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# Feeding Guilds Among Artificial-Reef Fishes in the Northern Gulf of Mexico

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To examine the diets of 25 demersal artificial-reef-associated fish species, 540 fishes were collected with spears and hand-nets off Panama City, Florida, in the summer of 1993. Fishes were preserved whole in the field. Stomach contents were later analyzed by frequency of occurrence, numerical abundance, and percent volume. These measures were combined into an Index of Relative Importance (IRI). The data set was then analyzed with cluster and detrended correspondence (DCA) analyses. Forage items of the reef fishes were dominated by fishes, xanthid crabs, unidentified items, squids, polychaetes, and penaeid shrimps. The DCA and cluster analysis revealed that these 25 artificial reef fishes could be organized into seven feeding guilds: lower structure pickers, ambush predators, lower structure crustacean predators, upper structure pickers, upper structure predators, water column pickers, and reef-associated open-water feeders. All of the demersal gamefish in this study were in the same feeding guild (i.e., reef-associated open-water feeders). Species in this feeding guild were associated with artificial reefs diurnally and foraged away from reefs nocturnally. Our data indicate that many important artificial-reef-associated fishes in the northern Gulf of Mexico obtain most of their energy foraging away from the artificial reef structure.

Artificial reefs attract and retain fish assemblages soon after deployment (Gascon and Miller, 1980; Brock and Norris, 1987; Bohnsack, 1991). Moreover, they have tremendous potential in the management of habitat-limited species (Polovina, 1991). However, the trophic habits and competitive interactions of artificial-reef fish assemblages have not been studied extensively. Most studies thus far have characteristically focused on only a few species (Bohnsack, 1991). Bailey-Brock (1989:580) described several possible feeding schemes for Hawaiian reef fish on an artificial reef; these include feeding, "...on the developing benthos, foraging over adjacent natural reefs, utilizing both feeding grounds, and some may use the reef solely for cover and forage some distance from the reef." Information on coral reef fishes indicates the importance of the soft-bottom communities surrounding reefs as a source of prey organisms (Jones et al., 1991). Bohnsack (1989) reported that fishes associated with artificial reefs feed both on organisms associated with the reef structure and on the surrounding benthic communities. Although studies of artificial-reef fish foraging have been conducted (Davis et al., 1982; Hueckel and Stayton, 1982; Steimle and Ogren, 1982; Hueckel and Buckley, 1987; Ambrose and Anderson, 1990), the results provide no clear paradigm. It is still unknown where most of the prey organisms for reef-associated predatory fishes originate.

Researchers studying both coral and artificial reef ecology have called for further examination of the trophic dynamics of reef fish assemblages (Bohnsack and Sutherland, 1985; Bohnsack, 1989; Jones et al., 1991). Researchers in other fields have found that studying functional groups of organisms can provide insights to food web dynamics. Utilization of the guild concept has been a useful approach under these circumstances. Austen et al. (1994) reviewed the importance of the guild concept in fisheries management and indicated that if statistically delineated guilds based on key resources (described as a "super species") were used, then guild management could be effective in managing fisheries stocks.

Root (1967) provided ecologists with a conceptual tool to examine how groups of organisms interact. He introduced the term "guild" to ecology and defined the term as a group of organisms that use the same resource in a similar manner. This term is not limited by taxonomic boundaries (Root, 1986). If, for example, two organisms being studied use the same food resources in a similar manner, they are considered members of the same feeding guild (Gerking, 1994). For the present investigation, a feeding guild will be considered as a portion of the reef fish assemblage that uses similar prey items without regard to feeding morphology. While guilds can be based on several factors or combinations of factors (diet, morphology, behavior, etc.) we have chosen to ex-

amine diet directly because literature reports are contradictory on the usefulness of measures such as feeding morphology in determining guild membership (e.g., Weins, 1977; Vitt and De Carache, 1995), especially in fishes (Zaret and Rand, 1971).

The present study was designed to examine the prey taxa of 25 of the most common demersal artificial-reef assemblage fishes in the northern Gulf of Mexico, compare the relative importance of various prey taxa in the diets of these reef fishes, determine the guild membership of these fishes, and comment on the partitioning of resources among them. The results of this study provide information on the diets of the most common artificial-reef assemblage fishes, preliminary data that will lead to an enhanced understanding of where artificial-reef assemblage fishes feed (which will, in turn, contribute information on the optimal spacing of artificial reefs), and a guild structure that can then be examined more directly by fish ecologists studying competition and resource partitioning.

## METHODS

Fishes were collected from artificial reefs composed of bridge rubble off Panama City, Florida (Fig. 1). The reefs were 2–5 km from shore and in shallow water (<22 m). Each reef site selected for this study had an established benthic community including hydroids, barnacles, and algae. Individuals of 25 resident demersal fish species were collected that represented common artificial-reef assemblage fishes in the northern Gulf of Mexico (Bortone et al., in prep.). However, the inclusion of a given fish species in this study was not necessarily due to its actual numerical abundance, but to the divers' ability to collect representatives of that species.

All fish collections were made by divers using SCUBA. Collections generally occurred in the morning hours (0700–1200 CDT) to take advantage of the nocturnal and crepuscular feeding habits predicted for diurnal reef inhabitants (Hobson, 1973). Because most fishes were being collected in the morning hours, digestion of stomach contents was expected to be minimal. Also, to minimize variation in food habits owing to seasonal differences, all fish were captured in July and August 1993. The primary collection technique was spear fishing with multipronged spears of various sizes. Hand-nets and small drop-nets were also used on a limited basis to collect fish. Several authors have identified these methods as the least

likely to bias the stomach contents by regurgitation or feeding during collection (Randall, 1967; Bowen, 1983; Helfman, 1983).

Once captured, fish were placed into mesh bags and retained by the divers for the duration of the dive (typically not more than 20 min). All fishes were chilled in an ice brine for 15–20 min to anesthetize them before fixation and to reduce the possibility of regurgitation. Fishes were subsequently fixed in 10% Formalin-seawater. Before immersion in the Formalin-seawater solution, however, larger fishes had their body cavities slit open to facilitate fixation and minimize digestion. After fixation for 7 d, samples were rinsed in tap water for 15 min to remove excess Formalin, and stored in 40% isopropyl alcohol.

In the laboratory, fishes were measured to the nearest 1.0 mm (fork length, FL) and weighed (whole body, wet weight) to the nearest 0.1 g. The gape (maximum distance between the jaws when forced open) of each fish was measured with calipers to the nearest 0.1 mm. The stomachs were then removed. For fishes without a distinct stomach (e.g., *Halichoeres bivittatus*) the first quarter of the gut was considered the stomach (Hueckel and Stayton, 1982). On removal, a stomach fullness index (SFI) was determined for each stomach (0–5 highest subjective score). The stomachs were stored in 40% isopropyl alcohol until identification and analysis could be completed. Stomachs without contents (SFI = 0) were noted but not retained.

