

FEEDING ECOLOGY OF THE SCHOOLMASTER SNAPPER, *LUTJANUS APODUS* (WALBAUM), FROM SOUTHWESTERN PUERTO RICO

Jay R. Rooker

ABSTRACT

Stomach contents from 449 schoolmaster snapper, *Lutjanus apodus*, from southwestern Puerto Rico were examined. Hierarchical cluster analysis identified two primary trophic groups: ≤ 70 mm FL and > 70 mm FL. Small *L. apodus* (≤ 70 mm) fed almost exclusively on crustaceans (89% by weight; 95% by number; 98% frequency of occurrence), particularly amphipods and crabs. By contrast, *L. apodus* greater than 70 mm preferred piscine prey (57% by weight; 37% by number; 63% frequency of occurrence) and supplemented their diets with crabs, shrimp, and stomatopods. Ontogenetic patterns in diet were related to changes in jaw morphology (i.e., gape dimensions). Moreover, spatial and temporal variations were size-related and appeared to play some role in structuring the diet of *L. apodus*. Small *L. apodus* (≤ 70 mm) were found only in mangrove prop-root habitats and showed peak feeding at midday. Larger *L. apodus* (> 70 mm) were present in both mangrove and coral reef habitats and showed little variation in diurnal feeding periodicity. Prey selection patterns of *L. apodus* were influenced by habitat and season.

The schoolmaster snapper, *Lutjanus apodus* (Lutjanidae), is the most commonly encountered lutjanid on coral reefs in the Caribbean (Randall, 1983) and Bahamas (Böhlke and Chaplin, 1968). *L. apodus* appears confined to reefs more than other snappers (Randall, 1967); however, it has also been reported as the predominant lutjanid in areas adjacent to or inside mangrove prop-root habitats (Austin, 1971; Austin and Austin, 1971; Kimmel, 1985; Rooker and Dennis, 1991). *L. apodus* is a highly esteemed food fish and an integral part of the commercial and sport fisheries in the West Indies and other areas of its geographic range which extends from northern Brazil to Massachusetts (Allen, 1985).

Although *L. apodus* plays an important trophic role in tropical marine communities, little is known regarding its feeding ecology in such ecosystems. Investigations of the food habits of *L. apodus* are limited to large-scale ichthyofaunal studies in which diet information is presented in qualitative terms and drawn from small sample sizes (Beebe and Tee-Van, 1928; Longley and Hildebrand, 1941; Randall, 1967; Austin and Austin, 1971; Starck, 1971). Detailed quantitative assessment of the food habits of *L. apodus*, including the effect of ontogeny, is lacking. The objectives of this study were to describe the diet of *L. apodus* quantitatively, determine ontogenetic patterns in diet, and determine the relevance of diel feeding periodicity, habitat, and season to these patterns.

MATERIALS AND METHODS

Study Area.—Mangrove and coral reef habitats located off La Parguera, Puerto Rico were selected as sampling sites for this study (Fig. 1). Habitat determination was based on random selection of sites from each of five habitat types. Mangrove collections were limited to two types: shoreline mangroves and mangrove keys. Mangrove sites were dominated by the red mangrove (*Rhizophora mangle*) and characterized by shallow (< 1.0 m) water. Three different coral reef habitats were distinguished and sampled: a) Inshore, shallow water (Ahogado, Collado), b) Inshore, moderate depth (Enrique, Margarita, Media Luna), and c) Offshore, moderate (Turumote) to shelf edge depth. Inshore shallow water reefs were characterized by large stands of elkhorn coral (*Acropora palmata*) near the surface, with fire coral (*Millepora alcicornis*) dominant at the base of the reef (ca. 4 m). Inshore, moderate depth reefs ranged in depth from 5 to 10 m. Coral composition was similar to shallow water reefs with the

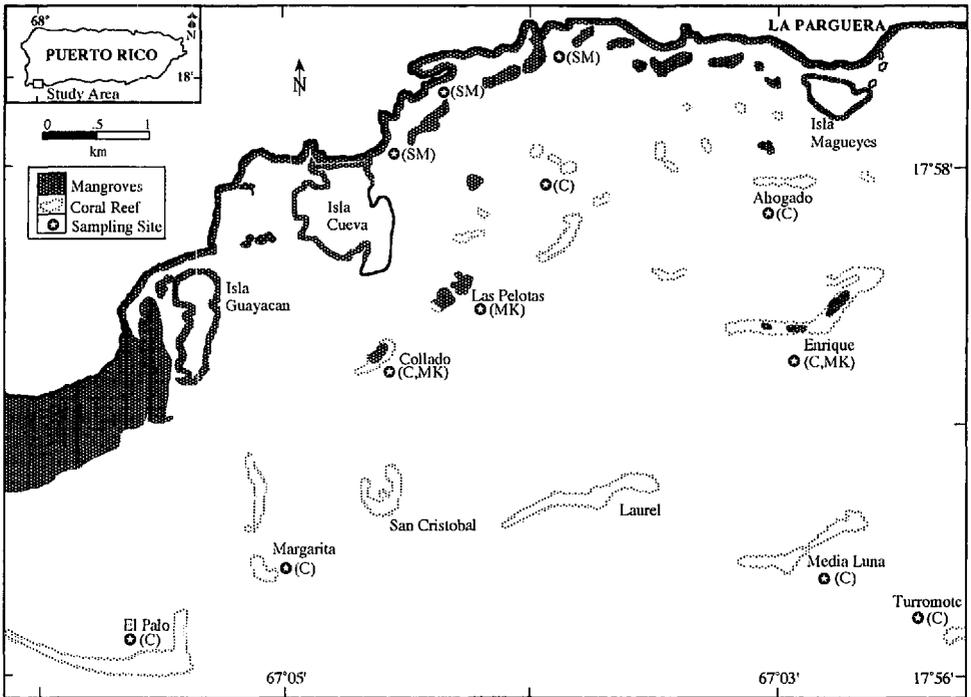


Figure 1. Location of collection sites and inshore habitats found off La Parguera, Puerto Rico (SM = shoreline mangroves, MK = mangrove key, C = coral reef).

addition of more massive-type corals (*Diploria* and *Montastrea*) at depth. Offshore coral reefs ranged in depth from 15 to 30 m and were characterized by both massive (*Diploria* and *Montastrea*) and foliose (*Agaricia*) hermatypic coral species.

