on the day that they were processed were stored in a desiccator to prevent hygroscopic weight gain. Muscle and liver samples were shipped to the Stable Isotope Facility of the University of California, Davis, for stable isotope analysis and processed with an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer. Samples were prepared in accordance to the University of California, Davis, protocol regarding sample preparation for analysis of ^{13}C and ^{15}N in solids by using an elemental analyzer and isotope ratio mass spectrometer (UC Davis[3]).

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[2] Wuenschel, M. J., G. R. Shepherd, R. S. McBride, R. Jorgensen, K. Oliveira, E. Robillard, and J. Dayton. 2012. Sex and maturity of black sea bass collected in Massachusetts and Rhode Island waters; preliminary results based on macroscopic staging of gonads with a comparison to survey data. A working paper for SARC 53- [*sic*] black sea bass data meeting, September 2011. *In* 53rd Northeast regional stock assessment workshop (53rd SAW) assessment report. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 12-05, p. 529–546. [Available from website.]

[3] UC Davis (Regents of the University of California, Davis). 2023. Carbon and nitrogen in solids: carbon (^{13}C) and nitrogen (^{15}N) sample preparation. UC Davis Stable Isot. Facil. Last updated 2 May 2023. [Web page, accessed June 2016.]

Samples of mucus were treated in accordance with methods adapted from Church et al. (2009). Fish were removed from the freezer, which was set to −27°C, and still in their respective bags, thawed for 5 min or until mucus was present on the epidermis of the fish. Mucus was gently scraped from the dorsal side of the fish and placed into a glass scintillation vial, and then the collected mucus was rinsed 3 consecutive times with 5 mL of reverse osmosis water. Samples were shaken between each addition of reverse osmosis water. The filtrate of mucus and water was then passed through a 5-µm polycarbonate filter. A final rinse of 5 mL of reverse osmosis water was passed through the filter before the filtrate was decanted into a 50-mL plastic test tube. Subsequently, the filtrate was frozen at 0°C for at least 24 h and then cryodesiccated for 48 h in a lyophilizer. A spatula was used to mix the sample, which was then weighed, enclosed in tin capsules, and shipped to the Stable Isotope Facility for stable isotope analysis as described in the previous paragraph.

Results from analysis of stable isotope composition at the University of California, Davis, were reported in δ notation, scaled in parts per thousand (‰), which can be expressed in the following equation (adapted from Hayes, 2004), originally introduced by McKinney et al. (1950):

$$\delta^{A}X_{STD} = ([{}^{A}R_{Sample} / {}^{A}R_{STD}] - 1)1000, \tag{3}$$

where $\delta^{A}X_{STD}$ = "the abundance of isotope A of element X in a sample relative to the abundance of that same isotope in a [. . .] standard" (Hayes, 2004);
${}^{A}R_{Sample}$ = the ratio of the abundance of isotope A in a sample; and
${}^{A}R_{STD}$ = the ratio of the abundance of isotope A in an isotopic standard.

Stable isotope composition was compared by using 2-way analyses of variance to determine whether significant differences existed between the 2 habitat types or among fish sizes and whether an interaction of habitat type and fish size existed. The assumptions that the observations were independent, normally distributed, and had constant variance, as advocated by Ogle (2016), were met. The following linear model was the one tested by using analyses of variance:

$$D_T \sim (H_i \times S_i) + \varepsilon, \tag{4}$$

where D = either the δ^{15}N or δ^{13}C value;
T = tissue type;
H = habitat type;
S = size (TL in centimeters); and
ε = experimental error.

The analyses of variance were evaluated with the critical P-value set at 0.01, less than the standard threshold of 0.05, to account for some of the multiple comparisons inherent in the use of multiple tissue types. Scatterplots with ellipses were used to display overlap of δ^{15}N and δ^{13}C data, with ellipses representing the 95% confidence intervals. Ellipses were created by using the function stat_ellipse in the R package ggplot2, vers. 2.2.0 (Wickham, 2016).

To compare isotopic niches between fish sampled at artificial habitats and those sampled at natural habitats, the R package SIBER (vers. 2.1.0; Jackson et al., 2011) was used. In part of this package, Bayesian statistics are used to make models that help display isotopic niches among groups in a community. The SIBER package is used to compare isotopic niches between groups of samples, as advocated by Suca and Llopiz (2017).