The stomach contents for each fish species were removed and sorted into various taxa. Prey groups were then identified to the lowest practical taxon. Voucher specimens for each prey taxon were retained for identification. Bowen (1983) stated that in most studies of predator–prey interactions, order or family is a low enough taxon for prey identification and little information is gained by identifying to the species level. For each taxon, the number of food items was recorded. If the items were not whole, particular parts were counted to roughly estimate the number of organisms (e.g., eye stalks, claws, or opercula). If the item was not recognizable as an individual but could be identified as belonging to a particular taxon (e.g., sponges), the taxon was divided into bite sized clumps based on gape information, to estimate number of individuals.

Volume, percent frequency of occurrence, and numerical abundance were determined for each prey item. The taxa volumes were primarily determined by water displacement in a graduated cylinder to the nearest 0.1 ml. The
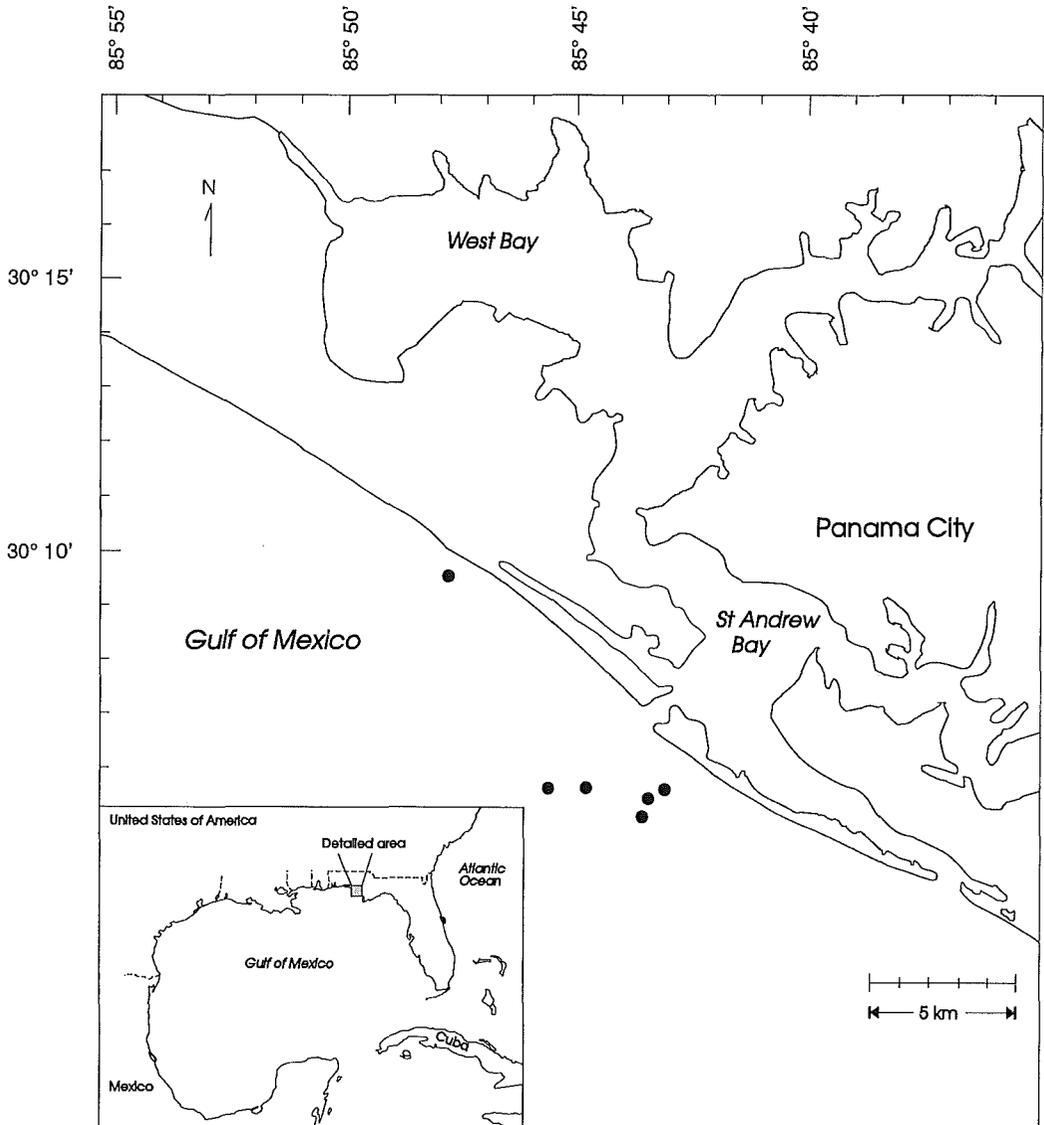
Fig. 1.    Map of the study area in the northern Gulf of Mexico. Filled circles indicate sample locations.

volume of a taxon was the total volume of wa- ter and prey items minus the volume of water delivered from a burette. For items such as eggs, volumes were calculated based on micro- scopic observations; the area covered by the eggs (on graph paper) was multiplied by the mean diameter of the eggs to give volume (Windell, 1971).

Frequency of occurrence (%O) was calculat- ed as the number of stomachs containing at least one food item of a group divided by the total number of fish examined per species (Bowen, 1983). Numerical abundance (%N) was calculated as the number of prey items per

taxa divided by the total number of prey items per stomach (Hyslop, 1980). The percent vol- ume (%V) was calculated as the percent, by volume, each item contributed to the total vol- ume of the stomach contents (Hyslop, 1980).

From the above information (i.e., %O, %N, and %V), an Index of Relative Importance (IRI) was calculated for each prey taxon for each species (Berg, 1979; Hyslop, 1980; Levy and Yesaki, 1982). The IRI was calculated as:

$$IRI = (\%V + \%N)\%O.$$

The IRI was used because each of the three calculated variables above have certain biases

that can be reduced by using this index (Hyslop, 1980). The IRIs for all prey taxa were averaged for each predatory fish species to provide a manageable data set. The percent IRI was calculated as the IRI value for that prey item divided by the sum of IRI values for all prey items of that species. This provided a data matrix appropriate for multivariate analyses.

For analysis, the fish species were considered operational taxonomic units (OTUs) and the prey taxa were considered characters ordinated by mean IRI values. The matrix was analyzed with two-way indicator species analysis (TWINSPAN; Hill, 1979a), detrended correspondence analysis (DCA) using DECORANA (Hill, 1979b), and cluster analysis using UPGMA (unweighted pair-group method, arithmetic averages) clustering on Bray-Curtis coefficients with NTSYS-pc software (Rohlf, 1989).

RESULTS

A total of 540 fish, representing 25 species, were collected for this study in July and August 1993 (Table 1). Two species were only represented by a single individual [*Epinephelus morio* (red grouper) and *Lachnolaimus maximus* (hogfish)]. Only one species was collected that had no stomach contents (*L. maximus*).