Data Collection.—Sample collections of *L. apodus* were taken by diving, using various spear types depending on fish size (micro-spear, pole-spear, and spear gun). Collections were concentrated in quarterly periods throughout the year: July–September 1988, October–December 1988, January–March 1989, and April–July 1989. Approximately 25 fish per 50-mm size grouping (51–100, 101–150, 151–200, and 201–250 mm fork length) were collected during each quarterly sampling period. An annual total of 20 specimens per 10-mm size class was targeted. Fish less than 50 mm or greater than 250 mm were infrequently encountered and therefore collected whenever possible. Diel feeding periodicity was examined by collecting specimens at 0800, 1200, 1600 and 2000 (± 1 hour). Stomach fullness (SF = prey weight/predator weight:1,000) and general condition of prey were evaluated. A series of 50 specimens, spanning the complete size range sampled, was examined for ontogenetic changes in jaw morphology. Gape height and width were measured to the nearest 0.1 mm using a vernier caliper.

Specimens were placed in ice-filled coolers in the field and later into the lab freezer to minimize post-capture digestive activity. Dissected stomach contents were placed in vials and preserved with 10% formalin. All food items were identified to lowest possible taxonomic level. Number, weight (blotted wet weight) and maximum dimension of each prey item were recorded. Relative importance of prey items was determined using three dietary coefficients: percent composition by weight, percent composition by number, and percent frequency of occurrence.

Dietary coefficients were combined to assess overall prey importance for *L. apodus* using the "Index of Relative Importance" (IRI) developed by Pinkas et al. (1971). This method combines separate prey measures into a single index, allowing prey items to be ranked. The IRI is defined as: $IRI = (\% \text{ composition by weight} + \% \text{ composition by number})(\% \text{ frequency of occurrence})$. For statistical testing, percent composition by weight estimates were used as the preferred prey measure since such values most closely approximate the relative importance of prey items as indicated by IRI estimations from this study.

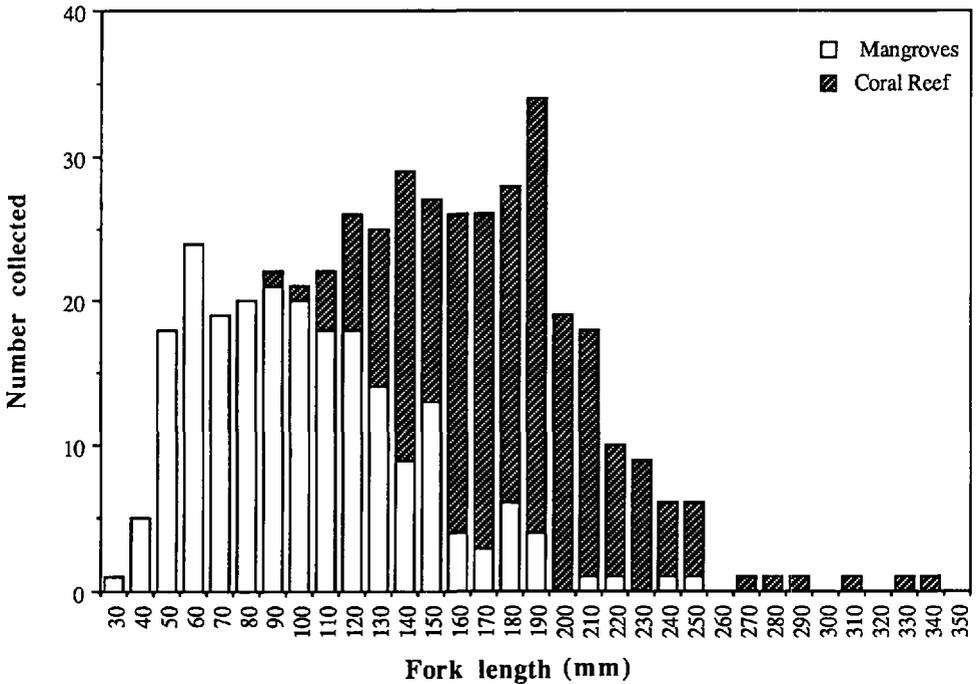


Figure 2. Length frequency distribution of *Lutjanus apodus* collected from mangrove and coral reef habitats off La Parguera, Puerto Rico from July 1988 through July 1989 (N = 449).

Statistical Treatments.—Hierarchical cluster analysis was used in this study to examine ontogenetic patterns in the diet of *L. apodus* (Hartigan, 1975) and to divide the set of 22 size classes into natural trophic groups. Euclidean distance was the selected similarity measure and average linkage (amalgamation) was used for clustering. Data were grouped into 10-mm size classes from 50–250 mm, plus groups for fish <50 mm and >250 mm. Clustering was based on weight percentage of major prey-species taxa. Other similarity measures (Pearson), linkage methods (single, median), and clustering algorithms (divisive clustering) were employed but produced similar results to the chosen cluster design. Therefore, only hierarchical clustering is presented. The statistical software package SYSTAT was used for cluster analyses (Wilkinson, 1989).

Analysis of variance (ANOVA) was used to examine spatial and temporal variability in feeding habits. To satisfy ANOVA assumptions, an angular transformation (arcsine) was used on proportional (percent weight) prey data. Significant ($\alpha = 0.05$) ANOVA results were examined further with Tukey's HSD test to determine which main effect was significant.

RESULTS

Quantitative assessments of feeding habits were made from 449 specimens of *L. apodus*. Three hundred and twelve (69%) specimens contained full or partially full stomachs. Specimens ranged in size from 39 mm (1.2 g) to 345 mm (824 g) (Fig. 2).

Habitat type and locality had considerable influence on the size of specimen collected. *L. apodus* less than 90 mm were all taken from mangrove habitats while larger fish (>90 mm) were collected from both coral reef and mangrove habitats. The largest specimen taken from the mangrove keys measured 255 mm, while that from shoreline mangroves measured 180 mm. The smallest specimen taken from a shallow water reef locality was 98 mm. A gradual transition from mangrove to reef habitats occurred over a restricted size range of 100–190 mm. Upon reaching 150 mm *L. apodus* was well established on coral reef habitats.