Results

In this study, 407 black sea bass were caught: 107 fish in 2016 and 300 fish in 2018 (Suppl. Table 1). Fish were sampled from 2 types of reef habitats: 194 fish at artificial reefs and 213 fish at natural reefs. Of the 300 fish caught in 2018, 280 fish were used for age analyses. As expected for individuals of a protogynous hermaphroditic species, female black sea bass were caught more often than males. This pattern occurred for fish caught through rod-and-reel angling, with 235 females, 165 males, 6 transitional fish, and 1 fish of unknown sex, as well as for fish in the data from NOAA bottom-trawl surveys, with 874 females, 323 males, 2 transitional fish, and 105 fish of unknown sex (Fig. 2). As expected, males were larger than females. Among fish captured by using rod and reel, males had a mean size of 27.2 cm TL (standard error [SE] 0.41) and females had a mean size of 23.9 cm TL (SE 0.26) (t=6.83, P<0.001). In the data for fish captured during bottom-trawl surveys, the mean size of males and females was 26.7 cm TL (SE 0.46) and 23.7 cm TL (SE 0.24) (t=5.89, P<0.001). In terms of habitat, the size of fish sampled by using rod-and-reel gear did not differ between artificial and natural habitats (Kolmogorov–Smirnov test: D=0.82, P=0.49).

Age–length analysis

The estimated age of the fish caught for this study ranged from 2 to 6 years, with the age of the majority of the fish between 2 and 4 years (Fig. 3). Fish age did not differ between types of reef habitat, whether ages were estimated directly from otoliths (sample size [n]=280) (Student's t-test: P=0.0015) or, for a larger subsample of fish caught by using rod-and-reel gear, ages of some fish were estimated with an age–length key (n=407; Student's t-test: P>0.11).

Stomach content analysis

Arthropods dominated the diets of black sea bass at artificial and natural habitats by percent number, weight, and frequency of occurrence, with relatively higher PSIRI values for annedlids and mollusks in natural habitats. A graphic display of PSIRI values for components of the diet of black sea bass is provided in Figure 4. Calculated PSIRI values for the prey categories of annelids, arthropods, fishes, and mollusks in stomach contents of fish caught at

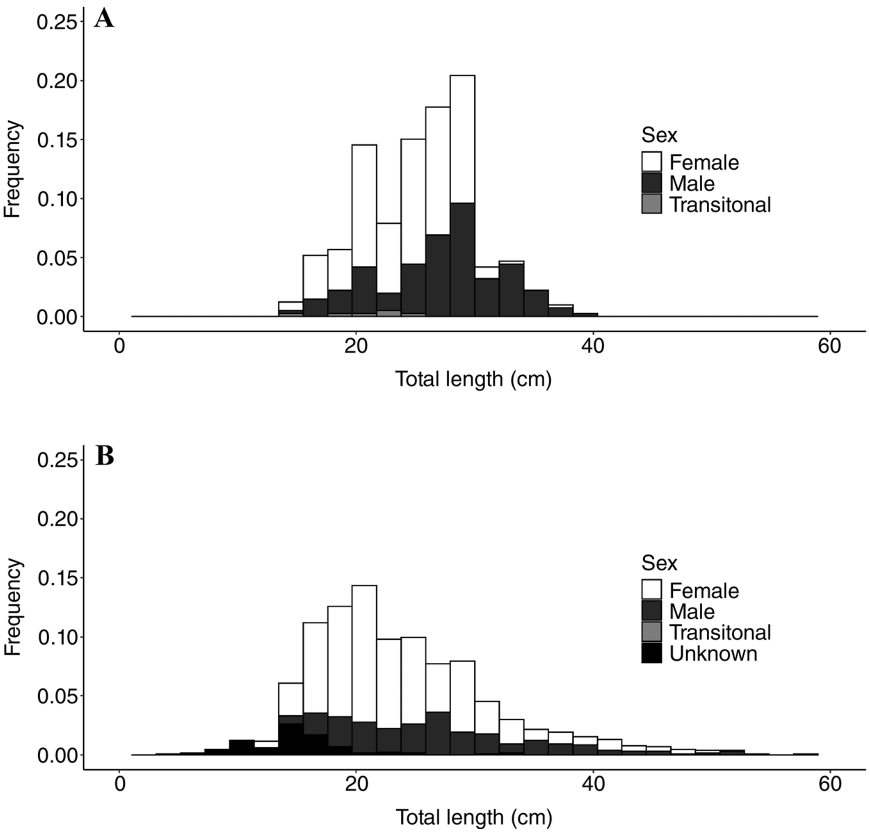

Figure 2

Length–frequency distributions for black sea bass (*Centropristis striata*) sampled (**A**) with rod and reel in 2016 and 2018 off the coast of Maryland and (**B**) during NOAA bottom-trawl survey in 2000–2016 from New Jersey to North Carolina. The sex of fish was categorized as female, male, transitional, or unknown.