The prey of the artificial-reef assemblage fishes belonged to 44 taxa recognized in this study (Table 2). The food items belong to two algal divisions—Chlorophyta and Rhodophyta—and eight animal phyla—Porifera, Cnidaria, Annelida, Mollusca, Arthropoda, Ectoprocta, Echinodermata, and Chordata. Each algal division was represented by a single family (Cladophorales and Rhodomelaceae). The annelids in this study were all polychaetes. Three molluscan classes (bivalves, gastropods, and cephalopods) were found as prey items. The arthropods were most often represented by barnacles and decapods; the echinoderms were represented by two groups, brittle stars and sea urchins; and the chordates were dominated by nine fish families.

Sixteen of the 25 fish species had a dominant prey item (i.e., an IRI > 25; Table 2). Fishes were a preferred item by the two-spot cardinalfish, *Apogon pseudomaculatus* (50% of total IRI); tomtate, *Haemulon aurolineatum* (33.9%); gag, *Mycteroperca microlepis* (100%), grey snapper, *Lutjanus griseus* (79.2%); gulf flounder, *Paralichthys albigutta* (100%); and greater amberjack, *Seriola dumerili* (60%). Xanthid crabs were preferred by the bank seabass, *Centropristis ocyurus* (34.8%); cubbyu, *Equetus*

*umbrosus* (77.3%); gulf toadfish, *Opsanus beta* (32.6%); whitespotted soapfish, *Rypticus maculatus* (65.9%); and belted sandbass, *Serranus subligarius* (58.7%). Polychaetes were preferred by pigfish, *Orthopristis chrysoptera* (24.8%), and cocoa damselfish, *Pomacentrus variabilis* (32.3%). Barnacles were preferred by striped burrfish, *Chilomycterus schoepfi* (49.8%). Sponges were preferred by Atlantic spadefish, *Chaetodipterus faber* (50%), and hermit crabs were preferred by red grouper *Epinephelus morio* (100%).

There were no clear prey preferences (an IRI of <25 for any one item) for 6 of the 25 fish species examined (i.e., *Calamus* sp., *Diplodus holbrooki, Haemulon plumieri, Halichoeres bivittatus, Lagodon rhomboides,* and *Monacanthus hispidus*). Porgies, *Calamus* sp., consumed xanthid crabs, polychaete worms, bivalves, and gastropods. Spottail pinfish, *D. holbrooki,* consumed sponges, polysiphonia, and ectoprocts. White grunt, *H. plumieri,* consumed gastropods, xanthid crabs, and fish, while slippery dick, *H. bivittatus,* consumed gastropods, bivalves, and xanthid crabs. Pinfish, *L. rhomboides,* consumed fish, portunid crabs, and bivalves. Planehead filefish, *M. hispidus,* consumed several encrusting organisms while over 50% of its stomach contents were unidentified material.

Six of the 44 prey taxa dominated the stomach contents among the 25 fish species examined. These taxa were: fishes (25.9% of the total IRI for all fish families combined), xanthid crabs (16.3%), unidentified items (10.5%), squids (6.7%), polychaete worms (5%), and penaeid shrimps (2.1%).

Algae were poorly represented among the prey taxa. Only three fishes consumed algal material (i.e., *D. holbrooki, P. variabilis,* and *R. aurorubens*). The consumption of algal material by *R. aurorubens* represents a single occurrence among nine fish and is probably a case of incidental consumption. The consumption of algae by *D. holbrooki* and *P. variabilis* was more likely intentional since algae comprised 18.8% and 11.8% of their diets, respectively. Both *D. holbrooki* and *P. variabilis* were not considered obligate herbivores because they had other items in their diets that were more important than algae.

To obtain a perspective on how these fishes interact, the artificial-reef-associated fish were clustered using the Bray-Curtis and two-way indicator species (TWINSPAN) clustering algorithms. The resulting dendrograms were compared using resource overlap values (Morisita's modified index; Pianka 1973). This comparison was performed by averaging the resource

TABLE 1.   Summary statistics for the fish collected and the presence of stomach contents. Abbreviations here are used throughout the tables and figures. SD = Standard deviation.

| Species | Abbre-viation | Number of fish | Mean length (mm) | SD | Mean mass (g) | SD | Mean gape (mm) | SD | Number of fish with contents present | % with contents |
|---|---|---|---|---|---|---|---|---|---|---|
| *Apogon pseudomaculatus* | APSE | 11 | 88.82 | 10.93 | 13.26 | 4.81 | 15.09 | 3.57 | 4 | 36 |
| *Balistes capriscus* | BCAP | 29 | 238.55 | 35.09 | 329.27 | 124.42 | 9.60 | 4.27 | 13 | 45 |
| *Calamus* sp. | CASP | 9 | 250.89 | 21.39 | 414.11 | 131.99 | 14.22 | 4.55 | 3 | 33 |
| *Centropristis ocyurus* | COCY | 32 | 172.03 | 45.93 | 88.74 | 86.68 | 19.58 | 4.92 | 18 | 56 |
| *Chaetodipterus faber* | CFAB | 21 | 257.29 | 47.54 | 602.50 | 284.43 | 11.50 | 2.37 | 2 | 10 |
| *Chilomycterus schoepfi* | CSCH | 13 | 233.31 | 35.44 | 437.75 | 189.12 | 14.60 | 6.67 | 6 | 46 |
| *Diplodus holbrooki* | DHOL | 22 | 180.14 | 26.76 | 156.30 | 76.68 | 8.84 | 2.81 | 15 | 68 |
| *Epinephelus morio* | EMOR | 1 | 375.00 | | 771.30 | | 33.50 | | 1 | 100 |
| *Equetus umbrosus* | EUMB | 36 | 179.06 | 33.42 | 91.64 | 56.31 | 14.75 | 3.54 | 19 | 53 |
| *Haemulon aurolineatum* | HAUR | 38 | 122.92 | 15.72 | 35.22 | 16.11 | 21.91 | 3.24 | 13 | 34 |
| *Haemulon plumieri* | HPLU | 33 | 171.61 | 45.04 | 142.76 | 170.78 | 27.88 | 9.53 | 12 | 36 |
| *Halichoeres bivittatus* | HBIV | 31 | 162.77 | 26.89 | 51.14 | 27.37 | 7.99 | 1.39 | 19 | 61 |
| *Lachnolaimus maximus* | LMAX | 1 | 240.00 | | 330.20 | | 21.10 | | 0 | 0 |
| *Lagodon rhomboides* | LRHO | 27 | 194.59 | 44.83 | 160.56 | 120.88 | 10.07 | 2.61 | 14 | 52 |
| *Lutjanus griseus* | LGRI | 4 | 266.50 | 21.01 | 331.25 | 128.86 | 18.78 | 2.20 | 3 | 75 |
| *Monacanthus hispidus* | MHIS | 4 | 247.75 | 2.05 | 273.40 | 9.57 | 8.58 | 0.75 | 3 | 75 |
| *Mycteroperca microlepis* | MMIC | 3 | 458.67 | 83.73 | 1,102.07 | 369.10 | 42.63 | 5.00 | 1 | 33 |
| *Opsanus beta* | OBET | 32 | 302.41 | 57.53 | 765.52 | 522.96 | 18.28 | 5.63 | 8 | 25 |
| *Orthopristis chrysoptera* | OCHR | 39 | 169.00 | 14.57 | 72.63 | 21.61 | 12.25 | 1.88 | 7 | 18 |
| *Paralichthys albigutta* | PALB | 11 | 335.36 | 72.08 | 319.85 | 177.12 | 21.96 | 5.75 | 3 | 27 |
| *Pomacentrus variabilis* | PVAR | 33 | 107.52 | 13.69 | 42.44 | 15.84 | 7.26 | 1.35 | 28 | 85 |
| *Rhomboplites aurorubens* | RAUR | 40 | 119.98 | 7.22 | 27.69 | 4.58 | 12.53 | 1.31 | 9 | 23 |
| *Rypticus maculatus* | RMAC | 33 | 197.42 | 24.40 | 145.82 | 56.81 | 16.08 | 4.78 | 11 | 33 |
| *Seriola dumerili* | SDUM | 5 | 274.40 | 39.09 | 423.88 | 225.81 | 20.56 | 5.00 | 5 | 100 |
| *Serranus subligarius* | SSUB | 32 | 88.16 | 8.06 | 14.70 | 4.15 | 11.91 | 2.15 | 25 | 78 |