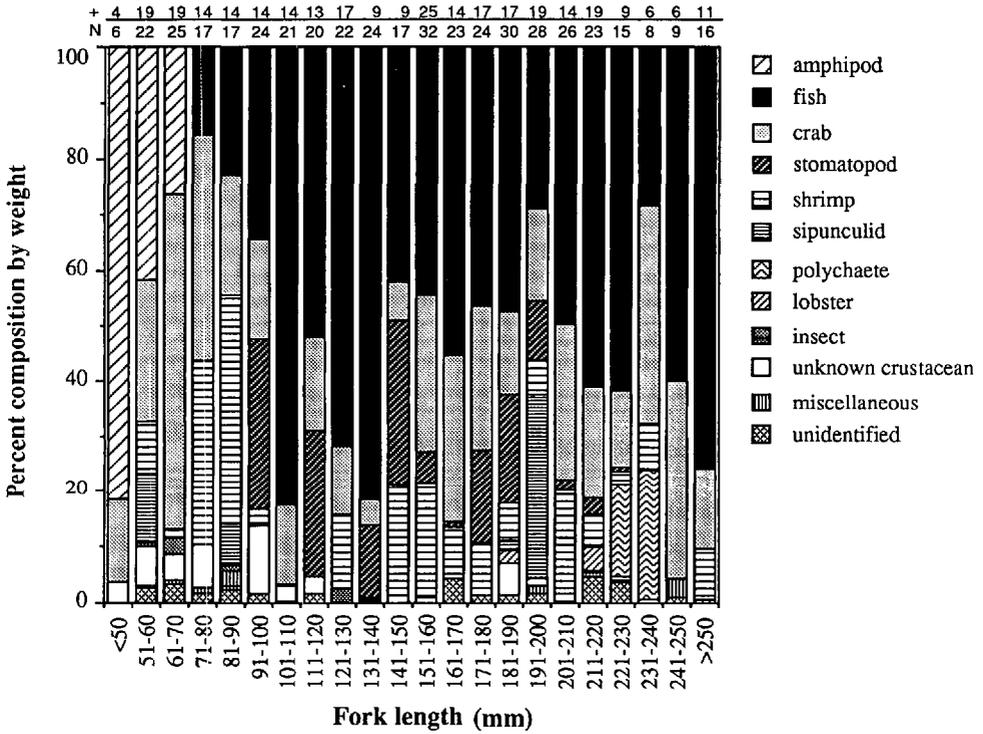


Figure 3. Ontogenetic changes in diet of *Lutjanus apodus* from mangrove and coral reef habitats. Histogram for each size class shows relative proportions (percent weight) of food items. Number collected per size class is given as N and (+) indicates number with partial or full stomachs.

Eleven major taxonomic groups were identified in the stomachs of *L. apodus*: amphipods, copepods, crabs, fishes, isopods, insects, lobsters, polychaetes, shrimp, sipunculids, and stomatopods. Diets changed with fish size (Fig. 3). Amphipods and crabs dominated the diet of small *L. apodus* (≤ 70 mm). As fish size increased to 100 mm, crab, shrimp, and fish selection increased. Fish greater than 100 mm fed most heavily on fishes and supplemented their diets with crabs, shrimp, and stomatopods.

Cluster Analysis.—Cluster analysis was performed on the five major taxonomic food groups: amphipods, crabs, fishes, shrimp, and stomatopods. IRI estimates for these five prey items represent over 99% of the overall IRI value, so the importance of other food items was minimal. Cluster analysis using all food items was also performed. However, results were less distinct and showed more variability. Thus, limiting further discussion to the restricted data set will simplify the analysis without sacrificing significant detail.

Hierarchical cluster analysis identified two distinct trophic groups for *L. apodus*: ≤ 70 mm and > 70 mm (Fig. 4). Discontinuity of the size spectrum within clusters was used as the objective criterion for identifying trophic groupings. Within each primary trophic group, there was evidence for further separation. Size class 1 (< 50 mm) and size classes 4–5 (71–90 mm) could each be separated from all larger size classes within their respective primary groups to form four trophic groups with similar levels of dissimilarity (Fig. 4). However, dietary information in smaller trophic groups was limited and may have biased ontogenetic

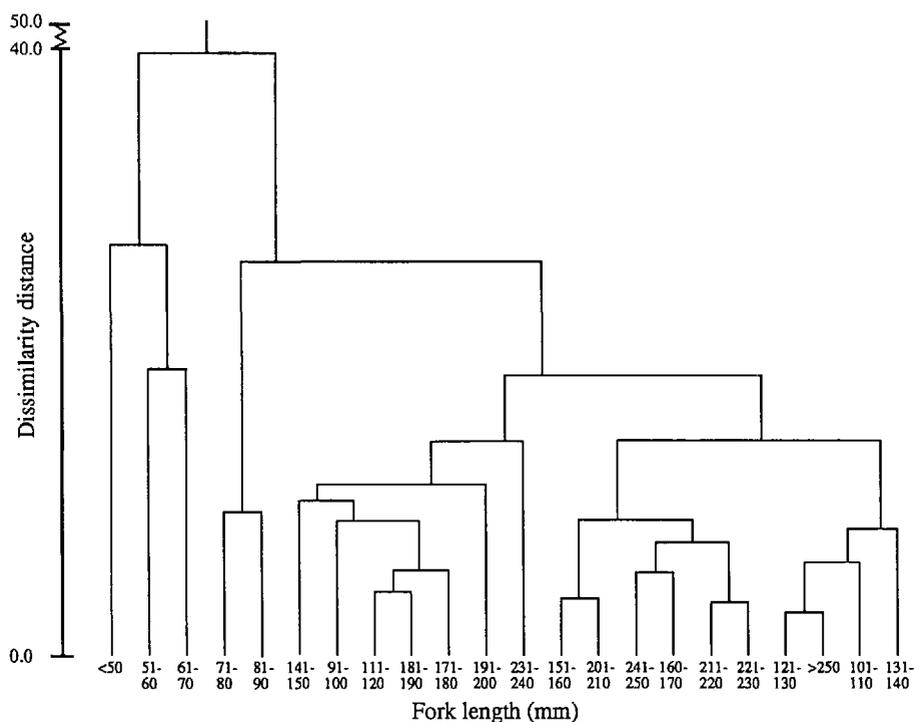


Figure 4. Dendrogram for hierarchical cluster analysis of diet similarity among 22 size-classes of *Lutjanus apodus*. Clustering was based on percent weight of top prey items. Average linkage clustering and euclidean distance were used.

groupings. For example, cluster group 1 was comprised of size class 1 (<50 mm), which contained only 4 specimens with food. For this reason, further analyses and quantitative descriptions of the diet of *L. apodus* will concentrate on the two primary trophic groups, ≤ 70 mm and >70 mm.

