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FLEXIBLE FEEDING STRATEGIES OF JUVENILE GRAY TRIGGERFISH (*BALISTES CAPRISCUS*) AND PLANEHEAD FILEFISH (*STEPHANOLEPIS HISPIDUS*) WITHIN *SARGASSUM* HABITAT

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ABSTRACT: *Sargassum*-associated juvenile gray triggerfish and planehead filefish exhibited flexible feeding strategies in terms of their use of epifauna or pelagic zooplankton. Four diet samples represented instances of co-occurrence and segregated occurrence. Co-occurring gray triggerfish had the most specialized diets consisting mainly of pelagic copepods and hyperiid amphipods. Conversely, segregated triggerfish as well as both co-occurring and segregated filefish had broader diets mainly consisting of *Sargassum* epifauna, such as bryozoans, portunid crabs, and hippolytid shrimp. Still, co-occurring planehead filefish also consumed somewhat more zooplankton than segregated planehead filefish. Ontogenetic diet transitions were not as distinct for gray triggerfish as for planehead filefish. Our study demonstrates that juvenile tetradonts can be flexible in their use of benthic versus pelagic feeding strategies. Consequently, the influence of these key consumers on *Sargassum* food webs may vary spatiotemporally.

KEYWORDS: fish feeding strategies, gray triggerfish, planehead filefish, *Sargassum*, Tetraodontiformes

INTRODUCTION

Brown macroalgae in the genus *Sargassum* forms extensive free-floating mats of structured habitat in surface waters of the Gulf of Mexico (GOM) and the Atlantic Ocean. *Sargassum* has recently been designated as Essential Fish Habitat (EFH) by the South Atlantic Fisheries Management Council (SAFMC 2002 in Casazza 2008). Functionally, the *Sargassum* complex provides potential refuge, feeding and spawning habitat for various pelagic fishes (Dooley 1972, Bortone et al. 1977, Kingsford and Choat 1985, Kingsford 1992, 1993, Druce and Kingsford 1995, Moser et al. 1998, Wells and Rooker 2004). As a mobile habitat, *Sargassum* also provides a vehicle of transport and dispersal for juvenile fishes and other organisms (Casazza 2008).

A growing awareness of the ecological importance of *Sargassum* has motivated recent studies of its role as a unique nursery habitat in the northwestern GOM (Rooker et al. 2004, 2006, Wells and Rooker 2004, Turner and Rooker 2006), the north-central GOM (Comyns et al. 2002), and the northwestern Atlantic (Casazza 2008, Casazza and Ross 2008). Although few organisms directly consume *Sargassum* (Rooker et al. 2006), the *Sargassum* complex consists of a diverse trophic network of epifaunal and epiphytic constituents (Coston-Clements et al. 1991). Marine rafting fauna represent all major trophic categories, including suspension-feeding, grazing, and boring organisms (Thiel and Gutow 2005). Pelagic-derived zooplankton also concentrate near *Sargassum* (Yeatman 1962), thus enhancing the pelagic feeding option for *Sargassum* occupants.

Juvenile gray triggerfish (*Balistes capriscus*) and planehead filefish (*Stephanolepis hispidus*) represent two of the most abundant fishes associated with *Sargassum* (Dooley 1972, Bortone et al. 1977, Coston-Clements et al. 1991, Settle 1993, Casa-

zza and Ross 2008). Planehead filefish usually ranks as the most abundant member of the *Sargassum* ichthyofauna, and gray triggerfish typically ranks among the top 3 most abundant fishes associated with *Sargassum*. Although there is some seasonal non-overlap, juveniles of both species often co-occur in association with *Sargassum* (Dooley 1972). As tetradonts, the body design of these fishes exemplifies agile maneuverability enabled by independently undulating paired and median fins (Arreola and Westneat 1996). This derived body design combined with a nimble but strong oral-jaw apparatus and dentition also promotes feeding plasticity (Kotrschal 1989, Turingan 1994, Vose and Nelson 1994).

Previous studies have noted that diets of juveniles of both fishes contain *Sargassum* associated epifauna as well as pelagic zooplankton (Dooley 1972, Coston-Clements et al. 1991, Harper and McClellan 1997, Turner and Rooker 2006, Casazza 2008). However, previous studies have not considered whether such diet breadth might represent flexible feeding strategies. The overall goal of this study was to compare the diets of *Sargassum*-associated juvenile planehead filefish and gray triggerfish to assess feeding flexibility among the limited set of ecological circumstances. Four population samples represented instances of co-occurrence and segregated occurrence for these fishes. Diet patterns were examined in terms of (1) the relative use of pelagic versus *Sargassum*-associated prey, (2) diet breadth and (3) diet dissimilarity. We hypothesized that variability in diets of these 4 populations of tetradonts reflect flexibility in feeding strategies relative to *Sargassum* versus nearby open water as sources of food. As a caveat, the limited set of diet samples was not robust enough for generalizing about co-occurring versus segregated settings or seasonal diet patterns.

MATERIALS AND METHODS

Sample collections

Four population samples of planehead filefish or gray triggerfish taken in association with *Sargassum* and representing different ecological settings were used for this study. A sample containing 74 planehead filefish was collected on 21 May 2000 from patchy *Sargassum* habitat at 29° 32.54'N and 87° 02.81'W. Samples of 69 planehead filefish and 55 gray triggerfish were collected on 15 October 2000 from a *Sargassum* mat at 28° 44.82'N and 87° 42.28'W. Another sample containing 70 gray triggerfish was collected on 10 July 2002 from patchy *Sargassum* habitat at 29° 02.29'N and 88° 48.68'W.

