Feeding habits of 2 reef-associated fishes, red porgy (Pagrus pagrus) and gray triggerfish (Balistes capriscus), off the southeastern United States

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SEDAR82-RD18

June 15, 2021

NOAA
National Marine
Fisheries Service

Fishery Bulletin
established 1881

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Feeding habits of 2 reef-associated fishes, red porgy (*Pagrus pagrus*) and gray triggerfish (*Balistes capriscus*), off the southeastern United States

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Abstract—The feeding habits of red porgy (*Pagrus pagrus*) and gray triggerfish (*Balistes capriscus*) were investigated by examining the gut contents of specimens collected during 2009–2011 from live bottom habitats off the southeastern United States. Red porgy had a diverse diet of 188 different taxa. Decapods, barnacles, and bivalves were their main prey. Canonical correlation analysis indicated that depth, season, and fish length were statistically significant factors determining the degree of variability in the diet of red porgy. Gray triggerfish also had a diverse diet, composed of 131 different prey taxa. Barnacles, gastropods, and decapods were their main prey. Of the 4 explanatory variables, latitude was highly significant, and season, depth, and length were statistically significant. Red porgy and gray triggerfish were observed to have a generalized feeding strategy of feeding opportunistically on a wide range of prey. This study contains fundamental trophic data on 2 important fishery species in the southeastern United States. Most importantly, it provides fisheries managers with some of the data necessary for the implementation of an ecosystem-based approach to fisheries management.

There have been numerous calls and mandates to adopt an ecosystem-based approach to fisheries management (Link, 2002; Latour et al., 2003; NMFS, 2009). An ecosystem-based approach to fisheries management requires extensive knowledge of the dynamics of the ecosystem in question, the trophic ecology of individual species, and the food web as a whole (Byron and Link, 2010), as well as information on environmental and biological and economic factors. As fisheries managers move toward an ecosystem-based approach to management, the data inputs for ecosystem models, including diet information, must be acquired (Link et al., 2008; NMFS, 2009; SAFMC[1]). These models require long-term monitoring of the food web and information on species interactions—data that are lacking for most species in the southeastern United States (SAFMC[1]).

Red porgy (*Pagrus pagrus*) and gray triggerfish (*Balistes capriscus*) support commercial and recreational fisheries along the entire southeastern U.S. Atlantic continental shelf, often referred to as the South Atlantic Bight (SAB) (Bearden and McKenzie[2]; Manooch, 1977; Antoni et al., 2011), and both species are in the snapper grouper complex managed by the South Atlantic Fisheries Management Council. Much of the fishery-independent data used by managers for the snapper grouper complex are provided by the Marine Resources Monitoring, Assessment, and Prediction program, which is a cooperative, long-term, fishery-independent monitoring survey. A recent report on analysis of data from this survey program revealed that red porgy and gray triggerfish were the third and fifth most commonly caught species in chevron traps used in this survey, respectively (MARMAP[3]).

Manuscript submitted 23 April 2015.
Manuscript accepted 6 May 2016.
Fish. Bull. 114:317–329 (2016).
Online publication date: 26 May 2016.
doi: 10.7755/FB.114.3.5

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[1] SAFMC (South Atlantic Fishery Management Council). 2009. Fishery ecosystem plan of the South Atlantic region. Volume V: South Atlantic research programs and data needs, 177 p. SAFMC, North Charleston, SC. [Available at website.]

[2] Bearden, C. M., and M. D. McKenzie. 1969. An investigation of the offshore demersal fish resources of South Carolina. South Carolina Wildl. Resour. Dep., Tech. Rep. 2, 19 p. [Available at website.]

[3] MARMAP (Marine Resources Monitoring, Assessment, and Prediction). 2014. Semi-annual progress report. [Project report for the period 1 May–31 October 2014. Available from MARMAP, South Carolina Dep. Nat. Resour., 217 Fort Johnson Rd, Charleston, SC 29412.]

Previous studies regarding the trophic habits of red porgy and gray triggerfish in the SAB were limited in scope or are dated and, therefore, may not reflect possible recent dietary shifts that result from natural or anthropogenic disturbances. There has been, for example, only one published study on the feeding habits of red porgy in the southeast (Manooch, 1977). Although that study was very comprehensive and had a large sample size (*n*=779), it was completed more than 40 years ago. Additionally, we found a report from 1984 (SCWMRD[4]) on feeding of red porgy in the SAB in which diet by size class and calculated diet overlap were examined in relation with other common reef fishes. Information on the food habits of gray triggerfish is also limited, and the few studies that have been undertaken have focused on their feeding behavior on artificial reefs (Blitch, 2000; Kauppert, 2002) and on their interactions with sand dollars (Frazer et al., 1991; Kurz, 1995).

Ecological dynamics and processes can be influenced by changing environmental conditions and anthropogenic disturbances (Byron and Link, 2010), such as fishing. It is likely that intense fishing pressure has an impact on predator–prey relationships, and when these relationships are altered the food web can become unstable (Holling, 1973). Therefore, it is reasonable to postulate that intense fishing pressure over the last several decades not only has affected predatory fish species, such as red porgy and gray triggerfish, directly but has also altered other ecological interactions. An additional change in the trophic dynamics of fish species of the U.S. southeastern waters has been the accidental introduction of piscivorous lionfishes (*Pterois* spp.) (Whitfield et al., 2002; Meister et al., 2005) The scale of the ecological impact of lionfishes is uncertain as its range expands, but studies have indicated that lionfish predation has caused a reduction in prey communities and, therefore, a decrease of prey for native predators (Albins and Hixon, 2008; Morris and Akins, 2009).

This article provides descriptions of the current feeding habits of red porgy and gray triggerfish collected from natural, live bottom habitats in the SAB. This study is the first one on feeding habits of gray triggerfish on natural reefs off the Carolinas and Georgia. The primary objectives of this study were 1) to qualitatively and quantitatively describe the diet of red porgy and gray triggerfish; 2) to determine whether prey consumption differs significantly among seasons, depth zones, and latitudes; 3) to describe ontogenetic shifts in diet; 4) to determine the feeding strategy of each species; and 5) to provide data on diet to managers that use ecosystem-based models for fisheries management.

