**Abstract**–We examined stomach contents of 385 bonefish that ranged in length from 228 to 702 mm FL. Relatively few prey species made up most of the diet by weight—xanthid crabs (29.9%), gulf toadfish, *Opsanus beta* (17.2%), portunid crabs (10.9%), alpheid shrimp (9.2%), and penaeid shrimp (7.7%) together made up 74.9%. A variety of gastropods (17 families and 24 species) and bivalves (9 families and 16 species) were eaten, but gastropods made up only 2.7% of the diet by weight and bivalves made up only 2.5%. Polychaetes, represented by at least seven families, were important in the diet numerically (37.1%) but made up little of the diet by weight (1.4%). Cluster analysis and ordination of stomach contents permitted bonefish to be grouped according to length. Large bonefish (>439 mm FL) ate more xanthid crabs, alpheid shrimp, *Callinectes* spp., and *O. beta* than did small bonefish; penaeid shrimp were more important in the diet of small bonefish (<440 mm FL). The stomach contents of bonefish caught in Florida Bay were significantly different from those of bonefish caught on the ocean (Florida Straits) side of the Florida Keys, but the differences were slight and the same prey taxa dominated the diet in both areas. Xanthid crabs, alpheid shrimp, *O. beta*, penaeid shrimp, and *Callinectes* spp. together made up over 50% of the dissimilarity in diet of bonefish between the two areas. Some seasonal effects on diet were found, but variable sample sizes among seasons in the respective sampling areas made it difficult to detect seasonal trends. Bonefish fed selectively on some prey groups, but other common prey groups were not selected and were less common in stomachs than in the prey environment. The suite of epibenthic crustaceans and fishes found in bonefish stomachs was significantly different from that available as prey in the environment. Our results suggest that teleosts, mainly *O. beta*, are more important in the diet of bonefish than reported in previous studies.

# Feeding habits of bonefish, *Albula vulpes,* from the waters of the Florida Keys

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Bonefish, *Albula vulpes*, are the basis of an economically important recreational fishery in the Florida Keys and many parts of the Caribbean. In the Florida Keys, fishing for bonefish is a year-round activity and provides an important source of income to professional fishing guides. Most bonefish are caught in relatively shallow (<2 m) water over either seagrass or sandy bottom, and it is common for bonefish to forage in water less than 0.3 m deep, where their tails and dorsal fins can often be seen extending from the water as they feed on benthic and epibenthic prey. Bonefish are known for their wariness when approached in shallow water and for their strong fighting abilities when hooked. In Florida, the commercial sale of bonefish is prohibited, and regulations on the recreational fishery include a bag limit of one fish per angler per day and a minimum total length of 457 mm (390 mm fork length). Bonefish are not considered a food fish in Florida, and therefore most bonefish caught are released.

Crabtree et al. (1996, 1997) recently described the age, growth, and reproduction of bonefish from South Florida waters and found that bonefish can attain ages of 19 years. In the Florida Keys, 50% of male bonefish reach sexual maturity at 418 mm and an age of 3.6 years, and 50% of female bonefish reach sexual maturity at 488 mm FL and an age of 4.2 years. Bonefish gonadal activity in the Florida Keys is seasonal and spawning occurs during November–May.

Feeding habits of bonefish have been studied by Warmke and Erdman (1963) in Puerto Rico, by Bruger (1974) in the Florida Keys, and by Colton and Alevizon (1983) in the Bahamas; however, none of these studies have adequately described the diet of bonefish. Warmke and Erdman (1963) identified only mollusks, Bruger (1974) presented frequency of occurrence data for crustaceans but did not quantify noncrustacean prey, and Colton and Alevizon (1983) sorted prey into 10 broad taxonomic categories but did not quantify the abundance of each prey species. Consequently, the relative importance of each prey species in the diet of bonefish is unknown. This information is needed to evaluate the effects of habitat changes on Keys bonefish populations and is particularly important considering the recent seagrass die-offs that have been documented in Florida Bay (Robblee et al., 1991; Carlson et al., 1994; Durako, 1994; Butler et al., 1995; Matheson et al.[1]). If changes in the benthic epifauna and infauna

have resulted from the seagrass die-off, these changes could potentially affect both feeding and occurrence of bonefish in Florida Bay. In this article, we describe the feeding habits of bonefish from waters off the Florida Keys. We consider both length-related and seasonal changes in bonefish diet. In addition, we compare the diets of bonefish collected from two important Keys areas: Florida Bay (including parts of Everglades National Park and adjacent waters) and ocean-side (Florida Straits) fishing areas off the Florida Keys.

## Methods

### Collections

We examined stomach contents of 385 bonefish collected from South Florida waters from December 1991 to April 1995. Most of these bonefish were caught with hook-and-line gear in waters off the Florida Keys, Florida Bay, and Biscayne Bay during daylight hours either by biologists or by a single professional bonefish guide and his anglers. Supplemental collections of small bonefish (<425 mm FL, $n$=22) were made with seines and gill nets of various sizes in waters off the Florida Keys. Bonefish were placed on ice immediately after capture. Fork length (FL) was later measured to the nearest millimeter (mm), stomachs were removed, and the contents preserved in 10% buffered formalin. Contents of individual stomachs were sorted and identified to the lowest possible taxon. Fragments of prey organisms were counted as one, unless countable parts such as eye lenses were found. Weights of prey organisms were measured by blotting prey items on filter paper and weighing them on an analytical balance. The number of individuals of each food type as a percentage of the total number of identifiable prey items (percent numerical abundance, $N$), the percentage of stomachs containing prey in which a particular prey taxa occurred (frequency of occurrence, $F$), and wet weight as a percentage of the total weight of all prey items (percent weight, $W$) were determined. For the larger and more abundant prey taxa (alpheid shrimp, penaeid shrimp, portunid crabs, xanthid crabs, and *Opsanus beta*), we measured prey size to examine the relation between predator and prey size. We measured total length (TL, tip of the rostrum to tip of the uropod) of shrimp, carapace width of crabs, and standard length (SL) of *O. beta*.

[1] Matheson, R. E., D. A. Camp, S. M. Sogard, and K. A. Bjorgo. 1998. Changes in seagrass-associated fish and crustacean communities on Florida Bay mud banks: the effects of recent ecosystem changes? Manuscript in review.

We compared the abundance of prey found in bonefish stomachs with the abundance of benthic and epibenthic crustaceans and fishes from typical Florida Keys bonefish habitat. Information on the abundance of potential prey in Florida Bay is based on meter-square throw-trap collections by Matheson et al.[1] during 1994–96. We used data for Buchanan Bank ($n$=30 collections) in the Atlantic subenvironment as described by Zieman et al. (1989) and followed by Matheson et al.[1] The Atlantic subenvironment, and specifically the Buchanan Bank area sampled by Matheson et al.,[1] is an area where many of our Florida Bay bonefish were caught. Data on prey abundance from ocean-side (Florida Straits) areas of the Florida Keys are from 54 samples that we collected following the methods of Sogard et al. (1987) and Matheson et al.[1] with meter-square throw traps. Ocean-side samples were taken during September 1996 ($n$=14) and January 1997 ($n$=40) at various locations from the middle Keys north to Elliot Key. We sampled areas where we had previously caught bonefish and that appeared to be representative of typical ocean-side bonefish flats. Throw-trap samples were collected over a different time period (1994–97) than that for our bonefish specimens (1991–95), and we assumed for our comparisons that prey availability did not change over this time. If prey abundance changed during 1991–97, this change could have biased our comparisons.

### Data analysis

Nonparametric multivariate techniques were used to analyze feeding data. Similarity matrices were constructed with pairwise Bray-Curtis similarity coefficients (Bray and Curtis, 1957). Square-root-transformed, percent-standardized prey-weight data were used to generate similarities. Prey weight was used for all comparisons except feeding selectivity comparisons, because this measure more closely reflects the energetic importance of a prey species in the diet than does either frequency of occurrence or percent numerical abundance. Percent numerical abundance was used in feeding selectivity comparisons because we were interested in the relative abundance of prey in stomachs and in the environment. Hierarchical agglomerative cluster analysis that incorporated a group-average linking method was used to search for groups among bonefish stomach contents. A nonparametric ordination technique, nonmetric multidimensional scaling (MDS), was used to ordinate sites on the basis of the similarity matrix. The contribution of the various prey categories to the percentage similarity within groups and the differences among groups were estimated with a simi-

larities percentage (SIMPER) procedure (Clarke, 1993; Clarke and Warwick, 1994). All multivariate analyses were performed with Plymouth Routines in Marine Environmental Research (PRIMER) programs (copyright M. R. Carr and K. R. Clarke, Marine Biological Laboratory, Plymouth, UK; Clarke and Warwick, 1994).