Quantitative Description of Diet (by Weight).—*L. apodus* less than 70 mm fed primarily on crabs (46.2%) and amphipods (34.1%). Grapsid crabs, particularly *Pachygrapsus transversus*, comprised 12.7% of the diet. Xanthid and majid crabs were present but in much lower quantities (2.1 and 0.4%, respectively). Although these figures appear low, the majority of crabs examined in the stomachs of juvenile fish were unidentifiable to family. In fact, 31.0% of the diet was composed of unidentifiable crab taxa. Five different amphipod taxa were observed, and overall this prey represented 34.1% of the diet. Less abundant prey items identified included sipunculids (4.7%), shrimp (4.5%), and insects (1.7%).

With increasing size the diet of *L. apodus* shifted. Piscivory first appears in size class 4 (71–80 mm), with fishes comprising 14.6% of food items consumed. The importance of fishes as prey continues to increase with size through size classes 5 (81–90 mm) and 6 (91–100 mm), accounting for 22.2% and 34.7% of the diet, respectively. By size class 7 (101–110 mm) piscivory was well established with fishes representing 82.6% of all food items taken. The remaining size classes, 8 (111–120 mm) through 22 (>250 mm), were primarily piscivorous. Composition of diet by weight in size groups 8 through 22 were: fishes (53.7%), crabs (20.6%), stomatopods (10.7%), and shrimp (8.5%).

Ontogenetic changes in piscine prey were also identified for *L. apodus* greater than 70 mm and possibly indicated additional trophic separation. All identifiable fishes from the stomachs of 70–160 mm *L. apodus* were clupeoids: Clupeidae (*Jenkinsia* spp.) and Engraulidae (*Anchoa* spp.). Within this group, *L. apodus* between 71–120 mm selected mainly clupeids, while larger fish (121–160 mm) consumed mostly engraulids. Both groups supplemented their diet with the other baitfish taxa. In contrast, *L. apodus* greater than 160 mm fed mostly on demersal fishes. Juvenile acanthurids (*Acanthurus* spp.) and scarids (*Sparisoma* spp. and *Scarus* spp.) were the primary prey species consumed by this group, together accounting for 71.5% of the diet. Scarids alone accounted for approximately three quarters of all demersal fish taken by *L. apodus*. Additional fishes consumed by *L. apodus* in order of dominance by weight included: Priacanthidae (7.2%), Labridae (4.2%), Muraenidae (4.1%), and Clinidae (1.5%).

Ontogenetic variation within crab prey taxa was also observed. *L. apodus* less than 100 mm fed heavily on grapsid crabs (69.1%), particularly *Percon gibbesi*. Hermit and xanthid crab consumption was much lower and accounted for only 11.1% and 16.1%, respectively. Crab consumption by 100–200 mm fishes was highly variable with grapsid, majid, and xanthid crabs accounting for most of the weight. Large *L. apodus* (>200 mm) were more selective than smaller fish. Majid crabs, particularly *Mithrax sculptus*, were the main crab prey item and made up 43.0% of all identifiable crabs. Grapsid, portunid, and xanthid crabs each accounted for approximately 18–20% of the total crab component of the diet.

Quantitative Description of Diet (by Number and Frequency of Occurrence).—The relative importance of different prey taxa was also examined using alternative quantitative measures: % composition by number and % frequency of occurrence (Fig. 5). For small *L. apodus* (≤ 70 mm), alternative prey indices amplify the importance of amphipods as prey. Percent composition by number and percent frequency of occurrence measures for amphipods were 78.4 and 73.0, respectively. The same prey measures for crabs were 9.1 and 35.2%, respectively. IRI values for primary prey taxa consumed by small *L. apodus* (≤ 70 mm) are as follows: amphipods (8,206), crabs (1,934), shrimp (176), insects (89), and polychaetes (1). Estimates of percent composition by number and percent frequency of occurrence for larger *L. apodus* (>70 mm) were very similar to percent composition by weight. The five primary food items by percent number include: fishes (36.5%), crab (28.9%), shrimp (12.6%), stomatopods (4.3%), and polychaetes (0.7%). Percent frequency of occurrence estimates were also very similar: fishes (63.6%), crabs (53.8%), shrimp (16.5%), stomatopods (9.3%), and polychaetes (0.9%). The relative importance of fishes (5,913) as prey items based on IRI calculations is approximately twice that of crabs (2,706). IRI values given for the remaining primary prey items are as follows: shrimp (333), stomatopods (112), and polychaetes (2).

Jaw Morphology and Prey Size.—Ontogenetic shifts in the diet of *L. apodus* appear to be correlated with changes in jaw morphology. Functional regression analyses compared fish size (mm FL) with gape dimensions ($N = 50$). Results showed progressive increases in gape height and width with increasing fish size. Equations for gape height and width are $y = 1.5603 + 0.0910 \cdot \text{FL}$ ($R^2 0.961$) and $y = 0.7514 + 0.0659 \cdot \text{FL}$ ($R^2 0.981$), respectively. To facilitate comparisons to systematic work, the conversion equation from fork to standard length (SL) is: $\text{FL} = 3.3199 + 1.1748 \cdot \text{SL}$ ($R^2 0.990$; $N = 200$).

Linear regression analysis was then used to determine if increasing jaw dimensions influenced the size of prey taken by *L. apodus*. Maximum dimensions of