Materials and methods

Collections

Red porgy and gray triggerfish were collected during seasonal cruises (May–October) from 2009 through 2011 in the SAB (Fig. 1) with hook-and-line fishing. The hooks were baited with cut squid (*Illex* sp.) and cut round scad (*Decapterus* sp.). Sampling was conducted during the day and night while the research vessel was anchored or drifted over hard-bottom reef habitat. Ten specimens of each species were targeted in each of 16 sampling zones. Each sampling zone consisted of 1 of 2 depth zones (20–50 m or >50 m) and 1 of 8 latitudinal zones (1° from 27°N through 34°N).

All specimens were weighed to the nearest gram, and total length (TL) was measured in millimeters. The digestive tract (gut) was excised from the esophagus to the anus and individually labeled. Intestines were included because both species consume prey with some anatomical features that are particularly resistant to digestion, and gray triggerfish lack a distinct stomach. Guts were fixed in 10% formalin for at least 14 days and then rinsed with freshwater. After rinsing, gut contents were scraped into individual jars containing 70% ethanol and stored for identification.

Identification of gut contents

Gut contents were sorted by taxa, enumerated, and weighed (wet weight to the nearest 0.001 g) with a Sartorius[5] balance, model BP211D (Sartorius AG, Goettingen, Germany). Prey items were identified to the lowest possible taxon. Multiple fragments of individual organisms were counted as single individuals, unless the number could be estimated by counting structures, such as eyes, claws. Colonial organisms (i.e., bryozoans and tunicates) were counted as one individual. Fishes were identified according to the identification guide of Carpenter (2002a, 2000b), decapods were identified by using Williams (1984), bivalves and gastropods were identified by using Abbott (1968), zooplankters were identified by using Johnson and Allen (2005) and Boltovsky (1999), echinoderms were identified by using Hendler et al. (1995), and isopods were identified by using Schultz (1969). Voucher specimens from the Southeastern Regional Taxonomic Laboratory of the South Carolina Department of Natural Resources were used to confirm some identifications.

Diet analyses

Description of general diet To quantify feeding habits, the relative contribution of food items to the total diet was determined by using 3 traditional indices: percent frequency of occurrence (%F), percent composition by number (%N), and percent composition by weight (%W).

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[4] SCWMRD (South Carolina Wildlife and Marine Resources Department). 1984. Final report: South Atlantic OCS Area Living Marine Resources Study, Phase III, vol. 1, 223 p. Prepared for Minerals Management Service, Washington, D.C., under contract 14-12-0001-29185. [Available from Mar. Resour. Library, South Carolina Dep. Nat. Resour., 217 Fort Johnson Rd., Charleston, SC 29412.]

[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

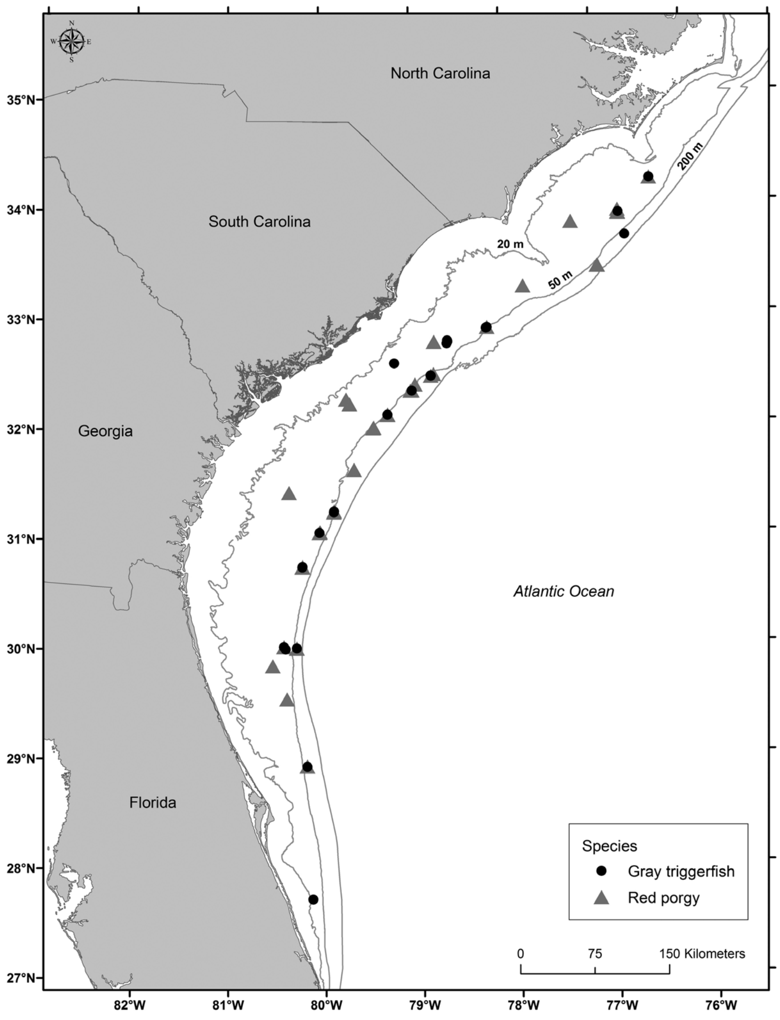

Figure 1

Map of catch locations off the southeastern United States, where specimens of red porgy (*Pagrus pagrus*) and gray triggerfish (*Balistes capriscus*) were collected for analysis of gut content in 2009–2011. Gray lines represent bathymetry (in meters).

Ontogenetic, temporal, and spatial changes in diet Prey were pooled on the basis of taxonomy (e.g., decapods and gastropods). Percent composition by weight was calculated for guts grouped by intervals of TL, season, depth (in meters), and latitude, and this metric was used for all analyses. For analytic purposes, prey types that contributed less than 1% by weight to the diet were excluded.

Canonical correspondence analysis (CCA; ter Braak, 1986), a multivariate direct gradient analysis technique, was used to determine the degree of variability in the diets of red porgy and gray triggerfish, explained by the canonical axes. The canonical axes are linear combinations of the 4 explanatory variables correlated to weighted averages of the prey within the cells of the response matrix (ter Braak, 1986; Garrison and Link, 2000). The CCA was performed with the community ecology package vegan, vers. 2.0-10 (Oksanen et al., 2013), an extension to the statistical software R, vers. 3.1.2 (R Core Team, 2014).

