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NOTE

DIET COMPOSITION OF JUVENILE BLACK GROUPER (*MYCTEROPERCA BONACI*) FROM COASTAL NURSERY AREAS OF THE YUCATÁN PENINSULA, MEXICO

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Groupers (Epinephelinae, Epinephelini) are top-level predators that influence the trophic web of coral reef ecosystems (Parrish, 1987; Heemstra and Randall, 1993; Sluka et al., 2001). They are demersal mesocarnivores and stalk and ambush predators that sit and wait for larger moving prey such as fish and mobile invertebrates (Cailliet et al., 1986). Groupers contribute to the ecological balance of complex tropical hard-bottom communities (Sluka et al., 1994), and thus large changes in their populations may significantly alter other community components (Parrish, 1987).

The black grouper (*Mycteroperca bonaci* Poey, 1860) is an important commercial and recreational fin fish resource in the western Atlantic region (Bullock and Smith, 1991; Heemstra and Randall, 1993). The southern Gulf of Mexico grouper fishery is currently considered to be deteriorated and *M. bonaci*, along with red grouper (*Epinephelus morio* Valenciennes, 1828) and gag (*Mycteroperca microlepis* Goode and Bean, 1880), is one of the most heavily exploited fish species in this region (Colás-Marrufo et al., 1998; SEMARNAP, 2000). Currently, *M. bonaci* is considered a threatened species (Morris et al., 2000; IUCN, 2003) and has been classified as vulnerable in U.S. waters because male biomass in the Atlantic dropped from 20% in 1982 to 6% in 1995 (Musick et al., 2000).

The black grouper is usually found on irregular bottoms such as coral reefs, drop-off walls, and rocky ledges, at depths from 10 to 100 m (Roe, 1977; Manooch and Mason, 1987; Bullock and Smith, 1991; Heemstra and Randall, 1993). Juveniles have been captured infrequently in North Carolina and eastern Gulf of Mexico estuaries (Bullock and Smith, 1991; Ross and Moser, 1995) and observed in low densities in patch reefs and isolated coral heads in Key Largo, Florida (Sluka et al., 1994). They have also been found in mangrove swamps, and on soft, rocky or coral bottoms in shallow waters in Venezuela (Cervignón, 1991). Based on the limited data available on adult feeding habits, the black grouper is considered to be a piscivorous predator (Randall, 1967; Valdés-Muñoz, 1980; Bullock and Smith, 1991; Sierra et al., 1994). However, relatively little is known of its early life history, especially its juvenile diet and feeding ecology. Because fish survival and growth depend on the energy and nutrient input generated by feeding activities (Wootton, 1999), and food studies can contribute to our understanding of the interactions among trophic community members (Cailliet et al., 1986), the goal of the present study was to determine the diet composition of juvenile black grouper collected from three nursery areas located along the north coast of the Yucatán Peninsula.

Materials and Methods

Black grouper were collected between July 2000 and December 2001, in shallow waters (1–10 m depth) from three sites considered to be potential nursery areas for *M. bonaci* (Renán

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et al., 2003) off the north coast of the Yucatán Peninsula: Sisal (21°15′N, 90°15′W), Dzilam de Bravo (21°30′N, 88°45′W) and Río Lagartos (21°40′N, 88°10′W). The predominant condition at all three sites was irregular hard bottom of limestone outcrops or rocks surrounded by sandy areas. There were, however, some differences among the sites. Río Lagartos had more high vertical relief with crevices and caves than at Dzilam de Bravo, where small dispersed rocks were abundant; some areas of Sisal consisted of a shallow rocky reef habitat. Specimens were caught with spear guns, between 0700 and 1400 hrs, placed on ice immediately after capture, and examined within 2 hrs after capture. Regurgitation was rare during collection, and when it did occur the collector recovered and kept the prey items together with the specimen in a plastic bag. For each collected fish, total and standard lengths (TL, SL) and whole and gutted weights (WW, GW) were recorded and the entire stomach was removed and preserved in 10% formalin. Before the food material was analyzed, stomachs were rinsed in freshwater for 24 hrs, and stomach contents removed and stored in 70% ethanol.

