

Gulf of Mexico Science

Volume 26
Number 1 *Number 1*

Article 3

2008

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DOI: 10.18785/goms.2601.03

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Recommended Citation

Nagareda, B. H. and J. M. Shenker. 2008. Dietary Analysis of Batfishes (Lophiiformes: Ogcocephalidae) in the Gulf of Mexico. *Gulf of Mexico Science* 26 (1).

Retrieved from <https://aquila.usm.edu/goms/vol26/iss1/3>

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Dietary Analysis of Batfishes (Lophiiformes: Ogcocephalidae) in the Gulf of Mexico

BRONSON H. NAGAREDA AND JONATHAN M. SHENKER

Stomach content analyses, performed on three species of batfishes, *Haliieutichthys aculeatus*, *Ogcocephalus declivirostris*, and *Ogcocephalus pantostictus* collected in the Gulf of Mexico in summer (June–July) and fall (Oct.–Nov.) 2002 and 2003, revealed a variety of benthic invertebrates, particularly gastropods, polychaete worms, and xanthid crabs. Schoener's dietary overlap indices (SI) were calculated between the three species within the same seasons, and within each species between seasons. SI values indicated that each species consumed a different assemblage of prey and that two of the species exhibited temporal variation in diet.

The anglerfishes (order Lophiiformes) have evolved some of the most unusual morphological and ecological adaptations in the tremendously diverse and varied clade of bony fishes (class Osteichthyes) and are among the most specialized groups of fishes. The defining feature of the anglerfishes is the modified first dorsal-fin spine (illicium) and terminal bait (esca) that serves as an apparatus to attract prey. The batfishes, family Ogcocephalidae, represent one of 18 families within the order, presently containing 10 genera and 68 species, of which five genera and 15 species are known from the western Atlantic Ocean (Bradbury, 2003). It is a poorly known group of small (< 300 mm) benthic fishes found worldwide in tropical and subtropical seas, from shallow inshore waters to depths as great as 3,000 m. They generally reside on continental shelves and slopes, on flat, relatively open-bottom habitats of rubble, sand, and mud (Bradbury, 1980, Richards and Bradbury, 1999).

Previous studies of ogcocephalids have focused primarily on taxonomy and systematics (Hubbs, 1958; Bradbury, 1967, 1980, 1988, 1998, 1999; Bradbury et al., 1999; Endo and Shinohara, 1999), although ogcocephalids have been briefly discussed in a few studies of the trophic ecology of a given region (e.g., Reid, 1954; Randall, 1967). Of the few studies on the natural history of batfishes, Winans (1975) examined the stomach contents of *Ogcocephalus rostellum* Bradbury, 1980, and *Haliieutichthys aculeatus* (Mitchell, 1818) off Cape Canaveral, Florida; and Gibran and Castro (1999) examined the stomach contents of *Ogcocephalus vespertilio* (Linnaeus, 1758) at Sao Sebastiao Channel, in southeastern Brazil. A histological study of the esca of *Ogcocephalus cubifrons* (Richardson, 1836) was conducted by Combs (1973) who hypothesized that the glandular esca secreted a chemical

attractant rather than acting as a visual stimulus for prey.

All lophiiform fishes studied to date are primarily piscivorous (Bertelsen, 1951; Randall, 1967; Bigelow and Schroeder, 1953; Pietsch and Grobecker, 1987), utilizing their lures to regularly obtain food. However, the few existing studies on the diets of batfishes suggest a different feeding strategy. Rather than the obvious adaptations for piscivorous macrophagy of nearly all other lophiiform taxa, exemplified best by their large anterodorsally directed mouths, ogcocephalids possess small, ventrally directed mouths, small villiform teeth, and a short gut, all adaptations for the capture of small demersal prey (durophagy), such as gastropods, small crustaceans, and polychaete worms (Wootton, 1994; McEachran and Fehhlm, 1998; Gibran and Castro, 1999). In an effort to demonstrate these trophic adaptations, as a unique approach to feeding among anglerfishes, dietary analyses assessing numerical importance and numerical similarities were conducted on three species of batfishes (*H. aculeatus*; *Ogcocephalus declivirostris* Bradbury, 1980; and *Ogcocephalus pantostictus* Bradbury, 1980) commonly found on the continental shelf of the northern and western Gulf of Mexico.

