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FOOD HABITS OF BLUELINE TILEFISH, *Caulolatilus microps*, AND SNOWY GROUPER, *Epinephelus niveatus*, FROM THE LOWER FLORIDA KEYS

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ABSTRACT: Dietary analyses of intestinal contents from 96 blueline tilefish *Caulolatilus microps* (mean TL = 528 ± 94 mm SD) and 32 snowy grouper *Epinephelus niveatus* (mean TL = 609 ± 146 mm SD) collected from the shelf environments (123-256 m) in the lower Florida Keys during July 1980 and May-October 1981, revealed that the two predatory species exhibited different feeding strategies. Blueline tilefish preyed principally on benthic invertebrates, and snowy grouper on fish. Copepods, ophiuroids, and gastropods comprised 60% of the numerical, and urochordates 40% of the volumetric intestinal contents of blueline tilefish. Frequency of occurrence of prey consumed by tilefish exceeded 50% only for two major taxa — Polychaeta and Natantia. Osteichthyes comprised 47% and 52% of the numerical and volumetric consumption of prey, respectively, by snowy grouper, and occurred in 72% of the intestines; cephalopods ranked second in numerical importance (18%), and brachyuran crabs second in volumetric importance (29%). Differences in prey taxa, space niche, and fish anatomy indicated that blueline tilefish and snowy grouper occupy different trophic niches, which reduces interspecific competition.

Two species of continental shelf fishes, the blueline tilefish, *Caulolatilus microps* Goode and Bean 1878, and the snowy grouper, *Epinephelus niveatus* (Valenciennes, 1828), are commercially exploited in the West-Central Atlantic and in the Gulf of Mexico, primarily off Florida. These species are harvested from the same biotopes, using the same gear and the same bait; however, little is known of their life history parameters, such as respective trophic niches.

The blueline tilefish has been described as an epibenthic browser (Dooley, 1978), and its diet includes polychaetes, mollusks, sipunculids, crustaceans, echinoderms, ascideans, and fish (Ross, 1982). Snowy grouper are presumed to feed near the bottom on fishes, crustaceans, and squid.

Investigational hypotheses were that blueline tilefish and snowy grouper, as predators, have evolved generalized feeding strategies to cope with the continental shelf environment, and that some degree of niche specialization exists to facilitate coexistence between the two species (Bielsa, 1982). Specific objectives of this study were to determine the dietary components of the blueline tilefish and snowy grouper, and to elucidate possible trophic interactions between the predatory fish species.

MATERIALS AND METHODS

Fish were collected from Atlantic offshore waters along the lower Florida Keys, between $24^{\circ}16' - 24^{\circ}26'$ N. Latitude and $81^{\circ}43' - 82^{\circ}0'$ W. Longitude. Samples were from the commercial catch, taken by hook-and-line at water depths between 123-256 m. Squid was the principal bait. Fish were collected in July 1980,

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and in May, June, July, and October 1981. All fish were measured for total length (mm TL).

Both fish species, when raised to the surface from deep waters, everted their stomachs because of the decompression of the gas bladder. Consequently, only intestinal contents were available for analysis, which could have biased the results in favor of food items that were resistant to digestion. Intestines were removed, labeled, and stored in 10% buffered formalin. Food items were later removed from the intestines, washed in water, and preserved in 50% isopropyl alcohol. Intestinal contents were separated to the lowest identifiable taxon. Identification was facilitated by texts and keys (Rathbun, 1898, 1925; Benedict, 1900; Williams, 1965; Manning, 1969; Pequegnat, 1970; Felder, 1973; Abbott, 1974; Nelson, 1976; Warner, 1977; Barnes, 1980). Each taxon was quantified by number, volume (water displacement), and frequency of occurrence of food items. The numerical proportion of each food category also was calculated for fish size-class: ≤ 500 mm, 501-600 mm, 601-700 mm, and ≥ 701 mm TL for tilefish; and ≤ 510 mm, 511-685 mm, and ≤ 686 mm TL for grouper. The relative importance of each food category was determined by computing the index of relative importance ($IRI = (N + V) F$), where N = numerical percentage, V = volumetric percentage; F = frequency of occurrence percentage (Pinkas *et al.*, 1971). The presence or absence of biogenic sediment also was recorded for each intestine.

RESULTS

Ninety-seven prey taxa were found in the intestines of 96 blueline tilefish (Table 1), and 17 prey taxa in the intestines of 32 snowy grouper (Table 2). In-

testines from three additional blueline tilefish and seven snowy grouper contained no traces of food, and were excluded from analyses. The tilefish exhibited a mean TL of 582 ± 94 mm SD, and a mean ungutted weight of 2.31 ± 1.35 kg SD ($N = 62$). The grouper had a mean TL of 609 ± 146 mm and a mean ungutted weight of 3.35 ± 2.17 kg ($N = 22$).