The sexual development of each collected black grouper was determined by histological examination of microscopic gonad structure according to Brulé et al. (2003). All were found to be sexually immature, and no signs of prior spawning activity, as defined by Shapiro et al. (1993) and Rhodes and Sadovy (2002), were evident in the gonads.

Prey (i.e., stomach contents) were sorted and identified to the lowest possible taxa, counted (except for plant material and unidentified remains), drained, and weighed to the nearest 0.01 g. All pieces identified as the same taxa within the same stomach were recorded as a single individual prey, unless two (or more) pieces obviously came from two (or more) different individuals. Stomach content analysis was done using percentage frequency of occurrence (%F), percentage number (%N), and percentage weight (%W; Hureau, 1970).

Schoener's dietary overlap index (Schoener, 1970) was calculated based on %F and %W of the main prey categories. This index ranges from 0 (no overlap) to 1 (complete overlap), and values above 0.6 were considered as significant overlap (Zaret and Rand, 1971; Wallace, 1981). Diet overlap was first analyzed between black grouper caught from each nursery area during different seasons, then between those collected from the three nursery areas, and finally, between specimens of different size classes. Seasonal changes in *M. bonaci* diet were analyzed between fish captured during the "cold" and "warm" seasons. This two-season division was based on Rivas (1968; 1970), who reported that temperature fluctuations in the Gulf of Mexico do not reflect a four-season cycle, but that recorded temperature fluctuations may be better interpreted in terms of an annual "cold" (November through April) and "warm" (May through October) season. In the southern Gulf of Mexico maximum and minimum average sea surface temperatures (SST) were observed in August (29.5°C) and March (23.5°C), respectively (Piñeiro et al., 2001).

Due to the low number of collected black grouper specimens, mean TL of the fish and the proportion of fish with empty stomachs were compared between seasons and nursery sites using non-parametric procedures, which are more efficient for small samples. The Mann-Whitney or Kruskal-Wallis tests were performed to compare sizes, and the chi-square goodness-of-fit or Fisher's "Exact" tests performed for proportion of empty stomachs (Steel and Torrie, 1984; Scherrer, 1984). Significance level, α, was 0.05 in all cases.

Results

Of the 120 black grouper analyzed, 58 were caught in Sisal, 28 in Dzilam de Bravo, and 34 in Río Lagartos (Table 1). Stomach contents yielded a total of 86 prey items from five main prey categories: plant material, natant decapods, reptant decapods, fish, and unidentified remains (Table 2).

Variation in the *M. bonaci* diet from the three nursery sites was analyzed on a seasonal basis (Table 3). Sizes of black grouper from Sisal differed significantly between seasons (Mann-Whitney test: df = 1, P = 0.047), while those from Dzilam de

Table 1. Juvenile black grouper collected in three nursery areas off the northern coast of the Yucatán Peninsula, between July 2000 and December 2001 (N_1 = total number of fish sampled; N_2 = number of fish with stomach contents; - = sample not available).

		Sisal		Dzilam de Bravo		Río Lagartos	
Season	Month	N_1	N_2	N_1	N_2	N_1	N_2
	July 2000	-	-	-	-	4	3
Warm	August	1	1	-	-	-	-
	September	1	0	1	1	-	-
	October	-	-	-	-	-	-
	November	5	4	4	0	0	0
	December	0	0	0	0	0	0
Cold	January 2001	5	3	1	0	3	1
	February	0	0	3	2	6	3
	March	6	6	0	0	9	8
	April	0	0	0	0	0	0
	May	9	7	1	0	1	1
	June	13	8	1	0	7	5
Warm	July	5	3	2	1	0	0
	August	6	3	4	1	1	1
	September	4	2	1	1	3	2
	October	1	0	0	0	0	0
Cold	November	2	0	4	1	0	0
	December	0	0	6	4	0	0
	Total	58	37	28	11	34	24
	Fish size range TL (cm)	12.0–45.3		8.7–35.4	17.5–35.4	18.7–41.1	