METHODS

Specimens were obtained during the National Oceanic and Atmospheric Administration/National Marine Fisheries Service (NOAA/NMFS) biannual groundfish survey between Brownsville, TX, and Pascagoula, MS, conducted by the R/V *Oregon II* in June–July and Oct.–Nov. 2002 and 2003. Trawls were made at randomly selected depth-stratified stations between 12 and 90 m, using a 16.8-m net otter trawl (2.54-cm mesh), with gear towed at an approximate speed of

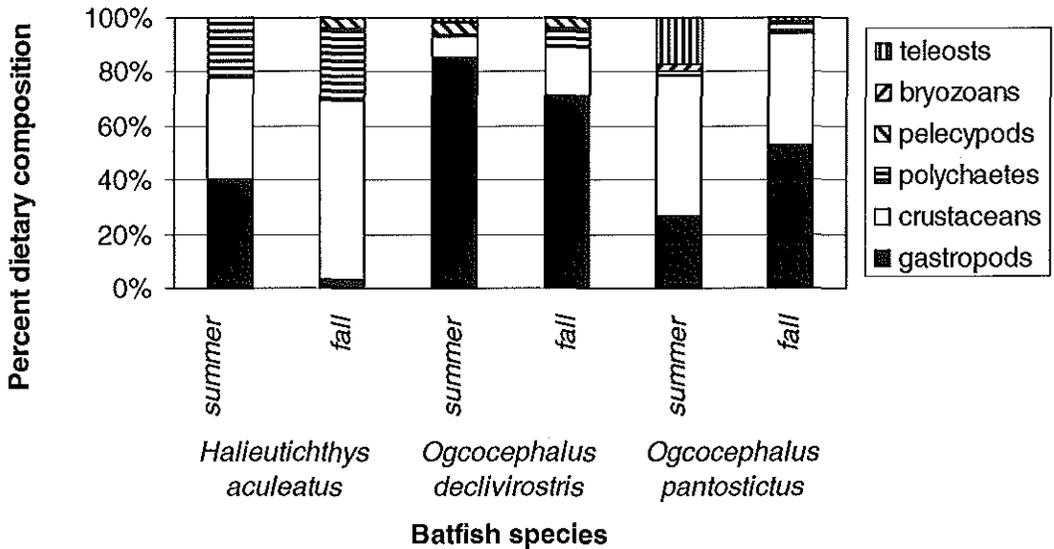


Fig. 1. Comparison of the dietary composition (%) of three species of batfishes taken from NOAA/NMFS groundfish surveys in the Gulf of Mexico in summer and fall 2002 and 2003.

1.3 m/sec for no less than 10 min, but not more than 55 min. During the survey, batfishes were opportunistically collected and frozen aboard ship for subsequent analysis. Once back at the laboratory, fishes were thawed, standard length and sex recorded, and stomach contents examined under a dissecting microscope. Prey items were counted, identified to the lowest possible taxon, and identified by H. Perry (Gulf Coast Research Laboratory, University of Southern Mississippi) and D. Shelton (Alabama Malacological Research Center).