overlap values for obvious clusters in the dendrogram. The highest resource overlap (>0.75) occurred between *R. maculatus* and *C. ocyurus* (0.754); *R. maculatus* and *E. umbrosus* (0.779); *S. subligarius* and *E. umbrosus* (0.968); and *L. griseus* and *R. aurorubens* (0.824). The lowest dietary overlap occurred among combinations of species with *M. hispidus,* which had a dietary overlap with only one other species (*C. ocyurus,* 0.062).

The Bray-Curtis cluster analysis dendrogram (Fig. 2) was found to have a high average diet overlap within groups and was used along with DCA to identify guilds and their associated factors of fish species for which more than five stomach samples were obtained. At 75% dissimilarity in diet, we recognize seven guilds. Guild A (lower structure pickers) contains *B. capriscus, C. schoepfi,* and *H. bivittatus.* Guild B (ambush predators) contains *O. beta.* Guild C (lower structure crustacean predators) contains *C. ocyurus, E. umbrosus, S. subligarius,* and *R. maculatus.* Guild D (upper structure pick-

ers) contains *D. holbrooki* and *L. rhomboides.* Guild E (upper structure predators) contains *H. aurolineatum, H. plumieri,* and *O. chrysoptera.* Guild F (water column pickers) contains *P. variabilis.* Guild G (reef-associated open water feeders) contains *R. aurorubens* and *S. dumerili.*

A detrended correspondence analysis (DCA) based on the IRI value for food items of each fish species was also used to help delineate factors associated with the guild relationships. Figure 3 indicates the arrangement of guilds in the physical habitat. Axis 1 represents foraging distance away from the reef center and axis 2 represents foraging height from the substrate (lower), up onto the reef structure and into the water column (higher). In Figure 3, the sum of the eigenvalue loadings for axes 1 and 2 were 0.693 and 0.562, respectively.

DISCUSSION

The diets of most of the 25 species of fishes correspond well with the previously published
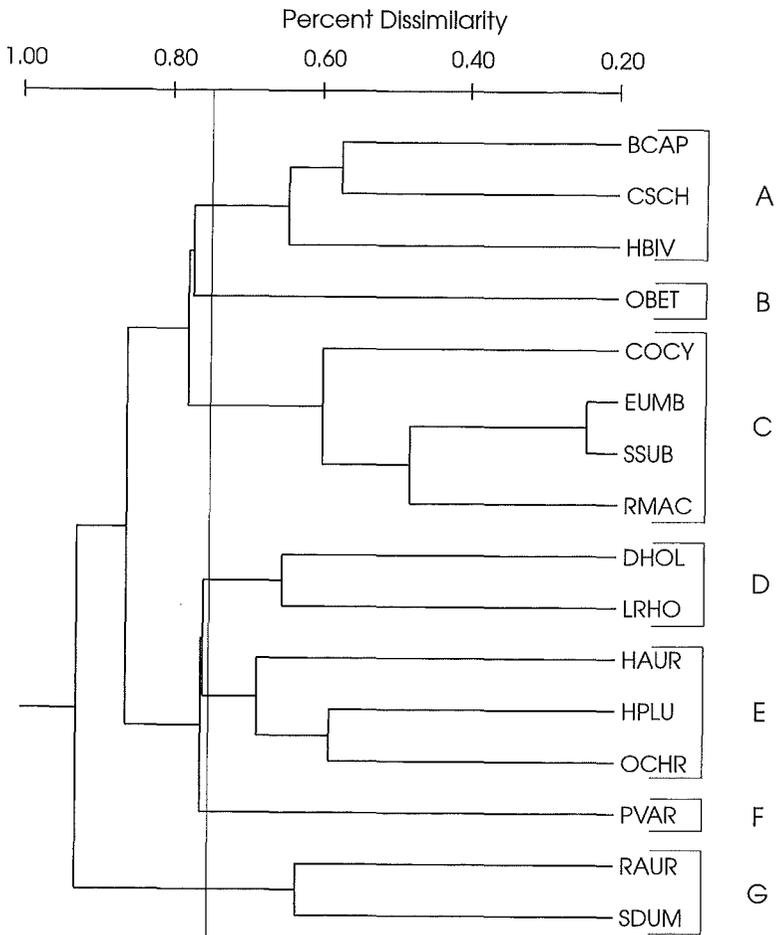
Fig. 2.   Dendrogram of the cluster analysis (UPGMA clustering of Bray-Curtis coefficient) for all fish species with five or more stomach samples. The letters indicate guilds: guild A, lower structure pickers; guild B, ambush predators; guild C, lower structure crustacean predators; guild D, upper structure pickers; guild E, upper structure predators; guild F, water column pickers; guild G, reef-associated open-water feeders. Fish abbreviations as in Table 1.

accounts (Table 3). It is because of this correspondence that we believe we can comment on the guild structure with sample sizes as small as five stomachs. The notable exceptions to the correspondence are *P. variabilis* and *D. holbrooki*. Based on the dietary reports of Randall (1967), it would seem that algae may be more important as a prey item than shown herein. In any case, we do not believe that these two fish play a major role in moving the energy of primary production through the food web. *D. holbrooki* was not found as a prey item and *P. variabilis,* when found, was not an important prey item. Due to the lack of obligate herbivorous fishes as prey, we suspect most of the trophic energy in the artificial-reef ecosystem comes from phytoplankton, which would imply the importance of filter feeding bait fish and

invertebrates (both attached to the reef and in the surrounding substrate) for capturing the energy to drive this system.