Each element in the response matrix was the mean percent weight of each prey taxon in a given length category, season, depth, and latitude combination. Prey data (%W) were log-transformed ($\ln[x+1]$) to normalize the data. The explanatory variables were coded as ordinal variables with the exception of season, which was coded as a categorical variable. The variance inflation factor was used to detect nearly collinear constraints (environmental variables), although it must be noted that these constraints are not a problem with the algorithm that is used in the CCA function of the vegan package to fit a constrained ordination (Oksanen et al., 2013). Any useless constraints would have been removed from the estimation, and no biplot scores or centroids would have been calculated (Oksanen et al., 2013). Permutation tests were used to determine the significant explanatory variables (ter Braak, 1986). A biplot of prey species and explanatory factors was constructed to examine the correlations between the explanatory variables (factors) and the canonical axes and to observe any dietary patterns associated with these factors. A descriptive analysis was generated for each of the significant factors identified by the CCA.

Hydrographic conditions were used to derive seasonal categories: spring: April through June; summer: July through September, and autumn: October through December. Latitudes were grouped into 3 categories: southern (27–29°N), middle (31–32°N), and northern (33–34°N). To examine the effect of fish length on the diets of red porgy and gray triggerfish, specimens were grouped into 50-mm-TL categories so that all members of a category displayed a reasonably consistent diet composition, and %W was calculated for each group. Groups with low sample sizes ($n \leq 3$) were trimmed to minimize outliers. Cluster analyses (Euclidean distance, average linkage method) were used to group these length classes into broader categories that represented relationships among the diet compositions.

Feeding strategies The feeding strategies of each species were analyzed according to the graphical method of Costello (1990), modified by Amundsen et al. (1996). Through the use of this method, prey-specific abundance was plotted against %F, making it possible to explore feeding strategies as well as shifts in niche use. Prey-specific abundance was defined as

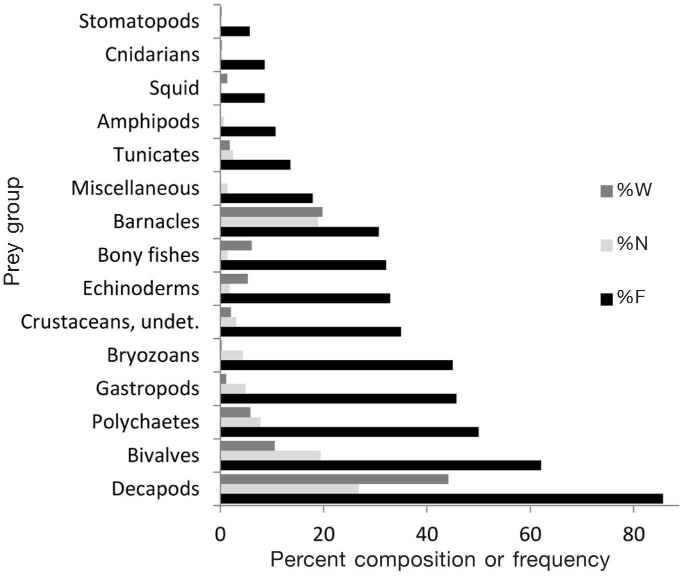

Figure 2

Percent frequency of occurrence (%F), percent composition by number (%N), and percent composition by weight (%W) of prey types present in the diet of 140 red porgy (*Pagrus pagrus*) captured in the South Atlantic Bight from 2009 through 2011. Prey items consumed by fewer than 5% of predators are not included. Miscellaneous=fish scales, foraminifera, eggs, macroalgae, and sediment.

$$P_i = (\sum S_i/\sum S_t)*100, \quad (1)$$

where S_i = the sum of prey *i*; and

S_t = the sum of all prey items found in only those predator guts that contained prey *i*. Percent composition by weight was the summed variable. On the graph that results from this method (Amundsen et al., 1996, fig. 3), the percent abundance, which increases along the diagonal from the lower left to the upper right corner, provides a measure of prey importance, with dominant prey on the top and rare or unimportant prey on the bottom. The vertical axis represents feeding strategy: specialization versus generalization. Prey points on the upper part of the graph represent prey on which predators have specialized, and prey positioned on the bottom half of the graph have been eaten occasionally or infrequently.

Results

Unidentified prey items were often encountered because both species bite or grind their food instead of consuming it whole. Fortunately, the majority of prey have parts that are resistant to digestion, making them easily identifiable on the basis of characteristic parts. For example, crab claws and legs, pieces of echinoderm test and spines, and pieces of barnacles were often seen in stomach contents. A full listing of prey items for both species is available in Suppl. Tables 1 and 2.

Red porgy

From 2009 through 2011, gut contents from 140 red porgy were collected. Lengths of red porgy ranged from 274 to 508 mm TL. Sample sizes were low at the extremes of our sampling range (i.e., 34°N and 27°N).

General diet description Red porgy had a diverse diet, composed of 188 different taxa that belong to 18 taxonomic groupings: decapods, bivalves, polychaetes, gastropods, bryozoans, unidentified crustaceans, echinoderms, bony fishes, barnacles, miscellaneous (e.g., fish scales and foraminifera), tunicates, amphipods, squid, cnidarians, stomatopods, isopods, ostracods, and protochordates. Decapods, barnacles, and bivalves were the main prey of red porgy, accounting for 44%, 20%, and 11% of the diet by weight, respectively (Fig. 2). The most frequently consumed decapods were parthenopid crabs (29%), portunid crabs (28%), calappid crabs (28%), and shrimps (28%). The most frequently consumed bivalve was the painted egg-cockle (*Laevicardium pictum*) (7%). Although polychaetes were consumed by 50% of red porgy, this taxon accounted for only 6% by weight and 8% by number. Other groups that were frequently consumed included gastropods (46%), bryozoans (45%), echinoderms (33%), and bony fishes (32%); however, these species contributed little by weight.

Ontogenetic, temporal and spatial changes in diet We determined that 6% of the total variability in the diet data was explained by the CCA. The first and second canonical axes accounted for 51% and 22%, respectively, of the constrained variation. Of the 4 environmental variables, depth and season were the most important ($P<0.001$), followed by length ($P<0.05$) (Fig. 3).

Although decapods were consumed in all seasons, fewer were consumed in the summer (29%) when barnacles were the primary food source (43%) (Fig. 4A). In the spring, red porgy consumed mostly decapods (50%) and bivalves (11%). In the autumn, decapods (53%) and polychaetes (20%) were the primary prey types.