Prey consumption was summarized in terms of percentage of frequency of occurrence (%F; proportion of stomachs containing a specific prey item) and percentage of the total numerical dietary composition (%N; proportion of the number of a specific prey item to the total number of prey items in all stomachs examined). Schoener's (1970) dietary overlap index (SI) was calculated to assess dietary overlap among the three co-occurring species within the same seasons (summer and fall) and within each species between seasons (Mathur, 1977), as follows:

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^n |P_{xi} - P_{yi}| \right)$$

where P_{xi} was the dietary composition proportion of food category i in the diet of sample x ; P_{yi} the dietary composition proportion of food category i in the diet of sample y ; and n , the number of food categories. SI values of ≥ 0.60 were taken to

indicate significant dietary overlaps (Zaret and Rand, 1971; Mathur, 1977).

RESULTS

The stomachs of *H. aculeatus* [$n = 230$, 37–72 mm standard length (SL)] (Table 1) contained primarily polychaetes (Nereidae), small gastropods (a species of *Nassarius* thought to be undescribed; H. Perry, pers. comm.), and small shrimps (Mysidae), although two additional species of gastropods and four other crustaceans were taken in low abundance (Fig. 1, Tables 1 and 2). *Nassarius* sp. was consumed only in the summer, whereas the other two dominant prey taxa occurred in both the summer and fall. This seasonal absence of gastropod prey is reflected in an SI value between the summer and fall samples of 0.568 (Table 3). Relatively few prey items were found in any one stomach, with a maximum of six gastropods and two polychaetes per stomach, although one contained 20 mysids. The hard-shelled prey items recovered were all small, approximately 1–4 mm in maximum dimension.

The stomachs of *O. declivirostris* ($n = 168$, 25–146 mm SL) (Table 1) contained a higher species diversity than those of *H. aculeatus*, but the prey were dominated by small (1–5 mm) gastropods, predominately *Cosmioconcha calliglypta* (Dall and Simpson, 1901) and *Nassarius* sp., two taxa that comprised over 90% of the diet (Fig. 1, Table 4), with as many as 28 gastropods found in a single stomach. Nereid polychaetes, pelyceps, crustaceans, and bryozoans were also found. Two specimens contained the shrimp eel

TABLE 1. Sample sizes and standard lengths of three species of ogcocephalids from the Gulf of Mexico. Summer samples were collected in June and July, fall samples in Oct. and Nov., 2002 and 2003. n = Number of fishes collected; SL = standard length.

Species	n	SL (mm)	Mean SL (mm)
<i>Halieutichthys aculeatus</i>			
Summer sample	125	49–67	58.2
Fall sample	105	37–72	53.5
<i>Ogcocephalus declivirostris</i>			
Summer sample	93	43–115	70.9
Fall sample	75	25–146	62.5
<i>Ogcocephalus pantostictus</i>			
Summer sample	26	47–275	190.1
Fall sample	11	39–268	145.6

Ophichthus gomesii (Castelnau, 1855). The diets of *O. declivirostris* remained consistent, with summer and fall collections having a SI value of 0.637 (Table 3).

The diet of *O. pantostictus* (n = 37, 39–275 mm SL) (Table 1) was dominated by xanthid crabs in the summer samples, and the lesser blue crab *Callinectes similis* (Williams, 1966) and the gastropod *C. calliglypta* in fall samples (Fig. 2, Table 5). Between seasons, *O. pantostictus* had an SI value of 0.376. Prey items were generally larger (10–25 mm) than those of the other two species, although most gastropod prey was similar in size (1–5 mm) than those found in the stomachs of *O. declivirostris*. Unlike the other species examined, *O. pantostictus* occasionally consumed fish: the remains of a 51-mm dwarf sand perch, *Diplectrum*

bivittatum (Valenciennes, 1828), were found in a 224-mm specimen, and small shrimp eels (*O. gomesii*) were found in the stomachs of several *O. pantostictus* specimens (176–275 mm SL).