Sightings of *Sargassum* by small aircraft pilots directed the R/V *Tommy Munro* to sampling sites. Upon arrival, surface collections were taken by towing a neuston plankton net (4 m long x 2 m wide x 1 m high, 3.22 mm nitex mesh) directly through weed lines, mats, or clumps to sample *Sargassum* along with associated epifauna and fishes. Accompanying hydrographic measurements included water clarity (Secchi), water temperature (°C), surface salinity and dissolved oxygen (mg/l). Time of day, cloud cover, sea state, sample depth, water depth, wind speed and direction, and latitude and longitude were also recorded for each collection site.

Net caught *Sargassum* was placed on fixed wire mesh suspended ~70 mm above the bottom of a 2.5m long fiberglass trough situated above a wash table. *Sargassum* samples were irrigated with seawater to wash associated organisms through a hole in the wash table and into a 0.505 mm mesh cone which retained the organisms. Organisms were fixed in 95% ethanol and labeled. Collections that were too large to preserve in entirety were subsampled by removing up to 50 kg wet weight of *Sargassum*. The remaining *Sargassum* along with associated organisms was then weighed and discarded.

Laboratory procedures

Diet Analysis. In the laboratory, fishes were removed from *Sargassum* samples and identified. Associated invertebrates were also retained and stored in ethanol. Each fish specimen was kept individually in 95% ethanol and assigned a unique number. For each specimen, total length (TL), standard length (SL), mouth width, head length, and body depth were measured to the nearest 0.01 mm using dial calipers. Blotted and gutted wet weights were taken for each fish to the nearest 0.01 g using an Ohaus® Analytical Plus microbalance.

For diet analysis, food items were recovered from the mouth cavity, gills, and complete digestive tract and preserved in 70% ethanol in labeled vials. First, guts were removed by making a ventral incision along the fish from the anus towards the operculum. The entire digestive tract from the esophagus to anus was removed and placed in a dish, incised and teased apart to remove any food items, and irrigated to remove any remaining food items.

All food items were identified to the lowest practical taxonomic level, usually family. For each fish, the volume of each type of food item was determined using a modified squash plate technique (Hellawell and Abel 1971), following Rako-

cinski and Zapfe (2005). Volumes of diet taxon fractions were estimated using a Nikon image analysis system consisting of a DMX 1200 Digital camera attached to a SMZ 1500 stereomicroscope and a PC. Using MetaVue 5.0 imaging software, prey volumes were estimated from two dimensional areas compressed to a uniform thickness between calibrated squash plates (Hellawell and Abel 1971). Multiple organisms were arranged to minimize the amount of unfilled space between them to ensure accurate volume estimates. Excess liquid was soaked up using a tissue before squashing. A digital picture was taken of the compressed area at a known magnification. Digital outlines of squashed diet fractions were traced twice to within a 0.1 mm² area tolerance in MetaVue 5.0 (Rakocinski and Zapfe 2005). Conversion factors specific to the calibrated squash plates facilitated volume (µL) estimations from mean areas (mm²). Volumes were recorded along with numbers of items for each prey type per fish.

Epifaunal Prey Abundances. Abundances and sizes (i.e., volumes) of epifaunal organisms were quantified as potential prey from *Sargassum* samples used for diet studies. First, *Sargassum* along with associated epifauna were subsampled into equal homogeneous fractions using a Motodo plankton splitter (Motodo 1959). One-fourth of the original sample was used for the segregated gray triggerfish and the co-occurrence sample; and a 1/8 fraction was used for the segregated planehead filefish sample. After removing all *Sargassum* fragments from retained fractions, the sorted organisms were split twice more, leaving 1/16 of the original epifauna for the segregated gray triggerfish and co-occurrence samples, and 1/32 of the original epifauna for the segregated planehead filefish sample. Organisms from the subsamples were identified and counted. Volumes for each taxonomic group were determined using the modified squash plate procedure as described above. Organisms that were too large for the squash plate procedure were placed in a drying oven for 48 hours at about 65°C before weighing them to the nearest 0.01 g (Hyslop 1980). Organisms from *Sargassum* samples retained by a 5.6 mm sieve were not regarded as potential prey due to gape size limitations of the fishes examined.

Data analysis

Diet Composition. Diets of 143 planehead filefish and 125 gray triggerfish were examined for this study. Basic diet metrics for each fish included counts and volumes for each prey type and frequency of occurrences (FO) for each fish sample. Diet analyses were mainly based on prey volumes to obviate biases associated with using counts for diet studies (e.g., 1 large prey versus equal volume made up of many small prey) and the problem of being unable to assign counts to some important prey types (e.g., colonial bryozoans and hydroids). Moreover, to avoid sacrificial pseudo-replication (Wallace 1981, Krebs 1999), diet proportions were calculated for each individual fish before averaging across the entire diet sample (VanderKooy et al. 2000). To consider ontogenetic diet shifts, fishes were subdivided into three natural size groupings (small (< 20 mm SL), medium (20–30 mm SL), and large (> 30 mm SL)). Lengths ranged from 9.8 mm to 71.2 mm SL for gray triggerfish and

from 19.1 mm to 71.2 mm SL for planehead filefish, although large fish were generally less than 50 mm SL. To ensure that the sample sizes (i.e., $n = 56 - 74$) of fishes adequately represented population-level diets and to estimate diet richness, the cumulative number of prey taxa was plotted against the number of pooled stomachs. Smoothed species-area curves representing every possible sequence of fish specimens within samples were generated, following Hartnoll (1983).