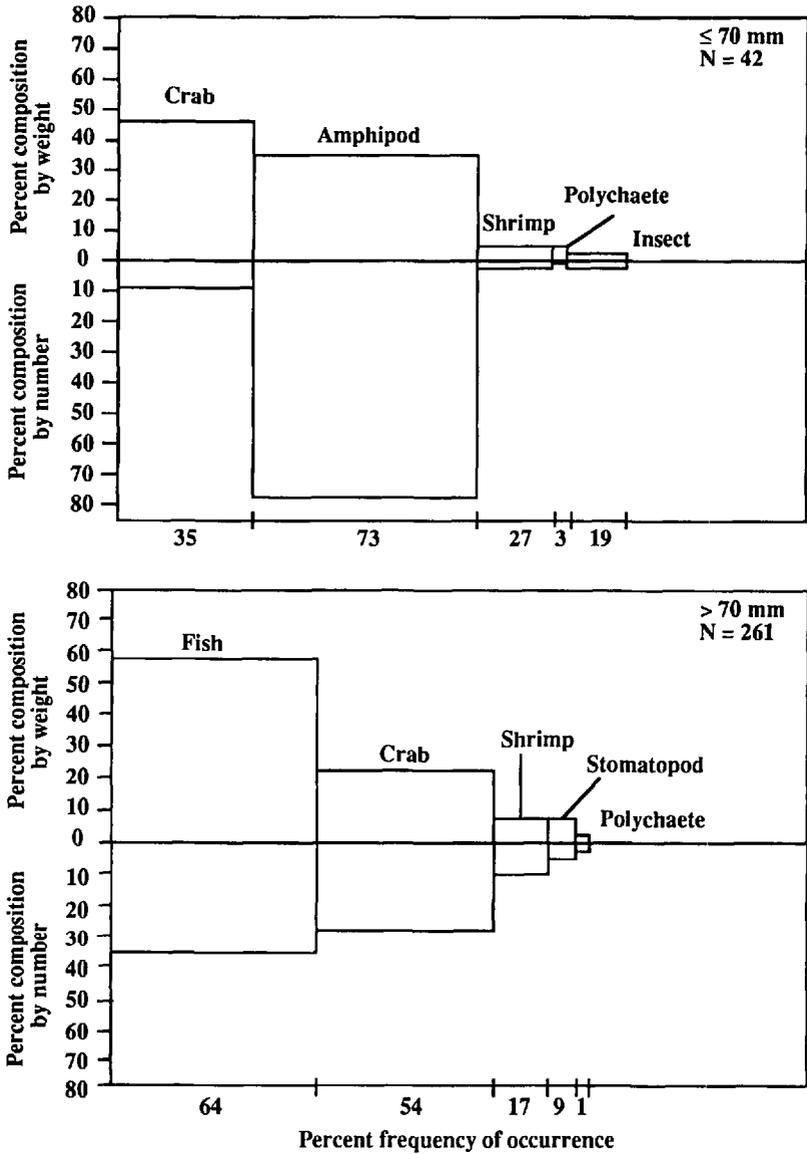


Figure 5. Diagram displaying measures of prey importance (percent weight, number, and frequency of occurrence) used to derive five IRI values for *Lutjanus apodus* $\leq 70\text{ mm}$ and $> 70\text{ mm}$. Top five prey items for each size group were used.

crab and amphipod/shrimp prey were positively correlated with predator size (Fig. 6). As *L. apodus* increased in size, they became capable of taking larger prey taxa. Maximum dimension of fish prey taken was highly variable and poorly correlated with predator size (R^2 0.058; $P > 0.05$); however, a slight positive trend was evident.

Gape dimensions of small *L. apodus* ($\leq 70\text{ mm}$) appear to influence ontogenetic changes by limiting their ability to consume piscine prey. On average, the smallest piscine taxa (i.e., clupeoids) taken ranged from 5 to 8 mm in body depth. Gape

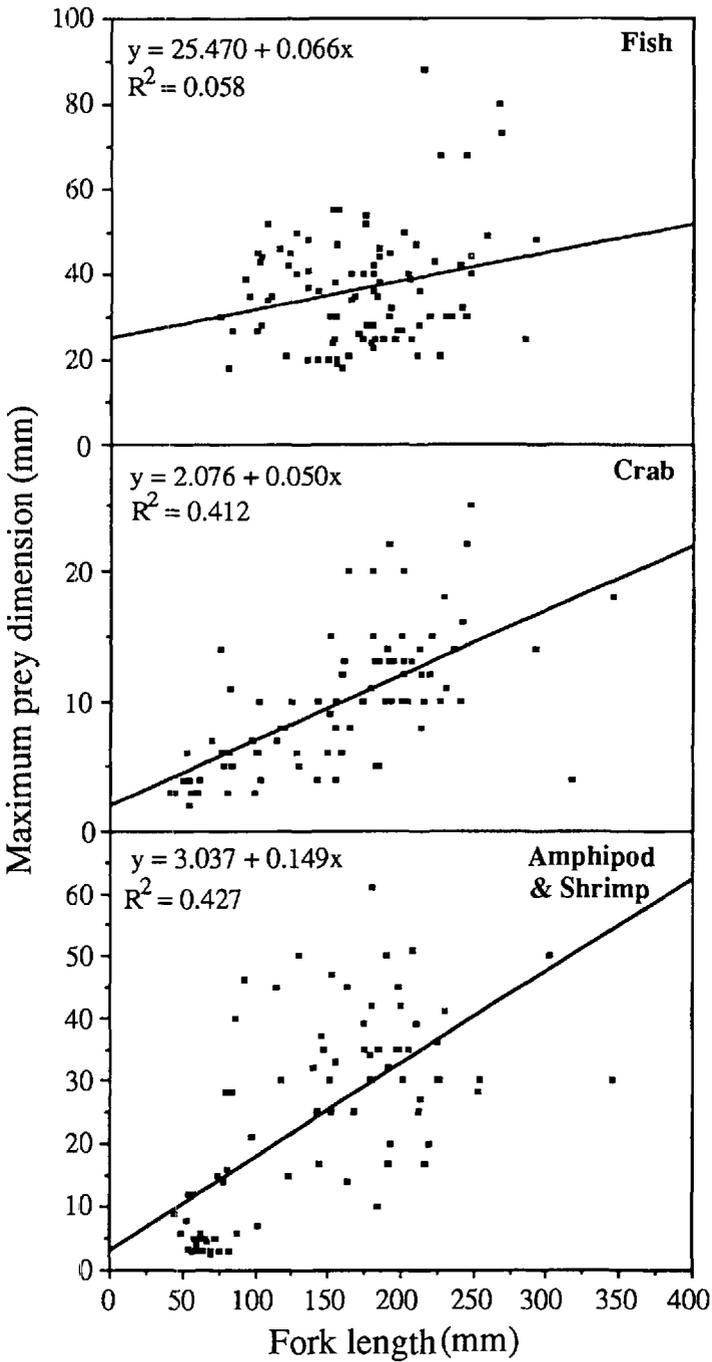


Figure 6. Linear regression of prey item size (maximum dimension) consumed as a function of predator (*Lutjanus apodus*) size. Prey categories include fish, crab, and amphipod/shrimp.

width and height of *L. apodus* at 70 mm (from regression equations) were estimated as 5.3 and 7.8 mm, respectively. Consequently, gape sizes of *L. apodus* less than 70 mm were close to or below the prey size (body depth) of the smallest piscine prey taxa. With increasing size, *L. apodus* was capable of taking larger prey; however, it often consumed fishes (i.e., baitfishes) much smaller in size (i.e., body depth) than gape constraints allowed.

Habitat Effect.—In an attempt to separate the influences of fish size and habitat on the diet of *L. apodus*, hierarchical cluster analyses were performed on mangrove and coral reef fish separately using weight percentages of the five primary prey taxa. Results were consistent with cluster analysis performed on all fishes (habitats combined). Two primary trophic groups identified for mangrove collected fish were ≤ 70 mm and > 70 mm. For the coral reef fish, which were all greater than 90 mm, cluster analysis could not distinguish additional trophic group separations, that is, no continuity existed in the size groupings.