There was no significant dietary overlap (SI \geq 0.60) between the three species in either summer or fall (Table 3). In summer, *H. aculeatus* showed SI values of 0.383 and 0.153, with *O. declivirostris* and *O. pantostictus*, respectively. *Ogcocephalus declivirostris* and *O. pantostictus* also showed very low dietary overlap with an SI value of 0.222 in the summer. Fall samples showed low dietary overlap as well, with *H. aculeatus* having SI values of 0.206 and 0.241 between *O. declivirostris* and *O. pantostictus*. The overlap in diet between *O. declivirostris* and *O. pantostictus* in the fall increased somewhat,

TABLE 2. Stomach contents of *Halieutichthys aculeatus* collected in the Gulf of Mexico in June–July and Oct.–Nov., 2002 and 2003. n = Number of stomachs examined; %F = frequency of occurrence; %N = numerical dietary composition; Max = maximum number of individuals of prey type in a gut.

Prey taxa	June–July			Oct.–Nov.		
	n = 125			n = 105		
	%F	Max	%N	%F	Max	%N
Polychaeta						
Nereidae	22.40	2	15.42	22.86	1	27.91
Gastropoda						
<i>Nassarius</i> sp.	24.8	6	26.06			
<i>Cylichnella bidentata</i>	14.40	3	11.70	0.10	2	2.33
<i>Cosmioconcha calliglypta</i>	4.80	2	3.72	0.10	1	1.16
Pelecypoda						
<i>Nuculana acuta</i>	5.60	2	4.26			
Crustacea						
Xanthidae	9.60	3	9.04	8.57	1	10.57
Stomatopoda	4.00	1	2.66	2.85	1	3.49
Isopoda	4.80	1	3.19			
Amphipoda						
Mysidacea	27.2	3	22.3	14.29	20	54.65
<i>Pagurus</i> spp.	1.60	2	1.60			

TABLE 3. Schoener dietary overlap indices for three species of batfishes collected in the Gulf of Mexico. Values in bold indicate intraspecific comparisons between summer (June–July, 2002 and 2003) and fall (Oct.–Nov., 2002 and 2003) samples. Values above the bold print indicate interspecific comparisons from fall collections. Values below the bold print indicate interspecific comparisons from summer collections.

	<i>Halieutichthys aculeatus</i>	<i>Ogcocephalus declivirostris</i>	<i>Ogcocephalus pantostictus</i>
<i>Halieutichthys aculeatus</i>	0.568	0.206	0.241
<i>Ogcocephalus declivirostris</i>	0.383	0.637	0.459
<i>Ogcocephalus pantostictus</i>	0.153	0.222	0.376

although not to any significant level (SI = 0.459).

DISCUSSION

Ogcocephalids are an exception to the primarily macrophagous, piscivorous feeding habits of other lophiiform fishes. In support of the few existing studies of batfish feeding (e.g., Winans, 1975; Gibran and Castro, 1999), batfishes in this study consumed almost exclusively small benthic invertebrates such as small snails, shrimps, crabs, and polychaetes. The three species of batfish in this study fed on somewhat different assemblages of prey. Stomach contents of *H. aculeatus* were dominated by nereid polychaetes and mysids. *Ogcocephalus declivirostris* consumed negligible amounts of polychaetes and no mysids, instead feeding primarily on gastropods (*Nassarius* sp. and *C. calliglypta*) and small xanthid crabs. Although there was some dietary overlap, with both species consuming *Nassarius* sp. in the summer, the majority of the diet was very different. *Ogcocephalus pantostictus* fed primarily on crabs (Xanthidae and *C. similis*) and gastropods (*C. calliglypta*). Small fishes [e.g., shrimp eels (*O. gomesii*) and dwarf sand perch (*D. bivittatum*)] were rarely found inside the stomachs of *O. declivirostris* and *O. pantostictus*, and their overall contribution to the diet appears limited. Larger individuals of *O. pantostictus* (> 215 mm SL) and two *O. declivirostris* (89 and 146 mm SL) were the only specimens found to contain fishes as prey items. While small fishes may not be a regular prey item, it is not surprising to find them in the stomachs of large batfishes as an opportunistic prey item. In addition to co-occurring in the same habitat, small fishes may mistake batfishes for a foraging or shelter structure in the same manner proposed for frogfishes by Pietsch and Grobecker (1987).