Red porgy captured on the inner shelf (depths: 20.1–50.0 m) consumed a higher percentage of barnacles and bivalves than did their counterparts on the outer shelf, but decapods dominated diets of red porgy regardless of depth. Outer shelf red porgy also consumed bony fishes and polychaetes (Fig. 4B).

Decapods were the dominant prey at all latitudes, but fewer of them were consumed in the middle latitudes (31–32°N) (Fig. 4C). Red porgy captured at the middle latitudes (31–32°N) consumed barnacles (27%) and bivalves (11%) in addition to decapods. Barnacles

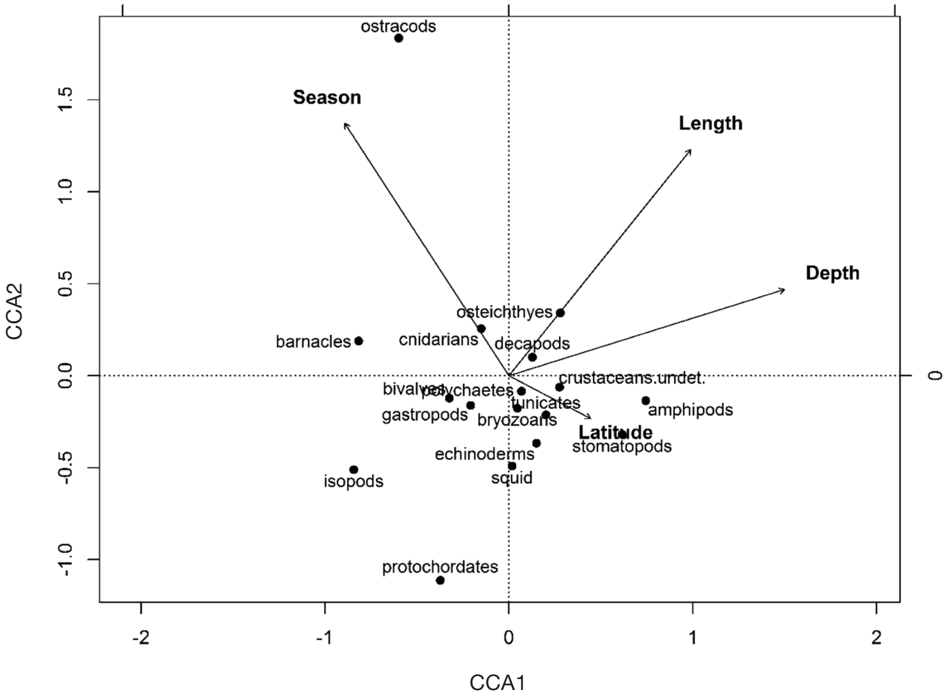

Figure 3

Biplot determined with canonical correspondence analysis (CCA) for the diet of red porgy (*Pagrus pagrus*) captured in the South Atlantic Bight from 2009 through 2011. Arrows represent significant explanatory factors, and dots represent prey types. The canonical axes represent linear combinations of the 4 explanatory variables (i.e., fish length, latitude of capture, season, and depth).

made up less than 1% of prey consumed at the northern latitudes (33–34°N).

The quantity of decapods in the diet of red porgy increased with increasing length (Fig. 4D), whereas smaller fish (<420 mm TL) consumed more barnacles and bivalves than their larger counterparts.

Feeding strategy According to the Amundsen graphical method, the feeding strategy of the red porgy population is generalized (points cluster lower on the y-axis of the graph) (Fig. 5), and therefore most prey types are eaten on occasion. Xanthid crabs were consumed by individual red porgy that were concentrating on this prey type as indicated by the point on the top left of the graph. The predator population had a broad niche width because most of the points are located along or below the diagonal from the upper left to the bottom right of the graph. A few prey items were eaten occasionally by most individuals, and these items are represented by the points on the bottom right of the graph (Fig. 5).

Gray triggerfish

Description of general diet Gut contents were collected from 82 gray triggerfish that ranged in size from 304 to 595 mm TL. Gray triggerfish had a diverse diet, composed of 131 different prey taxa that were combined into 19 broader taxonomic groups: gastropods, amphipods, decapods, unidentified crustaceans, polychaetes, bivalves, bryozoans, barnacles, bony fishes, echinoderms, tunicates, miscellaneous items (e.g., fish scales, foraminifera, and *Sargassum* spp.), stomatopods, isopods, cnidarians, ostracods, cephalopods, copepods, and unidentified mollusks. Barnacles, gastropods, and decapods were the main prey of gray triggerfish, accounting for 29%, 11%, and 11% of the diet by weight, respectively (Fig. 6). Although most gastropods were unidentified, 13 species were pelagic pteropods (group Thecosomata); cavolinid pteropods (40%) were the most frequently consumed pelagic pteropods. Unidentified shrimps were the most frequently consumed decapod (30%). Although amphipods were consumed by 63% of predators, this taxon accounted for only 0.5% of the diet by weight and 10% by number. Other species consumed frequently included unidentified crustaceans (59%), polychaetes (46%), bivalves (46%), and bryozoans (43%); however, these species contributed little by weight.

Ontogenetic, temporal, and spatial changes in diet We determined that 15% of the total variability in the diet data could be explained by the CCA. The first and second canonical axes accounted for 41% and 36% of the constrained variation, respectively. Latitude and season were the most important explanatory variables ($P<0.001$), followed by depth and length ($P<0.05$) (Fig. 7).