natural habitats from 2016 through 2018 are 2.9%, 17.4%, 0.5%, and 11.1%, respectively, and the PSIRI values for fish caught at artificial habitats during that same period are 0.1%, 51.5%, 1.1%, and 2.3% (Fig. 4, Suppl. Table 2). A full list of PSIRI values for prey items in the stomach contents of fish sampled is provided in Supplementary Table 2. Graphic representation of PSIRI values for prey items of the fish captured from artificial and natural habitats in 2018 can be found in Supplementary Figure 1.

The majority of arthropod taxa in the data from our stomach content analysis and in the data from NOAA bottom-trawl surveys were true (Brachyura) and hermit (Anomura) crabs (Suppl. Table 3). Annelids composed a higher percent weight (34%) but had a lower frequency of occurrence (0.07%) in the diets of black sea bass caught during bottom-trawl surveys than in those of black sea bass caught through rod-and-reel angling. For fish in the small and medium size classes, arthropods had the highest percent number, as shown in the graphic display of PSIRI values in Supplementary Figure 2. Approximately 40% (*n*=83) of the 205 fish caught at natural habitats had empty stomachs, but only about 13% (*n*=25) of 193 fish from artificial habitats had stomachs that were empty. For fish with prey present in their stomachs, results of a chi-square test of independence indicate that there were no significant differences in prey consumption by black sea bass between artificial and natural habitats, when examining the relationships of prey number and fish size (P=0.29, χ^2=2.43) or sex (P=0.18, χ^2=3.41). A full list of prey items found in stomachs of fish based on data from rod-and-reel angling and from bottom-trawl sampling can be found in Supplementary Table 3.

Stable isotope analysis

For all tissue types (liver, muscle, and mucus), δ^{13}C and δ^{15}N values overlapped between habitat types (artificial versus natural) and available fish size classes (medium versus small) (Fig. 5). Isotopic values differed between habitats for both stable isotope signatures and for all 3 tissue types except for δ^{15}N in muscle samples (Table 1). In addition, isotopic values differed by fish size only for δ^{13}C