To examine the question of how so many fish species can use so few key prey resources, the data were analyzed to determine patterns of association. The DCA of the feeding data indicates the importance of foraging distance from the reef and the height at which the organism forages (from sand up the structure into the water column). The various areas where fish feed in relation to artificial reefs in different environments have been discussed by several authors (Hawaii—Bailey-Brock, 1989; Washington—Hueckel and Stayton, 1982; Hueckel and Buckley, 1987; South Carolina—Steimle and Ogren, 1982). These studies found that adjacent, soft-bottom communities

TABLE 2. Percent of the mean total Index of Relative Importance (IRI) of each prey taxon for each artificial reef fish species examined. Fish species abbreviations are as in Table 1.

| Prey items | APSE | BCAP | CASP | COCY | CFAB | CSCH | DHOL | EMOR | EUMB | HAUR | HPLU | HBIV | LRHO | LGRI | MMIC | MHIS | OBET | OCHR | PALB | PVAR | RAUR | RMAC | SDUM | SSUB |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Algae | | | | | | | | | | | | | | | | | | | | 3.5 | 5.4 | | | |
| Cladophorales | | | | | | 3.1 | | | | | | | | | | | | | | 9.3 | | | | |
| Polysiphonia | | | | | | 15.7 | | | | | | | | | | | | | | | | | | |
| Demospongiae | | | | 50.0 | | 25.4 | | | | | 8.3 | | 16.5 | | | 1.1 | | | | 1.7 | | | | |
| Hydrozoa | | | | | | | | | | | | | | | | | | | | 10.1 | | | | |
| Polychaeta | | 18.8 | | | | | | | 5.0 | | 8.2 | | 6.8 | | | 6.0 | | 24.8 | | 32.3 | | | | 1.0 |
| Gastropoda | | 6.3 | | | | 8.9 | | | | | 20.5 | | | | | | | | | | | | | |
| Crepidulidae | | | | | | | | | | | | | | | | | 7.9 | | | | | | | |
| Nassaridae | | 18.0 | | | | | | | | | | | | | | | | | | | | | | |
| Potamididae | | | 2.9 | | | | | | | | | 1.7 | | | | | 20.3 | | | | | | | |
| Bivalvia | | 6.3 | | | | 9.1 | 5.4 | | | | | 23.9 | 10.7 | | | | | | | | | 3.9 | | |
| Arcidae | | | | | | | | | | | | 8.0 | | | | | | | | | | | | |
| Glycymeridae | | | | | | 14.6 | | | | | | 17.6 | | | | | | | | | | | | |
| Mytilidae | | 4.3 | | | | | 4.7 | | | | 8.3 | | | | | 0.8 | | | | | | | | |
| Pectinidae | | | | | | | | | | | | | | | | | | | | | | | | 2.0 |
| Veneridae | | | 17.5 | 2.9 | | | | | | | | 5.7 | | | | 5.5 | | | | | | | | |
| Teuthiodea | | | 25.2 | | | | 3.3 | | | 26.1 | | | | 20.7 | | | | | | 1.3 | 43.0 | | 40.0 | |
| Crustacea | | | | | | | | | | | | 2.6 | | | | | | 12.6 | | | 6.7 | | | |
| Balanomorpha | | 2.1 | | | 49.8 | 5.5 | | | | | | 1.2 | 5.5 | | | | | | | 4.9 | | | | |
| Dendrobranchiata | | 8.8 | | | | | | | | | 1.7 | | | | | | | | | | | | | 8.6 |
| Alpheidae | | | | | | | | | | | 8.3 | | | | | | | | | | | 4.7 | | |
| Penaeidae | 9.4 | | 11.5 | | | | | | 3.2 | 9.3 | 3.9 | | | | | | | | | | | 11.2 | | 2.4 |
| Brachyura | | 12.3 | | | | | | | | | | 14.1 | | | | | | | | | | | | |
| Majidae | | | | 9.1 | | | | | | | | | | | | | | | | | | | | |
| Paguridae | | | | 1.1 | | | | 100.0 | | | 1.7 | | | | | | 5.4 | | | | | | | 0.8 |
| Portunidae | | | | 5.8 | | | 0.8 | | | | | | | | | | | | | | | | | |
| Xanthidae | | 17.9 | 19.1 | 34.8 | | 17.6 | | | | 77.3 | 12.5 | 22.2 | 10.4 | | | 8.6 | 32.6 | 12.6 | | | | 65.9 | | 58.7 |
| Ectoprocta | | | | | | 10.7 | | | | | 4.5 | | 1.5 | | | 21.1 | | | | 0.3 | | | | |
| Amphipoda | 15.6 | | | | | 2.1 | | | | | | | | | | | | | | | | | | |
| Ophiotrichidae | | | | | | | | | | | 1.0 | | | | | | | | | | | | | 9.3 |

TABLE 2.   Continued.

| Prey items | APSE | BCAP | CASP | COCY | CFAB | CSCH | DHOL | EMOR | EUMB | HAUR | HPLU | HBIV | LRHO | LGRI | MMIC | MHIS | OBET | OCHR | PALB | PVAR | RAUR | RMAC | SDUM | SSUB |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Arbacioida |  | 21.4 |  |  |  |  |  |  |  |  |  |  | 6.8 |  |  |  | 20.4 |  |  |  |  |  |  |  |
| Urochordata |  |  |  |  |  |  |  |  |  |  |  | 3.1 |  |  |  |  |  |  |  | 0.9 |  |  |  |  |
| Pisces | 25.0 | 28.7 |  | 8.5 |  |  |  |  | 6.9 | 33.9 | 11.1 |  | 16.8 | 45.9 |  |  |  | 12.6 | 66.7 | 7.3 | 45.0 | 9.5 | 20.0 | 7.3 |
| Blenniidae |  |  |  | 5.4 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 2.0 |
| Bothidae |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 40.0 |  |
| Clupeidae |  |  |  | 3.0 |  |  |  |  |  |  |  |  |  |  | 100.0 |  |  |  |  |  |  |  |  |  |
| Gobiidae |  |  |  | 0.7 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 9.5 |  |  |
| Grammistidae | 25.0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Pomacentridae |  |  |  | 0.7 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Pomadasyidae |  |  |  |  |  |  |  |  |  |  |  |  |  | 33.3 |  |  |  |  | 33.3 |  |  |  |  | 5.5 |
| Sciaenidae |  |  |  |  |  |  |  |  |  | 2.5 |  |  |  |  |  | 13.3 |  |  |  |  |  |  |  |  |
| Serranidae |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 2.3 |
| Eggs | 25.0 |  |  |  |  |  | 3.1 |  |  |  |  |  |  |  |  |  |  |  |  | 18.3 |  |  |  |  |
| Unidentified |  | 7.1 |  |  | 50.0 |  | 20.0 |  | 5.0 | 30.7 | 10.0 |  | 25.1 |  | 56.9 |  |  | 37.4 |  | 10.0 |  |  |  |  |

are important foraging areas for some fishes. Jones et al. (1991) and Posey and Ambrose (1994) discussed similar situations for fishes and forage areas on coral and temperate rocky reefs, respectively.