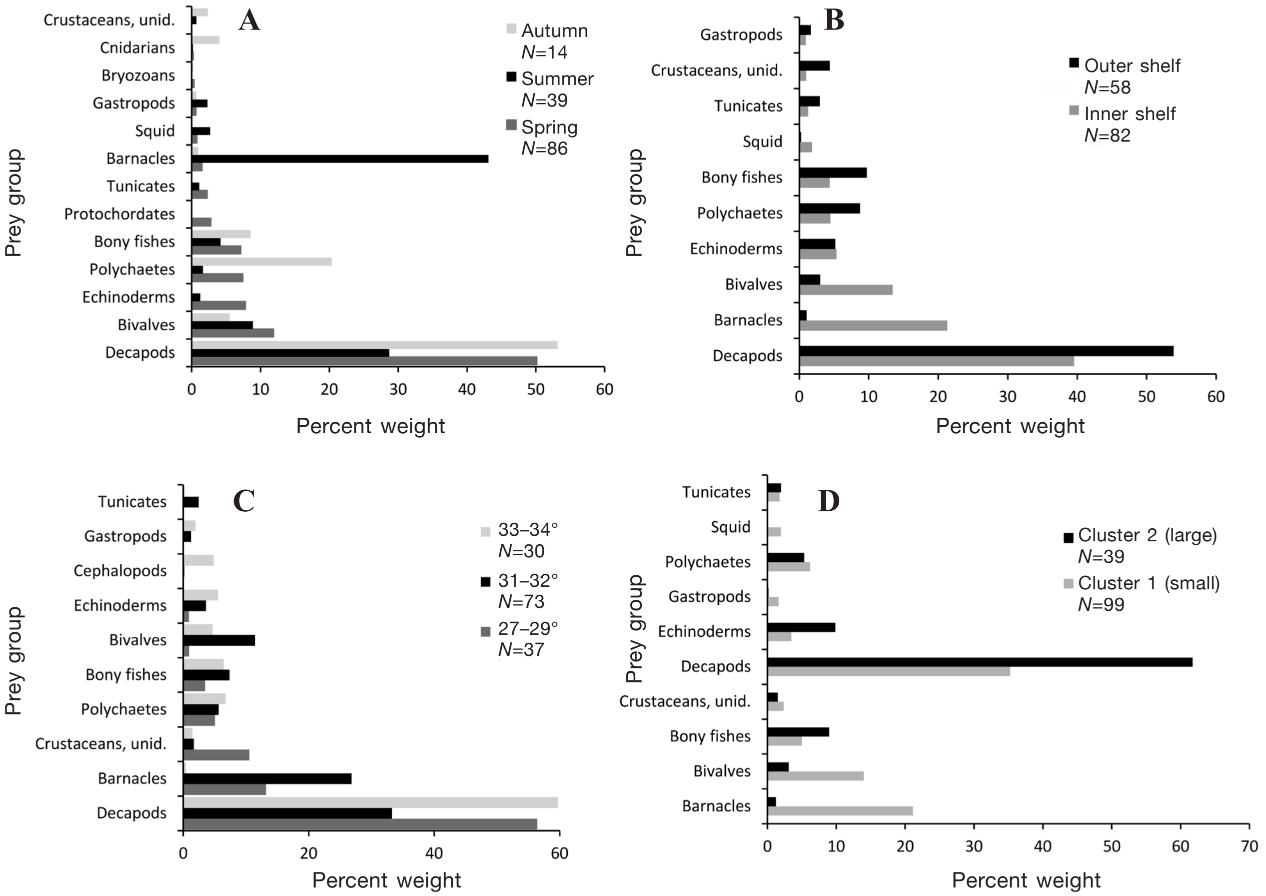

Figure 4

Diet composition by weight of red porgy (*Pagrus pagrus*) collected in the South Atlantic Bight from 2009 through 2011 presented by (**A**) season, (**B**) depth, (**C**) latitude, and (**D**) length. The number (*N*) of specimens collected in each season, at each depth zone, latitude range, or within each length cluster (small=321–420 mm in total length; large=421–520 mm TL) is given in the legends. unid=unidentified.

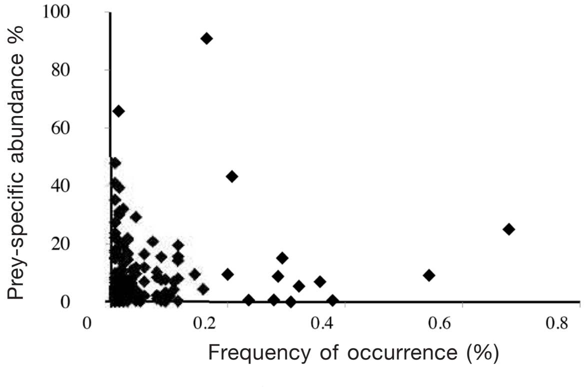

Figure 5

Graph of the feeding strategy of red porgy (*Pagrus pagrus*), captured during 2009–2011 in the South Atlantic Bight. The graph was developed in this study by using the Amundsen graphical method. Each dot represents a different prey species.

Barnacles (35%) and decapods (17%) were the primary prey for gray triggerfish captured in the spring (Fig. 8A). In the summer, the principal prey of gray triggerfish were barnacles (24%) and bivalves (23%), and, in the autumn, gray triggerfish consumed primarily gastropods (40%) and bony fishes (32%).

Gray triggerfish caught on the inner shelf consumed more barnacles, decapods, and polychaetes than did their outershelf counterparts, whereas, on the outershelf, they consumed more gastropods and bivalves (Fig. 8B).

Latitudinal differences in diet were substantial (Fig. 8C). Fish captured at the southern latitudes (27–29°N) preyed upon decapods (59%), and fish captured at the northern latitudes (33–34°N) consumed mostly barnacles (57%). Gray triggerfish caught in the central region (31–32°N) had a more diverse diet consisting of decapods, gastropods, barnacles, and bony fishes.

Small fish (<400 mm TL) consumed decapods and

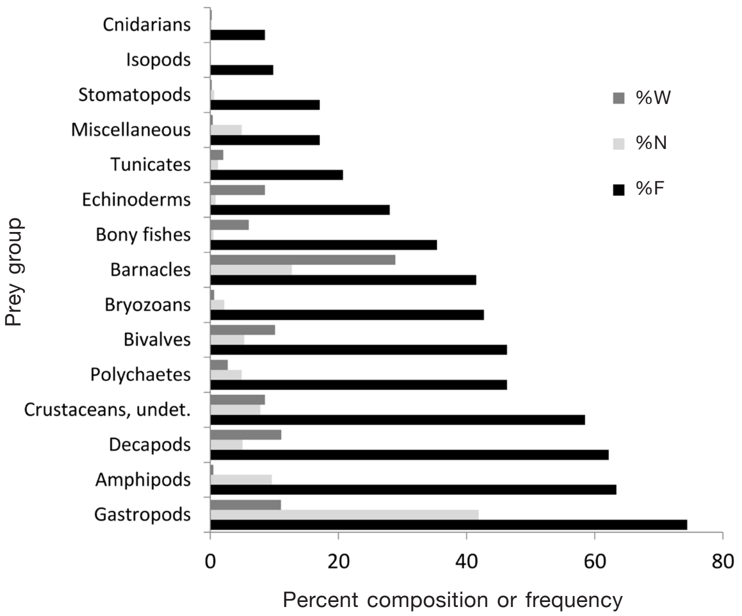

Figure 6

Percent frequency of occurrence (%F), percent composition by number (%N), and percent composition by weight (%W) of prey types present in the diet of 82 gray triggerfish (*Balistes capriscus*) captured in the South Atlantic Bight from 2009 through 2011. Prey items consumed by fewer than 5% of predators are not included.

relatively few bivalves. In contrast, large fish had a diet dominated by barnacles and bivalves. (Fig. 8D).