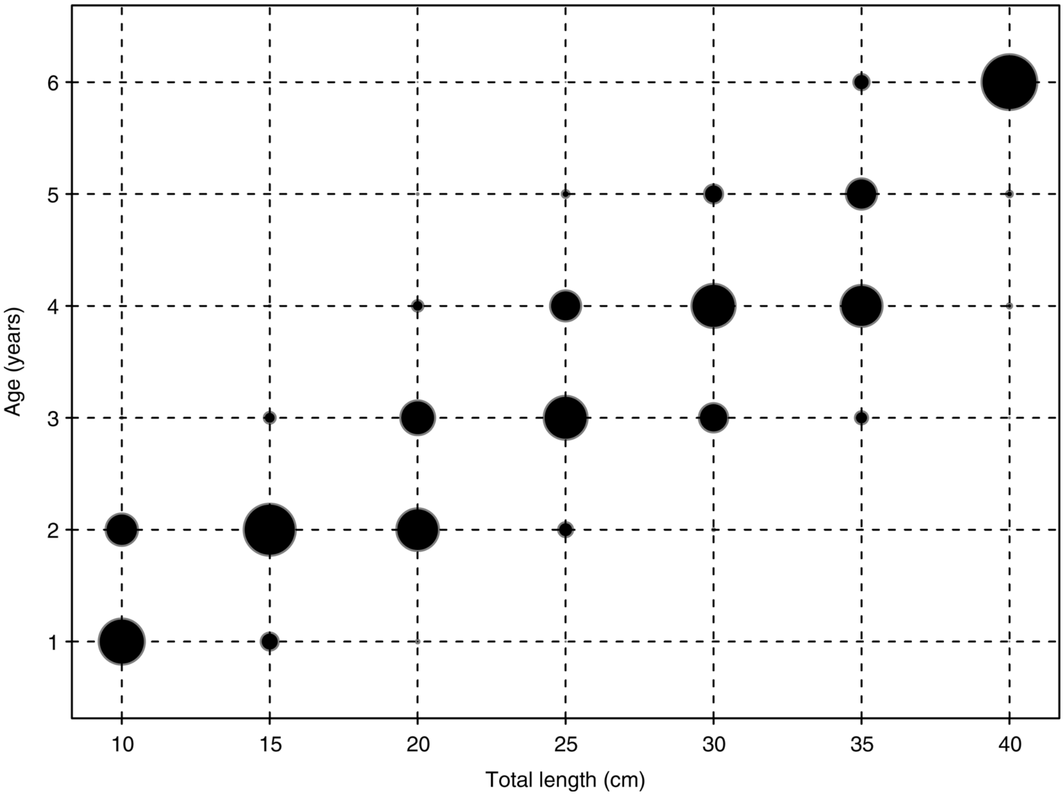

Figure 3

Length at age for 280 black sea bass (*Centropristis striata*) caught with rod and reel in 2018 off the coast of Maryland. Age and length did not differ between habitat types; therefore, samples caught at natural and artificial reefs were pooled. Bubble size is proportional to the relative number of fish per age and length interval.

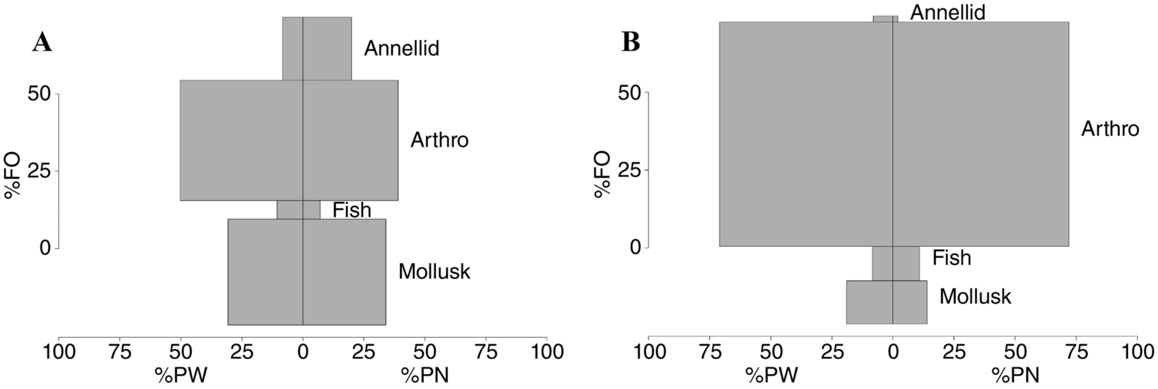

Figure 4

Values for components of the prey-specific index of relative importance (PSIRI) used to examine the diets of black sea bass (*Centropristis striata*) caught at (**A**) natural and (**B**) artificial reef habitats through rod-and-reel angling off the coast of Maryland in 2016 and 2018. Prey items include annelid, arthropod, fish, and mollusk taxa. The PSIRI is based on the following components: percent number (%PN), weight (%PW), and frequency of occurrence (%FO).

in mucus tissues, and they differed as an interaction of habitat and size only for δ^{13}C in muscle and mucus tissues.

Results from visual analysis for potential prey items sampled in 2018 indicate a lack of direct overlap in stable isotope signatures with the δ^{13}C and δ^{15}N values for sand dollars (*Echinarachnius* spp.), mussels (*Mytilus* spp.), clams (*Mercenaria* spp.), and scallops (*Pecten* spp.), indicating that the black sea bass is positioned at a higher trophic level.

For the SIBER analysis in which isotopic niches were compared between habitat types, the standard ellipse area is a proxy for isotopic niche and can be interpreted as the area that an ellipse would occupy on a Cartesian coordinate plane. The vertical length, representing the area, of each icon conveys the variability of the predator's prey consumption or how diverse a predator's diet may be in a food chain, with the assumption that this diet is reflected in the tissues sampled. The location of the plot symbol, as it relates to the *y*-axis, provides a general indication of where the animal feeds on a basic trophic scale, where an increase of one trophic level would be represented as an increase of 3–4‰^{2} in the stable isotope signatures shown. The SIBER analysis results indicate small differences (<5‰^{2} total) in the standard ellipse area, signifying isotopic niches in small and medium fish; these results also indicate inconsistency among tissue types (Fig. 6). Standard ellipse areas for liver and muscle samples were larger than those for mucus samples in a comparison of values between small and medium fish, regardless of habitat type. Isotopic niches between fish sampled at artificial and natural habitats did not differ greatly (<4‰^{2}), but for both groups, values for liver samples were consistently the highest, followed by those for muscle and mucus samples.