Separate analyses were performed to compare stomach contents between various length groups of bonefish, between seasons, and between areas (Table 1). To detect length-related differences in feeding, we pooled bonefish into 20-mm length intervals and used cluster and MDS analyses to compare stomach contents. Stomach contents of all 20-mm length groups within the 480- to 699-mm length range had a level of similarity >55%, so we restricted all other com-

parisons to this length group in order to minimize length-related dietary shifts that could have confounded comparisons of areas and seasons. We compared stomach contents of bonefish from two areas, Florida Bay and the ocean (Florida Straits) side of the Keys, using the analysis of similarity (ANOSIM) permutation test (Clarke, 1993; Clarke and Warwick, 1994). We did not include the lower Keys or Biscayne Bay in our area comparisons because we examined relatively few bonefish stomachs from these two areas. Bonefish move seasonally between Florida Bay and ocean-side areas; thus for any given month sample sizes were rarely the same for the two areas. To reduce confounding from seasonal effects that could result from unequal seasonal representation of the two areas, we eliminated some stomachs from our analysis to achieve equal monthly sample sizes for the two areas for each month. We pooled samples from all years, totaled the number of samples by month for each area, and then randomly eliminated stomachs for each month from the area with the greatest sample size so that, for any given month, both areas had equal sample sizes. The resulting sample of 50 stomachs from each area contained equal sample sizes from both areas for each month, but the total sample size varied from month to month (Table 1). To detect seasonal dietary shifts, collections were pooled into four seasonal groupings: January–March, April–June, July–September, and October–December. We used ANOSIM to make seasonal comparisons of the diets of bonefish separately for the two principal sampling areas. Six pairwise comparisons were made among seasons for each area. No adjustment of significance levels exists for ANOSIM to account for the increased possibility of type-1 error associated with multiple comparisons (Clarke and Warwick, 1994).

To determine feeding selectivity, we used ANOSIM to compare the species of crustaceans and fishes found in the stomachs of bonefish 480–699 mm long to those found in samples collected in the potential-prey environment. We included only bonefish collected during the same seasons as those when the throw-trap collections were made. For Florida Bay comparisons, bonefish collected during March, May, June, and September were included; for ocean-side comparisons, bonefish collected during January, February, August, September, and October were included (Table 1). Significant differences in the suite of crustaceans and fishes found in bonefish stomachs and the potential prey available in the environment would imply selective feeding. We used SIMPER to indicate the percentage of dissimilarity contributed by each prey species and thus show which prey were selected or not selected. Taxa that were not selected

**Table 1**

Sample sizes, and collection months and years for data included in ANOSIM comparisons. Numbers in parentheses are the number of samples collected during a particular month. Bonefish, *Albula vulpes*, fork lengths for all comparisons ranged from 480 to 699 mm.

| Comparison | n | Months | Years |
|---|---|---|---|
| Area | | | |
| Florida Bay | 50 | Jan (5), Feb (3), Mar (2), Apr (5), May (7), Jun (1), Jul (4), Aug (4), Sep (3), Oct (6), Nov (7), Dec (3) | 1991–1995 |
| Ocean side | 50 | same monthly sample sizes as Florida Bay | 1991–1995 |
| Season | | | |
| Ocean side | | | 1991–1995 |
| Jan–Mar | 39 | | |
| Apr–Jun | 43 | | |
| Jul–Sep | 6 | | |
| Oct–Dec | 33 | | |
| Florida Bay | | | 1991–1995 |
| Jan–Mar | 8 | | |
| Apr–Jun | 25 | | |
| Jul–Sep | 70 | | |
| Oct–Dec | 18 | | |
| Stomach throw trap | | | |
| Ocean side | | | |
| Stomachs | 39 | Jan. (7), Feb (13), Aug (4), Sept (3), Oct (12) | 1991–1995 |
| Throw traps | 54 | Jan (40), Sep (14) | 1996–1997 |
| Florida Bay | | | |
| Stomachs | 45 | Mar (2), May (9), Jun (10), Sep (24) | 1991–1995 |
| Throw traps | 30 | Mar (6), May (6), Jun (6), Sep (12) | 1994–1996 |

could have been avoided, not preferred, or only incidentally ingested by bonefish. Alternatively, taxa that were not selected could have been preferred, but were able to evade capture.
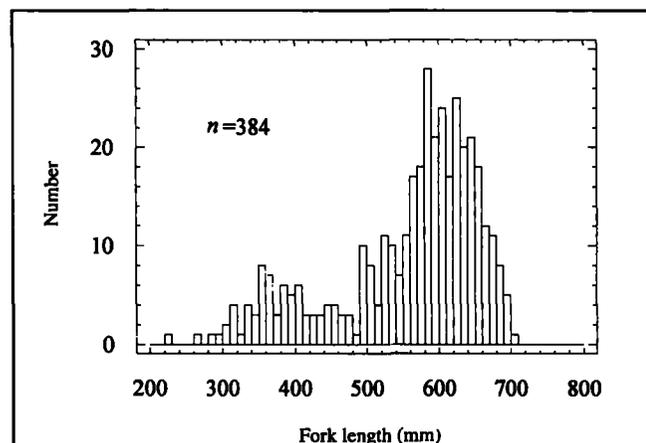
## Results

Stomachs of 385 bonefish that ranged in length from 228 to 702 mm contained prey (Fig. 1) consisting mostly of small benthic and epibenthic organisms (Table 2). Stomachs of 67 of the bonefish we examined were empty. Decapods and teleosts dominated the diet by weight, but gastropods and bivalves were among the most speciose prey categories. Relatively few prey species made up most of the diet by weight; xanthid crabs ($W$=29.9%), the gulf toadfish, *Opsanus beta* ($W$=17.2%), portunid crabs ($W$=10.9%), alpheid shrimp ($W$=9.2%), and penaeid shrimp ($W$=7.7%) together made up 74.9% of the diet. At least 17 families and 24 species of gastropods and 9 families and 16 species of bivalves were recognized, but gastropods made up only 2.7% of the diet by weight and bivalves made up only 2.5%. Polychaetes, represented by at least seven families, were important numerically ($N$=37.1%) but made up only 1.4% of the diet by weight.

Both the cluster analysis and the MDS ordination grouped bonefish stomach contents according to fish length (Fig. 2). Cluster analysis organized the 23 length groups into two principal clusters that were linked at a level of similarity greater than 20% and one outlying group of bonefish 280–299 mm long (group 2) that was linked to the other clusters at a



**Figure 1**

Length-frequency distribution of 384 bonefish, *Albula vulpes*, whose stomachs contained recognizable prey. The tail of one of the 385 bonefish whose stomach contents were examined was eaten by a shark during capture, so that fish was not measured.

level of similarity less than 10%. One principal cluster contained bonefish 260 to 439 mm long, and a second principal cluster contained mostly larger fish 400 to 702 mm long. Bonefish in the 400–419 mm length interval (group 8) were classified with larger fish, and bonefish in the 420–439 mm length interval (group 9) were classified with smaller bonefish. In Table 3, stomach contents are summarized separately for small bonefish (<440 mm) and large bonefish (>439 mm) on the basis of cluster analysis, but we reassigned bonefish stomachs in the 400–419 mm length interval (group 8) into the <440 mm group to avoid any overlap in the table between lengths of small (<440 mm) and large (>439 mm) bonefish. In the SIMPER analysis (Table 4), bonefish stomachs were grouped according to the cluster analysis shown in Figure 2, and no groups were reassigned. Levels of similarity among stomach contents of the 20-mm length groups within the 260–439 mm cluster were less overall than the levels of similarity of stomach contents of the 20-mm length groups of bonefish in the 400–699 mm cluster. Stomach contents of bonefish length groups ranging from 480 to 699 mm had a high level of similarity (>55%) and were tightly grouped in the MDS; we chose this length group as the basis for all other statistical comparisons.