Consumption of *Sargassum* Epifauna versus Zooplankton. The extent to which fishes consumed *Sargassum*-associated epifauna or zooplankton was examined for each species-size group. Epifaunal and zooplankton groupings were assigned to food items based on the literature (Morris and Mogelberg 1973, Coston-Clements et al. 1991, Smith and Johnson 1996). For each fish, epifauna and zooplankton volumes were normalized by the total amount of food in the diet, and resulting proportional values were arcsine square root transformed. Gut fullness (i.e., total prey mass/fish mass) was also compared among size class groups.

Diet Breadth. Diet breadth based on prey volume was calculated using Levins' Index (B) and then standardized so it was expressed on a scale from 0 to 1.0, following Krebs (1999). The proportion of items in the diet (p_j) represented by each of food category j was estimated by N_j/Y , where N_j = number of individuals in j and $Y = \sum N_j$ (i.e., total number of individuals sampled).

Levins' Index was calculated as:

$$B = 1/\sum p_j^2.$$

Levins' B ranges from 1 to n , where n is the total number of prey types. To make interpretation easier, the values were standardized by dividing the total number of prey types into B, after correcting for a finite number of prey types (Krebs 1999):

$$B_A = (B - 1)/(n - 1);$$

where B_A = Levins' standardized niche breadth, B = Levins' index of niche breadth, and n = number of possible resource states (i.e., prey types). After standardization, 0 signifies a minimum niche breadth and extreme specialization, whereas 1.0 signifies maximum niche breadth and extreme generalization. Levins' Index of diet breadth was calculated both for each fish sample as whole, and separately for each size class within samples.

Diet Ordination. Diet similarity patterns were examined using non-metric Multi-Dimensional Scaling (NMDS) in Primer ver. 6.0. Percent volumes for prey types were square root transformed before conversion into a resemblance matrix of Bray-Curtis similarity values, which were subsequently subjected to NMDS ordination. The Bray-Curtis similarity coefficient is considered the most appropriate index for comparing biological communities (Clarke and Gorley 2006). Similarity values range from 0 to 100, with 100 signifying perfect similarity. Coordinates in NMDS plots represented diets of individual fish in 2 dimensional NMDS space, and distances between coordinates reflected diet dissimilarity.

ANOSIM and SIMPER Analyses. Analysis of Similarity (ANO-

SIM) followed by the Similarity Percentages Routine (SIMPER) elucidated overall differences in the diet composition of fishes. ANOSIM tests in Primer ver. 6.0 compared diets among samples and size classes of planehead filefish and gray triggerfish. The ANOSIM permutation test statistic, R, is centered on 0 (no differences among the groups). As R approaches 1, the null hypothesis is rejected indicating a significant difference among groups (Clarke and Gorley 2006).

SIMPER in Primer ver. 6.0 was used to attribute dietary differences to particular prey types when ANOSIM tests were significant (Clarke and Gorley 2006). SIMPER breaks down the average Bray-Curtis dissimilarity into percentage contributions from each prey type, thus showing which prey types primarily contributed to dietary differences. An overall two-way SIMPER analysis compared diet dissimilarity between gray triggerfish and planehead filefish as well as between segregated and co-occurring size-classes. In addition, one-way SIMPER tests elucidated diet dissimilarity between size classes.

RESULTS

Diet overview

A total of 32 prey types were recognized among all 4 samples. Predominant epifaunal prey types included bryozoans, hydroids, hippolytid shrimp, portunid crabs, caprellid amphipods, nereid polychaetes, triphorid gastropods, serpulid polychaetes, and phoxichilid sea spiders. Important pelagic prey types included calanoid copepods, cyclopoid copepods, corycaeid copepods, hyperiid amphipods, and fish eggs. Partially digested food was generally categorized as unidentified (unid) shrimp, unid brachyuran, unid copepod, unid gastropod, or unid miscellaneous material. Guts of 4 of the 74 segregated planehead filefish (5.4%; $n = 70$) were empty; as well as 1 of the 69 co-occurring planehead filefish (1.4%; $n = 68$); 0 of the 55 co-occurring gray triggerfish (0%; $n = 55$), and 3 of the 70 segregated gray triggerfish (4.3%; $n = 67$).

Smoothed species-area curves indicated that the sample sizes were sufficient, and thus provided comparable estimates of diet richness (Figure 1). The segregated gray triggerfish sample exhibited the highest diet richness, as signified by a curve that leveled out at about 25 prey types. In contrast, co-occurring gray triggerfish exhibited the lowest diet richness of about 14 prey types. Curves for both segregated and co-occurring planehead filefish reached similar values of around 20 and 22 prey types, respectively. However, the curve for co-occurring planehead filefish began to level off prior to that for the segregated filefish, reflecting fewer infrequent prey types in the co-occurring sample.

Epifaunal prey abundance and gut fullness

Prey abundances were quantified as standardized volumes (ml/kg) of epifaunal prey taxa, except organisms retained by a 5.6 mm sieve that were excluded from consideration. This criterion excluded mostly larger portunid crabs and palaemonid shrimp. Consequently, the total volume of potential epifaunal prey was highest for the segregated planehead filefish *Sargassum* sample (1144.6 ml/kg; included prey = 15.6 % of total volume); followed by the co-occurring *Sargassum* sample