Some studies have shown that fishes feed on reef-related organisms. For example, Hueckel and Buckley (1987) found that fishes became more abundant with time as artificial reefs aged, and that the attached benthic community increased in complexity and biomass. On older reefs, fishes predominantly fed on algal-mat-associated species. Hueckel and Buckley (1987) also found that some fish species also fed on the surrounding sand epifauna. They concluded that artificial reef communities change over time. The first stage of community development was an aggregating stage where prey organisms are predominantly from the surrounding benthic communities. Second, piscivores colonize the reef and feed on the assemblage of fishes feeding on the surrounding benthic community. Finally, the reef begins to produce sufficient prey organisms to support a fish fauna feeding on these reef-attached organisms. In Hueckel and Buckley's (1987) study, 70% of the reef fish assemblage was supported by reef-attached prey items.

Other studies have shown that organisms closely associated with reef structure and the proximate benthos are important sources of food for reef fishes. Thus, fish that occupy reef edges can benefit by foraging in both micro-habitats. Steimle and Ogren (1982) studied the diets of fish assemblages on artificial reefs off New York and South Carolina. Their results showed little evidence to support the hypothesis that temperate fish species on artificial reefs are dependent on reef-associated fauna or flora for food. They found that typical temperate reef fishes [e.g., cunner (*Tautogolabrus adspersus*) and tautog (*Tautoga onitius*)] fed on organisms that occurred both on and off the reef structure.

In another example of fish benefiting from both microhabitats, in Puget Sound, Hueckel and Stayton (1982) found that small members of several species preyed on both sand fauna and plankton, while larger individuals of the same species in the reef assemblage fed on reef-associated organisms (e.g., caridian shrimps and brachyuran crabs). Hueckel and Stayton (1982) also found that striped seaperch (*Embiotoca lateralis*) could not be characterized as sand or reef foragers because their prey organisms (epibenthic crustaceans) were located both on and away from the reef structure.
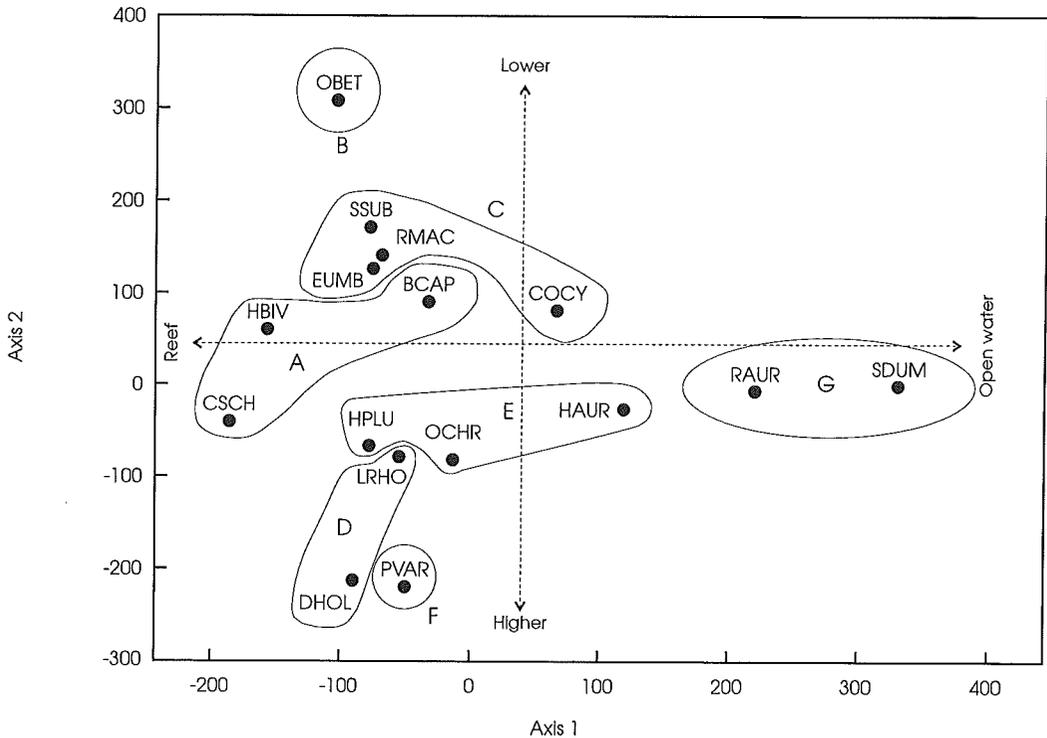
Fig. 3.  Scatter plot of the eigenvector loadings for the first two DCA axes for all fish species with five or more stomach samples. Guild definitions as in Figure 2. Fish species abbreviations as in Table 1.

A third set of studies examine fish foraging away from the reef structure and how these fishes can create "halos" of decreased abundance among benthic prey around reefs. Davis et al. (1982) examined the impact of man-made structures on the surrounding sand bottom community and found that foraging by reef-associated fishes profoundly changed epifaunal community structure. For example, the sea pen, *Stylatula elongata,* had a significantly lower abundance and less evidence of fish foraging damage (i.e., missing polyps) near the reef. This study did not examine fish foraging on organisms attached to the reef, only on the benthic community around reef structures.

Ambrose and Anderson (1990) examined the physical influence of artificial reefs and their associated fishes on the surrounding infauna. They found that currents moving around artificial reefs can influence infaunal communities via scouring, which changes the physical habitat immediately adjacent to the reef. This change in habitat led to changes in abundance (both increases and decreases) for only 13% of the examined fauna in the study area. Ambrose and Anderson (1990) also found that reef-associated fishes influenced the abundance of infaunal organisms.

Fraser et al. (1991) examined the impact that a predator may have on the abundance of forage items in the communities surrounding an artificial reef. They found that gray triggerfish (*B. capriscus*) reduced the abundance of sand dollars around artificial reefs. While the overall importance of sand dollars in triggerfish diet is unknown, this study does suggest a link between the reef assemblage and the surrounding benthic communities.

Lindquist et al. (1994) studied the food habits of fishes associated with artificial reefs off North Carolina. They concluded that the sand-substrate-associated organisms that occurred around reefs are probably an important source of energy to the associated artificial-reef fish assemblage. Moreover, they warned that a necessary amount of surrounding sand bottom may be essential to support the reef-associated fishes that forage over the sand substrate. Posey and Ambrose (1994) also found a similar situation near a natural rock outcrop off North Carolina. They noted a trophic link between the fishes associated with the rock outcrop and the soft-bottom community 10–75 m from the reef.