Food Habits of the Blueline Tilefish

Copepods, ophiuroids, and gastropods comprised 60% of the number, but only 16% of the volume of prey contained in the intestines of blueline tilefish (Table 3). Volumetrically, urochordates were the most prevalent food item for tilefish (40%), followed by ophiuroids (15%). Osteichthyes, due to the large mass of a fish prey consumed by a single tilefish, were third in volumetric importance (13%), but comprised only 2% of the number of items consumed by the tilefish. Frequency of occurrence of prey found in the intestines of tilefish exceeded 50% for only two major taxa — Polychaeta and Natantia. Brachyuran crustaceans occurred in 40% of the intestines. Biogenic sediment was found in 58% of the intestines from blueline tilefish. Collectively, as reflected by the IRI , urochordates, natantian decapods, and ophiuroids were the three most important foods for blueline tilefish, contributing 20%, 19% and 18%, respectively, to the overall diet of the tilefish (Fig. 1).

Ophiuroids, gastropods, and crustaceans (copepods, natantian and brachyuran decapods) were the three most important prey taxa consumed by tilefish ≤ 500 mm TL, comprising 39%, 20% and 20% of the number of prey consumed (Table 4). Crustaceans contributed 36% to the numerical occur-

Table 1. List of prey taxa identified in intestines of 96 *C. microps* collected from continental shelf environments in the lower Florida Keys. Those taxa preceded by an asterisk (*) designate the lowest taxon identified.

*Porifera
Cnidaria
*Hydrozoa
*Schyphozoa
Anthozoa
*Octocorallia
*Zoantharia
Mollusca
Gastropoda
Prosobranchia
Fasciolaridae
*Fusinus sp.
Marginellidae
*Hyalina c.f. <i>H. avenella</i> Dall
Atlantidae
*Atlanta peronii Lesueur, 1817
*Turritellidae
*Bullidae
*Other (unidentified)
Opisthobranchia
Thecosomata
*Cavolinia longirostris (Blainville, 1821)
*Cavolinia cuatridentata (Lesueur)
*Cavolinia tridentata (Niebuhr, 1775)
*Cavolinia uncinata (Range, 1828)
*Cavolinia sp.
*Cuvierina sp.
*Hyalocylis striata (Range, 1828)
*Creseis acicula (Range, 1828)
*Creseis sp.
*Clio cuspidata (Bosk, 1802)
*Clio pyramidata (Linne, 1767)
*Diacria trispinosa (Blainville, 1821)
Bivalvia
Cardiidae
*Laevicardium sp.
Nuculanidae
*Nuculana sp.
Cephalopoda
*Teuthoidea
*Other (unidentified)
Annelida
Polychaeta
*Aprhoditidae
*Glyceridae
Goniadidae
*Goniada sp.
*Other (unidentified)
*Eunicidae
Onuphidae
*Diopatra sp.
*Other (unidentified)
Arabellidae
*Arabella sp.
*Lumbrineridae
*Chaetopteridae
*Flabelligeridae

Table 1. (cont.)

*Capitellidae
*Sabellidae
*Serpulidae
Other
* <i>Palacostrema cidariophilum</i>
*Other (unidentified)
*Sipunculida
Priapulida
* <i>Priapulus</i> sp.
Arthropoda
Crustacea
*Ostracoda
Copepoda
*Calanoida
*Cirripedia
Eumalacostraca
Stomatopoda
*Pseudosquillaidae
*Squillaidae
Decapoda
Natantia
Penaeidea
Aristeidae
* <i>Ceratopsis</i> sp.
Penaeidae
* <i>Trachypenaeus</i> sp.
* <i>Parapenaeus longirostris</i> (Lucas)
Caridea
Pasiphaeidae
* <i>Parapasiphae sulcatifrons</i> (Smith)
Eugonatonotidae
* <i>Euonatonotus crassus</i> (A. Milne Edwards 1881)
*Other (unidentified)
Reptantia
Anomura
Galatheididae
* <i>Munida</i> sp.
Paguridae
* <i>Pylopagurus</i> sp.
Diogenidae
* <i>Dardanus</i> sp.
Brachyura
Raninidae
* <i>Ranilia</i> sp.
* <i>Raninoides</i> sp.
* <i>Lyreides</i> sp.
Dromiidae
* <i>Dromidia antillensis</i> (Stimpson)
* <i>Dromia</i> sp.
Homolidae
* <i>Homola barbata</i> (Fabricius)
Calappidae
* <i>Calappa flamea</i> (Herbst)
* <i>Calappa</i> sp.
Portunidae
* <i>Bathynectes</i> sp.
*Other (unidentified)
Majidae

Table 1. (cont.)