Habitat-related feeding variability was further investigated by comparing data from the five habitats sampled: shoreline mangroves, mangrove key and three coral reef habitats (inner, middle and outer). Amphipod, fish, shrimp, and stomatopod consumption each varied significantly (ANOVA, $P < 0.05$) among the different habitats sampled. Tukey's HSD test results showed that piscivory by *L. apodus* from shoreline mangroves was significantly lower than from mangrove key and coral reef habitats. Moreover, no significant difference (ANOVA, $P > 0.05$) in piscivory was detected among coral reef habitats when analyzed separately. Habitat-related trends in shrimp consumption were less evident than other prey taxa. Results from Tukey's HSD test indicated shrimp consumption by *L. apodus* occupying shallow-water coral reef habitats was significantly higher than mangrove key habitats. Multiple comparisons on amphipod and stomatopod consumption could not be tested since such taxa were completely absent from certain habitats (no variance). Amphipods were only found in the stomachs of *L. apodus* collected from shoreline and mangrove key habitats. Stomatopods were part of the diet of *L. apodus* from all habitats except shoreline mangroves.

Diurnal Feeding Periodicity.—Although nocturnal collections were attempted at 2000, small sample sizes precluded any diel comparisons. Hence, results will only address diurnal feeding periodicity. Fish size and habitat had considerable impact on diurnal feeding activity of *L. apodus* (Fig. 7). Stomach fullness of small *L. apodus* (≤ 70 mm; mangroves) varied significantly among three time periods with peak intensity between 1100–1300 (SF = 13.7; ANOVA, $P < 0.05$). Prey items found in the stomachs of *L. apodus* less than 70 mm collected from 1100–1300 were relatively undigested and intact. Feeding intensity was reduced at 0700–0900 and 1500–1700 with fullness values of 4.7 and 8.7, respectively. Condition of prey items from these sampling periods was poor with most food being well digested. Larger *L. apodus* (> 70 mm) showed constant prey consumption throughout the day with no significant peaks in stomach fullness (ANOVA, $P > 0.05$). This lack of strong diurnal feeding periodicity was present for both mangrove and coral reef collected specimens. Stomach fullness indices for intermediate- to adult-sized *L. apodus* inhabiting mangrove habitats were approximately twice those of their coral reef counterparts. Fullness values for fish collected from mangrove habitats ranged from 9.2 to 11.9 during diurnal periods, while coral reef fish ranged from 5.0 to 5.9 (Fig. 7).

Seasonal Effect.—Seasonal analysis of the ontogenetic trophic groups identified through cluster analysis (≤ 70 mm and > 70 mm) was examined with each prey measure (Table 1). For small mangrove-dwelling *L. apodus* (≤ 70 mm), amphipods

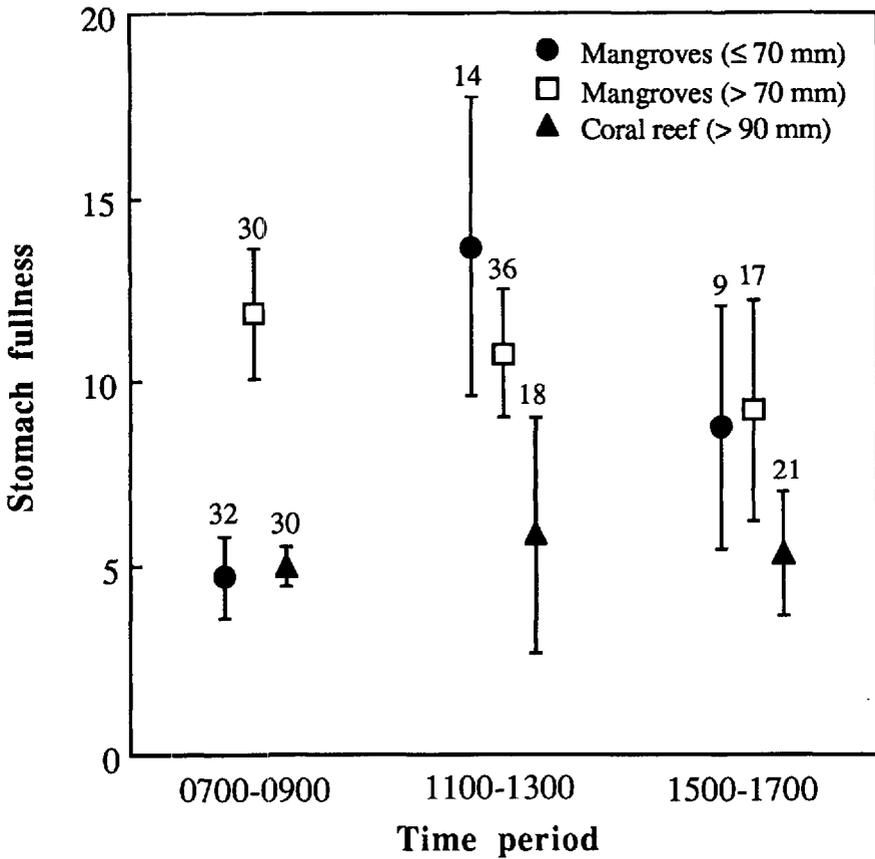


Figure 7. Diurnal feeding periodicity based on mean stomach fullness (± 1 SE) for *Lutjanus apodus* ≤ 70 mm and > 70 mm from mangrove and coral reef habitats. Numbers above error bars represent sample sizes.

accounted for approximately half of all prey consumed by weight during each season. Percent composition by number estimates were also consistent among seasons, but higher than percent weight estimates, ranging from approximately 70 to 80%. Frequency of occurrence for amphipod prey taxa ranged from approximately 50 to 80% with peak values occurring from July to December. Consumption of crabs and shrimp was more variable than amphipods. In July to December, crabs and shrimp each accounted for approximately 15–30% of the diet by number and weight. From January to June, shrimp consumption was reduced to less than 3% of the diet by number and weight, while crab consumption increased to levels similar to amphipods. Larger *L. apodus* (> 70 mm), taken from mangrove habitats, showed strong seasonal differences in prey consumption. In July through December, fishes accounted for approximately 75% of prey weight consumed by *L. apodus*. Crabs, shrimp, and stomatopods contributed the remainder of the diet. During January to June, consumption of fishes declined precipitously to less than 15% of the diet by weight. Decreased fish consumption was matched by increasing selection for crustaceans, namely crabs and stomatopods. Crabs comprised 65 and 42% of prey weight for *L. apodus* (> 70 mm) in mangrove habitats during January–March and April–June, respectively. Similar sea-

Table 1. Seasonality in the diet of *Lutjanus apodus* from mangrove and coral reef habitats (July 1988 to June 1989). Percent weight, percent number, and percent frequency of occurrence are given for small (≤ 70 mm) and large (> 70 mm) fish. Numbers represent prey types (1 = amphipod, 2 = crab, 3 = shrimp, 4 = stomatopod, and 5 = fish).

