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## Development of an Epifaunal Assemblage on an Estuarine Artificial Reef

TONY R. MARTIN AND STEPHEN A. BORTONE

Twelve Polyolefin<sup>®</sup> cones were placed in Choctawhatchee Bay, Okaloosa County, Florida, on 20 Oct. 1987, as an artificial reef to examine the succession of the associated epibenthic invertebrate assemblage and its relationship to environmental factors. Ninety-five epifaunal settling plates with individual surface areas of 706.5 cm<sup>2</sup> were removed from the reefs. The epifaunal settling plates bore 124,893 organisms from 90 taxa. The number of taxa and individuals associated with the reef gradually increased from deployment in Oct. to a maximum in June. Species diversity tended to increase through the 12-mo study. Coverage by the epifauna stabilized after 4 mo of deployment. A canonical correlation model attributed 86% of the variation in taxa abundance to variation in the independent variables equatorial moon position, salinity, temperature, reef module surface area, absolute time from noon, and vertical height of each settling plate above the substrate. Initial colonizers were typically motile organisms that were gradually succeeded by sedentary organisms. Arborescent bryozoans may have created a complex microhabitat, which facilitated the colonization of grazing species such as gastropods.

Artificial reefs have intrigued fishermen for many years with their apparent ability to develop an abundant and diverse marine assemblage. Concomitantly, artificial reefs have intrigued scientists as platforms from which to test ecological hypotheses related to the development of the associated faunal assemblage (Carr and Hixon, 1997). Polovina (1991) offered a model to explain how artificial reefs may permit an increase in total biomass. However, whether or not artificial reefs actually increase total biomass or merely attract fishes to an area and increase fishing efficiency has not been resolved (Bohnsack, 1989; Grossman et al., 1997). Details on succession and colonization of associated faunal assemblages, as well as on the food web dynamics of artificial reefs, are not known (Bohnsack and Sutherland, 1985).

To date, several studies have examined succession of the fish assemblages on artificial reefs (e.g., Bohnsack et al., 1991; Bortone et al., 1994). Only a few studies have examined the succession and colonization patterns that occur among the associated epibenthic invertebrates (e.g., Ardizzone et al., 1989; Bailey-Brock, 1989; Fitzhardinge and Bailey-Brock, 1989). Even fewer studies have examined the associated environmental factors that may be responsible for the epifaunal assemblage characteristics on artificial reefs in any detail (e.g., Relini et al., 1995).

Development of fish assemblages on artificial reefs has been studied in many parts of

world, but few studies have examined faunal development on artificial reefs that occur within estuaries. Bortone et al. (1994) examined the fish assemblage development associated with an estuarine artificial reef in the northern Gulf of Mexico. The present study, reported herein, was conducted simultaneously with their study and is concerned with the development of the epibenthic invertebrate assemblage. An examination of the characteristics of epifaunal invertebrate development, along with an investigation into the associated environmental variables, should permit a more thorough understanding of the development of the associated reef fish assemblage. Because this study was conducted on a reef located within the confines of an estuary, the study results present a unique opportunity to more fully understand the potential of estuarine artificial reefs. Information on the epibenthic fauna associated with an estuarine artificial reef should provide some of the data needed to determine if artificial reefs can indeed play a role in increasing the total biomass of target species within a limited area.

### METHODS

*Study area.*—Choctawhatchee Bay is located in the western portion of Florida. It receives water from the Choctawhatchee River, small coastal streams, and ground water (Livingston, 1990). The Bay discharges into the Gulf of Mexico at Destin, FL, through East Pass. The

following description is taken chiefly from Hastings (1979). The low-energy offshore coastal area is biologically monotonous, and the substratum is white quartz sand along the beaches and inshore areas. Maximum surface salinity at the Choctawhatchee River mouth is 30 ppt. Water temperature in Choctawhatchee Bay can vary from 9 C in January to 32 C in August. Tidal regimes vary from 0.6 to 1.0 m and are diurnal and minimal; however, river runoff conditions contribute to strong ebb tidal surges (Livingston, 1990).

The artificial reef group (*sensu* Grove and Sonu, 1985) examined herein was established in Choctawhatchee Bay approximately 800 m NW of Destin, FL, in 6.5 m of water on a coarse sand substratum (30°24'40"N, 80°30'30"W). Initially the reef site was flat; however, during the study, sand "waves" up to 0.5 m high became established in the immediate area. The reef site was within 500 m of the intracoastal waterway, and there was substantial recreational activity in the area, including boating, fishing, and SCUBA diving.