Although some prey taxa were commonly consumed by all three species, the consumption of other prey types resulted in low values (< 0.60) of Schoener's dietary overlap index among

species and between seasons within a species (except *O. declivirostris*; see Table 3) suggesting there is relatively little overlap in diets among species in the Gulf of Mexico. This may be in part because of spatial habitat differences as batfish species do not regularly co-occur in trawl collections. Most of the lowest dietary overlap values occurred between *H. aculeatus* and both species of *Ogcocephalus*. *Halieutichthys aculeatus* rarely occurred in trawls with *O. declivirostris* and never with *O. pantostictus*. Furthermore, *O. declivirostris* and *O. pantostictus* also rarely occurred in the same collections. The SI values between these two species were low in the summer but increased (although not significantly) in the fall. This was reflected by the increase in diet of *C. calliglypta* by *O. pantostictus* in the fall (Tables 3 and 5). The summer SI value between *H. aculeatus* and *O. declivirostris* was higher than most other values between species and this resulted from the presence of *Nassarius* sp. in the diet of *H. aculeatus* during the summer.

Although spatial habitat differences between species may explain the large differences in dietary overlap values, in some collections batfishes co-occurred (*H. aculeatus*/*O. declivirostris* and *O. declivirostris*/*O. pantostictus*). Despite this co-occurrence, the SI values between species remained low. This may reflect prey resource partitioning by the different batfishes where they co-occur. Seasonal changes in some of the available prey species of these fishes may also account for the differences in diet, although the possibility cannot be discounted that these differences simply reflect different microhabitats sampled by individual trawls.

Only *O. declivirostris* showed a persistent and significant dietary similarity between the summer and fall samples; its primary prey of gastropods remained consistent between seasons. The SI value of 0.568 for *H. aculeatus* between seasons indicated some similarity as it approached the 0.60 threshold value (Zaret and Rand, 1971; Mathur, 1977) to indicate significant dietary overlap. Dominant prey items such as nereid polychaetes and mysids were consistent in the

TABLE 4. Stomach contents of *Ogocephalus declivirostris* collected in the Gulf of Mexico in June–July and Oct.–Nov., 2002 and 2003. n = Number of stomachs examined; %F = frequency of occurrence; %N = numerical dietary composition; Max = maximum number of prey type in a gut.

Prey taxa	Summer			Fall		
	n = 93			n = 75		
	%F	Max	%N	%F	Max	%N
Polychaeta						
Nereidae	4.30	1	0.90	10.67	2	6.77
Gastropoda						
<i>Nassarius</i> sp.	26.88	18	23.67	16.00	20	24.81
<i>Cylichnella bidentata</i>	10.75	9	6.18	6.67	2	5.26
<i>Cosmioconcha calliglypta</i>	35.48	21	31.56	14.67	5	14.29
<i>Niso aeglees</i>	2.15	1	0.40	4.00	1	2.26
<i>Polystira albida</i>	15.05	17	10.87	6.67	1	3.76
<i>Kurtziella</i> sp.	8.6	28	8.74	4.00	1	3.01
<i>Terebra arcas</i>	12.90	6	4.05	1.33	1	0.75
<i>Natica marochiensis</i>	2.15	3	1.07	1.33	1	0.75
<i>Compsodrillia</i> sp.				12.00	3	14.89
Pelecypoda						
<i>Argopecten</i> sp.	1.08	7	1.49			
<i>Nuculana acuta</i>	12.90	3	3.20	5.33	2	3.76
Crustacea						
Xanthidae	31.51	2	6.37	16.00	4	12.78
<i>Raninoides</i> sp.	2.15	1	0.40	2.67	3	3.76
<i>Trachypenaeus similis</i>				1.33	1	0.75
<i>Pagurus</i> spp.	1.08	1	0.20			
Bryozoa	1.08	1	0.20	1.33	2	1.50
Teleostei						
<i>Ophichthus gomesii</i>				2.67	1	1.50