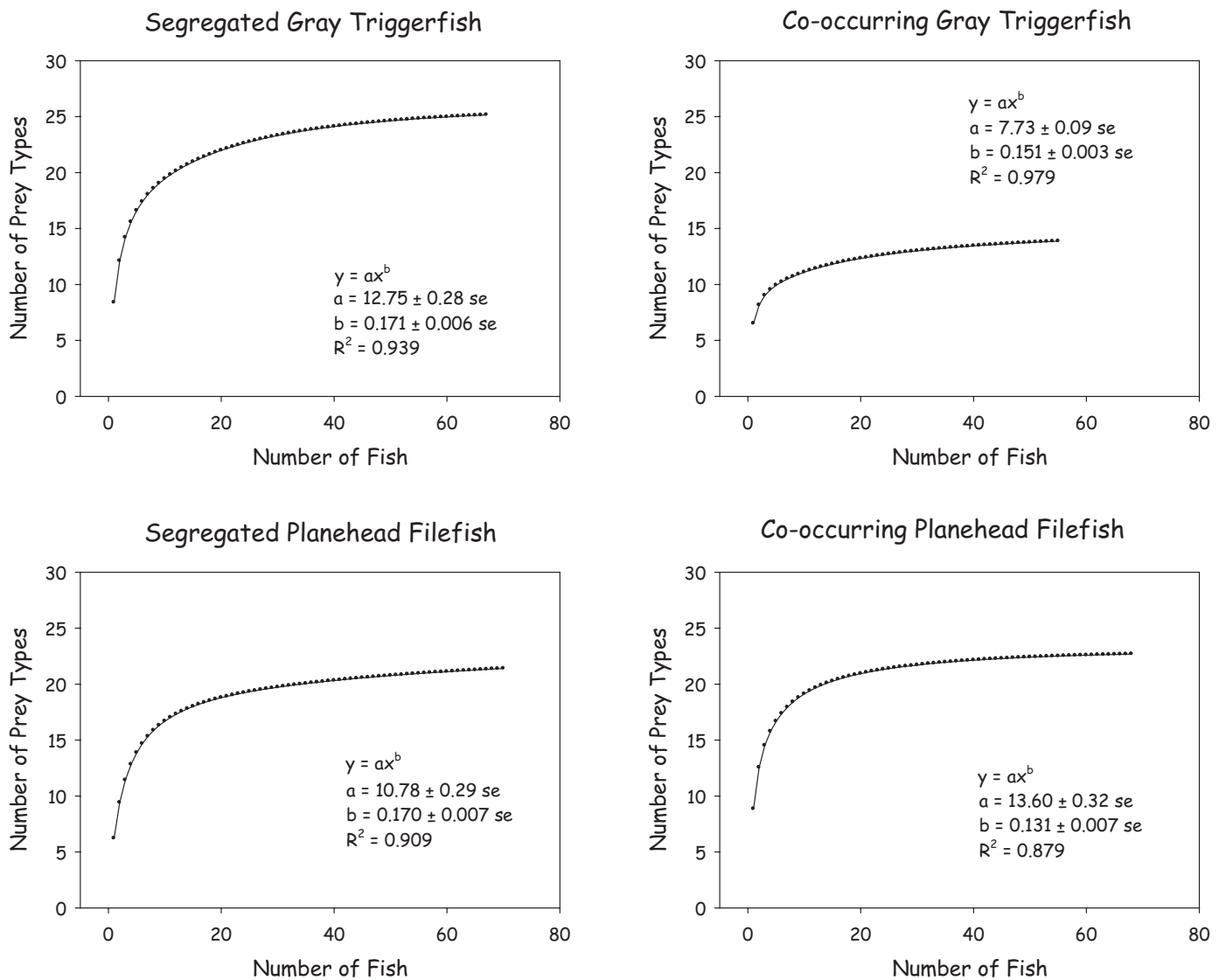


Figure 1. Smoothed species–area curves for segregated gray triggerfish, segregated planehead filefish, and for co-occurring gray triggerfish and planehead filefish samples.

(915.4 ml/kg; included prey = 84.9 % of total volume), and by the segregated gray triggerfish *Sargassum* sample (712.4 ml/kg; included prey = 71.3 % of total volume). Relative abundances of smaller, more vulnerable potential prey were highest for the co-occurring *Sargassum* sample, as implied by the relatively steep slope and high intercept of the normalized biomass–size spectrum (NBSS) (slope = -1.07 , intercept = 4.78 ; $r^2 = 0.73$, $n = 8$ for co-occurring species vs. slope = -0.701 , intercept = 3.78 , $r^2 = 0.59$, $n = 8$ for segregated triggerfish and slope = -0.44 , intercept = 3.07 , $r^2 = 0.58$, $n = 10$ for segregated filefish).

Together, hippolytid, palaemonid, and unidentified shrimp, in addition to serpulids and planocerids (planocerid flatworms) made up over 90% of the total biomass of recovered potential epifaunal prey in the segregated triggerfish *Sargassum* sample. Hippolytid shrimp was the most prevalent prey item within the segregated filefish *Sargassum* sample, making up almost 80% of the potential prey biomass. Palaemonid and unidentified shrimp

made up an additional 10% of the biomass of potential prey in this sample. Relative prey proportions for the co-occurrence *Sargassum* sample were very similar to those for the two segregated samples. Hippolytid shrimp alone made up 91% of the potential prey biomass for the former sample. Together, palaemonid and unidentified shrimp also contributed an additional 4.7% of the potential prey biomass for this *Sargassum* sample.

Segregated gray triggerfish showed the lowest gut fullness, and segregated planehead filefish showed somewhat lower gut fullness than co-occurring fishes (Figure 2). Co-occurring fishes of both species contained relatively similar amounts of food in their guts. There was no consistent pattern among size classes in the relative amounts of food in the guts, although medium sized fish contained slightly more food than large and small fish, especially within segregated samples.

