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Stephen A. Bortone University of West Florida

Robert K. Turpin University of West Florida

Richard C. Cody University of West Florida

Charles M. Bundrick University of West Florida

Ronald L. Hill University of Puerto Rico

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Factors Associated with Artificial-Reef Fish Assemblages

STEPHEN A. BORTONE, ROBERT K. TURPIN, RICHARD C. CODY, CHARLES M. BUNDRICK, AND RONALD L. HILL

Visual census (5-min point-count, 100 m²) was used to estimate fish assemblage parameters associated with artificial reef variables from 64 reefs over a 3-yr period in the northern Gulf of Mexico. Dependent variables, recorded by divers [i.e., number of species, number of individuals, length (TL in cm), and species diversity (H')], were analyzed for their associations with potentially underlying environmental attributes using stepwise regression, TWINSPAN, and canonical correspondence analyses (CCA). The fish assemblages (dominated by haemulids, labrids, and serranids) were qualitatively and quantitatively similar to the assemblages described by others from the same general area. Pelagic fishes (carangids and scombrids) associated with the reefs were among the most numerous and were the largest predators in the assemblage. The stepwise regression analysis was able to account for fairly high percentages of the variation in number of species (37%), number of red snapper (43%), and size of red snapper (52%). TWINSPAN allowed the recognition of fish assemblages based on their inshore-offshore biotopes. Vermilion snapper was identified as a key indicator species. The CCA helped identify species groups and factors associated with them. The affinity of pinfish and spottail pinfish with rock jetty was evident, as was the association of triggerfish with vertical steel structure. Although the axis loadings using CCA did not identify a clear species/factor relationship, this analytical method should prove useful in recognizing environmental factors that can be controlled to optimize species-specific artificial reef construction.

The world's fisheries resources are currently at, or may soon attain, the limits of their maximum sustainable yield (Houde and Rutherford, 1993; Knauss, 1994). Many fish species of these fisheries are limited by processes such as recruitment, migration, harvesting, and available food resources (Pitcher and Hart, 1982). In addition, some reef-associated species are thought to be limited by lack of suitable habitat (Bohnsack, 1989). Recently, efforts to thwart the decline of some fishes have involved the deployment of artificial habitats or reefs as a management strategy (Polovina, 1991). Artificial reef development for hard-bottom-associated fish species has been carried out under the assumption that many of these species are limited by the amount of appropriate substrate. Since many nearshore and continental shelf areas of the world lack hard substrate, there is potential for increasing hardbottom-associated, habitat-limited organisms such as reef fishes by increasing the amount of hard bottom through effective artificial reef deployment (Grossman et al., 1997). Overall, artificial reefs have many potential uses, only some of which have been realized to date. However, a long-term and effective management strategy for demersal nearshore fisheries that uses habitat modification through the deployment of artificial reefs has yet to be developed.

The development of artificial reefs as a management alternative has been hindered by a lack of information that could reliably predict their utility in improving the existing stocks. Most artificial reefs in the United States have been constructed in an opportunistic manner using readily available materials, presumably obtained at a low cost. While the number of artificial reefs in coastal waters continues to grow, the questions concerning their optimum construction and deployment to attain management objectives remain unanswered. Specifically, we need to know optimal ways to construct these reefs in terms of design, materials, and location (Bohnsack and Sutherland, 1985).

A previous study (Bortone and Van Orman, 1985) and a review of the literature (Bohnsack et al., 1991) indicate that the parameters of the associated artificial reef variables are not established to a sufficient degree to permit optimal use of the limited funds available for their construction. In a recent study of an estuary in the northern Gulf of Mexico, Bortone et al. (1994) used several multivariate approaches to determine the factors significantly associated with the dependent variables: number of species, in-

dividuals, size, species diversity, and biomass. Their study showed that temperature and succession attributes were the underlying factors that dominated fauna composition and features. However, the reefs in that study had not "stabilized" in that colonization, and successional features strongly masked the impact of the reef attributes and environmental factors surrounding the reefs.

The objective of this study was to examine the relationship between the fish assemblage and the environmental features and variables, toward a final goal of using this information to improve reef design and placement. The present study was conducted with replicate visual fish surveys on a large number of artificial reefs from a single biotic province over several years. This improvement in sampling strategy over previous efforts permitted more careful examination of the environmental variables associated with the fish assemblage variables and with individual species abundance. The results of this examination are directed toward accurately and precisely knowing the environmental attributes of artificial reefs that are associated with the species, numbers of individuals, species diversity (H'), and size of individuals that constitute the artificial-reef fish assemblages. In addition, herein, we focus on identifying the reef-attribute and environmental variables with which specific reef assemblage fishes are associated.

STUDY AREA

The northern Gulf of Mexico study area (Fig. 1) has a mixed tropical and temperate fish fauna (Hastings, 1979). Depths of the reefs in the study were 3.0–35.1 m, bottom temperature was 20.0–30.3 C, bottom salinity was 19– 38 ppt, and the substrate was generally coarsegrained sand and shell 0.24–1.78 mm in diameter with little natural relief except for occasional limestone outcroppings. Within each of the general areas, the specific artificial reefs were chosen to give a diversity of environmental and artificial-reef attributes. This permitted the association of variation in the environmental independent variables with variation in the dependent variables of the fish assemblage.

Methods

Each summer (June, July, and August) for 3 yr (1991–93), 64 different artificial reefs located along the northern Gulf of Mexico were visually surveyed for fish fauna, with each survey being replicated three times for a total of 564

https://aquila.usm.edu/goms/vol15/iss1/3 DOI: 10.18785/goms.1501.03 surveys (some survey sites were not found on subsequent visits). The reefs had a broad range of associated parameters for each variable. The duplication of most variable parameters at more than one reef permitted an evaluation of their relationships with reef assemblage features. The 3-yr sampling period was necessary to determine the degree of interannual faunal variation in species composition and abundance, as well as to note the impact of varying environmental parameters at each site. Summer sampling took advantage of warmer diving conditions, calmer seas, a more complete fauna, and reduction of the impact of seasonal variation. Much of the fish fauna in the northern Gulf moves offshore during the winter and repopulates in the spring and early summer (Hastings, 1979).

At each reef, three replicate visual fish counts were made following the visual survey methods detailed by Bortone et al. (1991). Upon arriving at the reef, a diver (using SCU-BA) took a position near the reef structure and set down a 5.64-m-long weighted radius line to allow estimation of the size of the visual census circle. The diver occupied the center of the circle and counted (by species) and estimated the sizes [total length (TL) in cm] of all fishes that passed through the circle during a 5-min period. All data were recorded on waterproof paper attached to a white plastic slate. The plastic slate had a centimeter rule along its edge to help the diver estimate fish size. During the observation period, the diver turned slowly through a 360 degree visual sweep to observe all fish in the survey area. No fish was intentionally recorded more than once, and if part of a school swam through the circle, then the entire school was included in the count (Brock, 1954). Three visual-survey replicates were conducted at each reef site; each from a different position on the reef. From the observations, we calculated number of species, total number of individuals, and species diversity (the Shannon-Wiener diversity index-H'; Pielou, 1966).