SIMPER analysis suggested that much of the dissimilarity between the two principal length clusters was due to xanthid crabs, penaeid shrimp, alpheid shrimp, and *O. beta* (Table 4). The large values of the ratios ($\delta_i$/SD($\delta_i$)) between the mean contribution ($\delta_i$) to the overall level of dissimilarity and the standard deviation (SD) of the $\delta_i$ values across all stomachs suggest that these taxa consistently contributed to the level of dissimilarity, and so they are probably reliable discriminating prey taxa characteristic of one or the other length clusters. Bonefish longer than 439 mm consumed more decapods (alpheid shrimp, xanthid crabs, and *Callinectes* spp.) and teleosts than smaller bonefish (Tables 3 and 4). The most striking difference was in the consumption of teleosts, principally *O. beta*, which was not eaten by bonefish shorter than 440 mm but made up 17.8% of the diet of bonefish longer than 439 mm. Penaeid shrimp made up a larger proportion of the diet of small bonefish ($W$=40.5) than large bonefish ($W$=6.7), but they were eaten by bonefish of all sizes. Portunid crabs were eaten in nearly equal amounts by both length groups of bonefish, but this finding is misleading because all the *Portunus* spp. eaten by small bonefish were eaten by a single individual collected in Florida Bay; thus the importance of portunid crabs in the diet of small bonefish is probably less than what is suggested in Table 3. No crabs of the genus *Callinectes* were eaten by small bonefish.

## Table 2

Food items found in stomachs of bonefish, *Albula vulpes*, caught in the waters of the Florida Keys (n=385). W = percent weight, F = percent frequency of occurrence, N = percent numerical abundance.

| Taxon and prey item | W | F | N | Taxon and prey item | W | F | N |
|---|---|---|---|---|---|---|---|
| Plant material | 0.6 | 34.5 | — | Olividae | | | |
| Algae | <0.1 | 0.5 | — | Unidentified Olividae | <0.1 | 0.8 | <0.1 |
| *Halimeda* | <0.1 | 8.1 | — | *Jaspidella jaspidea* | 0.2 | 8.3 | 0.7 |
| Unidentifiable seagrass | 0.1 | 8.1 | — | Marginellidae | | | |
| *Halodule* | <0.1 | 7.0 | — | Unidentified Marginellidae | <0.1 | 1.3 | <0.1 |
| *Syringodium* | <0.1 | 1.6 | — | *Prunum apicinum* | 0.3 | 8.1 | 1.7 |
| *Thalassia* | 0.3 | 19.2 | — | *Prunum* sp. | <0.1 | 1.3 | <0.1 |
| Annelida | | | | *Volvarina avena* | <0.1 | 1.6 | 0.1 |
| Total Polychaeta | 1.4 | 39.5 | 37.1 | Cystiscidae | | | |
| Unidentified Polychaeta | 0.2 | 6.8 | 1.7 | *Persicula catenata* | <0.1 | 1.6 | <0.1 |
| Amphinomidae | 0.3 | 1.3 | <0.1 | *Persicula pulcherrima* | <0.1 | 0.3 | <0.1 |
| Lumbrinereidae | | | | Conidae | | | |
| *Lumbrinereis* spp. | <0.1 | 0.8 | 0.7 | *Conus stearnsi* | <0.1 | 0.3 | <0.1 |
| Opheliidae | 0.7 | 30.1 | 33.0 | Bullidae | | | |
| Spionidae | <0.1 | 0.8 | 0.4 | *Bulla striata* | <0.1 | 2.3 | 0.7 |
| Orbiniidae | <0.1 | 1.3 | 0.9 | Nudibranchia | <0.1 | 0.3 | <0.1 |
| Capitellidae | | | | Total Bivalvia | 2.5 | 24.9 | 2.9 |
| Unidentified Capitellidae | <0.1 | 1.6 | 0.1 | Unidentified Bivalvia | 0.5 | 5.2 | 0.4 |
| *Dasybranchus* spp. | <0.1 | 0.5 | <0.1 | Mytilidae | | | |
| Sabellidae | <0.1 | 1.0 | 0.1 | *Brachidontes modiolus* | <0.1 | 0.5 | 0.3 |
| Mollusca | | | | Pteriidae | | | |
| Unidentified Mollusca | 1.6 | 15.6 | 0.8 | *Pinctada imbricata* | <0.1 | 0.5 | <0.1 |
| Total Gastropoda | 2.7 | 31.2 | 5.9 | Limidae | | | |
| Unidentified Gastropoda | 0.3 | 8.6 | 0.6 | *Limaria pellucida* | 0.1 | 3.9 | 0.6 |
| Acmaeidae | | | | Pectinidae | | | |
| Unidentified Acmaeidae | <0.1 | 0.3 | <0.1 | Unidentified Pectinidae | <0.1 | 0.8 | <0.1 |
| *Patelloida pustulata* | <0.1 | 0.3 | <0.1 | *Argopecten irradians* | 0.5 | 2.1 | 0.1 |
| Trochidae | | | | *Argopecten* spp. | <0.1 | 0.8 | <0.1 |
| *Tegula fasciata* | <0.1 | 0.3 | <0.1 | Lucinidae | | | |
| Turbinidae | | | | Unidentified Lucinidae | 0.2 | 1.6 | 0.1 |
| *Turbo castanea* | <0.1 | 0.3 | <0.1 | *Codakia orbicularis* | <0.1 | 0.3 | <0.1 |
| *Eulithidium affine* | <0.1 | 1.3 | 0.5 | *Codakia orbiculata* | <0.1 | 0.3 | <0.1 |
| Turritellidae | | | | Carditidae | | | |
| *Torcula acropora* | <0.1 | 0.3 | <0.1 | *Carditamera floridana* | <0.1 | 1.3 | <0.1 |
| Modulidae | | | | Cardiidae | | | |
| *Modulus modulus* | <0.1 | 1.8 | 0.1 | Unidentified Cardiidae | <0.1 | 0.5 | <0.1 |
| Cerithiidae | | | | *Americardia media* | <0.1 | 0.3 | <0.1 |
| Unidentified Cerithiidae | <0.1 | 1.0 | <0.1 | *Laevicardium mortoni* | <0.1 | 0.3 | <0.1 |
| *Cerithium eburneum* | <0.1 | 0.8 | <0.1 | *Trachycardium muricatum* | <0.1 | 0.3 | <0.1 |
| *Cerithium muscarum* | <0.1 | 0.5 | <0.1 | Tellinidae | | | |
| Triviidae | | | | Unidentified Tellinidae | <0.1 | 1.0 | <0.1 |
| *Trivia quadripunctata* | <0.1 | 0.5 | <0.1 | *Strigilla carnaria* | <0.1 | 0.3 | <0.1 |
| Naticidae | | | | *Tellina fausta* | <0.1 | 0.3 | 0.1 |
| *Natica canrena* | <0.1 | 0.8 | <0.1 | *Tellina similis* | <0.1 | 3.9 | 0.3 |
| Columbellidae | | | | *Tellina tampaensis* | <0.1 | 0.5 | 0.1 |
| Unidentified Columbellidae | <0.1 | 0.3 | <0.1 | *Tellina* spp. | <0.1 | 1.3 | <0.1 |
| *Anachis avara* | <0.1 | 1.0 | <0.1 | Veneridae | | | |
| *Columbella rusticoides* | <0.1 | 0.3 | <0.1 | *Chione cancellata* | 0.6 | 6.5 | 0.4 |
| *Zafrona taylorae* | <0.1 | 0.5 | <0.1 | *Transennella conradina* | <0.1 | 0.3 | <0.1 |
| Nassariidae | | | | Crustacea | | | |
| *Nassarius* sp. | <0.1 | 0.3 | <0.1 | Unidentified Crustacea | <0.1 | 1.6 | <0.1 |
| Fasciolariidae | | | | Copepoda | <0.1 | 0.3 | <0.1 |
| *Leucozonia nassa* | <0.1 | 0.3 | <0.1 | Total Stomatopoda | 2.0 | 10.9 | 1.0 |
| *Fasciolaria tulipa* | 1.5 | 6.8 | 0.6 | Unidentified Stomatopoda | 1.0 | 5.7 | 0.6 |
| *Fasciolaria* spp. | <0.1 | 0.5 | <0.1 | *Pseudosquilla ciliata* | 1.0 | 5.2 | 0.3 |

There was a significant positive correlation between prey size and bonefish length for xanthid crabs ($n$=286, $r$=0.262, $P$<0.001) and portunid crabs ($n$=58, $r$=0.465, $P$<0.001), but not for alpheid shrimp ($P$=0.630), penaeid shrimp ($P$=0.063), or *O. beta* ($P$=0.782). The largest prey consumed were *O. beta* (largest 113 mm SL), the portunid crab *Callinectes sapidus* (largest 106 mm carapace width), and penaeid shrimp (largest 100 mm TL; Fig. 3). Most of these relatively large animals were consumed only as juveniles by bonefish.