Feeding strategy On the basis of Amundsen graphical method, the feeding strategy of the gray triggerfish population is generalized (cluster of points lower on the *y*-axis of the graph) (Fig. 9); several prey items are eaten occasionally by most individuals. As with red porgy, the predator population has a broad niche width (points are all located below the diagonal from the upper left to the bottom right of the graph) (Fig. 9).

Discussion

Red porgy

Across the broad sampling range of this study, red porgy had a very diverse diet. Much of this diversity is likely a reflection of localized prey assemblages rather than a preference for specific prey items (Bearden and Mckenzie[2]; Manooch, 1977). Manooch (1977) and SCWMRD[4] reported findings similar to those of our study in that they found the red porgy to be a generalized predator. However, Manooch (1977) and SCWMRD[4] identified only 69 and 80 prey taxa, respectively, compared with the 188 taxa found in our study. In the case of the Manooch (1977) study, the difference in number of prey taxa may be attributed to the limited geographic range of his investigation; samples in that study came from only North and South Carolina, whereas samples from our study came from an area spanning from North Carolina to Florida.

It is also possible that the abundance of certain prey has shifted and, therefore, that red porgy have had to diversify their food resources. SCWMRD[4] found the preferred prey were decapods and fishes and that fishes made up the greatest volume of prey. We found fishes to be far less important prey (6%W). In contrast to Manooch (1977) and our study, SCWMRD[4] identified more nektonic and fewer benthic prey. In addition, SCWMRD[6] found very few mollusks in comparison with our study. The scientists at SCWMRD suggested that, because Manooch (1977) used stomach and intestine of red porgy and shelled organisms are slow to be digested, bivalves and gastropods would appear to be present more frequently than taxa such as small crustaceans and polychaetes. This suggestion could be one explana-

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[6] SCWMRD (South Carolina Wildlife and Marine Resources Department). 1981. South Atlantic OCS Area Living Marine Resources Study, vol. 1, 297 p. Prepared for Bureau of Land Management, Washington, D.C, under contract AA551-CT9-27. [Available from Mar. Resour. Library, South Carolina Dep. Nat. Resour., 217 Fort Johnson Rd., Charleston, SC 29412.]

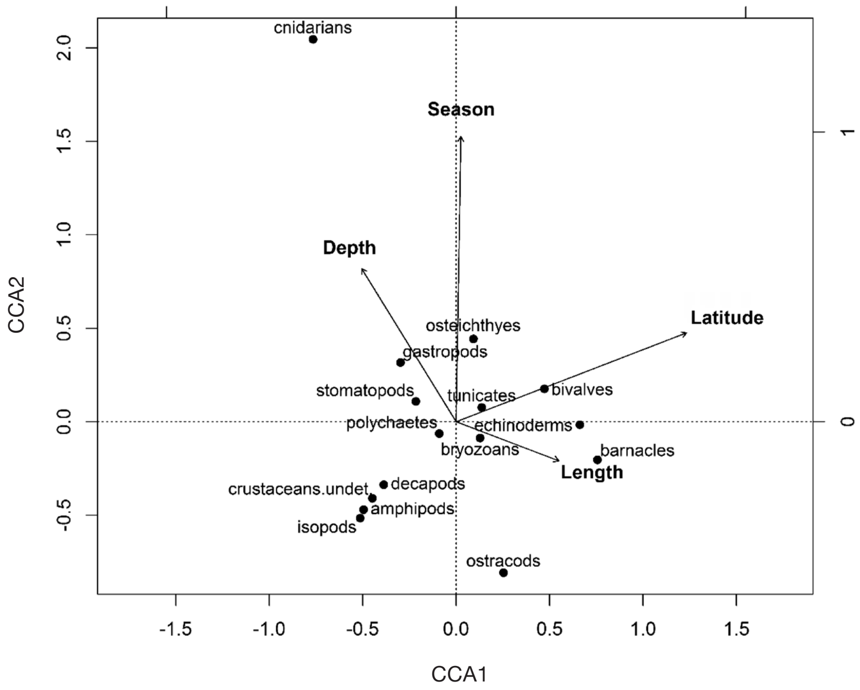


Figure 7

Biplot determined with canonical correspondence analysis (CCA) for the diet of gray triggerfish (*Balistes capriscus*) captured in the South Atlantic Bight from 2009 through 2011. Arrows represent significant explanatory factors, and dots represent different prey types. The canonical axes represent linear combinations of the 4 explanatory variables (i.e., fish length, latitude of capture, season, and depth [shown in bold type]).

tion for the frequently observed bivalves and gastropods in the diet of red porgy in our study.