Feeding strategies

Dependence on benthic or pelagic feeding strategies varied

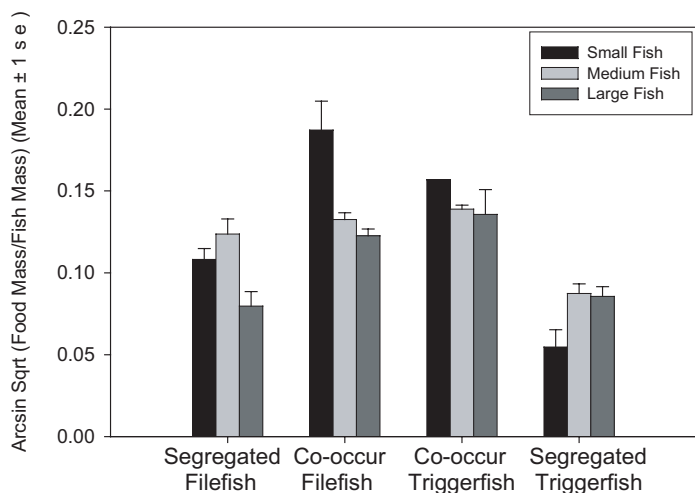


Figure 2. Relative gut fullness (mean \pm se) for 3 size classes of segregated and co-occurring samples of planehead filefish and gray triggerfish. Lack of error bar reflects small n for small co-occurring triggerfish. Size classes represent small (< 20 mm SL), medium (20–30 mm SL), and large (> 30 mm SL) fishes.

among the 4 samples of tetraodontids. Overall, co-occurring gray triggerfish consumed the highest relative amounts of zooplankton; whereas segregated triggerfish consumed the highest relative amounts of epifaunal prey (Figure 3). Both co-occurring and segregated planehead filefish consumed relatively high amounts of epifaunal prey. However, co-occurring planehead filefish consumed somewhat greater relative amounts of zooplankton than segregated filefish. Large co-occurring planehead filefish relied much more heavily on epifaunal sources of food than either small or medium fish; however, this was not the case for segregated filefish.

Diet Breadth. Overall, co-occurring gray triggerfish displayed the narrowest diets whereas co-occurring planehead filefish had the broadest diets (Table 1). Segregated gray triggerfish also had much broader diets than co-occurring triggerfish. Conversely, segregated planehead filefish had somewhat narrower diets than co-occurring filefish. Surprisingly, large size classes typically had narrower diets than small or medium size classes.

NMDS Ordination. NMDS plots depicted diet similarity patterns for samples of planehead filefish and gray triggerfish (Figure 4). A stress value of 0.18 indicated that diet variation was fairly well represented by the first two NMDS dimensions. Segregated planehead filefish and gray triggerfish occupied much broader regions of NMDS space than their co-occurring counterparts; coordinates of co-occurring individuals were relatively aggregated within NMDS space. Co-occurring gray triggerfish occupied the narrowest and most exclusive diet-ordination space. In contrast, co-occurring planehead filefish characterized a much broader region of ordination space. However, segregated planehead filefish occupied the most extensive region of NMDS space.

Ontogenetic diet transitions were also apparent within NMDS ordination space (Figure 4). Generally, size classes of planehead filefish were discernible as dispersion patterns within ordination space. Size classes of the co-occurring planehead

filefish were more discernible than those of the segregated planehead filefish. Conversely, ontogenetic diet transitions were not as apparent for gray triggerfish. For example, size classes of segregated gray triggerfish were not sharply delineated in NMDS space, even though they occupied a fairly broad region of ordination space. In contrast, all 3 size classes of co-occurring gray triggerfish clustered within a narrow region of NMDS diet-ordination space.

ANOSIM and SIMPER. ANOSIM showed that diet composition strongly differed between co-occurring and segregated gray triggerfish (ANOSIM $R = 0.817$; $p < 0.001$) and SIMPER confirmed the marked difference in diet composition (average dissimilarity = 89.69%) and illustrated how it was expressed. Consumption of pelagic calanoid copepods (74.27% vs. 2.94% volume) and hyperiid amphipods (8.39% vs. 0.26% volume) accounted for much of the diet dissimilarity between these samples. Segregated gray triggerfish mainly consumed large epifaunal prey, including bryozoans (17.50% volume), portu-

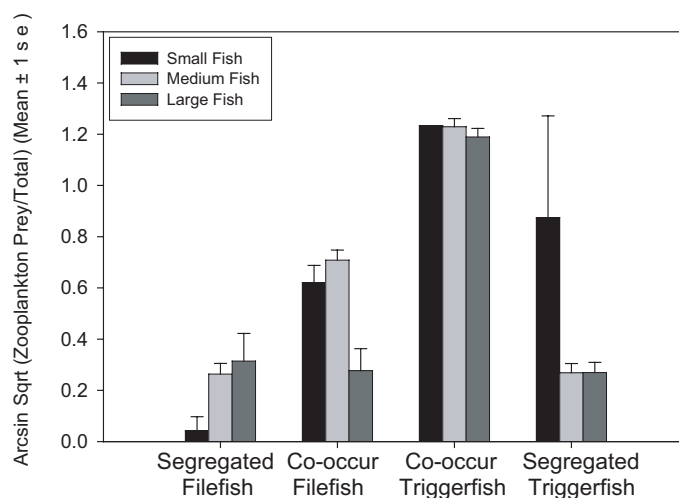
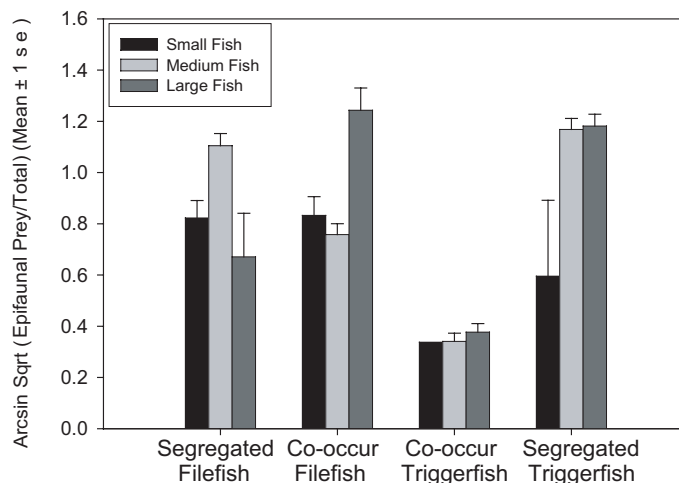