* <i>Euprognatha rastellifera marthae</i> (Rathbun)
* <i>Podocheila</i> sp.
*Other (unidentified)
Parthenopidae
* <i>Parthenope agona</i> (Stimpson)
*Other (unidentified)
Tanaidacea
*Apseudidae
Isopoda
Cirolanidae
* <i>Cirolana</i> sp.
* <i>Excirolana</i> sp.
*Idoteidae
*Other (unidentified)
Amphipoda
Hyperiliidae
* <i>Primo</i> sp.
* <i>Vibilia</i> sp.
Aoriidae
* <i>Rildardanus</i> sp.
*Other (unidentified)
*Other crustaceans (unidentified)
*Bryozoa
Echinodermata
*Asteroidea
Ophiuroidea
* <i>Ophiura</i> c.f. <i>O. sarsi</i> Lutken
Echinoidea
*Echinidae
*Spatangoida
Urochordata
*Ascidae
Chordata
Osteichthyes
*Clupeidae
*Ophichthidae
*Gadidae
Sternoptychidae
* <i>Argyropelecus</i> sp.
*Scaridae
*Other (unidentified)
Organic deposits
*Calcareous deposits
Inorganic deposits
*Silt
*Clay
*Other residuals

rence in the 501-600 mm TL size class, and gastropods and ophiuroids, 24% and 19%, respectively. The only numerically important food taxon consumed by tilefish in the 601-700 mm TL size class was crustaceans, which accounted for 81% of the number of prey consumed. Ophiuroids and gastropods, together,

numerically contributed 55% of the food items in tilefish ≤ 701 mm TL.

Food Habits of the Snowy Grouper

Osteichthyes was the most important prey found in the intestines of grouper (Table 3). This taxon comprised

Table 2. List of prey taxa identified in intestines of 32 *E. niveatus* collected from continental shelf environments in the lower Florida Keys. Those taxa preceded by an asterisk (*) designate the lowest taxon identified.

Cnidaria
Anthozoa
*Octocorallia
Mollusca
*Gastropoda
*Cephalopoda
Annelida
Polychaeta
*Goniadidae
*Other (unidentified)
Arthropoda
Crustacea
Copepoda
*Calanoida
Eumalacostraca
*Stomatopoda
Decapoda
Natantia
Penaidea
Aristeidae
* <i>Ceratopsis</i> sp.
*Other (unidentified)
Reptantia
Brachyura
Raninidae
* <i>Ranilia</i> sp.
Calappidae
* <i>Calappa ocellata</i> Holthuis
*Portunidae
*Other (unidentified)
*Urochordata
*Ascidacea
Chordata
Osteichthyes
*Clupeidae
*Other (unidentified)
Organic deposits
*Calcareous ooze
Inorganic deposits
*Silt
*Clay

47% of the number and 52% of the volume of prey consumed, and occurred in 72% of the intestines. Cephalopods ranked second in numerical importance (18%), and brachyuran crabs second in volumetric importance (29%). Biogenic sediment occurred in 19% of the intestines. Overall, osteichthyes dominated the *IRI*, contributing 78% of the diet (Fig. 1).

The numerical consumption of osteichthyes was relatively uniform among the three size classes of snowy grouper, ranging from 43% to 65% (Table 5). The importance of cephalopods increased with the increasing fish size; numerically, they comprised 6% of the number of prey in the smallest fish (≤ 510 mm TL), and 18% in both the intermediate size class (511-685 mm TL)

Figure 1. Composition of diets of *C. microps* (n = 96) and *E. niveatus* (n = 32) from continental shelf environments (123-256 m) in the lower Florida Keys. Numbers indicate the index of relative importance (*IRI*) for a particular taxon; percentages indicate the proportionate contribution of that taxon to the total diet. *Miscellaneous = Porifera, Cnidaria, Bivalvia, Sipunculida, Priapulida, Ostracoda, Cirripedia, Stomatopoda, Anomura, Tanaidacea, Isopoda, Amphipoda, unidentified crustaceans, Bryozoa, Asteroidea and Echinoidea. + Miscellaneous = Cnidaria, Gastropoda, Polychaeta, Copepoda, Stomatopoda, Urochordata, and unidentified crustaceans.

and the largest fish (≥ 686 mm TL). Gastropods were numerically important in the diet of the groupers ≤ 510 mm TL, as were brachyuran crustaceans for groupers ≤ 686 mm TL. The most diverse diet was exhibited by intermediate-sized snowy groupers.