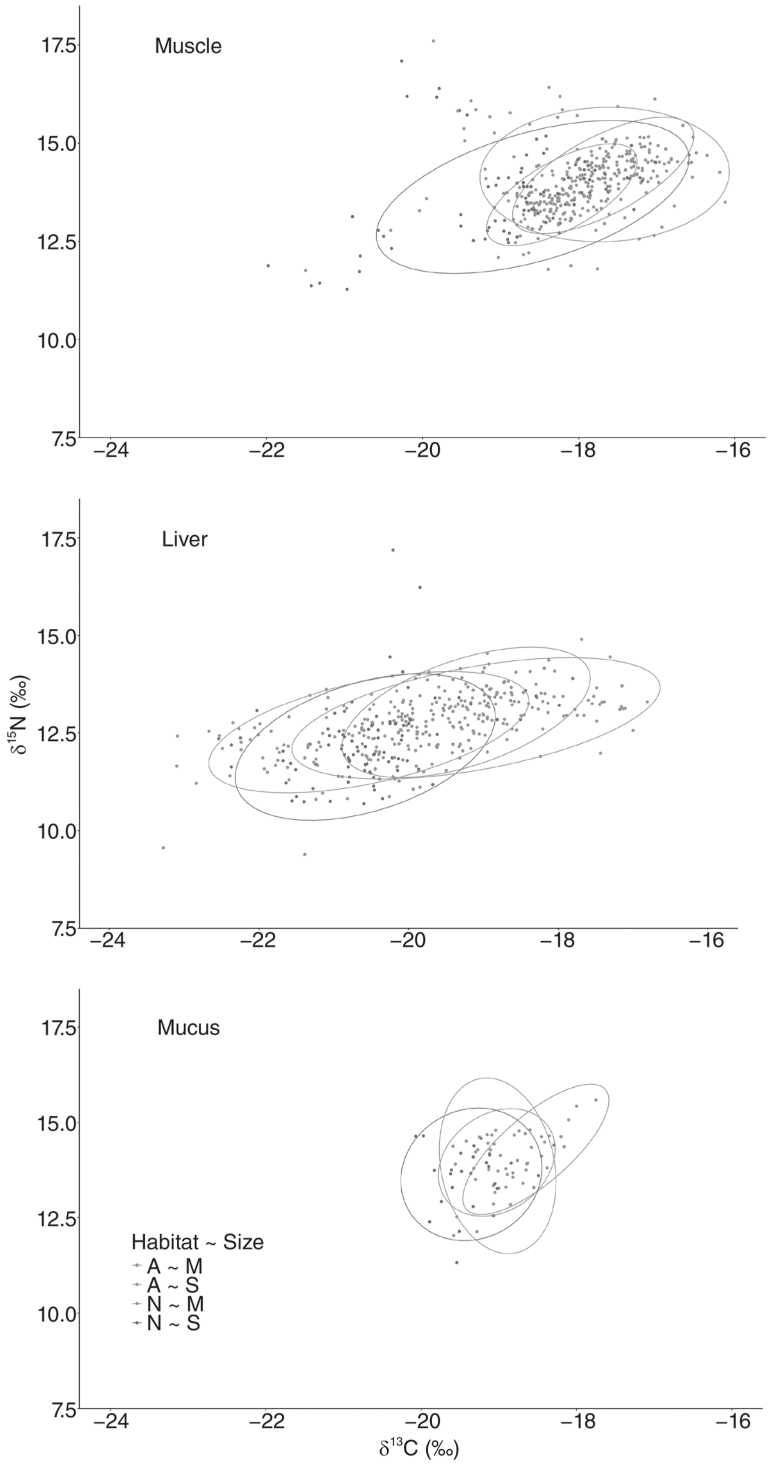

Figure 5

Stable isotope signatures, δ^{13}C and δ^{15}N, in muscle, liver, and mucus tissues of medium (M) and small (S) black sea bass (*Centropristis striata*) caught in natural (N) and artificial (A) reef habitats off the coast of Maryland in 2018. Fish were categorized as small if they measured 0–25 cm in total length (TL) and medium if they measured 25–50 cm TL. Ellipses represent 95% confidence intervals.

Discussion

Artificial reefs function similarly to natural reef habitats for black sea bass in marine waters off Maryland and New England, given that individuals sampled at sites of both habitat types were similar in several traits that we examined: age, length, length at age, and gut contents. The initial expectation of this

Table 1

Comparison of stable isotope signatures, δ^{15}N and δ^{13}C, in liver, muscle, and mucus tissues of black sea bass (*Centropristis striata*) caught in 2018 near Ocean City, Maryland, based on analysis of variance for habitat type (natural versus artificial) and size class (small [0–25 cm in total length] versus medium [25–50 cm in total length]) and for the interaction of those 2 variables and the interaction between habitat type and consumer level (predator versus prey). *P*-values from analysis of variance were assessed at 2 levels of significance: $P<0.001$ and $P<0.01$.