*Artificial reef features.*—The reef group was deployed on 20 Oct. 1987 at a depth of 6.5 m (Bortone et al., 1994). It consisted of 12 modular Polyolefin<sup>®</sup> cones anchored in four sets, with three cones per set. Two sets consisted of tall cones with a vertical height of 3.9 m and base diameter of 2.9 m, and two sets had short cones 1.4 m high and 2.3 m in diameter. Cones in each set bore several openings of one diameter: either 15, 20, or 25 cm. Disks, made from the 15-cm diameter holes cut from the Polyolefin cones, were attached to the sides of the cones to serve as settling plates for encrusting epifauna. Each settling plate had a surface area of 706.5 cm<sup>2</sup>. Settling plates were numbered and marked with a letter corresponding to the cone to which they were attached. Surface area of the cones varied from 36.0 to 121.6 m<sup>3</sup> (depending on the size of the cone and the size and number of openings).

*Sampling strategy.*—Sampling was conducted on or about the 20th day of each month from Nov. 1987 through Oct. 1988. Eight settling plates were removed from either a tall or short cone on each sampling date (one plate was lost during sampling in July). Two plates were collected from each of four compass positions (NW, NE, SE, SW): four plates 1.5–3.0 m above the substrate and four plates within 0.5 m of the substrate. These vertical positions were recorded on a plastic slate as high or low along with the compass orientation and the identifying

reef letter and plate number. During plate retrieval, one diver removed the plate while another held a plastic bag directly beneath the plate to reduce the loss of motile organisms. The entire epifaunal assemblage attached to the plates was fixed in 10% seawater formalin. The fixative was replaced with 40% isopropyl alcohol after at least 1 wk.

*Independent variables.*—Equatorial moon position: Lunar cycles have often been observed to be a significant factor in influencing the abundance and distribution of marine organisms (Sanders et al., 1985). Potential influence of lunar cycle was estimated using the relative position of the moon in reference to the equator [i.e., equatorial moon position (EMP)] calculated using NOAA tide tables for 1987 and 1988. Equatorial moon position was calculated (modified from Sanders et al., 1985) as follows

$$\text{EMP} = \text{FD}[(\text{CD} - \text{ED})/\text{CD}];$$

where

- EMP = equatorial moon position on the day of collection,  
 FD = the farthest position of the moon north (+) and south (-) of the equator,  
 CD = the total number of days in the equatorial moon cycle, and  
 ED = the day the sample was collected in the equatorial moon cycle.

A longitudinal value was assigned to the position of the moon from the equator on each sample date.

Absolute time from noon: Previous studies have indicated that time of day may be an important factor when investigating artificial reef faunal assemblages (e.g., Sanders et al., 1985). This is because behavioral activity and species associations often differ relative to the time of day. Most studies use local time; however, this time is only an approximation of celestial events such as noon, sunrise, and sunset. Thus, to more accurately reflect a relevant time of day, we employed absolute time from noon (ATFN) in this study. This measure is used to account for behavioral responses that could affect sampling results. ATFN was calculated using the method described by Sanders et al. (1985). ATFN represents the deviation of time from the exact midpoint of sunlight hours that a sample was taken.

Other independent variables: Prior to collection of epifaunal samples, bottom tempera-

tures were measured to the nearest 1 C by a diver with a field thermometer. Bottom salinity was measured using a temperature-compensating refractometer accurate to the nearest 1 ppt from a diver-collected, 200-ml water sample.

*Dependent variables.*—Area covered by attached organisms was estimated using the methods of Woodin and Jackson (1979) and Bohnsack (1979), by viewing transparencies on a microfilm projector under a dot planimeter with 8,000 total dots (200/12.5 cm<sup>2</sup>). Transparencies of the disks were taken at a fixed distance with the camera mounted on a copy stand. The presence of a sessile organism under a dot was recorded and its percent coverage was calculated. Percent cover for encrusting bryozoan species was measured by using a digitizer. Total abundance of echinoderms associated with cone surfaces was estimated from videotapes taken on each sampling date (Bortone et al., 1994).

Sessile epifauna attached to settling plates were removed by thoroughly scraping the surface with a razor blade while the plates were submerged in water. Removed epifauna were gathered on sieves of different mesh sizes: no. 5 (4.0 mm), no. 14 (1.4 mm), and no. 30 (0.595 mm). Organisms retained on each sieve were preserved in jars for later identification.