The independent/environmental variables recorded during each survey and used in the analyses are presented below (along with their abbreviations used in the tables and figures) with a description of the protocol used to measure them: Yr Blt (year built)—the year of deployment; Year—year of the survey; Waves (wave height)—estimated wave height (trough to crest) in meters; Wind Str—wind strength, estimated on a scale (i.e., 0 = 0 knots, 2 = 5knots, 4 = 10 knots, 5 = 15 knots); Surf Str strength of surface current, estimated on a

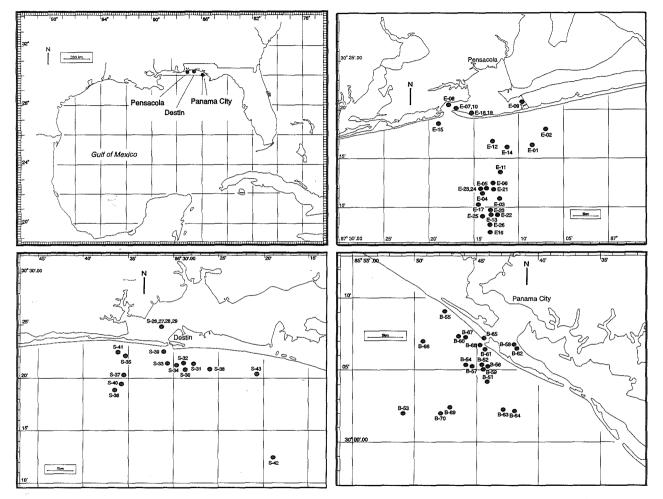


Fig. 1. General (upper left) and specific locations of the artificial-reef study sites in the northern Gulf of Mexico. The specific sites were coded with an E (Pensacola, E-01 through E-26), S (Destin, S-26 through S-43), or B (Panama City, B-51 through B-70) for a total of 64 artificial reefs.

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qualitative scale (0 = none, 5 = strongest);Secchi (secchi depth)-distance below the water surface (as viewed from the boat) that a secchi disk can be seen (to nearest 0.1 m) as an indicator of water clarity; Sur Sal (surface salinity)-refractometer (temperature compensating) reading in ppt of water sampled 0.5 m below the surface; Sur Tmp-surface temperature, measured to the nearest 0.1 C, 0.5 m below the surface; Thermocl (thermocline depth)-depth of the beginning of a noticeable change in water temperature recorded with a depth gauge in meters by divers; Substr-substrate, recorded as a "dummy" indicator variable (1 = rock, 2 = sand, 3 = sand)and shell, 4 = shell, 5 = sand and mud, 6 =shell and mud); Ridge L (ridge length)-distance in meters from crest to crest of a typical sand wave along the bottom; Ridge D-ridge depth, measured from crest to trough of a typical sand wave in centimeters; Vis (visibility)horizontal secchi disk reading in meters recorded at depth (A diver sets the disk down and moves away to the point where the disk is barely visible.); Bot Tmp-bottom temperature, recorded to the nearest 0.1 C by divers with a hand-held thermometer, 1 m above the bottom; Bot Sal (bottom salinity)-a water sample was captured in a vial at depth 1 m above the bottom; upon return to the surface, a refractometer was used to record the refractive index; Cur Str (current strength)-estimated bottom current on a qualitative scale according to strength of surface current; Light (light level)—using a photographer's light meter in an underwater housing, the shutter speed was set at $\frac{1}{45}$ of a second and held horizontal to the bottom at a height of 1 m above the substrate (The reading on the light meter is a relative measurement of the amount of light at depth.); Depth—the maximum bottom depth in meters as recorded by divers with a depth gauge; Struc Dep (structure depth)depth of the uppermost structure of the reef in meters (Subtracting this from the depth will give the height of the artificial reef.); Dis Shre (distance from shore)—nearest (straight line) distance to land in kilometers; N Outfall (nearest outfall)-distance (in km) to the nearest outflow from an estuary; estimates of the percentage of each material that comprised the reef [Concrete; Steel; Tires; Plastic (plastic and PVC); Alum (aluminum); Fbrgls (fiberglass); Rock; Ceramic; and Other]; Btm Cvg (bottom coverage)—estimated percentage of substrate covered by the reef at the specific survey site; Length-length of the reef in meters; Widthwidth of the reef in meters; Height-estimated

average height of the reef above the substrate in meters; Area-area calculated (in m²) from the length and width information above; Volume-volume calculated (in m³) from the length, width, and average height information above; estimated percentage of hole sizes present at a particular reef site (in cm): <10, 11-100, and >100; Complexity-a qualitative assessment of the reef complexity (on a scale from 1 to 20) as a measure of cryptic habitat: 1 is a box with no holes (i.e., no complexity), and 20 is a bridge trestle with numerous entrances and passages (i.e., extremely complex); Growth-estimated percentage of reef surface covered by fouling or attached organisms; Void—estimation of the relative percentage of internal reef volume that was void or empty; Median-the median grain sediment size of a sand sample (in mm) [Sand was gathered in a plastic bag by the divers, within 10 cm of the surface and no closer than 1 m from the reef. Upon return to the laboratory, the sample was dried and shaken to be retained on standard geological sieve sizes (0.063, 0.090, 0.125, 0.180, 0.250, 0.355, 0.425, 0.850, 2.000 mm)]; Sort-sorting coefficient of the grain sediment size calculated from the sieved sand sample; Q1 (first quartile)—the grain sediment size of the first quartile in the sediment sample; Q3 (third quartile)-the grain sediment size of the third quartile in the sediment sample. Tide stage (high, flooding, low, or ebbing) was also recorded. Tide stages were treated as dummy variables (similar to substrate condition) for the stepwise regression models.

Analyses included descriptive statistics of the reef variables and their associated fish fauna and stepwise regression analyses conducted using SAS (1985) to determine the significance and degree of the relationships between the independent variables (i.e., the environmental variables for each reef) and the dependent variables: number of species, number of individuals, species diversity (H'), and average total length (cm). Because our objectives were to identify reef and environmental attributes useful in species-specific management, the number of red snapper, Lutjanus campechanus, and their average size were also used as dependent variables in regression models. Canonical correspondence analyses (using CANOCO; ter Braak, 1992) and two-way indicator species analyses (using TWINSPAN; Hill, 1979) were also conducted to identify multifactor interrelationships among the dependent and independent variables.

RESULTS

General description of the fish assemblage.—The summary of statistics for the total fish assemblage (Table 1) indicate that the mean number of species observed per each of the 564 dependent surveys was 9.5, and the mean number of individuals was 1,680.8. The mean species diversity calculated among all surveys was 0.39, and the mean length of all fish observed was 11.8 cm TL.