Bravo and Río Lagartos did not (Mann-Whitney test: df = 1, P = 0.705 and df = 1, P = 0.707, respectively). The proportion of juveniles with empty stomachs did not differ significantly between cold and warm seasons at any of the sites (Sisal: $\chi^2 = 0.26$ with $\chi^2_{0.05\,(df=1)} = 3.84$; Dzilam de Bravo and Río Lagartos: Fisher's "Exact" test: P = 0.68 and P = 0.44, respectively). Schoener's index showed significant dietary overlaps in the main prey categories between cold and warm seasons at all three sites (Table 4). At each nursery site, fishes were the dominant prey during both warm and cold seasons. Natant crustaceans were also ingested all year round, except during the warm season at Sisal.

Because no significant change was detected in juvenile diet composition between seasons, the data from each nursery site were pooled for the 18 mo of sampling (Table 5). Fish size did not differ significantly among sampling sites (Kruskal-Wallis test: df = 2, P = 0.524). However, the proportion of juveniles with empty stomachs was significantly different among nurseries ($\chi^2 = 8.43$ with $\chi^2_{0.05\,(df=2)} = 5.99$). Schoener's index showed significant dietary overlaps in the main prey categories between the three studied nursery areas (Table 6), with fishes and natant crustaceans always being the dominant prey items in the stomachs of black grouper from the three sites.

No significant geographical differences were noted in juvenile black grouper diet composition, therefore the relationship between size and diet was analyzed by pooling all collected fish with stomach contents into seven, 5-cm TL size classes (Table 7). Significant diet overlap was evident between all size classes when %W of the main prey categories was considered (Table 8). The lowest Schoener's indices, indicating no significant overlap between diets (0.25–0.56), were produced in comparisons of

Table 2. Food items observed in stomach contents of juvenile black grouper collected in three nursery areas off the northern coast of the Yucatán Peninsula (+ = present; – = absent).

Food items	Sisal	Dzilam de Bravo	Río Lagartos
Plant material	+	–	+
Crustaceans			
Decapoda Natantia			
Penaeidae			
Aristeinae	–	–	+
Penaeinae			
Farfantepenaeus sp.	–	+	–
Unidentified	–	+	+
Palaemonidae	–	–	+
Alpheidae			
Alpheus sp.	–	–	+
Unidentified	+	+	+
Decapoda Reptantia			
Brachyura	–	+	–
Fishes			
Osteichthyes			
Carangidae	+	–	–
Ballistidae			
Monacanthus sp.	–	–	+
Labridae			
Halichoeres sp.	–	–	+
Lutjanidae			
Lutjanus sp.	–	–	+
Pomadasyidae			
Orthopristis crysoptera	–	–	+
Scaridae			
Cryptotomus roseus	–	–	+
Unidentified	+	+	+
Unidentified remains	+	+	+

prey frequencies of occurrence among size classes with < 5 specimens with stomach contents (10.5–15.5 cm TL; N = 4, and 40.6–45.5 cm TL; N = 3). This was likely an artifact of the low sample sizes.

Discussion

Groupers are dependent on their habitat for food, shelter, and cleaning (Sluka et al., 1999), and tend to have secretive habits, occupying caves, crevices, and ledges (Smith, 1961). Juvenile black grouper habitat on the northern coast of the Yucatán Peninsula mainly consists of sandy-rocky bottoms with some ridges and crevices (Renán et al., 2003), which is different from that described for Atlantic (grass beds in estuarine areas) and eastern Gulf of Mexico (coral reefs) coastal waters (Bullock and Smith, 1991; Sluka et al., 1994; Ross and Moser, 1995). Specimens analyzed in the present study were all considered to be juvenile because they ranged in size from 12.0 to 45.3 cm TL, were sexually immature, and did not manifest signs of prior spawning activity in the gonads. In the southern Gulf of Mexico black grouper stock, 50%

Table 3. Percent frequency of occurrence (%F), percent number (%N) and percent weight (%W) of main prey categories of juvenile black grouper collected during cold and warm seasons in three nursery areas off the northern coast of the Yucatán Peninsula (N_1 = total number of fish sampled; N_2 = number of fish with stomach contents; analysis based on N_2).