	P-value					
	δ^{15}N			δ^{13}C		
Variable	Liver	Muscle	Mucus	Liver	Muscle	Mucus
Habitat type	<0.001	<0.001	0.07	<0.001	<0.001	<0.001
Fish size class	0.01	0.99	0.03	0.74	<0.001	<0.001
Habitat × size	0.88	0.79	0.81	0.92	<0.001	0.54
Habitat type × consumer level	<0.001	<0.001	<0.001	<0.01	0.28	<0.01

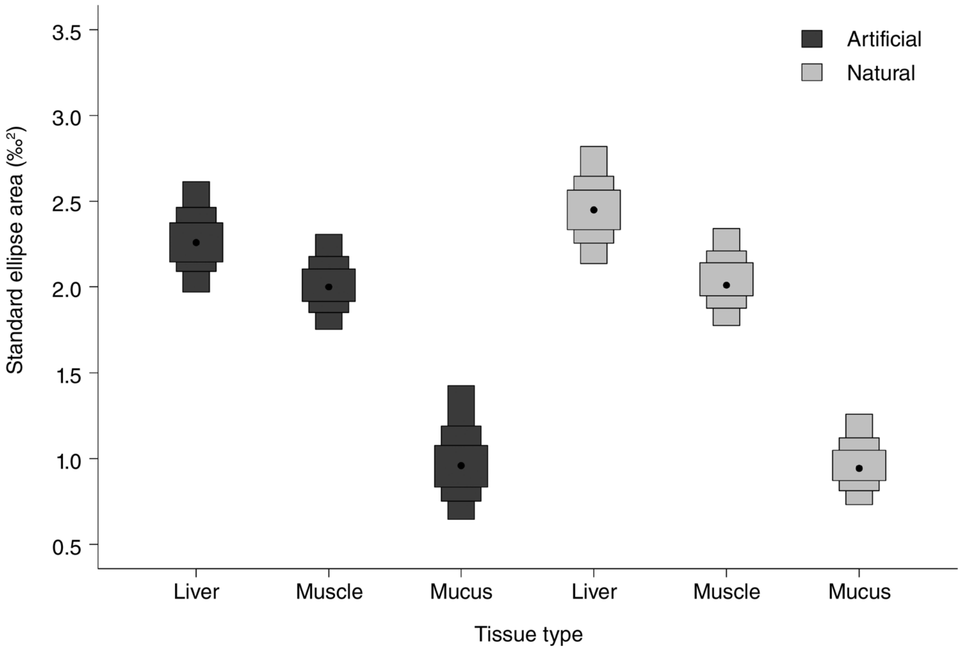

Figure 6

Standard ellipse areas, by tissue type and corrected for small sample size, for small (0–25 cm in total length [TL]) and medium (25–50 cm TL) black sea bass (*Centropristis striata*) sampled at natural and artificial reef habitats off the coast of Maryland in 2018. The lines on each box represent the 95%, 75%, and 50% credible intervals. The standard ellipse area is a proxy for isotopic niche, the location of the plot symbol in relation to the *y*-axis indicates the general trophic level of black sea bass based on stable isotope analysis of tissues, and the vertical length of each box indicates variability in prey consumption.

study was that habitat differences might drive variance in diet and subsequent differences in size or age, as suggested by Lawson et al. (2018). If black sea bass had a more calorically rich diet (e.g., one composed primarily of fish) at one habitat—but a calorically poorer diet (e.g., one composed of primarily crabs) at another habitat—this difference in diet could have affected fish size, particularly size at age, between habitats. The interactions between feeding and growth, as well as survival, are in fact complex (Goodrich and Clark, 2023); therefore, it was not surprising that we did not find evidence of such a simple postulation.

Nonetheless, values of stable isotope composition differed between fish of both size classes captured at natural and artificial habitats. There were notable differences in habitat traits and prey composition based on data from otter trawl collections near sampling habitats: natural habitats consisted mostly of large shell and cobble, with sea robins (*Prionotus* spp.) and squid egg mops, and otter trawl hauls at natural habitats mostly consisted of shrimp (Crangonidae) and small shells.