We observed 122 fish species or taxonomic units, including larvae and unidentified species (Table 2). The majority of these species could be considered type A or type B species according to Nakamura (1985; type A-species that have direct contact with the reef; type B-species closely associated with the reef without direct contact). Only about 20 of the 122 species recorded (16.4%, mostly carangids and clupeids) were type C species (i.e., species which occupy the mid- and surface layers of water above and some distance from the reef). Clearly, the majority of species were those that have an affinity for the reef substrate. The most frequently occurring fish species in our samples (i.e., occurring in more than 200 of the total 564 surveys) were Haemulon aurolineatum (72% frequency of occurrence), Halichoeres bivittatus (66%), Serranus subligarius (63%), Pomacentrus variabilis (48%); Centropristis ocyurus (45%), Rypticus maculatus (44%), and Equetus umbrosus (36%). The 10 most abundant species (excluding larvae) per survey were: Decapterus punctatus (mean number of individuals per survey 619.7), Haemulon aurolineatum (289.9), Rhomboplites aurorubens (98.6), Anchoa sp. (69.3), Harengula jaguana (56.4), Trachiurus lathami (29.7), Sardinella anchovia (22.8), Orthopristis chrysoptera (12.1), Lagodon rhomboides (8.9), and Halichoeres bivittatus (8.5). Of these species, only R. aurorubens, O. chrysoptera, L. rhomboides, and H. bivittatus could be considered species that associate with hard, reeflike substrates. The majority of individuals by abundance are clearly pelagic schooling species (type C) that are only indirectly associated with reef biotopes. All of the most commonly occurring species are considered type A species.

The largest fishes by mean total length are the predatory, pelagic carangid and scombroid fishes such as *Caranx* spp., *Seriola dumerili*, and *Scomberomorus* spp., as well as muraenid eels (*Gymnothorax* spp.) and rays (i.e., *Dasyatis* spp. and *Mobula hypostoma*). Stepwise regression.—Stepwise regression was performed to determine the associations of the independent variables with the dependent variables. Stepwise models were produced for the independent variables: number of individuals, number of species, species diversity, and mean fish length (in cm). Additionally, models were constructed for the number of red snapper and mean length of red snapper (i.e., No. LCAM and TL LCAM in Table 3, respectively). Variables were included in the models at the 0.15 level of significance.

A summary of the stepwise models is presented in Table 3 for each of the dependent variables. A total of 36.96% of the variation in the number of species is explained by the model using 12 variables that were significant at the 0.15 level. Of these, bottom salinity (9.94%), void space (5.46%), and substrate type (sand and mud) (3.87%) were among the independent variables that accounted for most of the variation in the number of species. With regard to the number of individuals, a total of 13 variables were identified as being significantly associated and cumulatively accounted for 24.84% of the variation. The most important of these were location off Pensacola (4.69%), surface salinity (2.78%), and hole sizes greater than 100 cm (2.51%). With regard to the species diversity (H') recorded during the surveys, a total variation of 22.19% was accounted for by eight independent variables. Among the most influential of these in predicting H' were location off Pensacola (4.45%), bottom temperature (3.98%), and the presence of fiberglass (2.43%). Also contributing to the model was variation in bottom salinity (2.33%), surface salinity (2.01%), and the presence of hole sizes less than 10 cm (1.68%). Variation in size, as measured by estimating the total length, of fish observed during our surveys was accounted for by 15 variables identified as significant at the 0.15 level, for a total of 21.86% of the variation. The most important of these were reef height (2.49%), distance to the nearest outfall (1.96%), presence of plastic (1.91%), and distance to shore (1.87%). Variation in the number of red snapper present on the reefs during our surveys was attributable to 18 variables that accounted for 42.87% of the total variation in species abundance. Among the most associative of these variables were survey year (8.99%), location off Destin (7.38%), and the presence of aluminum (6.18%). An even greater amount of variation in the size of red snapper (52.23%) was shown to be significantly accounted for by 26 variables. The most influential of these were:

Variable ^a	n	Mean	SD	Minimum	Maximum
Yr Blt*	112	1978	18.33	1907.00	1990.00
Year*	189	92.04	0.79	91.00	93.00
Waves*	173	0.52	0.47	0.00	2.50
Wind Str*	185	2,29	1.70	0.00	10.00
Sur Str*	136	1.67	0.99	0.25	5.00
Secchi*	162	7.86	3.33	1.50	21.00
Sur Sal*	178	27.81	6.26	10.00	36.00
ur Tmp*	175	27.16	1.36	22.50	30.00
Thermocl*	131	11.04	4.33	1.50	24.40
Ridge L*	62	0.59	0.39	0.00	1.50
Sidge D*	62	3.73	4.49	0.30	35.00
7is*	186	8.39	4.69	1.50	42.00
Growth*	189	84.82	14.26	30.00	100.00
8tm Tmp*	176	24.45	2.16	20.00	30.30
stm Sal*	184	31.99	3.62	19.00	38.00
Cur Str*	79	1.49	1.15	0.00	5.00
.ight*	176	7.07	6.85	0.50	64.00
Depth +	189	18.49	7.57	3.00	35.10
truc Dep +	189	14.96	8.34	0.00	33.50
Dis Shre +	189	6.16	5.84	0.00	20.20
V Outfall +	189	7.67	7.85	-14.60	22.60
Concrete +	189	20.43	33.84	0.00	100.00
teel +	189	47.32	43.63	0.00	100.00
ires +	189	2.81	12.30	0.00	90.00
lastic +	189	10.54	28.90	0.00	100.00
lum +	189	4.49	20.19	0.00	100.00
brgls +	189	2.38	13.36	0.00	95.00
kock +	189	11.69	31.64	0.00	100.00
Ceramic +	189	0.24	1.88	0.00	15.00
Other +	189	0.02	0.20	0.00	2.00
	189	63.89	28.68	5.00	100.00
Stm Cvg +	189	37.62	42.66	3.50	300.00
ength +	189		8.77	1.75	
Vidth +	189	$\begin{array}{c} 13.89 \\ 2.27 \end{array}$	2.28	0.30	36.00 12.30
leight +					
rea	189	621.03	788.63	6.12	3,717.00
olume	189	1,839.54	4,488.84	9.19	28,800.00
<10 +	189	25.64	17.72	2.00	80.00
1-100 +	189	47.12	21.23	0.00	90.00
100	189	27.24	23.87	0.00	98.00
Complexity +	189	9.74	5.44	2.00	20.00
oid +	189	46.38	26.17	0.00	95.00
fedian +	57	0.46	0.24	0.24	1.78
O +	57	1.50	0.44	1.14	3.03
21 +	57	0.76	0.55	0.30	2.80
23 +	57	0.32	0.10	0.19	0.82
lo. of species	564	9.52	3.29	2.00	20.00
lo. of individuals	564	1,680.81	3,310.16	14.00	30,011
I'	564	0.39	0.23	0.00	1.00
lean length	564	11.75	6.60	1.96	70.53

TABLE 1. Summary of independent and dependent variables. Explanations for the variable abbreviations are found in the text.