Season	Predator Size	Habitat	N	Prey															
				% Composition by weight					% Composition by number					% Freq. of occurrence					
				1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
Jul.-Sep. 1988	Small	Mangrove	12	53	31	13	0	0	70	19	2	0	0	0	0	73	27	0	0
	Large	Mangrove	22	0	12	6	0	74	2	19	8	0	42	5	36	14	0	50	
	Large	Coral reef	34	0	23	21	6	50	0	25	23	5	29	0	47	53	15	56	
Oct.-Dec. 1988	Small	Mangrove	5	47	22	31	0	0	81	8	4	0	0	0	80	40	0	0	
	Large	Mangrove	38	0	6	0	9	79	10	12	7	3	59	3	24	3	11	76	
	Large	Coral reef	24	0	48	11	5	37	0	49	16	3	23	0	67	29	4	54	
Jan.-Mar. 1989	Small	Mangrove	7	54	38	1	2	0	82	2	3	1	0	57	14	14	0	0	
	Large	Mangrove	27	0	65	14	8	10	3	39	11	2	4	4	67	26	4	11	
	Large	Coral reef	39	0	29	13	19	39	0	31	24	9	26	0	41	41	21	54	
Apr.-Jun. 1989	Small	Mangrove	14	46	52	0	0	0	79	4	2	0	0	50	29	14	0	0	
	Large	Mangrove	23	1	42	13	26	15	25	18	15	3	8	17	39	13	9	22	
	Large	Coral reef	36	0	9	4	2	77	0	25	6	2	41	0	50	19	6	78	

sonal trends were present for larger mangrove fish (>70 mm) using percent composition by number and percent frequency of occurrence measures.

Seasonal prey selection patterns were also present for reef dwelling *L. apodus*. Fishes were the preferred prey during all quarterly sampling periods. Fishes accounted for approximately 35–50% of the diet by weight between July and March, rising above 75% in April–June. Similarly, percent composition by number estimates for fishes was lowest during July and March (20–30%) and increased in April–June (41%). Crabs, and to a lesser degree shrimp and stomatopods, accounted for the remaining prey taxa, which was minimal in terms of percent weight (i.e., <10%). However, percent composition by number and percent frequency of occurrence estimates were more substantial for such prey taxa. By number, crabs and shrimp accounted for 25–39% and 6–24% of the diet during all seasons, respectively. Moreover, percent frequency of occurrence of crab taxa was over 40% during each season.

DISCUSSION

Lutjanus apodus from southwestern Puerto Rico undergo ontogenetic shifts in habitat and diet. Small juveniles (≤ 70 mm) inhabit shallow-water mangrove habitats. Their dietary regime is fairly rigid, with crustaceans accounting for almost the entire diet. As *L. apodus* matures, feeding and habitat shifts occur. Fish begin to appear on coral reef habitats when they reach intermediate size (ca. 100 mm). Although some intermediate- to adult-sized fish remain in the mangroves, the majority emigrate to established coral reef populations. Feeding patterns become more varied and fishes become the dominant prey taxa with increasing size.

Relative importance (i.e., percent composition) of primary prey chosen by *L. apodus* indicates selective feeding is operating throughout ontogeny. Diminutive prey, namely amphipods, were preferred by small fish (≤ 70 mm) and taken in large quantities, often numbering between 20 and 50 prey items per individual. Evidently, small *L. apodus* (≤ 70 mm) exploit amphipods and opportunistically feed on larger prey (i.e., crabs). Similarly, *L. apodus* >100 mm prefer to feed on fishes. In contrast to small fish, prey selected by larger *L. apodus* (>100 mm) were generally large (ca. 25–50 mm maximum dimension) and present in smaller quantities (ca. 2–3 per specimen). Similar to juveniles, prey selection by larger *L. apodus* (>100 mm) was essentially limited to one or two primary prey taxa which accounted for most of the diet based on IRI estimates.

Ontogenetic shifts in feeding habits often correspond with morphological changes (Werner, 1974; Stoner and Livingston, 1984). Likewise, dietary shifts of *L. apodus* appear to be related to changes in jaw morphology during ontogeny. Changes in gape dimensions during ontogeny of *L. apodus* may have affected prey size selectivity. Gape sizes of juvenile *L. apodus* less than 70 mm ranged close to the prey size (body depth) of the smallest and most abundant piscine prey taxa available (i.e., baitfishes). As a result, morphological gape limitations may preclude small juveniles (≤ 70 mm) from feeding on baitfishes which dominate mangrove habitats in Puerto Rico (Kimmel, 1985; Rooker and Dennis, 1991). Chao and Musick (1977) suggest that morphological constraints are responsible for structuring the diets of fishes. Similarly, ontogenetic shifts in the diet observed in this study (i.e., shift to piscivory) for *L. apodus* appear to display morphological control.

While changes in morphology appear to influence the ontogenetic shift from crustacean to piscine prey taxa, spatial distribution (i.e., habitat) also appears to be important in structuring the diet of *L. apodus*. Variations in diet within locales

have been reported for a congener of *L. apodus*, the gray snapper (*L. griseus*) (Longley et al., 1925; Starck, 1971). In like manner, the diet of *L. apodus* differed depending upon the habitat and area from which it was collected. In particular, distinctly different prey selection patterns were observed for mangrove and coral reef dwelling *L. apodus*. *L. apodus* (>100 mm) from mangrove habitats consumed large quantities of mid-water baitfishes (i.e., clupeids, engraulids) while their coral reef counterparts focused on demersal fish taxa (i.e., scarids, acanthurids). This piscine shift was also size-related with *L. apodus* less than 160 mm feeding almost entirely on baitfishes, while larger specimens focused on scarids and acanthurids. Such patterns are consistent with size-related habitat shifts observed in this study for *L. apodus* and prey abundance patterns found in such habitats in southwestern Puerto Rico (Kimmel, 1985; Rooker and Dennis, 1991).