Randall (1967) reported that lutjanids tended to seek cover on coral reefs by day and to

forage out over sand and grass flats by night. He also indicated that bothids foraged on the sand flats around coral reefs; furthermore, he described *S. dumerili* as a roving predator. Grimes (1979) and Sedberry and Cuellar (1993) reported on nocturnal foraging of *R. aurorubens* away from reef structures off the Carolinas. These reports support part of the pattern depicted in Figures 2 and 3 by confirming that members of guild G tend to feed the farthest away from reef structures.

The explanation of the second trend (i.e., feeding height above the reef structure) suggested in the DCA is supported by several authors based on the following literature reports: Levins (1968) argued that, by segregating in multiple directions, species can minimize resource overlap. Randall (1967) reported that fishes of the family Apogonidae (cardinal fishes), members of guild F, fed some distance from the substrate. Furthermore, Wellington and Victor (1988) found that some species of damselfish (Pomacentridae) "cultivate" algae in defended territories. It may benefit individuals to establish their territories higher on reef structures where "cultivated" algae could capture the most light energy. While it has been reported that *P. variabilis* (guild F) fed predominantly on algae (Randall, 1967); that was not found to be the case here. While we do not offer a definitive reason for the difference in diet, the selection of the prey items found is probably due to the damselfish's normal position on the reef and may represent the typical diet where or when algae is not available in sufficient quantities.

Further argument for spatial and temporal segregation by species and guilds comes from the observations of project divers during collection that *P. variabilis* was often found high on the reef structure. Oppositely, divers most often observed members of guilds B and C low on, or even under, reef materials. Additional support for a complex three-dimensional spacing of the feeding guilds can be found in reports of tropical stream fish feeding guilds. Zaret and Rand (1971) reported a guild structure that varied both in food habits and in physical position in a stream.

The cluster analysis, also based on diet, also reveals spatial trends similar to those suggested by the DCA. The first branching in Figure 2 divides guild G from other species. Guild G consists of the major piscivores that may swim the farthest from the reef in search of food. The next branching separates fishes who fed heavily on crustaceans (guilds A–C) from those which fed on a broad variety of organisms

(guilds D–F). If the apparent environmental associations with feeding guilds in the DCA are correct, then this branching also separates lower reef fishes (Guilds A–C) from those on the upper reef (guilds D–F).

The prey of the open water feeders in guild G (e.g., *Seriola dumerili*) was dominated by fish and squid. There was some dietary overlap with the upper structure predators (guild E). However, the greatest overlap for these fish is within their own guild. The overlap between guilds G and E may be due to the fact that most fish (as prey items) could not be identified to family or species. Identification of food fish taxa would allow for a differentiation between a prey species from open water and one from the reef.

Two of the three lower structure guilds are dominated by a single prey species. Both the ambush predator (guild B, *Opsanus beta*) and the lower structure predators (Guild C, *Equetus umbrosus*) consume large amounts of xanthid crabs, *Pseudomedaeus agassizi*. This crab is typically associated with both natural and artificial reefs (Williams, 1965). Members of guild C show a high degree of internal resource overlap, exemplified by *Serranus subligarius* and its feeding overlap with *E. umbrosus* (96.8%).

There was also a high degree of overlap between *R. maculatus* and *O. beta*. *Opsanus beta* is not included in guild C because its diet is also similar to *Balistes capriscus* due to the consumption of whole urchins (*Arabacia punctata*) and the single occurrence of two prey taxa: a gastropod of the family Crepidulidae and a single *S. subligarius*. These may not be normally targeted food items. The gastropod was found in a stomach containing a large hermit crab, shell and all; the snail was probably attached to the crab's shell at the time of consumption. The *S. subligarius* was intact and undigested. Although care was taken in handling captured specimens, it may have been consumed after capture. If so, it may represent a case of "net feeding."

Guild A is not dominated by a single prey taxon as are the other guilds. The dominant prey items of the lower level pickers were barnacles, bivalves, and fish. The first two items can be easily picked from the reef or the sand at the edge of the reef (depending on the bivalve species). The consumption of fish (28.7% IRI) by *B. capriscus* is not as easy to explain. Perhaps they steal bait from fishing lines, consume small fish, or ingest fish parts remaining from the feeding activities of larger predators. The diets of the members of guild A overlap with those of fish in other guilds.

TABLE 3. Summary of prey items from various sources of species examined herein. 1—This study; 2—Randall (1967); 3—Fraser et al. (1991); 4—Adams (1976); 5—Wilson et al. (1982); 6—Bullock and Smith (1991); 7—Grimes (1979); 8—Sedberry and Cuellar (1993); 9—Heck and Weinstein (1989); 10—Hastings (1978); 11—Hastings and Bortone (1980); 12—Sedberry (1989); 13—Stoner (1980). Asterisk (*) indicates prey items of particular importance.

| Taxa | Algae | Sponges | Hydro-zoans | Antha-zoans | Poly-chaetes | Gastro-pods | Bivalves | Cepha-lopods | Chi-tons |
|---|---|---|---|---|---|---|---|---|---|
| Apogonidae | | | | | | | | | |
| Apogon pseudomaculatus | | | | | 2 | | | | |
| Balistidae | | | | | | | | | |
| Balistes capriscus | | | | | | | | | |
| Monacanthus hispidus | 2 | 1 | | | 1 | 1 | 1 | | |
| Batrachoididae | | | | | | | 5 | 4, 5 | |
| Opsanus beta | | | | | | 1 | | | |
| Bothidae | | | | | | | | 2 | |
| Paralichthys albigutta | | | | | | | | | |
| Carangidae | | | | | | | | | |
| Seriola dumerili | | | | | | | | 1 | |
| Diodontidae | | | | | | 2 | 2 | | |
| Chilomycterus schoepfi | | | | | | 1, 4 | 1, 4 | | |
| Ephippidae | | | | | | | | | |
| Chaetodipterus faber | | 1, *2 | | | | | | | |
| Grammistidae | | | | | | | | | |
| Rypticus maculatus | | | | | | | | | |
| Labridae | | | | | | | | | |
| Halichoeres bivittatus | | | | | 2 | 2 | *1 | | |
| Lachnolaimus maximus | | | | | | 2 | 2 | | |
| Lutjanidae | | | | | | | | | |
| Rhomboplites aurorubens | | | | | | 7 | | 1, 7, 8 | |
| Lutjanus griseus | | | | | | | | 1 | |
| Pomacentridae | | | | | | | | | |
| Pomacentrus variabilis | 1, *2 | | 1 | | *1, 2 | | | | |
| Haemulidae | | | | | | | | | |
| Haemulon aurolineatum | | | | | 2 | | | 1 | |
| Haemulon plumieri | | | | | 2 | *1 | | | |
| Orthopristis chrysoptera | | | | | 1 | | | | |
| Sciaenidae | | | | | | | | | |
| Equetus umbrosus | | | | | | | | | |
| Serranidae | | | | | | | | | |
| Centropristis ocyurus | | | | | 6 | 1 | | 1 | |
| Epinephelus morio | | | | | | 6 | | 6 | |
| Mycteroperca microlepis | | | | | | | | | |
| Serranus subligarius | | | | | | | | | |
| Sparidae | | | | | | | | | |
| Calamus sp. | | | | 12 | 1, 2, 12 | 1, 12 | 1, 2, 12 | | |
| Diplodus sp. | *2 | | | | | 2 | | | 2 |
| Diplodus holbrooki | 1 | 1 | | | | | 1 | | |
| Lagodon rhomboides | 1 | | | | | 13 | | | |

The upper structure pickers, guild D (e.g., *Diplodus holbrooki*), fed predominantly on sponges and unidentifiable items. This group is equipped with dental and pharyngeal structures for picking and grinding food from upper portions of the reef. The diets of guild D members overlap each other more than they overlap fishes outside the guild.