^a See text for explanation of abbreviations. Environmental-condition variables are indicated with asterisks; reef-attribute variables are indicated with plus signs.

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TABLE 2. Summary of the numbers and sizes of fishes observed on the reefs studied from 1991 to 1993. Abundance averages are based on data from all 564 samples. Length averages are based on data for which the species is present.

	Species	No. of	No. of	No. o	f individuals per sar	nple	Fish length			
Species"	code	fish	samples	Mean	SD	Maximum	Mean	SD	Minimum	Maximun
Abudefduf saxatilis	ASAX	24	8	0.043	0.500	10	8.775	5.617	2	15
Acanthurus chirurgus	ACHI	17	9	0.031	0.317	5	19.822	8.604	7	30
Acanthurus randalli	ARAN	1	1	0.002	0.042	1	25.000		25	25
Acanthurus sp.	ACSP	3	3	0.005	0.073	1	7.000	1.732	5	8
Alectis ciliaris	ACIL	20	1	0.035	0.842	20	25.000		25	25
Aluterus monoceros	AMON	3	1	0.005	0.126	3	40.000		30	45
Aluterus schoepfi	ASCH	4	3	0.007	0.103	2	10.000	0.000	10	10
Aluterus scriptus	ASCR	4	3	0.007	0.103	2	20.000	5.000	15	25
Anchoa sp.	ANSP	39,107	25	69.339	538.833	10,000	3.231	1.198	1	8
Antennarius ocellatus	AOCE	3	3	0.005	0.073	1	21.666	2.887	20	25
Apogon pseudomaculatus	APSE	493	114	0.874	2.787	23	7.447	2.611	2	16
Archosargus probatocephalus*	APRO	47	30	0.083	0.468	6	32,906	10.449	10	50
Bairdiella chrysoura	BCHR	66	6	0.117	2.166	50	13.333	4.719	8	20
Balistes capriscus*	BCAP	265	97	0.470	2.225	38	26.182	8.375	10	60
Blennius sp.	BLSP	591	116	1.048	3.838	67	4.782	1.651	1	12
Brotula barbata	BBAR	1	1	0.002	0.042	1	60.000		60 -	. 60
Calamus leucosteus	CLEU	1	1	0.002	0.042	1	12.000		12	12
Calamus sp.*	CASP	129	46	0.229	0.909	13	25.502	6.874	10	50
Caranx bartholomaei	CBAR	438	30	0.776	8.084	150	16.422	7.441	5	40
Caranx crysos	CCRY	1,245	44	2.207	14.041	204	25.587	5.910	10	35
Caranx hippos	CHIP	316	5	0.560	12.642	300	59.000	31.504	25	95
Caranx ruber	CRUB	39	14	0.069	0.599	10	16.928	3.100	10	20
Centropristis ocyurus*	COCY	2,727	256	4.835	13.009	130	13.385	5.055	2	35
Centropristis philadelphica	CPHI	2	. 2	0.004	0.059	1	7.000	1.414	6	8
Centropristis striata	CSTR	41	23	0.073	0.578	12	17.746	5.172	7	25
Chaetodipterus faber	CFAB	831	61	1.473	7.844	100	26.948	6.896	10	50
Chaetodon ocellatus	COCE	101	56	0.179	0.624	8	14.850	3.944	. 5	25
Chaetodon sedentarius	CSED	7	4	0.012	0.151	2	15.000	4.082	10	20
Chaetodon striata	CSTR	1	1	0.002	0.042	1	10.000		10	10
Chilomycterus schoepfi	CSCH	· 19	15	0.034	0.224	3	18.600	7.696	6	30
Chromis enchrysurus	CENC	189	43	0.335	1.980	35	8.154	3.732	1	17
Chromis scotti	CSCO	204	29	0.362	2.164	25	7.797	2.816	2	12
Coryphopterus sp.	CORY	50	24	0.089	0.565	8	4.818	2.534	3	15
<i>Dasyatis americana</i> l by The Aquila Digital Community,	DAME	2	564	0.004	0.084	2	0.621	14.738	150	200

	Species	No. of	No. of	No.	of individuals per san	Fish length				
Species ^a	code	fish	samples	Mean	SD	Maximum	Mean	SD	Minimum	Maximum
Dasyatis say	DSAY	1	1	0.002	0.042	1	40.000		40	40
Decapterus macarellus	DMAC	4,000	3	7.092	107.048	2,200	6.455	1.878	4	8
Decapterus punctatus	DPUN	349,531	175	619.735	2,005.690	20,000	11.864	4.577	2	25
Decapterus sp.	DESP	1,000	1	1.773	42.107	1,000	5.000		3	7
Diplectrum formosum*	DFOR	184	73	0.326	1.109	11	14.042	5.634	4	27
Diplodus holbrooki*	DHOL	3,054	142	5.415	63.873	1,500	17.136	5.052	2	30
Écheneis neucratoides	ENEU	11	4	0.020	0.312	7	35.000	20.412	15	55
Elagatis bipinnulata	EBIP	8	1	0.014	0.337	8	25.000		25	25
Epinephelus cruentatus	ECRU	1	1	0.002	0.042	1	25.000		25	25
Epinephelus morio	EMOR	20	13	0.035	0.308	6	28.013	12.074	15	60
Equetus lanceolatus	ELAN	341	34	0.605	6.234	101	18.119	7.465	2	30
Equetus umbrosus	EUMB	833	205	1.477	3.391	41	13.112	5.990	1	35
Eucinostomus sp.	EUSP	68	8	0.121	1.870	40	5.625	3.502	2	12
Euthynnus alletteratus	EALE	89	8	0.158	2.046	40	45.000	5.345	40	50
Gobiosoma horsti	GHOR	1	1	0.002	0.042	1	4.000		4	4
Gymnothorax moringa	GMOR	7	7	0.012	0.111	1	44.285	26.209	15	90
Gymnothorax saxicola	GSAX	7	5	0.012	0.151	3	39.000	7.416	30	50
Haemulon aurolineatum*	HAUR	16,351	407	289.923	780.382	10,046	12.304	5.784	2	35
Haemulon plumieri*	HPLU	906	86	1.606	13.989	300	19.001	5.926	7	35
Haemulon sp.	HASP	500	1	0.887	21.054	500	2.000		2	2
Halichoeres bivittatus	HBIV	4,782	375	8.479	23.785	335	9.883	5.216	1	32
Halichoeres caudalis	HCAU	3	2	0.005	0.094	2	13.500	9.192	7	20
Halichoeres maculipinna	HMAC	2	2	0.004	0.059	1	15.000	0.000	15	15
Harengula jaguana	HJAG	31,795	27	56.374	406.096	7,000	7.858	4.804	3	20
Hemipteronotus novacula	HNOV	45	7	0.080	0.962	15	9.524	3.948	6	15
Heteroconger sp.	HESP	18	1	0.032	0.758	18	30.000		30	30
Holacanthus bermudensis	HBER	285	164	0.495	0.995	8	28.005	8.644	5	55
Hypleurochilus geminatus	HGEM	14	10	0.025	0.213	3	4.800	1.229	3	6
Hypsoblennius hentz	HHEN	1	1	0.002	0.042	1	7.000		7	7
Ioglossus calliurus	ICAL	12	3	0.021	0.315	6	7.777	3.288	4	12
Kyphosus sectatrix	KSEC	12	7	0.021	0.230	4	25.893	7.730	20	40

TABLE 2. Continued.