Larger branching and filamentous organisms were rinsed to remove any entangled organisms. Once rinsed, the arborescent bryozoans were examined under a dissecting microscope to remove any remaining epizootic organisms. Organisms remaining in the sorting pan, resulting from scraping the settling plates, and nonsessile organisms previously separated from arborescent bryozoans were also sorted by sieving. Specimens not retained by a U.S. standard no. 30 sieve were considered microinvertebrates (Weber, 1973) and were not included in this analysis.

The removed epifaunal taxa were assigned to three functional groups: motile, sedentary, and sessile as suggested by Woodin and Jackson (1979) and were identified to the lowest taxa possible for analytical purposes. For colonial organisms (e.g., bryozoans and cnidarians) the colonies were counted and their volume displacement in water was used as a measure of colony size. This procedure involved placing the organisms in a graduated cylinder with 500 ml of fresh water. Once the organisms were completely immersed, their displacement (to the nearest milliliter) was recorded.

TABLE 1. Dependent variables on the corresponding dates for the epifaunal surveys on an artificial reef group in Choctawhatchee Bay.<sup>a</sup>

Date	Temp (C)	Salinity (ppt)	EMP	ATFN
19 Nov. 1987	18	26	-9.50	124.5
18 Dec. 1987	14	29	-12.00	136.0
19 Jan. 1988	12	32	-19.00	310.0
23 Feb. 1988	14	32	12.20	219.0
22 March 1988	15	32	19.00	77.0
22 April 1988	19	28	24.20	219.0
23 May 1988	22	30	10.69	117.5
16 June 1988	25	31	21.38	220.0
20 July 1988	27	28	-4.07	196.0
25 Aug. 1988	28	34	-19.00	225.5
22 Sept 1988	27	30	-14.30	137.5
20 Oct. 1988	22	19	-12.00	189.5

<sup>a</sup> EMP, equatorial moon position; ATFN, actual time from noon.

*Data analysis.*—Dependent variables analyzed in this project included assemblage statistics, such as individual taxon abundance, numbers of species and species diversity [Shannon-Weaver H' according to Pielou (1966) using natural logarithms]. Using canonical correlation analysis (CANCORR; SAS, 1990), individual taxa abundances were dependent variables. Temperature, salinity, equatorial moon position, ATFN, height of settling plate above the substrate, and reef module surface area (calculated from each cone's dimensions with allowance for holes) were independent variables. CANCORR partitions the variance associated with correlations in a matrix created from the individual taxa abundances and associated environmental variables. CANCORR permits the determination of which independent variable, or combination of variables, had the highest associated influence in predicting the variance in the individual taxa abundances (Gauch and Wentworth, 1976).

## RESULTS

*Independent variables.*—A summary of measured and calculated independent variables is presented in Table 1. Temperature was lowest (12 C) in Jan. and highest (28 C) in Aug. Salinity varied throughout the study period due to tidal influence and periodic freshwater incursions from the Choctawhatchee River and onshore runoff. The lowest salinity recorded was 19 ppt and the highest was 34 ppt. There were no seasonal trends in salinity, equatorial moon position, or ATFN relative to our sampling dates.

TABLE 2. Estimates of abundance for 90 epibenthic faunal taxa collected from the Choctawhatchee Bay artificial reef.<sup>a</sup>

Taxa	Abrev.	Group	No. of individuals
Porifera			1
Gorgonia			2
Cnidaria			
Actinaria	ACTI	2	12
Bryozoa			
Arborescent bryozoan	ABRY	3	1,187.39*
<i>Membranipora</i> sp.	MEMB	3	230.45*
Annelida			
Unidentified Polychaeta	PHCA	1	45
Capitellidae			8
Eucinidae	EUCI	1	15
Hesionidae	HESI	1	18
Lumbrineridae			4
Nereidae	NERE	1	1,078
Onuphilidae			5
Ophellidae	OPHE	1	122
Orbiniidae			1
Pectinoridae			2
Phyllocidae	PHYL	1	252
Polynoidae	POLY	1	55
Sabellaridae			2
Sabellidae	SABE	1	84
Serpullidae	SERP	3	493
Spionidae	SPIO	1	236
Syllidae	SYLL	1	556
Terebellidae	TERE	1	470
Mollusca			
Class Bivalvia			
<i>Aequipecten muscosus</i>	AGIB	2	1
<i>Argopecten gibbus</i>			30
<i>Anadra ovalis</i>	ASIM	3	2
<i>Anomia simplex</i>			840
<i>Arcinella cornuta</i>			5
<i>Atrina semimuda</i>			1
<i>Barbatia candida</i>	BCAN	2	1,396
<i>Brachidontes exustus</i>	BEXU	2	80
<i>Chione grus</i>	CGRU	2	19,981
<i>Crassostrea virginica</i>	CVIR	3	554
<i>Hiatella azaria</i>			7
<i>Laevicardium</i> sp.			1
<i>Musculus lateralis</i>	MLAT	2	490
<i>Ostrea equestris</i>			1
<i>Tellina</i> sp.			16
Class Gastropoda			
<i>Aplysia</i> sp.	APLY	1	29
<i>Billium</i> sp.			13
<i>Calliostoma</i> sp.			2
<i>Cantharus</i> sp.	CANT	2	29
<i>Cerithiopsis</i> sp.			4
<i>Cerithium ebureum</i>	CEBU	2	18
<i>Cerithium</i> sp.	CERI	2	158