The stomach contents of bonefish caught in Florida Bay were significantly different from those of bonefish caught on the ocean side of the Keys (ANOSIM, $R$=0.034; $P$=0.013). The statistic $R$ can range from −1 to 1 with a value of 1 indicating that all replicates within a sample are more similar to each other than to any replicates from the other samples and with a value of 0 indicating that the similarities between and within samples are on average equal (Clarke and Warwick, 1994). Although the $R$ value of 0.034 was

## Table 2 (continued)

| Taxon and prey item | W | F | N | Taxon and prey item | W | F | N |
|---|---|---|---|---|---|---|---|
| Total Decapoda | 67.8 | 88.6 | 42.1 | Echinodermata | | | |
| Unidentified Dendrobranchiata | 0.2 | 8.3 | 0.9 | Ophiuroidea | 0.5 | 1.8 | 1.0 |
| Penaeidae | | | | Holothuroidea | 0.5 | 2.9 | 0.2 |
| Unidentified Penaeidae | 0.9 | 4.9 | 1.2 | Ascidiacea | <0.1 | 0.3 | <0.1 |
| *Penaeus* spp. | 3.8 | 17.9 | 2.9 | Chordata | | | |
| *Penaeus duorarum* | 3.0 | 5.5 | 1.1 | Total Teleostei | 20.5 | 44.9 | 4.9 |
| Palaemonidae | | | | Unidentified teleostei | 0.5 | 10.1 | 0.6 |
| Unidentified Palaemonidae | <0.1 | 8.6 | 1.1 | Ophicthidae | | | |
| *Brachycarpus biunguiculatus* | <0.1 | 0.8 | <0.1 | Unidentified Ophicthidae | 0.2 | 1.3 | 0.1 |
| Alpheidae | | | | *Ahlia egmontis* | 0.7 | 2.9 | 0.2 |
| Unidentified Alpheidae | 0.9 | 9.4 | 1.8 | *Myrophis punctatus* | 0.7 | 2.6 | 0.1 |
| *Alpheus floridanus* | <0.1 | 1.0 | <0.1 | Engraulidae | | | |
| *Alpheus normanni* | 7.6 | 35.3 | 13.2 | Unidentified Engraulidae | <0.1 | 0.3 | <0.1 |
| *Alpheus* spp. | 0.6 | 6.8 | 0.9 | *Anchoa* sp. | <0.1 | 0.3 | <0.1 |
| Hippolytidae | | | | Batrachoididae | | | |
| Unidentified Hippolytidae | 0.1 | 4.7 | 1.2 | *Opsanus beta* | 17.2 | 29.1 | 3.1 |
| *Thor* spp. | 0.3 | 19.7 | 5.6 | Bythitidae | | | |
| *Tozeuma* spp. | <0.1 | 0.5 | <0.1 | *Ogilbia cayorum* | <0.1 | 0.8 | <0.1 |
| Palinuridae | | | | Cyprinodontidae | | | |
| *Panulirus argus* | 0.6 | 0.5 | <0.1 | *Floridichthys carpio* | <0.1 | 0.3 | <0.1 |
| Unidentified Brachyura | 3.8 | 17.7 | 1.0 | *Lucania parva* | <0.1 | 1.0 | <0.1 |
| Majidae | | | | Syngnathidae | | | |
| Unidentified Majidae | 3.0 | 6.2 | 0.6 | Unidentified Syngnathidae | <0.1 | 1.6 | <0.1 |
| *Pitho mirabilis* | 0.2 | 0.3 | <0.1 | *Hippocampus zosterae* | <0.1 | 0.3 | <0.1 |
| *Pitho* spp. | 0.7 | 2.3 | 0.2 | *Hippocampus* sp. | <0.1 | 0.3 | <0.1 |
| Portunidae | | | | *Syngnathus floridae* | <0.1 | 0.5 | <0.1 |
| Unidentified Portunidae | 2.9 | 8.1 | 0.6 | *Syngnathus scovelli* | <0.1 | 0.3 | <0.1 |
| *Callinectes ornatus* | 1.3 | 1.0 | 0.2 | *Syngnathus* spp. | 0.1 | 1.6 | 0.1 |
| *Callinectes sapidus* | 2.5 | 1.8 | 0.2 | Lutjanidae | | | |
| *Callinectes* spp. | 3.1 | 7.0 | 0.5 | *Lutjanus griseus* | 0.1 | 0.3 | <0.1 |
| *Portunus* spp. | 1.1 | 1.0 | 0.5 | Scaridae | 0.2 | 0.8 | <0.11 |
| Xanthidae | | | | Gobiidae | | | |
| Unidentified Xanthidae | 29.9 | 49.6 | 8.2 | Unidentified Gobiidae | <0.1 | 1.3 | <0.1 |
| *Neopanope* sp. | <0.1 | 0.3 | <0.1 | *Gobiosoma robustum* | <0.1 | 0.3 | <0.1 |
| *Panopeus* spp. | 0.1 | 0.8 | 0.1 | Balistidae | | | |
| Grapsidae | | | | *Monacanthus ciliatus* | <0.1 | 0.3 | <0.1 |
| Unidentified Grapsidae | <0.1 | 1.0 | 0.1 | *Monacanthus hispidus* | 0.2 | 0.8 | <0.1 |
| *Sesarma* sp. | <0.1 | 0.3 | <0.1 | Ostraciidae | | | |
| Palicidae | | | | *Lactophrys* sp. | 0.1 | 0.3 | <0.1 |
| Unidentified Palicidae | <0.1 | 0.3 | <0.1 | Miscellaneous material | — | 28.1 | — |
| Mysidae | <0.1 | 0.5 | <0.1 | Nonfood material | | | |
| Tanaidacea | <0.1 | 2.9 | 4.0 | sandy debris | — | 1.8 | — |
| Isopoda | <0.1 | 0.3 | <0.1 | coral rock | — | 0.3 | — |

significantly different from zero, the difference was small and thus the differences between the stomach contents of Florida Bay and ocean-side bonefish were probably slight. Xanthid crabs, alpheid shrimp, *O. beta*, penaeid shrimp, and *Callinectes* spp. together made up over 50% of the dissimilarity between the two areas (Table 5). Although these taxa contributed to the overall level of dissimilarity, the ratios ($\delta_i$/ SD($\delta_i$)) between the mean contribution ($\delta_i$) to the overall level of dissimilarity and the standard deviation of the $\delta$ values across all stomachs were low for each prey taxa. Thus, these taxa did not consistently contribute to the level of dissimilarity, and are probably not reliable discriminating prey taxa characteristic of either area. In both areas, the same prey taxa dominated the diet (Table 6).