	Species	No. of	No. of	No. of individuals per sample				Fish length				
Species"	code	fish	samples	Mean	SD	Maximum	Mean	SD	Minimum	Maximum		
Opsanus pardus	OPAR	43	34	0.076	0.336	4	28.603	7.338	15	45		
Orthopristis chrysoptera	OCHR	6,851	163	12.147	45.510	550	18.498	4.543	3	35		
Parablennius marmoreus	PMAR	70	28	0.124	0.810	11	4.720	1.201	2	7		
Paralichthys albigutta	PALB	23	20	0.041	0.246	4	29.125	10.042	15	60		
Paralichthys lethostigma	PLET	1	1	0.002	0.042	1	40.000		40	40		
Pomacanthus arcuatus	PARC	1	1	0.002	0.042	1	30.000		30	30		
Pomacentrus dorsopunicans	PDOR	1	1	0.002	0.042	1	5.000		5	5		
Pomacentrus partitus	PPAR	2	9	0.039	0.365	5	8.533	1.913	5	12		
Pomacentrus variabilis	PVAR	2,224	260	3.060	8.753	135	7.891	3.383	1	20		
Prionotus sp.	PRSP	2	2	0.004	0.059	1	27.500	3.535	25	30		
Raja eglanteria	REGL	8	8	0.014	0.118	1	37.500	5.976	30	50		
Raja sp.	RASP	9	8	0.016	0.139	2	42.500	10.351	25	55		
Rhinobatos lentiginosus	RLEN	7	5	0.012	0.139	2	68.000	14.832	50	90		
Rhomboplites aurorubens*	RAUR	55,594	180	98.571	485.404	6,001	15.466	6.898	2	40		
Rypticus maculatus	RMAC	719	247	1.275	2.108	11	16.090	4.357	2	30		
Sardinella anchovia	SANC	12,832	14	22.752	243.238	5,000	13.357	5.597	5	20		
Scartella cristata	BCRI	7	4	0.012	0.163	3	4.000	0.816	3	5		
Sciaenops ocellatus	SOCE	9	2	0.016	0.282	6	30.833	5.893	25	35		
Scomberomorus cavalla	SCAV	6	3	0.011	0.178	4	51.666	22.546	30	75		
Scomberomorus maculatus	SMAC	52	21	0.092	0.589	7	40.079	6.135	35	60		
Scorpaena brasiliensis	SBRA	12	12	0.021	0.144	1	24.166	4.669	15	30		
Seriola dumerili*	SDUM	2,392	113	4.241	19.947	200	41.612	20.116	7	150		
Seriola faciata	SFAS	1	1	0.002	0.042	1	20.000		20	20		
Seriola rivoliana	SRIV	2	2	0.004	0.059	1	32.500	3.535	30	35		
Serranus subligarius	SSUB	1,308	353	2.319	3.345	21	8.095	2.243	2	25		
Sphoeroides parvus	SPAR	2	2	0.004	0.059	1	12.500	3.535	10	15		
Ŝphoeroides spengleri	SSPE	12	12	0.021	0.144	1	15.000	6.661	7	30		
Sphyraena barracuda	SBAR	16	5	0.028	0.356	6	36.000	13.416	30	60		
Sphyraena borealis	SBOR	1,252	21	2.220	25.504	500	17.087	6.153	5	30		
Sphyraena sp.	SPSP	1,164	19	2.064	22.351	400	14.175	7.068	6	25		
Synodus foetens	SFOE	14	8	0.025	0.244	4	8.438	2.665	5	12		
Trachurus lathami	TLAT	16,772	19	29.738	256.237	5,000	9.210	4.626	4	20		
Unidentified	UNID	1	1	0.002	0.042	1	20.000		20	20		

"Asterisks indicate species that are most sought after by fishers.

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TABLE 3.	Results of the stepwise linear regression. The values under each dependent variable indicate the	2
ar	nount of variation accounted for by the corresponding dependent variable in the model.	

	Dependent variables ^b										
Independent variables ^a	No. of species	No. of individuals	H'	Average TL	No, LCAM	TL LCAM					
Alum					0.0618	0.0906					
Area						0.0133					
3tm Cvg		0.0197									
Btm Sal	0.0994	0.0083	0.0233	0.0161	0.0076	0.0061					
3tm Tmp	0.0195	0.0262	0.0398		0.0253						
Complexity				0.0091		0.0051					
Concrete				0.0126							
Cur Str											
Depth					0.0279						
Destin	0.0365				0.0738	0.0595					
Dis Shre			0.0303	0.0187		0.0119					
brgls	0.0124		0.0243	0.0123	0.0112	0.0059					
Growth	0,0141	0.0153	0.0410	010140	0.0077	0.0052					
leight		010100		0.0249	0.0097	0.0085					
Length		0.0123		0.0410	0.0007	0.0000					
light		0.0140		0.0109							
Aonth				0.0161		0.0266					
N Outfall				0.0196	0.0062	0.0200					
Other		0.0097		0.0190	0.0002	0.0072					
-		0.0469	0.0445								
Pensacola			0.0445	0.0101							
lastic		0.0091		0.0191	0.0000	0.0700					
Rock		0.0100			0.0098	0.0729					
ecchi		0.0188			0.0000	0.0139					
teel					0.0099	0.0277					
ubstrate 2						0.0106					
Substrate 5	0.0387										
ubstrate 6					0.0071	0.0186					
bur Sal		0.0278	0.0201	0.0151	0.0169	0.0059					
ur Str	0.0315				0.0373	0.0269					
ur Tmp			0.0141	0.0078							
hermocl						0.0187					
ide 1		0.0171		0.0145	0.0056	0.0068					
ide 2	0.0071					0.0116					
ïres	0.0251	0.0121									
ïs	0.0146										
<i>'</i> oid	0.0545										
'olume			0.0087	0.0117	0.0077	0.0084					
Vaves					0.0133	0.0051					
Vidth						0.0082					
Vind Str	0.0171										
éar					0.0899	0.0404					
m <10			0.0168								
m >100	0.0132	0.0251		0.0101		0.0067					
otal	0.3696			0.2186	0.4287	0.5223					

* See text for explanation of abbreviations.

^b LCAM = red snapper.

presence of aluminum (9.06%), presence of rock (7.29%), location off Destin (5.95%) and year of the survey (4.04%).