Guild E, the upper structure predators (e.g., *Orthopristis chrysoptera*), is composed of fishes with unclear feeding preferences. Fish are important prey items, as are gastropods and unidentified items. All three species in this guild have at least 50% dietary overlap with *Lagodon rhomboides* from guild D. Most of the overlap was presumed due to large amounts of uniden-

TABLE 3.   Extended.

| Crustaceans | Bar-nacles | Xanthid crabs | Other crabs | Am-phi-pods | Cope-pods | Iso-pods | Ecto-procts | Echinoids | Sand dol-lars | Ur-chins | Ascid-ians | Fish eggs | Fishes | Uniden-tified |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *2 | | | | | | | | | | | 2 | 2 | | |
| 1 | | | | | | | | | | | | 1 | *1 | |
| 2 | | | | | | | | | | 2 | | | 2 | |
| | | 1 | 1 | | | | | | 3 | 1 | | | 1 | 1 |
| 2 | | | | | | | 1 | | | | | | | 1 |
| 4, 5 | | | 5 | | | | | | | | | | *4 | |
| 1 | | | | | | | | | | 1 | | | 1 | |
| 2 | | | | | | | | | | | | | *2 | |
| | | | | | | | | | | | | | *1 | |
| | | | | | | | | | | | | | *1, *2 | |
| 2 | | | | | | | | | | 2 | | | | |
| 4 | 1 | 1 | | | | | | | | 4 | | | | |
| | | | | | | | | | | | | | | 1 |
| 6 | | *1, 6 | 6 | | | | | | | | | 1, 6 | | |
| 1 | | 1 | 2 | | | | | | | 2 | | | | |
| | | | 7, 8 | 7 | | | | | | | | | *1, 8 | |
| | | | *2 | | | | | | | | | | *1, 2, *9 | |
| | | | | | 2 | | | | | | | 1 | | 1, 2 |
| 2 | | | | | | | | | | | | | 1 | 1 |
| 9 | | 1 | *2 | | | | | 2 | | | | | 1 | |
| 1, 4 | | 1 | 4 | 4 | | | | | | | | | | *1 |
| *2 | | *1 | | | | | | | | | | | | |
| 1, 6 | | *1, *6 | 6 | | | | | 6 | | | | | 1, 6 | |
| *2, 6 | | | *1, *2 | | | | | | | | | | 6 | |
| 4, 6 | | | | | | | | | | | | | *1, *2, 4, 6 | |
| 6, 10, 11 | | *1 | 6 | | | | | | | | | | 1, 6 | |
| 1 | 12 | *1 | 2 | | | | 12 | 2, 12 | | | | | 12 | |
| | 1 | | 2 | | | | | | | | | | | |
| | 13 | | 1, 4, 13 | | | | | | | | | | 1 | |

tified food items. Even discounting the unidentified prey, there was little overlap within the guild. These fish are apparently generalists in contrast with the lower structure predators.

Guild F consists of fish that apparently swallow individual organisms whole from the water column or off the structure while remaining very close to cover (e.g., *Pomacentrus variabilis*).

The feeding strategy of the fish in this guild differs from the pickers because the pickers use their teeth to scrape off what they consume. Guild F had wide prey preferences.

Our inability to assign *C. faber*, *P. albigutta*, and *M. microlepis* to any particular guild was most probably due to the low percentages of individuals of these species with stomach con-

tents. *E. morio* and *L. maximus* were only present as single individuals. *M. microlepis* and *E. morio* were outliers in our initial analyses. We believe that they belong to guild G based on published reports of their diets. *Chaetodipterus faber* and *P. albigutta* were tentatively assigned to guilds E and G, respectively. At the 75% level of diet dissimilarity, they each represent independent guilds. They were assigned to their respective guilds based on dietary overlap. *Lachnolaimus maximus* was represented by a single individual with no stomach contents. Based on Randall's (1967) description of the diet of *L. maximus,* it should belong to the same guild as *H. bivittatus* (guild A). Unfortunately, the commercially and recreationally important red snapper, *Lutjanus campechanus,* was not collected as part of this study because they were not observed on our study reefs. Based on the dietary descriptions of Bortone et al. (1981) and Parrish (1987), it would seem that red snapper are members of the open-water feeding guild as well.

The high levels of resource overlap both within and between some feeding guilds raise questions regarding resource partitioning. While we have no definitive answers regarding these questions, we can offer some possible hypotheses for consideration: (1) spatial partitioning—fishes could be feeding on the same resource on different parts of the reef or defending different feeding territories; (2) temporal partitioning—fishes might be using the same resources but at different times; or (3) resource flooding—fishes may prey on the same food item when it is extremely abundant and shift to another food item when that abundant item's density is lower.

This study has described the diets of the most common artificial-reef assemblage fishes in the northern Gulf of Mexico. A potential guild structure for these fishes has also been outlined. The guild structure could change over time due to seasonal or ontogenetic shifts in diet (see Winemiller and Pianka, 1990). This study could be strengthened by year-round sampling and sampling over a broader size range of fish. If the guild structure presented here remains as more data are collected, then the reef-associated gamefishes (snappers: *L. griseus, L. campechanus,* and *R. aurorubens*; flounder: *P. albigutta*; amberjack: *S. dumerili*; and probably the groupers: *M. microlepis* and *E. morio*) could be candidates for a guild management plan.

It has been argued that managing for a guild is easier than managing for a single species (Severinghaus and James, 1986). Moreover,

guild management has been in use, either intentionally or unintentionally, in fisheries for some time (Austen et al., 1994). If further ecological investigations of the reef-associated game fishes continue to show similar life histories, ecological requirements, and limitations, then managing either resources or recruitment for any one species will, in theory, benefit all guild members. If this guild is habitat-limited (i.e., larval production produces more potential recruits than there are available microhabitats), then one solution could be to provide more microhabitat. This would be in the form of artificial reefs (functioning as predator refugia) with sufficient foraging space between reefs to assure an adequate amount of sustainable forage items. Moreover, growth rates among artificial-reef-associated fishes may become impaired if suboptimal conditions occur as a result of overforaging by the attracted biomass (Sogard, 1994). Thus, proper spacing of artificial reefs may be paramount in the design and placement of structure to manage fisheries.

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