DISCUSSION

The blueline tilefish is a generalized feeder that consumes a diverse prey assemblage, comprised mostly of benthic invertebrates. In contrast, the snowy grouper is a relatively specialized feeder, with fish constituting the principal dietary component.

The diets of blueline tilefish and snowy grouper suggest that these predatory species occupy different realized niches. This niche differentiation is probably founded in the different anatomical adaptation of their mouth parts for capturing prey, which, subsequently, results in their spatial segregation in the water column.

In terms of space, the blueline tilefish, as evidenced by its diet, its closely associated with the bottom.

Urochordates, ophiuroids, polychaetes, cnidarians, and poriferans are obligate benthic organisms. Brachyuran crustaceans, though capable of swimming, are primarily benthic inhabitants. Natantian decapods and stomatopods, though adapted for swimming, are bottom dwellers, and swim only intermittently. Most of the gastropods (Thecosomata), and calanoid copepods are pelagic, but undergo vertical migrations that maintain them in close proximity to the bottom.

The blueline tilefish has morphological adaptations for benthic browsing: a terminal mouth and pointed snout to facilitate the extraction of organisms from crevices in the irregular substrate; upper and lower jaws with single rows of moderately large canines; and a medial patch of 4-5 rows of villiform teeth to facilitate grabbing, tearing and/or scraping benthic organisms from the substrate (Ross 1978). These anatomical features likely explain the high frequency of occurrence of biogenic sediment (58%) in the intestines of the tilefish.

The diet of the snowy grouper sug-

Table 3. Percentage numerical occurrence (N), volumetric occurrence (V) and frequency of occurrence (F) of foods, by major taxa, found in the intestine of *C. microps* (N = 96) and *E. niveatus* (N = 32) from continental shelf environments (1223-256m) in the lower Florida keys.

Food taxa	<i>C. microps</i>			<i>E. niveatus</i>		
	N	V	F	N	V	F
Gastropoda	19.0	0.6	40.6	5.3	1.0	3.1
Cephalopoda	0.8	12.2	18.8	18.4	7.6	28.1
Polychaeta	4.2	6.0	54.2	3.9	0.4	9.4
Copepoda	21.2	0.4	12.5	1.3	0.1	3.1
Natantia	15.4	8.6	61.5	6.6	6.4	12.5
Brachyura	3.9	2.4	39.6	9.2	29.0	15.6
Ophiuroidea	20.2	14.8	38.5	0	0	0
Urochordata	2.9	40.3	35.4	2.6	1.9	6.3
Osteichthyes	2.4	12.9	37.5	47.4	51.7	71.9
Miscellaneous*	10.0	1.8	60.4	5.3	1.9	12.5
Total	100.0	100.0		100.0	100.0	

**C. microps*: Porifera, Cnidaria, Bivalvia, Sipunculida, Priapulida, Ostracoda, Cirripedia, Stomatopoda, Anomura, Tanaidacea, Isopoda, Amphipoda, unidentified crustaceans, Bryozoa, Asteroidea, and Echinoidea. *E. niveatus*: Cnidaria, Stomatopoda, and unidentified crustaceans.

gests strongly that this species occupies a higher relative position in the water column than the blueline tilefish. The diet of the snowy grouper was dominated by clupeid fishes, which, as pelagic organisms, have a closer association with the water column than the bottom. Benthic and semi-benthic prey (brachyuran crustaceans, urochordates, polychaetes, natantian decapods, stomatopods, and calanoid copepods) were of secondary importance in the diet of this predatory species.

The presence of a large mouth, short and conical teeth, and a snout that is shorter than the jaw are adaptations of the snowy grouper to piscivorous food

habits. These anatomical features suggest that the snowy grouper has less of a demersal habit than the blueline tilefish. The comparatively low frequency of occurrence (19%) of biogenic sediment in the intestines of the snowy grouper supports the contention of pelagic feeding habits.

In summary, this study revealed that the blueline tilefish and snowy grouper differed in their food habits — the tilefish being benthic and euryphagic, and the grouper, pelagic and relatively stenophagic. These divergent feeding strategies were attributable principally to differences in the anatomical adaptations of the two species for capturing

Table 4. Percentage numerical occurrence of foods, by major taxa, found in the intestines of four size classes of *C. microps* from continental shelf environments (123-256 m) in the lower Florida Keys.