Figure 3. Relative amounts (mean \pm se) of epifaunal (top panel) and zooplankton (bottom panel) prey for 3 size classes of planehead filefish and gray triggerfish within segregated and co-occurring samples. Lack of error bars reflects small n for small co-occurring triggerfish. Size class definitions described in legend for Figure 2.

TABLE 1. Levins's diet breadth (B) and standardized Levins's diet breadth (B_A) for tetraodontid diet samples. Standardized diet breadth values (B_A) show that large fishes consistently exhibited the most specialized diets. Size classes represent small (< 20 mm SL), medium (20–30 mm SL), and large (> 30 mm SL) fishes

		Levins' Measure (B)	Standardized Levins' Measure (B_A)
Segregated Gray Triggerfish	Overall	10.6980	0.3879
	Small	5.0546	0.5068
	Medium	10.3995	0.4087
	Large	8.5564	0.3149
Co-occurring Planehead Filefish	Overall	10.0811	0.4128
	Small	6.8720	0.3091
	Medium	9.3272	0.3785
	Large	3.7693	0.1539
Co-occurring Gray Triggerfish	Overall	1.7660	0.0547
	Small	1.5692	0.0712
	Medium	1.7666	0.0639
	Large	1.7746	0.0596
Segregated Planehead Filefish	Overall	8.1687	0.3258
	Small	7.8354	0.3598
	Medium	7.8223	0.3790
	Large	4.1705	0.2114

nid crabs (13.79% volume), and hippolytid shrimp (12.41% volume).

Diet dissimilarity was also significant between co-occurring and segregated planehead filefish (ANOSIM $R = 0.376$; $p < 0.001$), as illustrated by moderately high SIMPER dissimilarity (average dissimilarity = 78.65%). Although bryozoans comprised roughly similar diet proportions in both samples of filefish (10.91% vs. 9.14% volume); co-occurring filefish consumed more planktonic calanoid copepods (16.41% vs. 7.14% volume), in addition to certain epifaunal prey, including hippolytid shrimp (15.53% vs. 2.89% volume), and triphorid gastropods (10.08% vs. 0.08% volume). Diets of segregated planehead filefish contained notably more unidentified miscellaneous material (24.79% vs. 7.90% volume) and hydroids (16.51% vs. 3.58% volume) than co-occurring filefish.

Although co-occurring gray triggerfish and planehead filefish were collected from the same *Sargassum* habitat, ANOSIM revealed significant diet dissimilarity between these population samples (ANOSIM $R = 0.463$; $p < 0.001$). SIMPER corroborated fairly high diet dissimilarity between these co-occurring fishes (average dissimilarity = 66.82%). Calanoid copepods mainly contributed to the difference in diets between the two co-occurring species; calanoids were much more prevalent in the diet of gray triggerfish (74.27% vs. 16.41% volume). Another zooplankton prey type, hyperiid amphipods, was almost equally represented in the diets of both fishes (8.39% triggerfish vs. 7.48% filefish volume). However, diets of co-occurring filefish also contained much higher amounts of several epifaunal prey, including hippolytid shrimp (15.53% vs. 0.11% volume), bryozoans (10.91% vs. 0% volume), and triphorid gastropods

(10.08% vs. 1.77% volume).

Diets of the size classes of co-occurring gray triggerfish were least distinct compared to other samples (average SIMPER dissimilarity = 27.71% – 32.48%). There were too few small fish ($n = 1$) to warrant reliable comparisons with this size class. However, the diets of medium and large size classes of co-occurring gray triggerfish were significantly different (ANOSIM $R = 0.212$; $p = 0.001$). Calanoid copepods largely contributed to size-related diet dissimilarity involving large fish (i.e., 7.50% SIMPER dissimilarity with medium fish); notwithstanding similar and high calanoid percent volumes for all three size classes (74.06% – 79.12%). In addition, the use of certain large prey, including unidentified shrimp, increased with fish size.

Pairwise ANOSIM showed a moderate difference in diet similarity between medium and large size classes of segregated gray triggerfish ($R = 0.068$; $p = 0.014$). There were too few small fish ($n = 2$) to warrant reliable comparisons with this size class. Diet dissimilarity between medium and large fish was mainly attributable to greater consumption of portunid crabs (10.19% dissimilarity), bryozoans (6.82% dissimilarity), and hippolytid shrimp (6.53% dissimilarity) by large fish. Diets of medium segregated gray triggerfish were further distinguished by the use of hydroids (9.42 % volume), and ostracods (10.62 % volume).