diet of this species between seasons; however, *Nassarius* sp. was a numerically important dietary item only in the summer samples of *H. aculeatus*, as it was absent in fall samples. This may reflect prey availability differences; however, *Nassarius* sp. was consistent in the diet of *O. declivirostris* between seasons suggesting it may be available throughout the year as a potential prey item and that resource partitioning occurs between these two species. Alternatively, if spatial habitat differences are normally an important factor in batfish diets, the increase of *Nassarius* sp. in the diet *H. aculeatus* may indicate increased sympatry with *O. declivirostris* during the summer. Prey consumption of *O. pantostictus* changed considerably between summer and fall. This species may be taking advantage of differences in recruitment and availability of prey by taking xanthid crabs in the summer and then switching to *C. similis* and *C. calliglypta* in the fall. A review of unpublished NOAA/NMFS collection data suggests that small juvenile *C. similis* were more abundant in fall trawl collections. A more intensive and focused study on *C. similis* may help determine whether this increase is because of recruitment. The stomachs of *O. pantostictus*

also contained larger prey items than those of the other two species studied. This may be a result of the larger size of specimens of *O. pantostictus* collected in the study (summer mean length, 190.1 mm; fall mean length, 145.6 mm).

Size, however, may not necessarily be a major factor in the size and type of prey taken. Nagareda (2005) analyzed a sample of *O. declivirostris* for relationships between prey size and batfish body and mouth size. The results showed only a slight increase in prey size with increasing predator body size and mouth gape. Although the gape parameters increased with increasing SL, this increase was not reflected in the consumption of significantly larger prey. Except for polychaetes and shrimp eels, all prey taken were short in length, with a maximum cross-sectional dimension of less than 5 mm. Despite being longer prey items, polychaetes and snake eels are soft and easily compressible, and had cross-sectional measurements similar to those of the gastropods and crustaceans taken by the batfish. Other constraints, including the availability of prey of larger sizes, or other morphological constraints such as pharyngeal

TABLE 5. Stomach contents of *Ogcocephalus pantostictus* collected in the Gulf of Mexico in June–July and Oct.–Nov., 2002 and 2003. n = Number of stomachs examined; %F = frequency of occurrence; %N = numerical dietary composition; Max = maximum number of individuals of prey type in a gut.

Prey taxa	Summer			Fall		
	n = 26			n = 11		
	%F	Max	%N	%F	Max	%N
Polychaeta						
Nereidae	3.85	1	2.44	9.09	3	4.17
Gastropoda						
<i>Nassarius</i> sp.	3.85	1	2.44	18.18	1	2.78
<i>Cosmioconcha calliglypta</i>	3.85	4	9.76	45.45	8	30.56
<i>Kurtziella</i> sp.				27.27	3	9.72
<i>Terebra arcas</i>				9.09	3	9.72
<i>Natica marochiensis</i>	3.85	1	2.44			
<i>Oliva sayana</i>	7.69	4	12.20			
Crustacea						
Xanthidae	19.23	4	24.39			
<i>Raninoides</i> sp.				9.09	1	1.39
<i>Callinectes similis</i>				54.54	9	37.50
<i>Persephona crinita</i>				9.09	2	2.78
Amphipoda	7.69	2	4.88			
<i>Pagurus</i> spp.	3.85	9	21.95			
Bryozoa	3.85	1	2.44	6.30	1	
Teleostei						
<i>Ophichthus gomesii</i>	15.38	2	14.63	9.09	1	1.39
<i>Diplectrum bioittatum</i>	3.85	1	2.44			

gape, may affect prey selection. The latter may be a significant constraint in batfish feeding because batfishes regularly take prey with hard exoskeletons or shells and do not crush them to get to the soft tissues. Further investigation in this aspect of batfish feeding biology may help determine what morphological limitations may exist in batfish feeding.