Two-way indicator species analysis.—Two-way indicator species analysis (TWINSPAN) is a polythetic, divisive clustering technique that divides the study sites or species into groups based on species abundance using reciprocal averaging (Gauch, 1982). The species cluster diagram was constructed, but no biologically meaningful interpretation could be gleaned from it;

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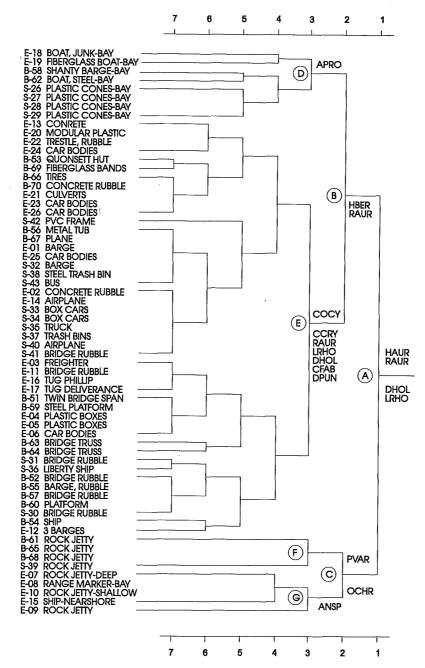


Fig. 2. Cluster dendrogram of the results of the TWINSPAN analysis to determine the patterns among the artificial reefs based on the 40 most abundant fish species in the study.

therefore, it is not presented here. Figure 2 presents the results of the TWINSPAN analysis used to group or classify the study sites (i.e., site cluster diagram) based on untransformed species abundances of the 40 most abundant species (i.e., those species for which 100 or more individuals were recorded during the study). The key species (identified by the species code listed in Table 2) that helped determine the clusters are indicated at the nodes on the dendrogram in Figure 2.

Four biologically meaningful clusters were formed at level 2. Cluster D is a group of reefs located within estuaries. Clusters F and G are reefs at the entrances to estuaries. Cluster E comprises the vast majority of reefs, and these are predominantly located offshore. The species that are primarily responsible for the cluster divisions (i.e., those species with maximum values along the ordination axes; Gauch, 1982) were generally the dominant species at the sites. Of note is Archosargus probatocephalus (APRO) which is an estuarine species that feeds predominantly on hard-shelled organisms attached to vertical structures. Its identification as an indicator species at bay sites on structures with high relief confirms its ecological affinities. Similarly, Pomacentrus variabilis (PVAR) is one of the dominant species of the rock jetty habitat at the entrances to estuaries and was identified as being an indicator species for this general habitat. While this species does indeed occur offshore, its dominance of the inshore rock assemblage is recognized by this analysis. Rhomboplites aurorubens (RAUR) was the only species to serve as an indicator species at levels 1, 2, and 3. Its abundance on high vertical relief structures at offshore reefs makes it an indicator species for this habitat in the northern Gulf of Mexico.

Canonical correspondence analysis.—Canonical ordination techniques such as canonical correspondence analysis (CCA) are useful in detecting patterns in the variation in species abundance that can be explained by the measured environmental variables (ter Braak, 1987). They also allow the simultaneous recognition of the relationships between species and environmental factors. One of the main purposes of our study was to identify attributes of the artificial reef environment that were associated with various fish species, especially those preferred by anglers. Because of the large number of variables that were measured in the field, however, the analyses became quite cumbersome. Therefore, the environmental data set was separated into two groups: (1) reef-attribute variables such as size, composition, and placement (i.e., variables a reefbuilder could control in the design, construction, and disposition of a reef; indicated by plus signs in Table 1) and (2) environmentalcondition variables (i.e., weather, sea state, water conditions, etc.; indicated by asterisks in Table 1). Variables such as area and volume were not included in the analyses, as these are obvious covariates with reef length, width, and height variables. Additionally, the variable hole size >100 cm was dropped from the analysis, because CANOCO detected extreme colinearity with this variable and several other variables. The untransformed data set on species abundance was used in our analyses, because it produced higher eigenvalue loadings on the first two axes than when using logarithm or square root transformed data sets.

The proper way to examine the results of the CCA is to superimpose parts A and B of each figure from similar analyses to identify specific factors associated with the presence and abundance of a particular species. To simplify the ordination scatter plots and to make them more meaningful, they are presented only for fish species (indicated by asterisks in Table 2) that are among the most sought-after by recreational and commercial fishers.

Reef attributes .- In Figure 3A, the preferred fish species are displayed according to their ordination values, derived from the species abundance matrix, on the first two canonical axes (eigenvalues of 0.571 and 0.337, respectively). The species-reef attribute correlations were 0.896 and 0.856 for axes 1 and 2, respectively. In Figure 3A, it can be noted that some species form groups presumably based on their common habitat affinities and abundance. Similarly, examining Figure 3A and B together permits some insight into the variables associated with the distribution of species according to the attributes of the reefs. Those variables farther from the center of the graph depict a stronger influence of the interrelationships. The vectors of the variables point from the center toward the periphery and indicate the positive influence of that variable. For example, Lagodon rhomboides (LRHO) and Diplodus holbrooki (DHOL) were generally associated with reefs composed of rock. None of the 15 most preferred species tended to be associated with fiberglass [with the possible exceptions of Lutjanus griseus (LGRI) and Mycteroperca microlepis (MMIC)]. Balistes capriscus (BCAP) was generally associated with reefs composed of steel. Haemulon plumieri (HPLU) was associated with reefs made of aluminum. A larger group of species was associated with reefs placed on a coarse sand substrate.

The preferred species analyzed here are not located far from the center on the ordination axes. This implies that the loadings for these species are low and that we cannot have a great deal of confidence that the groupings are significant. On the other hand, the fact that several reef-attribute vectors terminate far from the center of the ordination (i.e., fiberglass, rock, nearest outfall, depth, and distance to shore) implies that these factors are quite important in the distribution and abundance of several nonpreferred species. BORTONE ET AL.—FACTORS ASSOCIATED WITH ARTIFICIAL-REEF FISH 29

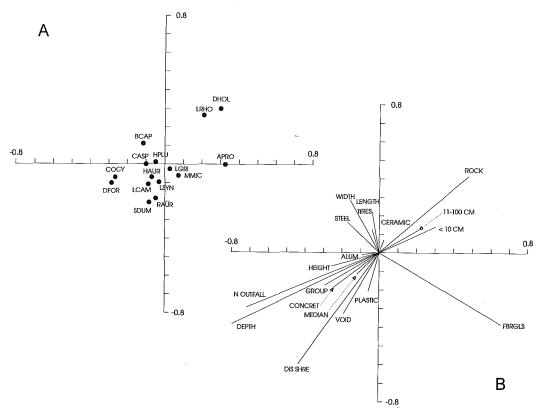


Fig. 3. Ordination of the CCA loadings for the 15 commercially and recreationally important fish species (A) and the corresponding reef attribute factors (B) associated with the artificial-reef assemblages.