As expected, arthropods, a common prey item for black sea bass, dominated gut contents of fish from focused rod-and-reel sampling and broad-scale bottom trawling. We did not observe an ontogenetic diet shift from invertebrates to finfish, as reported by Byron and Link (2010); however, black sea bass in the large size class (>50 cm TL) were not present in the habitats that we sampled. We did notice a higher proportion of empty stomachs at natural habitats, but this trend was not associated with slower growth of black sea bass.

Analysis of stable isotope composition was more sensitive than analysis of gut contents alone, indicating trophic differences between natural and artificial reef habitats for the fish size classes evaluated. Significant differences in values of δ^{13}C in liver samples between habitat types may indicate that fish at different reef habitats frequently prey on items with distinctive δ^{13}C values. Specifically, fish caught at artificial reefs had higher δ^{13}C values, indicating that they feed on prey from more littoral or benthic sources, such as sand dollars or snails, instead of pelagic prey, such as smaller finfish. Yet this distinction was not reflected in our diet analyses, or in data on prey types from NOAA bottom-trawl surveys. The cause of this apparent disconnect in results between analysis of stable isotope signatures and analysis of stomach contents at the 2 habitat types is challenging to assign. Isotopic turnover times in wild fish would likely vary, considering that wild fish may have a wide breadth of prey options, a need to forage, and arguably slightly higher metabolic demands, which can alter turnover time.

In mucus samples, δ^{13}C values were significantly different between habitat types, but δ^{15}N values were not. The former result was consistent with findings for the other tissues tested, indicating that it is possible to use mucus, which can be sampled in a nonlethal way, for black sea bass in future isotopic studies. The use of fish mucus for stable isotope analysis has great potential, but this approach would benefit from experimental validation. Altering the stable isotope signatures of black sea bass in a controlled diet-switching experiment, in which food amounts (offered and consumed) and growth would be tracked from a known fish age until the end of the experiment, could help verify how long it takes for isotopic signatures to change in certain tissues, which food items have the greatest effect on signatures, and how certain foods affect growth by isolating the variable of diet. In fact, the black sea bass is a suitable model species for this research because of its history of being reared in aquaculture facilities (Perry et al., 2007). The results presented herein (Fig. 7) can be used to inform selection of prey items for a prey-switching experiment over a season of growth.

Conclusions

In this study, black sea bass were found to feed and grow at identical rates at natural and artificial habitats, indicating that, from an ecological perspective, artificial reefs function in a similar manner as natural reefs as habitat for this species. Therefore, we conclude that risks of habitat alteration, or the addition of artificial habitat structures, associated with construction of wind energy systems should be relatively low for this common species on the continental shelf in this region. Nonetheless, the differences between habitat types in the stable isotope composition of tissue samples indicate functional differences in system energy flow that should be investigated further, not only for black sea bass but also for marine species that may also be affected by climate change or offshore wind energy development (Kleisner et al., 2017)—if we are to explain and predict the response of the many other such species in this region, we need to include them as well.

Resumen

El serrano estriado (*Centropristis striata*) se alimenta de presas epibentónicas, sobre todo decápodos, y se vuelve más piscívora a medida que crece, una tendencia que tiene consecuencias energéticas para su crecimiento. En las próximas décadas, la construcción de sistemas de energía eólica expondrá a el serrano estriado a una manipulación a gran escala de los hábitats de la plataforma continental en el noreste de Estados Unidos. En este estudio, probamos los efectos del tipo de hábitat (hábitats de arrecifes naturales versus artificiales) en el tamaño, la edad, el crecimiento, la dieta y la dinámica trófica del serrano estriado, utilizando 407 especímenes recolectados con caña y carrete cerca de Ocean City, Maryland, en 2016 y 2018. No hay diferencias significativas en la longitud, edad, talla a la edad o dieta de los peces atribuibles al hábitat. La composición de isótopos estables (δ^{13}C y δ^{15}N) en muestras de 3 tipos de tejidos (hígado, músculo y mucus) varía significativamente según el hábitat, excepto los valores de δ^{15}N en las muestras de mucus. En todos los tipos de tejidos, los valores de δ^{13}C son más elevados en los peces de hábitats artificiales, lo que indica una alimentación más litoral que pelágica. Concluimos que, aunque ambos tipos de hábitats arrecifales son ecológicamente equivalentes como fuente de crecimiento y dieta para el serrano estriado, las diferencias en las señales de isótopos estables indican diferencias funcionales en el flujo de energía del sistema que deberían investigarse más a fondo en esta y otras especies marinas que se verán afectadas por el desarrollo de la energía eólica marina.