A seasonal effect on feeding was found for ocean-side bonefish (ANOSIM, $R$=0.069; $P$=0.002) but not for bonefish collected from Florida Bay (ANOSIM, $R$=0.066; $P$=0.080). For both tests, the $R$ values were close enough to zero to suggest that any seasonal differences in diet were slight. On the ocean side of the Keys, pairwise tests between bonefish caught during January–March and those caught during all other seasons were significant at $P$<0.05; no other pairwise seasonal comparisons were significant. Xanthid crabs, alpheid shrimp, brachyuran crabs (excluding xanthids, portunids, and majids), *O. beta*, penaeid shrimp, and stomatopods accounted for most of the dissimilarity between stomach contents of bonefish collected during January–March and those of bonefish collected during other seasons (Table 7). The ratios ($\delta_i$/SD($\delta_i$)) between the mean contribution ($\delta_i$) to the overall level of dissimilarity and the standard deviation of the values across all stomachs were low for each prey taxa. No taxa consistently contributed to the level of dissimilarity, and there were no reliable discriminating prey taxa characteristic of any particular season. Variable sample sizes between seasons in both areas reduced the power of our seasonal comparisons; most ocean-side bonefish were caught during January–May, and most Florida Bay bonefish were caught during June–December. Only six stomachs were examined from ocean-side bonefish captured during July–September. Although the stomach contents of these six bone-
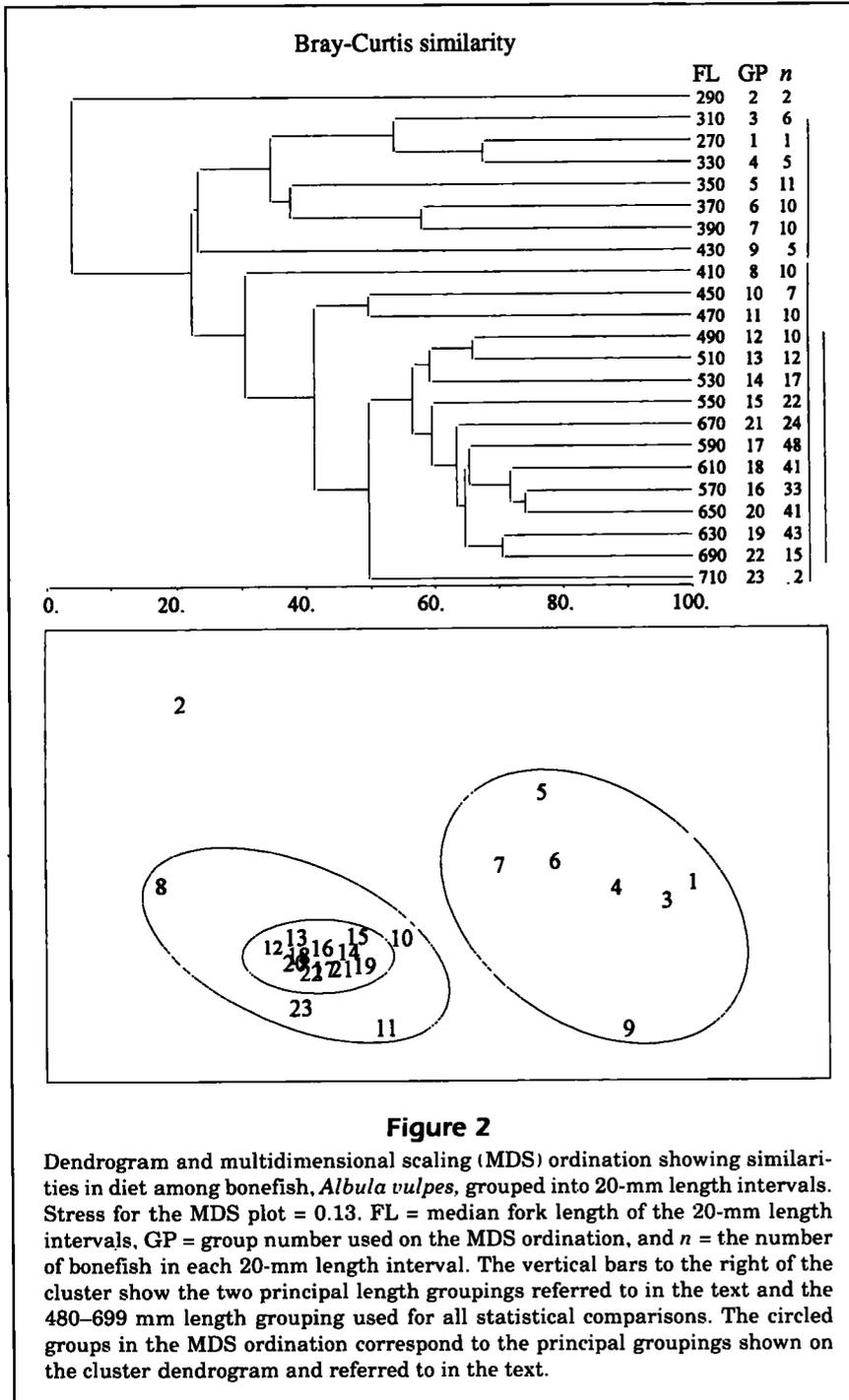


**Figure 2**

Dendrogram and multidimensional scaling (MDS) ordination showing similarities in diet among bonefish, *Albula vulpes*, grouped into 20-mm length intervals. Stress for the MDS plot = 0.13. FL = median fork length of the 20-mm length intervals, GP = group number used on the MDS ordination, and $n$ = the number of bonefish in each 20-mm length interval. The vertical bars to the right of the cluster show the two principal length groupings referred to in the text and the 480–699 mm length grouping used for all statistical comparisons. The circled groups in the MDS ordination correspond to the principal groupings shown on the cluster dendrogram and referred to in the text.

**Table 3**

Food items found in stomachs of bonefish, *Albula vulpes*, caught in the waters of the Florida Keys (n=384) by bonefish length interval. W = percent weight, F = percent frequency of occurrence, N = percent numerical abundance.

| Taxon and prey item | <440 mm FL (n=611) | | | >439 mm FL (n=323) | | |
|---|---|---|---|---|---|---|
| | W | F | N | W | F | N |
| Annelida | | | | | | |
| Polychaeta | 3.06 | 19.67 | 9.54 | 1.34 | 43.34 | 40.08 |
| Mollusca | | | | | | |
| Unidentified Mollusca | 2.29 | 19.67 | 1.82 | 1.56 | 14.24 | 0.67 |
| Gastropoda | 4.99 | 21.31 | 13.18 | 2.53 | 32.82 | 5.07 |
| Bivalvia | 4.64 | 22.95 | 3.51 | 2.39 | 25.70 | 2.81 |
| Crustacea | | | | | | |
| Stomatopoda | 2.26 | 3.28 | 2.52 | 2.03 | 12.38 | 0.79 |
| Decapoda | | | | | | |
| Penaeidae | 40.45 | 36.07 | 11.50 | 6.68 | 26.01 | 4.37 |
| Alpheidae | 0.35 | 8.20 | 1.12 | 9.36 | 51.70 | 17.52 |
| Hippolytidae | 1.87 | 11.48 | 7.99 | 0.33 | 26.01 | 6.76 |
| Majidae | 3.28 | 8.20 | 0.70 | 3.92 | 8.98 | 0.89 |
| Portunidae | 15.64 | 8.20 | 3.37 | 10.91 | 19.50 | 1.83 |
| Xanthidae | 7.43 | 13.11 | 1.68 | 31.49 | 56.97 | 8.94 |
| Chordata | | | | | | |
| Teleostei | 3.90 | 19.67 | 3.09 | 21.10 | 49.54 | 5.07 |
| Batrachoididae | | | | | | |
| *Opsanus beta* | 0.00 | 0.00 | 0.00 | 17.83 | 34.67 | 3.43 |

fish were significantly different from those of bonefish collected in January–March (ANOSIM, R=0.284, P=0.018), we have little confidence in this test because of the small sample size, and these results are not included in Table 7.