Environmental conditions.—The second CCA examined the relationship of the same 15 preferred fish species with environmental conditions on axes 1 and 2 (eigenvalues of 0.587 and 0.307, respectively). The species–environmental conditions correlations were 0.911 and 0.815 for axes 1 and 2, respectively.

Superimposing Figure 4A and 4B, one can appreciate the importance of environmental conditions in the distribution and abundance of preferred fish species on the reefs. Perhaps even more apparent than in the case for reefattribute analysis above, however, is the close distribution that all preferred species have about the origin of the ordination axes. This implies that the associations of these species are not strongly influenced by the environmental variables. One of the clearest and easiest to understand species-environment association patterns is seen in the position of Balistes capriscus (BCAP) relative to the amount of growth on the reef (Fig. 4A,B). Individuals of this species are pickers, and their association with attached growth is likely. Species such as Diplectrum formosum (DFOR), Calamus sp. (CASP), and Centropristis ocyurus (COCY) were

found more often and more abundantly at higher salinities, in areas with generally better water clarity. While other patterns of association may exist, they are not evident in this analysis.

DISCUSSION

There have been only a few studies conducted on artificial reefs in the same area of the northern Gulf of Mexico to which our survey results can be compared. The total number of species (122) observed in our study is lower than the 204 species observed by Hastings (1979) during his 3-yr study conducted at the inshore rock jetties at Destin and Panama City (sites S-39 and B-68, respectively). However, Hastings (1979) conducted fish faunal evaluations at these sites over the entire year for several years and used visual surveys as well as rotenone icthyocide to assess the fish assemblages. Bortone (1976) examined the impact that a hurricane had on the fauna of the same rock jetty at Destin (S-39). Bortone and Van Orman (1985) incorporated several similar sites from Pensacola (E-12, E-15), Destin (S-36,



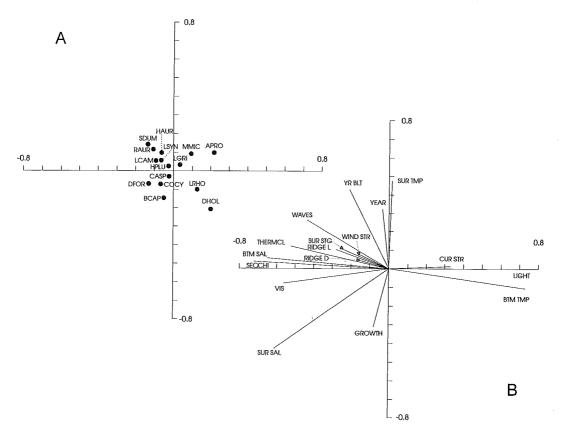


Fig. 4. Ordination of the CCA loadings for the 15 commercially and recreationally important fish species (A) and the corresponding environmental factors (B) associated with the artificial-reef assemblages.

S-41), and Panama City (B-60) in their surveys of artificial reef faunas around the state. Chandler et al. (1985) and Sanders et al. (1985) investigated the association of fish fauna with the features of two barges off Panama City (B-55). Hastings et al. (1976) also surveyed the stage platform reef of Panama City (B-60). Bortone et al. (1994) evaluated the initial colonization first-year succession by fishes on the plastic cones in the estuary in Choctawhatchee Bay (S-26, S-27, S-28, S-29). A comparison of the species lists from these studies indicates that the summer-early fall fauna at all of these locations and times are qualitatively similar to that of the respective sites examined in this study. The species abundances were not quantitatively comparable, because the abundance values were recorded using different methods (except for Bortone et al., 1994). Those species that were among the most abundant and frequently encountered in our study are mirrored in the results of the studies cited above.

Stepwise regression results.—The results of the stepwise regression analysis can be used to de-

termine the associations between the faunal dependent variables and the measured independent variables. Although no variation in a dependent variable was explained fully, it should be noted that a fair amount of variation was explained for number of species (37%), number of red snapper (43%), and size of red snapper (52%). Stepwise regression models can be useful in reducing the number of independent variables that have a significant impact on the dependent variables one wishes to manage. Although there are no firm "rules," it should be noted that attempting to control more than four or five variables in any management procedure could prove impossible or, at the least, frustrating. What is disheartening from a management perspective is that the lowest number of significant variables identified in this study was eight, for number of species (at the 0.15 level). The independent variables that helped account for the most variation among the assemblage-related dependent variables (i.e., number of species, number of individuals, H', and average size) were those environmental variables associated with temperature

and salinity. Reef attribute variables, such as materials of composition, configuration, and dimension, generally were among the least useful in accounting for variation among the assemblage-dependent variables.

Bortone and Van Orman (1985) used correlation and regression analyses to identify significant relationships among dependent variables (i.e., family abundance) and independent variables around Florida. At the 0.15 level of significance, they identified positive associations of serranid abundance with reef area and distance from shore, while negative associations were noted with steel and rubber materials, reef complexity, reef volume, and surface temperature. Carangids were positively associated with reef height and visibility and negatively associated with depth and bottom salinity. Lutjanids were positively associated with the presence of tires, reef height, surface and bottom temperature, and bottom salinity, while they were negatively associated with reef area and surface salinity. Haemulids were positively associated with reef height and distance to the pass, while their abundance was negatively associated with distance to shore.

In the northern Gulf off Panama City, FL, Chandler et al. (1985) examined the relationship between three substrate variables (i.e., rugosity, percent of substrate cover, and vertical relief). They indicated that greater species abundance and richness were noted from their offshore sites that had higher rugosity and percentage of substrate cover. They concluded that higher structural complexity of reefs was more important than vertical relief in attracting or concentrating fishes on artificial reefs composed of barges. As part of this same study, Sanders et al. (1985) noted that water temperature had the greatest impact on the reef fish assemblage attracted to an artificial reef, especially relative to the number of individuals and species that were linearly correlated with water temperature. They also noted that the number of individuals was positively associated with visibility. They noted that the numbers of species and individuals were negatively associated with current speed and that species diversity was generally higher during the summer and fall.

The temperature-dependent feature is generally recognized in the warm temperate waters in the northern Gulf (Hastings et al., 1976; Hastings, 1979; Bortone et al., 1994). We noted no association of water temperature with the dependent variables sampled during our study, but our study was purposefully conducted during the summer to reduce the impact that minor changes in temperature might have on the dependent variables. Nevertheless, bottom temperature still had a significant (0.15 level) association with number of species, number of individuals, species diversity, and number of red snapper in our study. Features noted as significant in the other studies were only somewhat influential in the dependent variables in our study. For example, reef height was noted by Bortone and Van Orman (1985) as being significantly associated with the abundance of carangids, lutjanids, and haemulids. This variable was only slightly influential on the dependent variables of fish size and the number of red snapper recorded in our study.

Regression analysis does indicate some common patterns of association among reef fishes associated with artificial reefs in the northern Gulf of Mexico. Higher salinities are generally associated with greater number of individuals, number of species, diversity, and size. This general association was noted in the present study as well as in those by Sanders et al. (1985) and Bortone and Van Orman (1985).