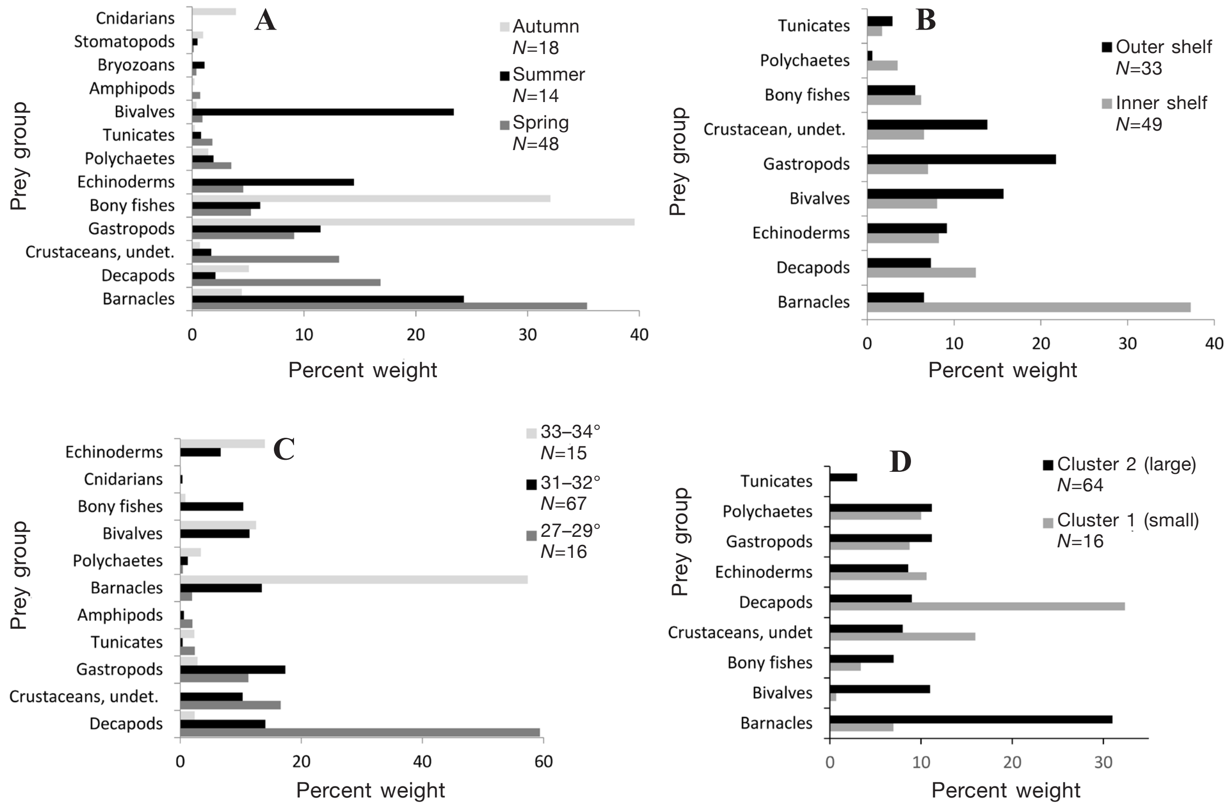
Season was the second most significant explanatory factor in the CCA in our study, but Manooch (1977) found only slight seasonal variation in several groups of invertebrates. In our study, barnacles were the main food source in the summer, whereas, in the autumn and spring, red porgy depended more heavily on decapod prey. This seasonal shift in diet could have been the result of lower decapod availability during the summer and that in turn would have led to red porgy consuming more barnacles. In fact, Manooch (1977) found that several groups of invertebrates varied seasonally both in volume and frequency. Red porgy are not dependent on one type of food source; therefore this species has the advantage of being able to switch prey as necessary with fluctuating seasonal prey populations.

There were significant differences in prey among length classes. Small fish (<420 mm TL) generally consumed small prey (barnacles and bivalves), and large fish consumed larger prey (decapods). The SCWMRD[4] study found that red porgy consumed more fishes and fewer decapods as they grew—a finding that also contrasts with our results. However, that study included smaller fish (51–350 mm in standard length) than those collected in our study (274–508 mm TL), and that size difference is likely to be the main reason for the reported differences in prey types by fish length.

A generalized feeding strategy (Fig. 5) is not unexpected for a species that consumes such a great diversity of prey items. Manooch (1977) suggested that the tremendously diverse diet of red porgy probably reflects localized forage assemblages rather than a preference for a specific food and supports the idea of classifying red porgy as trophic generalists. He also noted that they have certain behavioral and morphological characteristics that make it easy to feed on a diversity of prey: swimming speed and strong molariform teeth that enable these fish to crush armored prey, such as sea urchins, crabs, and gastropods. This feeding strategy has a selective advantage because red porgy are not dependent on a small number of food types, and, therefore, are less likely to face competition.

Gray triggerfish

Gray triggerfish were found to have a very diverse diet of 131 prey taxa across a broad sampling range. Unlike the prey that we found, previous researchers found the most important prey of gray triggerfish to be bivalves, barnacles, and echinoderms (Vose, 1990; Vose and Nelson, 1994; Kauppert, 2002). However, fish living around



Figures 8

Diet composition by weight of gray triggerfish (*Balistes capriscus*) collected in the South Atlantic Bight from 2009 through 2011 presented by (**A**) season, (**B**) depth, (**C**) latitude, and (**D**) length. The number (*N*) of specimens in each season, depth group, latitude range, or length cluster (small=350–400 mm in total length; large=401–600 mm TL) is given in the legends.

artificial structures (as opposed to the natural reefs examined in our study) were examined in those previous studies, and other research focused on gray triggerfish interaction with sand dollars (Frazer et al., 1991; Kurz, 1995). Vose (1990) wrote that gray triggerfish are highly dependent on reef-associated prey and found diets of gray triggerfish to be quite different for natural and artificial reefs. On natural reefs, bivalves were a common food, whereas artificial reefs that were examined were dominated by fouling organisms such as barnacles. Of the previously published work, only one study on gray triggerfish collected from artificial reefs in the Gulf of Mexico had findings similar to those in our study: Blitch (2000) found pelagic mollusks and crustaceans to be the most important prey.

In our study, echinoderms were found in 28% of guts, but this finding may be an underrepresentation of their importance in the diet of gray triggerfish because the soft tissue of echinoderms may have been digested before a gray triggerfish was caught. Frazer et al. (1991) cautions that because gray triggerfish eat only soft tissue and not the hard test, echinoderms may be underrepresented in studies of stomach contents because of different digestion rates. We were able to identify sand dollars in guts only when gray triggerfish had eaten an entire organism with its test.

The diet of gray triggerfish was dominated by gastropods (primarily pelagic pteropods) in the autumn, a result that confirms Kauppert's (2002) observations that feeding habits of gray triggerfish in the autumn shifted to 60% nektonic and planktonic feeding, especially when compared with substrate feeding in the spring and summer. Some species of pteropods are reported to reproduce in the spring and summer (Rampal, 1975; Dadon and de Cidre, 1992) and could result in increases in pteropod numbers in the autumn months and consequently the seasonal shift in predation. Furthermore, seasonal migrations occur in some species of pteropods (Sardou et al., 1996). Results from Sardou et al. (1996) and Franqueville (1971) indicate that the pyramid clio (*Clio pyramidata*), a pteropod species commonly consumed by gray triggerfish in our study, becomes abundant at shallower depths in autumn. This occurrence offers a plausible explanation for the increased pteropod predation in the autumn.