Diets differed significantly among all 3 size classes of co-occurring planehead filefish (ANOSIM $R = 0.322$ – 0.601 ; all $p = 0.001$); as further illustrated by SIMPER (average dissimilarity = 58.12% – 79.22%). Although small crustaceans, such as calanoid copepods and ostracods, contributed markedly to size-related diet dissimilarities (e.g., combined = 45.46% vs. 6.48% volume for small vs. large fish), other large epifauna, including hippolytid shrimp, as well as bryozoans, also contributed noticeably to size-related dietary differences (e.g., combined = 5.00% vs. 69.57% volume for small vs. large fish). Accordingly, hippolytid shrimp and bryozoans together made up 41.1% of the diet dissimilarity between small and large co-occurring planehead filefish.

SIMPER showed that the diets of all 3 size classes of segregated planehead filefish were fairly distinct (average dissimilarity = 66.23%–78.50%). The diet composition of large segregated planehead filefish differed significantly from diets of small and medium fish (ANOSIM $R = 0.321$ and 0.413 ; $p = 0.001$). Unidentified amorphous (miscellaneous) material contributed substantially to the diets of all 3 size classes of segregated planehead filefish (13.29–41.55% of volume). In addition, bryozoans mainly discriminated the diets of large segregated planehead filefish from small filefish (e.g., 3.58% vs. 21.13% volume for small vs. large fish); whereas the use of bryozoans was similar between large and medium fish (e.g., 19.92% volume for medium fish).

DISCUSSION

By virtue of their high abundances, juvenile planehead filefish and gray triggerfish likely play key roles within the food web of the *Sargassum* complex in the northern GOM. In addition to our study, previous studies have noted that diets of juveniles of both species include both *Sargassum*-associated epifauna as well

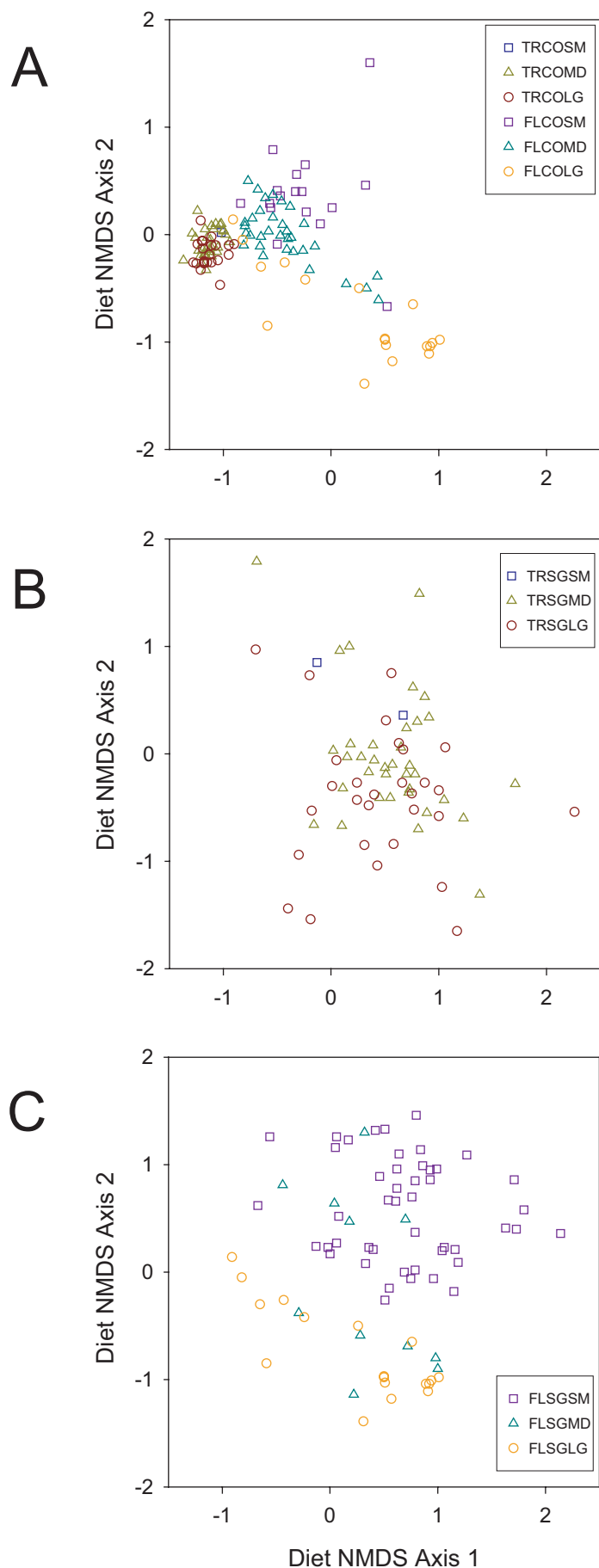


Figure 4. Non-metric multidimensional scaling (NMDS) ordination for individual fishes within the first two NMDS dimensions. **A.** Co-occurring gray triggerfish and planehead filefish coded by size class. **B.** Segregated gray triggerfish coded by size class. **C.** Segregated planehead filefish coded by size class. Size class definitions described in legend for Figure 2. Key: TRCOSM - small co-occurring triggerfish; TRCOMD - medium co-occurring triggerfish; TRCOLG - large co-occurring triggerfish; FLCOSM - small co-occurring filefish; FLCOMD - medium co-occurring filefish; FLCOLG - large co-occurring filefish; TRSGSM - small segregated triggerfish; TRSGMD - medium segregated triggerfish; TRSGLG - large segregated triggerfish; FLSGSM - small segregated filefish; FLSGMD - medium segregated filefish; FLSGLG - large segregated filefish.

as pelagic zooplankton. For example, juveniles of both species often feed on *Sargassum*-associated hydroids, bryozoans, polychaetes, and various crustaceans (Dooley 1972, Coston-Clements et al. 1991, Harper and McClellan 1997, Casazza 2008). Thus, they may rely considerably on *Sargassum*-associated secondary production as a food source. Pelagic copepods can also contribute substantially to the diet of juvenile gray triggerfish (Casazza 2008). Moreover, as seen in our study, planehead filefish also consume at least some zooplankton. But previous studies have not considered whether such diet variability might reflect flexible feeding strategies and food web impacts.