TWINSPAN.---The TWINSPAN analysis was useful in grouping the reef sites based on their associated fish assemblages. The faunal associations reflect the general habitat types of the reefs in the study area. Thus, three major groups of reefs (based on their associated fish assemblages) were formed: (1) those located offshore (group E in Fig. 3); (2) reefs located in estuaries (group D); and (3) reefs located at the entrances of estuaries (groups F and G). An often stated a priori assumption of most fishers in the area is that certain fish species tend to associate with one type of material more than they associate with another. However, reefs did not generally group together based on their materials of composition. It must be acknowledged, however, that this study does not represent a balanced design and the "materials of composition-faunal affinity" hypothesis may not have been fairly tested by our study. For example, no reefs composed of plastic cones were located offshore, rock jetties were only located at the entrances to estuaries, and no large barges and tugboats were located in estuaries. Nevertheless, there was no clear pattern of species-specific reef composition associations that was apparent from the analysis of our data.

The TWINSPAN analysis did indicate that the vermilion snapper, *R. aurorubens*, was one of the indicator species that was influential in forming groups at three different levels in the analysis. This is a dominant species of the off-

shore artificial-reef fish assemblage, as both juveniles and adults. Grimes et al. (1982) noted that it was one of the most common fishes of the offshore reef and rock outcropping community off the southeastern coast of the United States. Our study results indicate that it is a species that typically inhabits the artificial reefs in the northern Gulf and, unlike other species observed in our study, does not tend to have broader habitat affinities. Thus, the vermilion snapper may prove to be a key species in the identification of an offshore artificial reef fish assemblage in the northern Gulf of Mexico.

Canonical correspondence analysis.—CCA is an ordination technique that uses eigenvectors to maximally reveal the joint or common associations between the site-by-species matrix and the site-by-environmental-variable matrix in ecological studies. This method of analysis permits us to determine the dominant pattern relative to variation in species composition and to relate that pattern to the environmental variables (ter Braak, 1987). CCA is a multivariate, direct gradient analysis in which a set of species is directly related to a set of environmental variables. It is a distinct improvement over single-species (or dependent-variable) comparisons with environmental factors, which are especially cumbersome when the number of factors is greater than two or three (ter Braak, 1986). In addition, it is far superior to detrended correspondence analysis (DCA), in that the environmental variables associated with the ordination axes are not just inferred (e.g., Bortone et al., 1991), but clearly identified. Mc-Gehee (1994) was successful, however, in identifying several coral reef factors with fish species assemblages off Puerto Rico using DCA.

In our study, the CCA indicated a strong association of gray triggerfish, *B. capriscus*, with the amount of growth on the reef structure. Given the dietary habits of this species, this association is expected (Nelson and Bortone, 1996). The higher salinity association of *D. formosum* and *C. ocyurus* was also expected, given their general distribution and habitat affinities (e.g., Bortone, 1971).

Several species-reef-attribute associations were revealed by the CCA that were not apparent in the TWINSPAN or stepwise regression analyses. Specifically, the rock substrate associations of *L. rhomboides* and *D. holbrooki* are expected, given their general association with rock jetties (Hastings, 1979). These were identified in CCA but not with the other analytical techniques. The loadings of *L. campechanus* were not high enough in the CCA to be of any use in determining the habitat- or reef-attribute-associated variables. The CCA technique generally appears to be useful in defining species associations and identifying the underlying environmental factors that may have impacted these associations. For species that are habitatlimited, the CCA technique will be extremely useful in determining the suitable habitat features when management actions are directed toward species or similar species groups.

The paucity of faunal associations among species in our analysis may be due to the fact that species assemblages on artificial reefs are inconsistently composed within the northern Gulf. This suggests that, while ecological units in the form of guilds may be consistent on these reefs, the species composition of a guild is somewhat arbitrary. This gives some plausibility to the hypothesis that reef assemblages are chiefly orchestrated stochastically or through settlement and colonization factors that remain unpredictable (Sale and Dybdahl, 1975; Helfman, 1978; Sale, 1978, 1991; Bohnsack, 1983).

Many of the reef-attribute variables were not strongly associated with the abundance of any preferred fish species. This may indicate that reef attributes are not important to the distribution of these fishes. Alternatively, it may be difficult to distinguish the species-reef-attribute relationship when multiple factors are operating. For example, the CCA showed that greater amberjack, Seriola dumerili, were generally associated with greater distances offshore and with reefs composed of concrete and plastic with more void space. Additionally, gray snapper, L. griseus, and gag, M. microlepis, were associated with fiberglass reefs, but this association was weak. Statistical interference with the loadings from other variables may have reduced our ability to detect the true nature of the relationships between these species and the habitat features. While other statistical procedures suffer from this same feature, CCA may be the best alternative, at present, for revealing the layered impacts of multiple variables on fish assemblage associations.

It appears that regression analysis may be useful in identifying factors associated with general assemblage variables but may not be effective on species-specific associated factors, especially when the number of measured variables is large. CCA can be useful in building reefs or in planning their design in the future with respect to determining composition of materials, overall dimensions, and geographical position. Statistically, the associations with types of materials in the present study were

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weak. The rock-pinfish-spottail pinfish association was the strongest. Reef attributes related to reef size (length, width) were associated with triggerfish. Most instructive is that reef features such as placement depth and height had virtually no impact on these preferred species.

In the future, it will be possible to construct artificial reefs with a much greater degree of assurance that the limited resources currently available for artificial reef construction will be optimized. It is also projected that the outcome of this study will permit the construction of reefs designed to attract or maintain preferred species. One of the goals of any reef project is not necessarily to build reefs to have the highest standing biomass, but to build them so that they will hold or attract the sizes of species most preferred by recreational and/ or commercial users. For example, a result of this study would be the construction or modification of reefs to have a higher likelihood of attracting larger snapper and grouper, as opposed to attracting many more smaller, nonpreferred species, such as grunts or pinfish.

From this study, it would seem that there are still many unanswered questions regarding our ability to create artificial habitats in the marine environment with the specific features necessary to provide suitable conditions for preferred fish species or assemblage characteristics. It appears, however, that regression analysis may be a suitable way to determine the appropriate environment for assemblage characteristics, TWINSPAN can help determine the major environmental factors that determine assemblage structure; and CCA can be readily used to identify the environmental and reef-attribute characteristics associated with particular species in an assemblage.

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- (SAB, RKT, RCC) BIOLOGY DEPARTMENT AND (CMB) DEPARTMENT OF MATHEMATICS AND STATISTICS, UNIVERSITY OF WEST FLORIDA, PENSACOLA, FLORIDA 32514; AND (RLH) DE-PARTMENT OF MARINE SCIENCES, UNIVERSITY OF PUERTO RICO, MAYAGUEZ, PUERTO RICO 00709. Date accepted: May 27, 1997.