Bonefish fed selectively on some prey groups but did not select others. The suite of epibenthic crustaceans and fishes found in bonefish stomachs was significantly different from that collected with throw traps both on the ocean side of the Florida Keys (ANOSIM, R=0.261, P<0.001) and in Florida Bay (ANOSIM, R=0.419, P<0.001). Bonefish on the ocean side of the Florida Keys fed selectively on alpheid shrimp, xanthid crabs, *P. duorarum*, and *O. beta*, whereas they did not select the small but abundant crustaceans *Thor* spp. and *Periclimenes americanus* (Table 8). Similarly, Florida Bay bonefish fed selectively on xanthid crabs, alpheid shrimp, *O. beta*, *P. duorarum*, and *Callinectes* spp. but did not select the abundant but small crustaceans *Thor* spp., *Hippolyte zostericola*, and *P. americanus*, as well as the abundant goby *Gobiosoma robustum* (Table 9).

## Discussion

A variety of factors could have biased our description of the diet of bonefish. Some prey, particularly soft-bodied prey, may have been digested more rapidly than others with bony or chitinous skeletons. Consequently, we may have underestimated the importance of soft-bodied organisms such as polychaetes. Furthermore, bonefish have massive pharyngeal tooth plates capable of crushing shells and other hard structures. If bonefish are able to expel the crushed shells of mollusks and swallow only the soft-bodied organism, then we could have underestimated the importance of mollusks. This might explain why mollusks were relatively unimportant in our samples. Our sample consisted principally of bonefish caught with hook-and-line gear; therefore most of the fish we examined were probably actively foraging or they would not have consumed the bait presented by anglers. We do not believe that the number of fish with empty guts in our sample reflects the number of fish in the area that were not feeding, therefore we did not attempt to evaluate temporal feeding patterns. We cannot eliminate the possibility that some bonefish regurgitated prey during capture trauma; if some prey taxa were more likely to be regurgitated than others, this could have biased our results. Most of the bonefish in our sample came from relatively shallow (<2 m) grass, sand, or hard-bottom flats, but because the fish were caught by anglers, we did not have corresponding data on bottom type for each fish. Colton and Alevizon (1983) found differences in the

**Table 4**

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent weight) of bonefish, *Albula vulpes*, from the two principal clusters shown in Figure 2. Small bonefish ranged from 260 to 439 mm FL and large bonefish ranged from 400 to 699 mm FL. Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the two bonefish length groups. $\delta_i$ is the mean contribution of the *i*th species to the dissimilarity between the two groups, $\delta_i/$ $SD(\delta_i)$ is the ratio between the mean contribution of the *i*th species $(\delta_i)$ and the standard deviation of the values for that species $[SD(\delta_i)]$, $\delta_i\%$ is the contribution to the total dissimilarity scaled as a percentage, and Cum $\delta_i\%$ is the cumulative contribution to the total dissimilarity scaled as a percentage. Taxa that are likely to be reliable discriminators of the two length groups are indicated by ** in the $\delta_i/SD(\delta_i)$ column. Taxa proportionally more important in the diet of large bonefish than small bonefish are shown in bold type.

| Species | $\delta_i$ | $\delta_i/SD(\delta_i)$ | $\delta_i\%$ | Cum $\delta_i\%$ |
|---|---|---|---|---|
| Penaeidae | 8.13 | 1.94** | 10.47 | 10.47 |
| **Xanthidae** | 7.97 | 2.48** | 10.26 | 20.73 |
| **Alpheidae** | 5.29 | 1.84** | 6.81 | 27.54 |
| ***O. beta*** | 5.28 | 1.84** | 6.80 | 34.34 |
| **Portunidae** (unidentified) | 4.62 | 1.26 | 5.95 | 40.29 |
| Brachyura[1] | 3.68 | 1.37 | 4.73 | 45.02 |
| Majidae | 3.25 | 1.05 | 4.19 | 49.21 |
| *Portunus* spp. | 2.80 | 0.45 | 3.60 | 52.81 |
| Stomatopoda | 2.51 | 1.16 | 3.23 | 56.03 |
| ***Callinectes* spp.** | 2.50 | 0.97 | 3.23 | 59.26 |

[1] Excluding xanthids, portunids, and majids.

**Table 5**

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent weight) of bonefish, *Albula vulpes* (480–699 mm FL), caught on the ocean side of the Florida Keys (n=50) and in Florida Bay (n=50). Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the two study areas. Taxa proportionally more important in the diet of ocean-side bonefish than Florida Bay bonefish are shown in bold type. The low values of $\delta_i/SD(\delta_i)$ suggest that the data were variable and that no taxa were reliable discriminators of either area. Symbols are explained in the legend of Table 4.

| Species | $\delta_i$ | $\delta_i/SD(\delta_i)$ | $\delta_i\%$ | Cum $\delta_i\%$ |
|---|---|---|---|---|
| **Xanthidae** | 13.47 | 1.15 | 17.17 | 17.17 |
| **Alpheidae** | 8.56 | 1.06 | 10.91 | 28.08 |
| ***O. beta*** | 8.04 | 0.82 | 10.24 | 38.32 |
| Penaeidae | 7.49 | 0.82 | 9.55 | 47.87 |
| *Callinectes* spp. | 4.53 | 0.46 | 5.78 | 53.65 |

stomach contents of Bahamian bonefish collected over different bottom types, and this variation probably also occurs in the Florida Keys. There was also no evidence that bonefish do not feed in deeper waters than those traditionally fished by anglers; prey availability and bonefish feeding may be quite different at greater depths than in the shallow waters we sampled.

Most (77%) of the fish in our sample were longer than 500 mm (Fig. 1); consequently, the diet of large bonefish is better described by our data than that of small bonefish. The inadequacy of our description of the diet of small bonefish is reflected in the low levels of similarity among 20-mm length intervals of bonefish smaller than 480 mm (Fig. 2). Many of the length intervals smaller than 500 mm contained few fish and resulted in greater variation in diet among length intervals and probably caused the lower levels of similarity among 20-mm length groups of small bonefish than among large fish.

The changes in diet as length of bonefish increased in general reflect the expansion of the diet to include
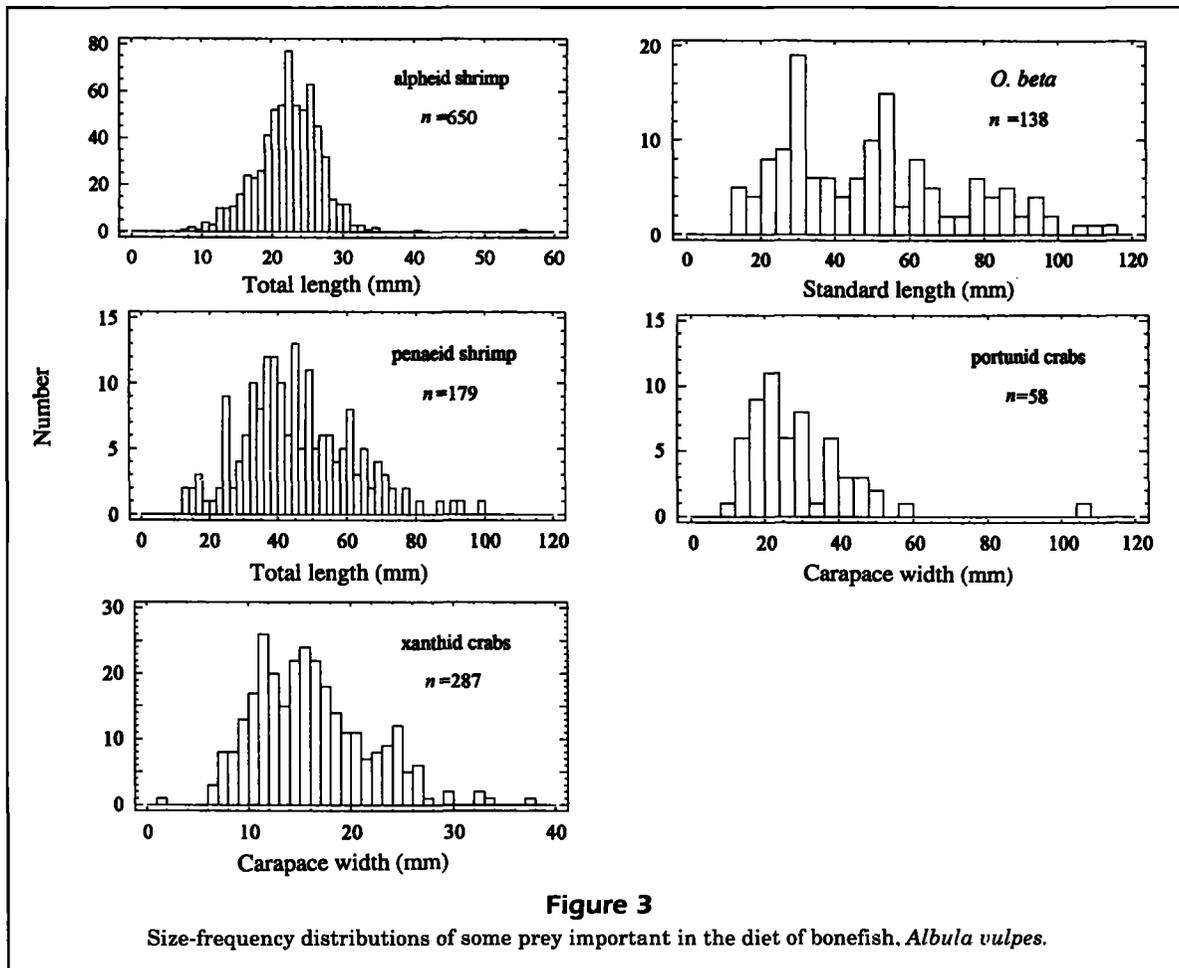
larger prey such as *O. beta* and crabs of the genus *Callinectes*. In some cases, for example xanthid and portunid crabs, prey size was positively correlated with predator length. In other cases, for example *O. beta*, prey were not eaten at all by small bonefish, and there was no correlation between prey size and predator length among large bonefish. Small but abundant crustaceans such as *Thor* spp., *H. zostericola*, and *P. americanus* were not important in the diet of the bonefish we examined. These small crustaceans may be eaten by smaller bonefish (<228 mm), but they are apparently outside of the size range of prey typically consumed by the size of bonefish we considered.