Food taxa	Numerical Occurrence (%)			
	≤ 500 mm TL (n = 16)	501-600 mm TL (n = 43)	601-700 mm TL (n = 19)	≥ 701 mm TL (n = 14)
Gastropoda	20.3	24.1	3.4	22.4
Cephalopoda	0.3	0.8	0.7	1.4
Polychaeta	5.7	5.9	1.6	2.0
Copepoda	1.2	21.6	54.3	0.7
Natantia	12.6	11.8	23.3	18.6
Brachyura	6.0	2.8	3.0	4.5
Ophiuroidea	38.5	18.6	1.8	32.8
Urochordata	1.7	2.0	5.1	2.9
Osteichthyes	1.7	3.7	0.7	2.5
Miscellaneous	12.0	8.7	6.1	12.2

Table 5. Percentage numerical occurrence of foods, by major taxa, found in the intestines of three size classes of *E. niveatus* from continental shelf environments (123-256 mm) in the lower Florida Keys.

Food taxa	Numerical Occurrence (%)		
	≤ 510 mm TL (n = 6)	511-685 mm TL (n = 17)	≥ 686 mm TL (n = 7)
Gastropoda	23.5	0	18.2
Cephalopoda	5.9	17.5	18.2
Polychaeta	5.9	5.0	0
Copepoda	0	2.5	0
Natantia	0	12.5	0
Brachyura	0	10.0	27.3
Ophiuroidea	0	0	0
Urochordata	0	5.0	0
Osteichthyes	64.7	42.5	54.5
Miscellaneous	0	5.0	0

prey, which, in turn, spatially stratified the predators on the basis of prey availability. Thus, the blueline tilefish and the snowy grouper, although inhabiting the same continental shelf biotype, occupy different trophic niches, which tends to reduce interspecific competition for food resources, and thereby, allows coexistence of the two predatory fish species.

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LITERATURE CITED

- Abbott, R.T. 1974. American seashells: the marine mollusca of the Atlantic and Pacific coasts of North America. 2nd edition. Van Nostrand Reinhold Co., New York, N.Y. 663 p.
- Barnes, R.D. 1980. Invertebrate zoology. 4th edition. Saunders College/Holt, Rinehart and Winston, Philadelphia, Pa. 1089 p.
- Benedict, J.E. 1900. The anomuran collections made by the *Fish Hawk* expedition to Porto Rico. Bull. U.S. Fish Comm. 20:129-148, 4 pls.
- Bielsa, L.M. 1982. Food-web community of two deep-water reef fish, *Caulolatilus microps* Goode and Bean 1978, and *Epinephelus niveatus* (Valenciennes, 1928), in the Lower Florida Keys. M.S. thesis, University of Florida, Gainesville. 34 p.
- Dooley, J.K. 1978. Systematics and biology of the tilefishes (Perciformes: Branchiostegidae and Malacanthidae), with descriptions of two new species. NOAA Tech. Rep., NMFS Cir. 411. 8 p.
- Felder, D.L. 1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. Louisiana State University Sea Grant Prog. Rep. 73-02. 103 p.
- Manning, R.B. 1969. Stomatopod Crustacea of the Western Atlantic. Studies in Tropical Oceanogr. 8, University of Miami Press, Coral Gables, Fla. 380 p.
- Nelson, J.S. 1976. Fishes of the world. John Wiley and Sons, Inc., New York, N.Y. 416 p.
- Pequegnat, L.H. 1970. Deep-sea caridean shrimps with description of six new species. Pages 59-124 in W.E. Pequegnat and F.A. Chase, Jr., eds. Contributions on the biology of the Gulf of Mexico. Texas A & M University Oceanogr. Studies 1.
- Pinkas, L., M.S. Oliphant, and I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Fish Game Fish. Bull. 152:1-105.
- Rathbun, M.J. 1898. The Brachyura of the biological expeditions of the Florida Keys and the Bahamas in 1893. Iowa State University Bull. Lab. Nat. Hist. 4:250-294, 9 pls.
- _____. 1925. The spider crabs of America. U.S. Natl. Mus. Bull. 129. 613 p., 283 pls.
- Ross, J.L. 1978. Life history aspects of the gray tilefish *Caulolatilus microps* (Goode and Bean, 1878). M.A. thesis, College of William and Mary, Williamsburg, Va. 120 p.
- _____. 1982. Feeding habits of the gray tilefish, *Caulolatilus microps* (Goode and Bean, 1878) from North Carolina and South Carolina waters. Bull. Mar. Sci. 32:448-454.
- Warner, G.F. 1977. The biology of crabs. Van Nostrand Reinhold Co., New York, N.Y. 202 p.
- Williams, A.B. 1965. Marine decapod crustaceans of the Carolinas. Fish. Bull. 65:1-298.