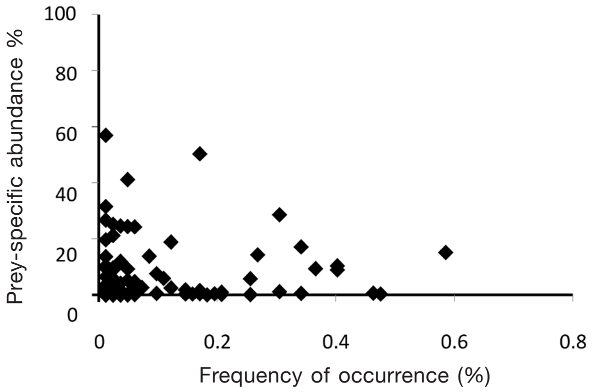


Figure 9

Graph of the feeding strategy for gray triggerfish (*Balistes capriscus*), captured from 2009 through 2011 in the South Atlantic Bight. The graph was developed by using the Amundsen graphical method. Each dot represents a different prey species.

Another reason for seasonal variation in diet could be the reproductive behavior of gray triggerfish. They spawn from April through September and peak spawning occurs from May through August (Kelly, 2014). During this time, they are found at deeper depths, and it is possible that their feeding behavior could change because they are nest guarders. Gray triggerfish caught on the outer shelf consumed more gastropods (primarily pteropods) than the gray triggerfish captured on the inner shelf. Pteropod distribution patterns remain poorly described (Bednaršek et al., 2012), but it has been reported that their distribution and migration vary seasonally (Dadon and de Cidre, 1992; Parra-Flores and Gasca, 2009).

Latitude was a highly significant explanatory factor in defining the diet for gray triggerfish, and there were changes in diet with fish length that might also have influenced our results. Small fish consumed more polychaetes and decapods, and large fish consumed more barnacles and bivalves (the opposite was true with red porgy). Decapod prey consumed by gray triggerfish were often smaller crab species or crustaceans in larval stages (i.e., crabs, shrimps, and lobsters). Gastropod consumption increased with predator size.

The percentages of explained variation found in this study are comparable to those in similar studies of diet composition (Jaworski and Ragnarsson, 2006; Latour et al., 2008). Although a relatively small proportion of the total variation is explained by the CCA, a small proportion is expected because the percentage-explained inertia (variance) for ecological data is typically low (<10%) (ter Braak and Verdonschot, 1995).

Some prey of gray triggerfish and red porgy have diel vertical migrations (at least 32 taxa) (Boltovskoy, 1973; Alldredge and King, 1980; Hopkins et al., 1994; Angel and Pugh, 2000). Pteropods, for example, exhibit diurnal vertical migrations along the depth range of 0–100 m. During the day, pteropods move to deeper waters but migrate to the surface at night (Angel and Pugh, 2000). They tend to concentrate in the upper layers during the night to feed and avoid predators (Hays, 2003). Gray triggerfish are rarely caught at night during cruises of the Marine Resources Monitoring, Assessment, and Prediction program (senior author, personal observ.), and they have been previously described as diurnal predators (Randall, 1968). It is possible that these fish are not caught on the bottom at night because this species migrates into the water column, following pelagic prey. Many fish species migrate in a diel pattern, both vertically (Narver, 1970; Blaxter, 1973; Begg, 1976) and horizontally (Baumann and Kitchell, 1974; Hobson, 1974; Bohl, 1979; Krumme, 2009), following prey migrations (Ahlbeck et al., 2012). Although gray triggerfish are highly reef associated, they also rely on migrating pelagic species as food sources. Other studies of reef fishes have reported trophic connections that are primarily dependent on these vertically migrating food webs (Weaver and Sedberry, 2001; Goldman and Sedberry, 2010).

Although competition between species was not a focus of our research, other studies have had results worth discussing in the context of our work. Johnson (1977) suggested that when %F exceeds 25% between 2 or more predators, competition is likely. In contrast, Pianka (1976) stated that competition for identical resources is only likely if resources are in short supply. Red porgy and gray triggerfish do share many of the same prey (e.g., decapods, gastropods, bivalves, bryozoans, echinoderms, polychaetes, and bony fishes), and, if food resources become scarce, then such scarcity could lead to competition. Possible causes for a short supply could be prey consumption by invasive lionfishes, ocean acidification, or other anthropogenic effects (e.g., fishing). In this study, we did not examine food availability, nor did we observe anything that indicated evidence of food scarcity.

Ocean acidification is of particular concern for gray triggerfish because a large part of its diet is composed of pelagic pteropods. Ocean acidification causes shell dissolution in pteropods and some benthic invertebrates that are $CaCO_3$-secreting organisms (Doney et al., 2009). Calcified structures provide protection from predators; therefore, pteropods would be adversely affected by the rising atmospheric CO_2 levels caused by human fossil fuel combustion and deforestation (Doney et al., 2009), and adverse effects on pteropods would, in turn, have serious effects on populations of gray triggerfish. This study is far more comprehensive than previous studies have been and covers a large geographic area, providing a baseline study that can be used to monitor potential dietary shifts that result from climate change.

The temporal and geographic differences in prey for red porgy and gray triggerfish highlight the need to incorporate information on fish food habits into ecosystem models. Many of the prey species consumed by fish in our study are not well studied in the southeast, and their population statuses are not well known. Changes in their status could have unanticipated consequences for commercial fish species like red porgy and gray triggerfish. The most significant predator–prey interactions are those between red porgy and decapods and bivalves and those between gray triggerfish and gastropods. The information reported here complements the findings of previous studies and provides a critical link between the biology of red porgy and gray triggerfish and their role as predators in marine ecosystems. Although both species rely primarily on hard-bottom habitats for feeding, opportunistic prey switching allows both red porgy and gray triggerfish to adapt to ecological changes. This research and that of similar studies contribute to our understanding of the role of predators in changing ecosystems and provide fisheries managers with some of the data necessary for the implementation of an ecosystem-based approach to fisheries management in the southeastern United States.

Acknowledgments

For their help with identification of prey items, we thank D. Burgess, J. Cowan, D. Knott, C. Willis, and D. Wyanski. Thanks are extended to the staffs of the Marine Resources Monitoring Assessment and Prediction program and of the Southeast Fishery-independent Survey, NOAA Southeast Fisheries Science Center, and to the crews of the RV *Palmetto* and RV *Savannah*. G. Sedberry, W. Anderson, C. Barans, K. Spanik, and W. Bubley provided helpful comments on early drafts at the manuscript stage. This work was supported through funds provided by the Southeast Area Monitoring and Assessment Program—South Atlantic. This paper is contribution number 734 from the South Carolina Marine Resources Division.

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