Bruger (1974) examined the stomachs of 129 bonefish ranging from 221 to 679 mm FL (reported as 210 to 656 mm SL) collected from the waters off the Keys and reported the frequency of occurrence of crustaceans in the diet. Of these 129 stomachs, 19 were empty. We recalculated his frequency of occurrences on the basis of only the number of stomachs with prey (n=110) to compare with our frequency data: the recalculated results were 85% crustaceans, 33% mollusks, and 17% teleosts. These results are in general agreement with our findings of 89% crustaceans, 51% mollusks, and 45% teleosts, except that our samples contained more teleosts than Bruger's. Among crustacean prey, Bruger's results resemble ours; penaeid shrimp, alpheid shrimp, portunid crabs, and xanthid crabs were the most frequently occurring crustacean prey. Although Bruger did not quantify by species the fishes found in stomachs, he did not include *O. beta* in his list of teleosts eaten by

**Figure 3**

Size-frequency distributions of some prey important in the diet of bonefish, *Albula vulpes*.

bonefish. In contrast, *O. beta* was the teleost most frequently eaten by the bonefish we examined (*F*=29.1%). Most of Bruger's bonefish were collected in the lower Keys between Marathon and Key West, but most of our bonefish were captured in the upper Keys from Marathon north to Key Biscayne and including Florida Bay. Although we have no data on prey availability in the lower Keys, habitat differences between the two study areas could account for some of the differences between our results and Bruger's.

Colton and Alevizon (1983) examined the stomach contents of 365 Bahamian bonefish ranging from 268 to 652 mm FL (reported as 256 to 630 mm SL). Bivalves made up 39.2% of the diet of Bahamian bonefish by dry weight, but they made up only 2.5% of the diet of Keys bonefish by weight. Bivalves were the most important prey of Bahamian bonefish both in terms of dry weight (39.2%) and frequency of occurrence (66.3%); portunid (*W*=20.1%; *F*=40.5%) and xanthid crabs (*W*=15.0%; *F*=24.8%) were also important. Teleosts (*O. beta* and *Bathygobius soporator*;

pooled *W*=4.9%), alpheid shrimp (*W*=4.6%), *Pseudosquilla ciliata* (*W*=3.2%), polychaetes (*W*=3.2%), gastropods (*W*=2.4%), and *Penaeus duorarum* (*W*=1.6%) occurred in 15–25% of the guts that Colton and Alevizon examined but made up little of the diet in terms of dry weight. The most notable difference between Keys and Bahamian bonefish diets was the greater importance of *O. beta* in the diet of Keys bonefish (*W*=17.2%).

Colton and Alevizon (1983) reported length-related changes in the diet of Bahamian bonefish that were similar to those that we observed in the Florida Keys. They found that bonefish larger than 416 mm FL (400 mm SL) ate more xanthid and majid crabs, alpheid shrimp, and teleosts than smaller bonefish did. Teleosts (gobiids, batrachoidids, ophichthids, and small lutjanids) were found principally in stomachs from bonefish larger than 575 mm FL (555 mm SL). In contrast to our conclusions, Colton and Alevizon (1983) found that small bonefish (<416 mm) ate more portunid crabs (*Callinectes ornatus*) than large bonefish did; we found no *Callinectes* spp. in any bone-

**Table 6**

Food items found in stomachs of bonefish, *Albula vulpes*, caught in Florida Bay (*n*=130) and on the ocean side (*n*=144) of the Florida Keys. Stomachs from all bonefish 480 to 699 mm FL collected during all months are included. W = percent weight; F = percent frequency of occurrence; N = percent numerical abundance.

| Taxon and prey item | Florida Bay | | | Ocean side | | |
|---|---|---|---|---|---|---|
| | W | F | N | W | F | N |
| Annelida | | | | | | |
| Polychaeta | 0.62 | 34.62 | 34.22 | 1.63 | 52.08 | 32.72 |
| Mollusca | | | | | | |
| Gastropoda | 1.86 | 33.85 | 4.94 | 2.83 | 32.64 | 3.52 |
| Bivalvia | 2.68 | 28.46 | 3.00 | 2.02 | 24.13 | 1.85 |
| Crustacea | | | | | | |
| Stomatopoda | 0.35 | 3.85 | 0.24 | 3.85 | 19.44 | 0.73 |
| Decapoda | | | | | | |
| Penaeidae | 8.30 | 35.38 | 6.72 | 4.30 | 15.97 | 1.35 |
| Alpheidae | 5.13 | 40.77 | 11.93 | 14.12 | 60.42 | 13.16 |
| Hippolytidae | 0.38 | 32.31 | 11.38 | 0.33 | 23.61 | 2.81 |
| Majidae | 1.97 | 4.62 | 0.28 | 4.45 | 9.72 | 0.67 |
| Portunidae | 17.06 | 23.85 | 2.96 | 5.00 | 14.58 | 0.60 |
| Xanthidae | 33.53 | 63.08 | 10.94 | 27.78 | 52.78 | 4.64 |
| Chordata | | | | | | |
| Teleostei | 21.25 | 56.92 | 7.43 | 24.87 | 43.75 | 2.31 |
| Batrachoididae | | | | | | |
| *Opsanus beta* | 18.94 | 48.46 | 5.85 | 19.87 | 25.00 | 1.19 |

**Table 7**

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent weight) of bonefish, *Albula vulpes* (480–699 mm FL), collected on the ocean side of the Florida Keys during January–March (*n*=39), April–June (*n*=43), and October–December (*n*=33). Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the seasonal samples. Taxa proportionally more important in the diet of bonefish collected during January–March than during other seasons are shown with bold type. The low values of $\delta_i/SD(\delta_i)$ suggest that the data were variable and that no taxa were reliable discriminators of any particular season. Symbols are explained in the legend of Table 4.

| Species | $\delta_i$ | $\delta_i/SD(\delta_i)$ | $\delta_i$ % | Cum $\delta_i$ % |
|---|---|---|---|---|
| Jan–Mar vs. Apr–Jun | | | | |
| Xanthidae | 12.44 | 1.16 | 16.02 | 16.02 |
| **Alpheidae** | 11.77 | 1.28 | 15.16 | 31.18 |
| **Brachyura**[1] | 6.71 | 0.69 | 8.64 | 39.81 |
| *O. beta* | 5.41 | 0.62 | 6.97 | 46.78 |
| Stomatopoda | 5.18 | 0.64 | 6.67 | 53.45 |
| Jan–Mar vs. Oct–Dec | | | | |
| **Alpheidae** | 11.52 | 1.27 | 14.52 | 14.52 |
| Xanthidae | 10.99 | 0.99 | 13.86 | 28.38 |
| **Brachyura**[1] | 7.26 | 0.75 | 9.16 | 37.54 |
| Penaeidae | 4.97 | 0.76 | 6.27 | 43.81 |
| *O. beta* | 4.90 | 0.56 | 6.18 | 50.00 |

[1] Excluding xanthids, portunids, and majids.

fish smaller than 440 mm, although crabs of the genus *Portunus* were eaten in large numbers by one 435-mm bonefish.