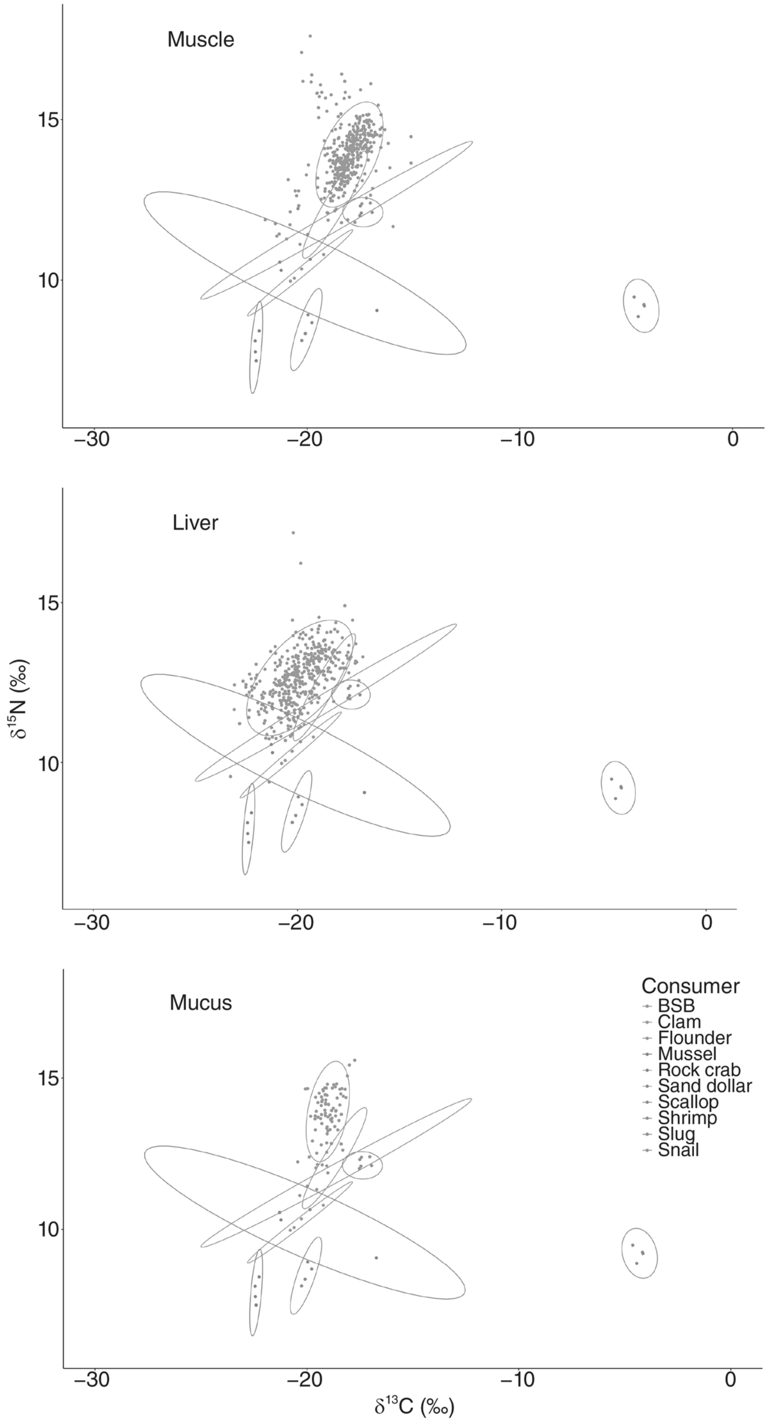

Figure 7

Stable isotope signatures, δ^{13}C and δ^{15}N, in muscle, liver, and mucus tissues of black sea bass (*Centropristis striata*) (BSB) caught with rod and reel off the coast of Maryland in 2016 and 2018, in relation to those for specimens of potential prey species collected with otter trawl in 2018 near the rod-and-reel sampling sites. Ellipses represent 95% confidence intervals.

Acknowledgments

Sea sampling was aided by Capt. C. Daniels, Capts. C. and W. Townsend, the Ecosystems Surveys Branch of the NOAA Northeast Fisheries Science Center, and the staff of NOAA research vessels. In Woods Hole, advice on sample processing was provided by J. Dayton, E. Robillard, S. Rowe, and B. Smith of the Northeast Fisheries Science Center. Special thanks to D. Secor, I. Oliver, N. Coit, I. Fenwick, and O. Scott Price. Base code for plotting PSIRI values was shared by S. Brown. This project was supported by the NOAA Living Marine Resources Cooperative Science Center (award no. NA16SEC4810007).

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