Temporal variations in feeding activity and prey selection were also observed. Evaluation of diel feeding activity indicates that a major ontogenetic change occurs when fish are approximately 70 mm in length. Smaller, younger individuals maintain a higher feeding intensity than larger individuals and with maturity shift from midday feeding to more continuous feeding throughout the day. Starck and Davis (1966) reported that feeding times of reef fishes are closely associated with the activities of their predators and prey. Microcarnivores which browse and pick at sessile organisms (e.g., amphipods) are generally active only during the day and seek cover at night for protection against predators (Hobson, 1965; Ebeling and Bray, 1976). By contrast, mesocarnivores, particularly piscivorous fishes, feed opportunistically during the day, but maintain peak activity during crepuscular or nocturnal periods (Collette and Talbot, 1972; Ebeling and Bray, 1976). Concentrated crepuscular or nocturnal feeding activity combined with opportunistic feeding during the day have been reported for other *Lutjanus* species (Hobson, 1965; Starck, 1971). Although adult *L. apodus* were observed feeding at night, small sample sizes precluded quantitative comparisons with diurnal collections necessary to confirm increased nocturnal feeding intensity. However, results from this study appear to support the general feeding strategy described above. Namely, juvenile and adult-sized *L. apodus* displayed feeding patterns of micro- and mesocarnivores, respectively.

Seasonal variation in prey selection patterns appeared to be related to fish size and habitat. Small *L. apodus* (≤ 70 mm) showed no marked changes in prey taxa selected among seasons, while larger fish (>70 mm), particularly those from mangrove habitats, showed strong seasonal differences in prey selection. Observed temporal patterns are probably related to seasonal variations in piscine prey. Inshore habitats often function as nursery areas for reef associated fishes, and recruitment to and emigration from such habitats is often variable (Ogden and Ehrlich, 1977; Lindeman, 1989). Consequently, seasonal fluctuations in species numbers may occur. Seasonal variations have been reported for a variety of fishes occupying Puerto Rican mangrove habitats (Rooker and Dennis, 1991), and some of these species were prey taxa consumed by *L. apodus* in this study. Thus, seasonal pulses, particularly in ichthyofaunal prey abundance, probably influence prey available to *L. apodus*.

ACKNOWLEDGMENTS

I am especially grateful to R. Appeldoorn and G. Dennis for their support and guidance. L. Fuiman, D. Hensley, J. Holt, A. Stoner, and two anonymous reviewers assisted with the evolution of the manuscript. A special thanks to A. Acosta, D. Goulet, A. McGehee, S. Reed, and R. Turingan for providing essential field assistance. This study was supported by the Department of Marine Sciences and Sea Grant Program, University of Puerto Rico.

LITERATURE CITED

- Allen, G. R. 1985. FAO species catalogue, Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. FAO Fish. Synop. (125), 208 pp.
- Austin, H. 1971. A survey of ichthyofauna of the mangroves of Western Puerto Rico during December, 1967–August, 1968. *Carib. J. Sci.* 11: 27–39.
- and S. Austin. 1971. The feeding habits of some juvenile marine fishes from the mangroves in Western Puerto Rico. *Carib. J. Sci.* 11: 171–178.
- Beebe, W. and J. Tee-Van. 1928. The fishes of Port-au-Prince Bay, Haiti, with a summary of the known species of marine fish of the island of Haiti, and Santo Domingo. *Zoologica*, N.Y. 10: 1–279.
- Böhlke, J. E. and C. C. G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingston Publ. Co., Wynnewood, Pennsylvania. 771 pp.
- Chao, L. N. and J. A. Musick. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the New York River estuary, Virginia. *Fish. Bull. U.S.* 75: 657–702.
- Collette, B. B. and F. H. Talbot. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *Bull. Nat. Hist. Mus. L.A. Co.* 14: 98–124.
- Ebeling, A. W. and R. N. Bray. 1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. *Fish. Bull. U.S.* 74: 703–717.
- Hartigan, J. A. 1975. Clustering algorithms. Wiley, New York, New York. 351 pp.
- Hobson, E. S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Res. Rep. U.S. Fish Wildl. Serv.* 73: 1–92.
- Kimmel, J. J. 1985. A characterization of Puerto Rican fish assemblages. Unpublished Ph.D. Thesis, University of Puerto Rico, Mayagüez, Puerto Rico. 106 pp.
- Lindeman, K. C. 1989. Coastal construction, larval settlement and early juvenile habitat use in grunts, snappers and other coastal fishes of southeast Florida. *Bull. Mar. Sci.* 44: 1068.
- Longley, W. H. and S. F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits and local distribution. *Pap. Tortugas Lab.* 34: 331 pp.
- , W. L. Schmitt and W. R. Taylor. 1925. Observations upon the food of certain Tortugas fishes. *Yearb. Carneg. Inst.* 24: 230–232.
- Ogden, J. C. and P. R. Ehrlich. 1977. The behavior of heterotypic resting schools of juvenile grunts (*Pomadasyidae*). *Mar. Biol.* 42: 273–280.
- Pinkas, L., M. S. Oliphant, I. L. R. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. *Fish. Bull.* 152, 139 pp. Calif. Dept. Fish Game.
- Randall, J. E. 1967. Food habits of reef fishes in the West Indies. *Stud. Trop. Oceanogr. Miami* 5: 655–847.
- . 1983. Caribbean reef fishes, 2nd ed. T. F. H. Publ. Inc., Jersey City, New Jersey. 318 pp.
- Rooper, J. R. and G. D. Dennis. 1991. Diel, lunar, and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bull. Mar. Sci.* 49: 684–698.
- Starck, W. A. 1971. Biology of the gray snapper, *Lutjanus griseus*, (Linnaeus) in the Florida Keys. *Miami Stud. Trop. Oceanogr.* 10: 12–150.
- and W. P. Davis. 1966. Night habits of fishes of Alligator Reef, Florida. *Ichthyologica* 38: 313–355.
- Stoner, A. W. and R. J. Livingston. 1984. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia* 1984: 174–187.
- Werner, E. E. 1974. The fish size, prey size, handling time relationships in several sunfishes and some implications. *J. Fish. Res. Bd. Can.* 31: 1531–1536.
- Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois.

DATE ACCEPTED: January 13, 1994.

ADDRESS: Department of Marine Sciences, University of Puerto Rico, Mayagüez, Puerto Rico 00709-5000; PRESENT ADDRESS: Department of Marine Science, The University of Texas at Austin, Port Aransas, Texas 78373-1267.