There was evidence of a seasonal effect on diet, but small sample sizes during some seasons in each of the respective sampling areas reduced our ability to detect significant differences. Colton and Alevizon (1983) also found seasonal differences in feeding in Bahamian bonefish. Bivalves were eaten more during the summer by bonefish of all lengths, whereas small bonefish (<416 mm) ate more portunid crabs during the winter. They also noted habitat-related differences in bonefish feeding. Penaeid shrimp were eaten almost exclusively by bonefish caught over grassy bottom and not by those caught over sandy bottom. Bonefish caught over sandy bottom ate relatively more crabs and bivalves than did bonefish caught over grassy areas.

Warmke and Erdman (1963) examined the stomach contents of 56 bonefish ranging from 292 to 663 mm FL (reported as 0.75 to 10.25 pounds) from Puerto Rican waters and, like Colton and Alevizon (1983), found that mollusks were the most important prey. Stomachs of Puerto Rican bonefish contained 56% mollusks, 42% crustaceans, and 2% other prey types by volume. In contrast, we found that mollusks accounted for only about 7% of the diet of Keys bonefish by weight and that crustaceans accounted for about 70% of the diet. Teleosts were part of Warmke and Erdman's "other" classification and made up less than 2% of the diet in their study; in the Keys, teleosts made up over 20% of the diet by weight. Warmke and Erdman identified only mollusks to species. The most important mollusk they found was the bivalve *Codakia costata*, which occurred in 62% of the stomachs they examined. *Codakia orbicularis* and *C. orbiculata* occurred in stomachs from Keys bonefish but made up less than 1% of the diet by numbers or weight. *Codakia costata* was not found in Keys bonefish stomachs and was not reported to occur in Florida Bay by Turney and Perkins (1972).

There were slight but significant differences between the diets of bonefish from Florida Bay and those from the ocean side of the Keys. These differences may reflect differences in prey availability in the two areas, but overall the dominant prey eaten by bonefish was the same in the two areas. The fauna of Florida Bay has been characterized as Gulf-Carolinian in nature, whereas that of the Keys ocean side is Antillean (Sogard et al., 1987; Holmquist et al.,

## Table 8

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent number) of bonefish, *Albula vulpes* (480–699 mm FL), caught on the ocean side of the Florida Keys (*n*=39) and throw-trap samples (*n*=54) from the ocean side of the Florida Keys. Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the two samples. Taxa proportionally more important in the diet of bonefish than suggested by their proportional abundance in throw-trap samples are shown with bold type. The low values of $\delta_i$/SD($\delta_i$) suggest that the data were variable and that no taxa were reliable discriminators of either sample source. Symbols are explained in the legend of Table 4.

| Species | $\delta_i$ | $\delta_i$/SD($\delta_i$) | $\delta_i$ % | Cum $\delta_i$ % |
|---|---|---|---|---|
| **Alpheidae** | 10.58 | 1.31 | 13.87 | 13.87 |
| **Xanthidae** | 7.89 | 1.13 | 10.35 | 24.23 |
| *Periclimenes americanus* | 6.83 | 0.93 | 8.96 | 33.19 |
| *Thor* spp. | 6.11 | 0.97 | 8.02 | 41.20 |
| ***P. duorarum*** | 5.95 | 0.88 | 7.81 | 49.01 |
| ***O. beta*** | 4.61 | 0.80 | 6.05 | 55.06 |

## Table 9

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent number) of bonefish, *Albula vulpes* (480-699 mm FL), caught in Florida Bay (*n*=45) and throw-trap samples (*n*=30) from Florida Bay (Matheson et al.[1]). Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the two samples. Taxa that are likely to be reliable discriminators of the two samples are indicated by ** in the $\delta_i$/SD($\delta_i$) column. Taxa proportionally more important in the diet of bonefish than suggested by their proportional abundance in throw-trap samples are shown with bold type. Symbols are explained in the legend of Table 4.

| Species | $\delta_i$ | $\delta_i$/SD($\delta_i$) | $\delta_i$ % | Cum $\delta_i$ % |
|---|---|---|---|---|
| *Thor* spp. | 18.13 | 1.97** | 23.03 | 23.03 |
| **Xanthidae** | 9.63 | 1.17 | 12.24 | 35.27 |
| **Alpheidae** | 7.61 | 1.23 | 9.67 | 44.94 |
| ***O. beta*** | 7.51 | 1.15 | 9.55 | 54.49 |
| ***P. duorarum*** | 5.17 | 0.81 | 6.57 | 61.06 |
| *Hippolyte zostericola* | 5.00 | 1.65** | 6.36 | 67.42 |
| *Periclimenes americanus* | 4.55 | 1.85** | 5.78 | 73.20 |
| ***Callinectes* spp.** | 3.23 | 0.48 | 4.10 | 77.30 |
| *Gobiosoma robustum* | 3.03 | 1.98** | 3.85 | 81.15 |

1989a, 1989b). Our sampling effort was over a large and diverse area, and this limited our ability to resolve area-specific differences in bonefish diet. Some Florida Bay areas that we sampled were near passes leading to ocean-side flats and may have more closely resembled ocean-side areas than some of the more remote areas in Florida Bay where we occassionally caught bonefish. Larger sample sizes, more intensive sampling of specific areas along with site-specific descriptions of habitat types, and sampling of prey availability concurrent with bonefish collections are needed to better describe spatial variation in the diet of Keys bonefish.

Comparisons of the stomach contents of bonefish collected in Florida Bay and ocean-side areas as well as seasonal comparisons were complicated by the variable monthly sample sizes from the two areas. We excluded over half of the bonefish in our sample from our area comparisons because seasonal sample sizes from the two areas were greatly unequal. The variable sample sizes from the two areas reflect general seasonal trends in bonefish availability in the two areas. Bonefish are typically most abundant in Florida Bay during summer and fall. Winter cold fronts tend to reduce Florida Bay temperatures more than ocean-side temperatures (Hudson et al., 1976; Roberts et al., 1982; Chiappone, 1996), and many productive summer–fall fishing areas in Florida Bay rarely hold bonefish during winter and spring because bonefish move to ocean-side areas with more moderate temperatures and closer proximity to deep water. Thus, most of our Florida Bay bonefish were captured during summer and fall, and most ocean-side bonefish were caught during winter and spring.

Seagrass die-offs have recently been documented in Florida Bay (Robblee et al., 1991; Carlson et al., 1994; Durako, 1994; Butler et al., 1995). Anecdotal evidence suggests that changes in the Everglades ecosystem have caused a decline in the quality of fishing in Florida Bay and the waters of the Florida Keys (Chiappone and Sulka, 1996). If changes in the benthic epifauna and infauna have resulted from the seagrass die-off, these changes could potentially affect feeding and occurrence of bonefish in Florida Bay. Data on the species composition and abundance of epifaunal crustaceans and fishes collected subsequent to the sea grass die-off and the studies of Sogard et al. (1987, 1989) and Holmquist et al. (1989a, 1989b) prior to the seagrass die-off suggest little evidence of declines in populations of important bonefish prey species (Matheson et al.[1]). One significant change reported by Matheson et al.[1] was an increase in the abundance of *O. beta* in some areas of Florida Bay since the 1980s. Whether the increased abundance of *O. beta* compared to that found in previous studies accounts for its greater prominence in stomachs of the bonefish we sampled is unknown.

# Acknowledgments

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