	Sisal						Dzilam de Bravo						Río Lagartos					
	Cold season $N_1 = 19$; $N_2 = 13$			Warm season $N_1 = 39$; $N_2 = 24$			Cold season $N_1 = 18$; $N_2 = 7$			Warm season $N_1 = 10$; $N_2 = 4$			Cold season $N_1 = 18$; $N_2 = 12$			Warm season $N_1 = 16$; $N_2 = 12$		
Main prey categories	%F	%N	%W	%F	%N	%W	%F	%N	%W	%F	%N	%W	%F	%N	%W	%F	%N	%W
Plant material	7.7	-	0.9	4.2	-	0.1	0	-	0	0	-	0	0	-	0	8.3	-	1.3
Natant crustaceans	7.7	9.1	1.4	0	0	0	14.3	16.7	8.7	25.0	20.0	18.7	25.0	38.5	5.1	16.7	13.3	0.2
Reptant crustaceans	0	0	0	0	0	0	0	0	0	25.0	20.0	0.2	0	0	0	0	0	0
Fishes	53.8	90.9	89.9	70.8	100.0	99.2	71.4	83.3	90.9	75.0	60.0	76.7	66.7	61.5	94.2	100.0	86.7	91.7
Unidentified remains	53.8	-	7.8	29.2	-	0.7	14.3	-	0.4	25.0	-	4.4	25.0	-	0.7	25.0	-	6.8
Fish size range TL (cm)	23.6– 45.3			12.0–44.8			22.9–29.8			17.5–35.4			18.7–41.1			18.8–35.5		

Table 4. Stomach contents dietary overlap between juvenile black grouper collected during cold and warm seasons in three nursery areas off the northern coast of the Yucatán Peninsula. %F = percent frequency of occurrence; %W = percent weight.

	%F	%W
Sisal	0.74	0.91
Dzilam de Bravo	0.75	0.86
Río Lagartos	0.75	0.93

maturity of females is reached at 72.1 cm fork length (FL), and the smallest sexually mature female reported to date was 58.0 cm FL (Brulé et al., 2003).

In the southern Gulf of Mexico, black grouper stomach contents and the proportion of fish with empty stomachs did not show seasonal variations at any of the three study sites. Fishes dominated juvenile black grouper diet year-round. Hard-bottom community composition and abundance are largely undescribed for the northern coast of the Yucatán Peninsula, and thus prey availability for juvenile *M. bonaci* and its variations in time and space could not be used in the present study to corroborate data from seasonal analysis of stomach contents. Lack of dietary seasonality coincides with Brulé et al. (1994), who reported similar results (i.e., no significant seasonal variation in diet composition) for juvenile red grouper from shallow waters of the Yucatán Peninsula. Ross and Moser (1995), in contrast, noted that dietary diversity of juvenile gag from North Carolina estuaries changed seasonally, with individuals eating more varieties of food items during late summer than during spring or early summer. Latitudinal differences in environmental conditions (i.e., mean and seasonal changes in SST) between nurseries in the Atlantic and the southern Gulf of Mexico coastal waters may explain this difference in seasonal feeding activity between juvenile gag and black grouper. For example, annual SST patterns along the Yucatán coast are closely linked to air temperature, which remains remarkably constant throughout the year, thus yearly SST fluctuation does not exceed 6 °C between the cold and warm seasons (Espejel, 1987; Piñeiro et al., 2001).

Despite some differences between nursery habitat characteristics, the diet overlap of juvenile black grouper collected from the three nurseries was significant. Fishes were the most important ingested prey, followed by natant crustaceans, and the prey fish species belonging to families common to the shallow coastal waters of this region (Vega-Cendejas et al., 1997; Ferreira et al., 2005).

Table 5. Percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of main prey categories of juvenile black grouper from three nursery areas off the northern coast of the Yucatán Peninsula (N_1 = total number of fish sampled; N_2 = number of fish with stomach contents; analysis based on N_2).