Flexible consumption of *Sargassum*-associated epifauna by juvenile tetradont fishes suggests potentially varying impacts upon the *Sargassum* food web. For example, some epifaunal prey organisms, including various small caridean shrimps and gastropods, likely graze upon epiphytic diatoms. Predation on grazing epifauna could potentially affect the condition of the *Sargassum* though cascading effects on epiphytic algae, as has been inferred for nearshore submerged vegetation (Drury-McCall and Rakocinski 2007). Conversely, suspension feeding epifauna like bryozoans and hydroids are linked to pelagic-derived production. Nevertheless, predation upon suspension feeding epifauna could also potentially enhance *Sargassum* by reducing fouling of this macroalgae.

Tetradont fishes possess derived morphological and behavioral traits that when taken together should facilitate feeding flexibility and a broad fundamental feeding niche. Notwithstanding the phylogenetic affinity between gray triggerfish and planehead filefish, they exemplified dichotomous feeding strategies in our study. When the species co-occurred in the same sample, juvenile gray triggerfish largely employed a pelagic feeding strategy on zooplankton; whereas planehead filefish mostly focused on *Sargassum*-associated epifauna. Segregated samples of both fishes largely relied on a benthic feeding strategy. Thus, our study shows that these tetradont fishes exercise flexible feeding strategies under different ecological scenarios. Previous studies have not emphasized the expression of such a flexible feeding dichotomy for these derived tetradont fishes.

Both pelagic and benthic feeding strategies may present viable options to consumers possessing suitable feeding adapta-

tions. The use of flexible feeding strategies should be mediated by prey availability in conjunction with the morphological and behavioral traits of consumers. In our study, prey availability did not appear to be any more limiting in the co-occurring sample than in the segregated samples. Moreover, both fishes in the co-occurring sample consumed some zooplankton. Despite the broad fundamental feeding niches shown by both of these tetradont fishes, gray triggerfish appeared better adapted for feeding on zooplankton. Indeed, Turner and Rooker (2006) surmised that gray triggerfish often consume pelagic copepods, based on Polyunsaturated fatty acid (PUFA) profiles characteristic of phytoplankton-derived particulate organic matter. Perhaps the fusiform shape of gray triggerfish predisposes this fish to feed on zooplankton, as opposed to the more laterally compressed shape of planehead filefish. A fusiform shape should favor rapid forward movements needed for capturing zooplankton and evading predators when making forays away from refuge; whereas a laterally compressed shape should facilitate the required maneuverability for feeding within habitat structure (Alexander 1974).

Coexisting fishes often avoid competition by partitioning food resources (Ross 1986); however, feeding disparities between co-occurring species alone do not imply competition for food (Connell 1980). Food availability did not appear to be limiting for fishes from the co-occurring sample in our study. Furthermore, co-occurring fishes of both species contained relatively more food than fishes from segregated samples. Instead of implying competition, interspecific dietary differences might simply reflect that gray triggerfish were better adapted for consuming zooplankton when the pelagic feeding strategy was relatively profitable (Gerking 1994). Alternatively, interference by planehead filefish might have discouraged gray triggerfish from accessing *Sargassum*-associated epifauna. As a corollary, competition for space within *Sargassum* habitat could explain feeding differences (Cody 1969, Heggenes et al. 1999). Indeed, Chen et al. (2001) documented territorial behavior in connec-

tion with dietary differences among juveniles of 3 co-existing triggerfishes.

Ontogenetic diet shifts have been documented for many species of marine fishes (Munoz and Ojeda 1998). Body-size related changes in food habits reduce diet overlap among size classes, resulting in a broader collective feeding niche (Labropoulou et al. 1997). In our study, ontogenetic shifts were expressed differently between species and ecological settings. In general, ontogenetic diet transitions appeared at a threshold size of about 30 mm SL, the large size class exhibited a narrower diet than smaller size classes, and diets of large segregated fishes were marked by the inclusion of decapod crustaceans. Although diets were only moderately dissimilar among size classes of segregated planehead filefish; distinct diet differences for small co-occurring planehead filefish suggested a broader feeding niche in this setting. In contrast, the feeding niche of gray triggerfish was much narrower within the co-occurring than in the segregated setting. Accordingly, the diets of all size classes of co-occurring gray triggerfish were very similar, mostly due to their common use of pelagic zooplankton.

The extent to which benthic versus pelagic feeding strategies are employed does not map commensurately to effects on epiphytic or pelagic trophic pathways. Many suspension-feeding epifauna depend on phytoplankton-derived particulate organic matter (POM). Indeed, based on PUFA profiles of selected *Sargassum*-associated invertebrates, Turner and Rooker (2006) proposed that the *Sargassum* food web was mainly supported by phytoplankton derived POM. The epiphytic trophic pathway only includes grazers on epiphytic algae and predators of said grazers. The influence of these key tetradont consumers on the structure of *Sargassum* trophic networks should vary accordingly. In conclusion, our study illustrates how the use of benthic versus pelagic feeding strategies by tetradont consumers within the biodiverse and biologically productive *Sargassum* complex is ecologically context-dependent.

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