Gibran and Castro (1999) suggested that gastropod shells recovered from the stomachs of batfish reflected predation upon mobile hermit crabs. In contrast to their study, almost all of the gastropod prey analyzed here included easily recognizable soft parts (antennae, siphons, opercula), demonstrating that the batfishes preyed on the gastropods themselves and not on hermit crabs. Compared to the overall number of gastropods, relatively few hermit crabs (*Pagurus* sp.) were found in the stomachs of the batfishes studied. They appear to be minor components of the diets of *H. aculeatus* and *O. declivirostris*; however, *Pagurus* sp. was a moderately numerically important prey item in the diet of summer-sampled *O. pantostictus*.

Winans (1975) investigated the sympatric species *O. rostellum* and *H. aculeatus* off Cape Canaveral, FL, and found that the diet of *H. aculeatus* there also consisted primarily of nereid polychaetes, whereas *O. rostellum* primarily con-

sumed the gastropod *Nassarius consensus* (Ravenel, 1861) and, in the cooler months, the scallop *Argopecten gibbus* (Linnaeus, 1758). Winans (1975) suggested that the minimal overlap of prey items between the sympatric batfishes was because of resource partitioning. Although spatial habitat differences in this study appeared to be a more important factor in the different diets of the species studied, the limited co-occurrence and low dietary overlap of these species also suggest that some resource partitioning occurs between batfishes in the Gulf of Mexico as well. Although the summer samples for *H. aculeatus* and *O. declivirostris* in this study both showed similar amounts of *Nassarius* sp. taken as prey, the primary types of prey taken by *H. aculeatus* (polychaete worms, small crustaceans) and the two species of *Ogcocephalus* (gastropods) were similar in both studies. Winans (1975) interpreted his observations in the diet shift of *O. rostellum* from *Nassarius* to *Argopecten* as an adaptation to a locally abundant prey source because the shift coincided with scallop recruitment. In this study, only *O. declivirostris* showed a significantly consistent diet between seasons. Although the SI value was not significant, two of the three primary prey items for *H. aculeatus* remained consistent between seasons, although the lack of *Nassarius* sp. in fall samples for this species may indicate a diet

shift for this species. *Ogcocephalus pantostictus* was the only batfish in this study that appeared to show a diet shift to possibly take advantage of the changes in its available prey between seasons.

Benthic sampling of the invertebrates and prey species in the same habitat as the batfishes may help clarify whether these fishes are taking prey because of availability or selection. Such studies may compare the feeding biology of batfish species taken at different locations for similarities or differences. Many species of batfishes occur over a large bathymetric range. Benthic and stomach samples compared from different depth strata may show different prey assemblages and feeding habits associated with depth. These and other studies on batfish feeding ecology are planned for the near future.

ACKNOWLEDGMENTS

BHN wishes to thank the following individuals for their assistance over the duration of this work. BHN extends his deepest gratitude to Theodore W. Pietsch (School of Aquatic and Fisheries Sciences, and Burke Museum of Natural History and Culture, University of Washington, Seattle) for providing exceptional guidance, advice, expertise on lophiiform fishes, and critiques to improve the manuscript. Gilmore Pellegrin, Jr., Kimberley Johnson, Andre Debose, Carrie Horton, and Lanora Lang (NOAA Southeast Fisheries Science Center, Pascagoula Laboratory) assisted in collecting specimens aboard the R/V *Oregon II*. Harriet Perry (Gulf Coast Research Laboratory, University of Southern Mississippi) and Doug Shelton (Alabama Malacological Research Center) provided identifications of invertebrate stomach contents. Marcus Zokan assisted in collecting specimens during several collection trips. In addition, several anonymous reviewers provided constructive comments on the manuscript.

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tober 27, 2008