	Sisal $N_1 = 58$; $N_2 = 37$			Dzilam de Bravo $N_1 = 28$; $N_2 = 11$			Río Lagartos $N_1 = 34$; $N_2 = 24$		
Main prey categories	%F	%N	%W	%F	%N	%W	%F	%N	%W
Plant material	5.4	-	0.3	0	-	0	8.3	-	0.5
Natant crustaceans	2.7	2.0	0.4	18.9	9.0	14.4	20.8	24.0	3.2
Reptant crustaceans	0	0	0	9.1	18.0	0.1	0	0	0
Fishes	64.9	98.0	96.8	63.6	73.0	82.8	75.0	76.0	93.2
Unidentified remains	37.8	-	2.5	18.2	-	2.7	25.0	-	3.1

Table 6. Stomach contents dietary overlap among juvenile black grouper from three nursery areas off the northern coast of the Yucatán Peninsula. %F = percent frequency of occurrence; %W = percent weight.

Nursery area		Río Lagartos	Dzilam de Bravo	Sisal
Sisal	%F	0.78	0.75	-
	%W	0.97	0.86	-
Dzilam de Bravo	%F	0.81	-	
	%W	0.89	-	
Río Lagartos	%F	-		
	%W	-		

Stomach contents of juvenile black grouper did not change substantially with increasing specimen length, within the examined size range. Parrish (1987) observed that change in the proportion of different food items with increasing age may represent a fairly general trend in groupers. Thus, very young grouper eat small items that are not important in the diets of larger grouper. For example, pelagic early-juvenile Nassau grouper *Epinephelus striatus* Bloch, 1792 (size range: 2.0–2.8 cm SL) from the Bahamas are reported to ingest dinoflagellates, fish larvae, and mysids (Grover, 1993), while Ross and Moser (1995) noted that as juvenile gags grow, their diet shifts from smaller (copepods and amphipods) to larger (penaeid shrimp and fish) prey. In

Table 7. Percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of main prey categories of juvenile black grouper from the northern coast of the Yucatán Peninsula, according to size of predator (N_1 = total number of fish sampled; N_2 = number of fish with stomach contents; analysis based on N_2; the only collected juvenile for 5.5–10.5 cm TL size class had an empty stomach).

		Main prey categories				
Size classes LT (cm)		Plant material	Natant crustaceans	Reptant crustaceans	Fishes	Unidentified remains
10.6–15.5	%F	0	0	0	25.0	75.0
N_1 = 15; N_2 = 4	%N	-	0	0	100.0	-
	%W	0	0	0	76.7	23.3
15.6–20.5	%F	0	25.0	0	62.5	25.0
N_1 = 15; N_2 = 8	%N	-	25.0	0	75.0	-
	%W	0	32.7	0	65.9	1.4
20.6–25.5	%F	13.3	13.3	0	60.0	33.3
N_1 = 25; N_2 = 15	%N	-	30.8	0	69.2	-
	%W	3.0	1.6	0	90.0	5.4
25.6–30.5	%F	0	6.0	6.0	82.0	18.0
N_1 = 24; N_2 = 17	%N	-	5.3	5.3	89.4	-
	%W	0	1.0	0.0	95.6	3.4
30.6–35.5	%F	7.0	7.0	0	67.0	33.0
N_1 = 21; N_2 = 15	%N	-	4.8	0	95.2	-
	%W	0.1	0.0	0	98.3	1.6
35.6–40.5	%F	0	20.0	0	90.0	20.0
N_1 = 14; N_2 = 10	%N	-	18.2	0	81.8	-
	%W	0	9.4	0	89.3	1.3
40.6–45.5	%F	0	0	0	100.0	0
N_1 = 5; N_2 = 3	%N	0	0	0	100.0	-
	%W	0	0	0	100.0	0

Table 8. Stomach contents dietary overlap between size classes of juvenile black grouper from the northern coast of the Yucatán Peninsula (*no significant dietary overlap). %F = percent frequency of occurrence; %W = percent weight.

Size classes TL (cm)		40.6–45.5	35.6–40.5	30.6–35.5	25.6–30.5	20.6–25.5	15.6–20.5	10.5–15.5
10.5–15.5	%F	0.25*	0.30*	0.51*	0.37*	0.48*	0.44*	-
	%W	0.77	0.78	0.78	0.80	0.84	0.67	-
15.6–20.5	%F	0.56*	0.81	0.81	0.74	0.82	-	
	%W	0.66	0.77	0.67	0.68	0.70	-	
20.6–25.5	%F	0.50*	0.68	0.90	0.68	-		
	%W	0.90	0.92	0.92	0.94	-		
25.6–30.5	%F	0.76	0.85	0.78	-			
	%W	0.96	0.92	0.97	-			
30.6–35.5	%F	0.60	0.72	-				
	%W	0.98	0.91	-				
35.6–40.5	%F	0.70	-					
	%W	0.89	-					
40.6–45.5	%F	-						
	%W	-						

South Carolina, ontogenetic shifts have also been observed in gag diet during the larval-juvenile transition (larvae =1.5–2.5 cm SL and juveniles = 2.6–15.7 cm SL; Mullaney, 1994; Mullaney and Gale, 1996).

The fishes that comprised the main prey items of juvenile black grouper can be categorized as inshore pelagic diurnal fishes (Carangidae), suprabenthic diurnal (Scaridae: *Cryptotomus roseus* and Labridae: *Halichoeres* sp.), or nocturnal (Lutjanidae) fishes (Valdéz-Muñoz and Mochek, 2001). Heemstra and Randall (1993) stated that adult black grouper feed primarily on fishes, while juveniles prey mainly on crustaceans. This is consistent with the presence of unidentified shrimp and amphipods in the stomachs of two juvenile black grouper (1.7 and 2. 1 cm SL) from Tampa Bay, Florida (Peters *in* Bullock and Smith, 1991). Natant and reptant decapods were also observed in the present study, but at much lower abundances than prey fishes, suggesting that crustaceans are secondary prey in the diet of juvenile black grouper from nursery areas along the Yucatán Peninsula coast. This may be unusual for groupers in general because other studies report that juvenile Nassau grouper (furcal sizes < 30 cm) from Cuba fed mainly on crustaceans (Silva-Lee, 1974), and Ross and Moser (1995) identified Caridean shrimp as the dominant food in the stomachs of young gag (1.1–18.6 cm SL) from North Carolina estuaries.

Along the northern coast of Yucatán, juvenile red grouper inhabit the same nursery areas as juvenile black grouper (Renán et al., 2003). Young individuals of both species are found in sandy-rocky bottom habitats, and eat reef-associated prey organisms. Despite their cohabitation, the dominant prey in the juvenile red grouper (13–55.5 cm TL) diet is crustaceans, particularly reptant decapods, while fishes and unidentified crustaceans are a secondary prey category (Brulé and Rodríguez-Canché, 1993; Brulé et al., 1994). Furthermore, prey captured by young red grouper are generally slow-moving benthic species while those consumed by black grouper are less bottom-dependant, faster-moving organisms. Based on these results, it appears that juvenile black and red groupers do not compete substantially for food when they co-occur in the same habitat. Specific morphological and behavioral characteristics may explain this low interspecies predatory interaction. In this sense, Randall (1967) stated that members of the genus *Mycteroperca* could be considered a predominantly piscivorous serranid fish group due to their slender body shape and well-developed canine teeth. *Mycteroperca* species also seem to be less intimately associated with the bottom than *Epinephelus* species, tending to forage higher above the bottom and appear to be stronger, more agile swimmers (Parrish, 1987).

Overall, the number of black grouper sampled in this study was relatively small (N = 120). As observed for young red grouper (Moe, 1969; Jory and Iversen, 1989), juvenile black grouper were scattered in low densities over hard bottoms off the Yucatán coast and were difficult to collect due to their cryptic behavior. Spearing was the most effective method used to capture juveniles in this habitat (Renán et al., 2003). Spearing is also the collection method most likely to assure unbiased evaluations of stomach contents (Randall, 1967). One concern in the present study is that gut samples were not immediately removed and fixed after capture, meaning post-capture digestion could cause a loss of valuable dietary information on ingested soft-bodied organisms, and thus bias the data toward less digestible animals (Randall, 1967; Bowen, 1992).

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