TABLE 2. Continued.

Taxa	Abrev.	Group	No. of individuals
<i>Crepidula</i> sp.	CREP	2	78
<i>Dentalium laqueat</i>			1
<i>Diadora</i> sp.			1
Gastropod veliger			3
<i>Latirus</i> sp.			4
<i>Mitrella tumata</i>	MLUN	2	323
<i>Porpeamussium dalli</i>			9
<i>Terebra</i> sp.	TERB	2	470
<i>Trigonostoma</i> sp.			1
<i>Turbo castaneus</i>	TCAS	2	17
<i>Zebina browniana</i>			3
Nudibranchs	NUDI	1	1,024
Arthropoda			
Class Cirrepedia			
<i>Balanus reticulatus</i>	BREC	3	18,204
Order Tanaidacea			
<i>Leptochelia rapax</i>	LRAP	1	3,001
Order Isopoda			
<i>Erichsonella attenuata</i>	EATT	1	19
Order Amphipoda			
<i>Corophium</i> spp.	CSPP	1	39,438
<i>Dulichieilla</i> (cf.) <i>appendiculata</i>	DAPP	1	29
<i>Elasmopsis levis</i>	ELEV	1	568
<i>Erichtonius brasiliensis</i>	EBRA	1	10,875
<i>Gitanopsis laguna</i>	GLUG	1	112
<i>Luconacia</i> (cf.) <i>incerta</i>	LINC	1	605
<i>Melita intermedia</i>			5
<i>Paracaprella tenuis</i>	PTEN	1	312
<i>Paracaprella pusilla</i>	PPUS	1	140
<i>Paracaprella</i> sp.	PARA	1	280
<i>Podocerus brasiliensis</i>	PBRA	1	773
<i>Stenothoe minuta</i>	SMIN	1	17,582
Class Malacostraca			
<i>Eurypanopeus abbreviatus</i>	XANT	1	37
Zoecal crab			2
<i>Palaemonetes pugio</i>			1
Alpheidae			1
Zoecal shrimp			5
Megalopa	MEGA	1	84
Rhyncocoela			
Rhyncocoela	RHYN	1	27
Nematoda			
	NEMA	1	553
Echinodermata			
<i>Arbacia punctulata</i>			75
<i>Lytechinus variegatus</i>			8
Echinoderm larvae			66
Ophiuroidea	OPHI	1	32
Holothuriidae	HOLO	1	77
Platyhelminthes			
Turbellaria	TURB	1	833

TABLE 2. Continued.

Taxa	Abrev.	Group	No. of individuals
Arachnida			
Pycnogonida	PYNC	1	336
Tunicata			
<i>Styela plicata</i>	STYL	3	337
Vertebrata			
<i>Blennius marmoratus</i>			1
Fish larvae			4

\* Group indicates functional group (1 = Motile, 2 = Sedentary, 3 = Sessile); Abrev., taxa abbreviation; \*, abundance estimated by displacement (ml).

*Dependent variables.*—Assemblage composition: Ninety-five settling plates were removed from the Choctawhatchee Bay artificial reef group, which resulted in 124,893 individual organisms from 90 taxa (Table 2). Thirty-one numerically dominant taxa accounted for 99% of the total individuals collected. A taxon was considered dominant if it contributed 0.01% or more (i.e., more than 12 individuals in the total assemblage) to the total number of individuals. Taxa with fewer than 0.01% contribution were not used in CANCECORR. These dominant taxa totaled 124,555 individuals. Crustacea was the most abundant major taxon, encompassing 73.85% of all individuals and including 17 lower taxa (32% of all taxa). Bivalve Mollusca was the second most abundant taxon, with 18.76% of the individuals and seven taxa (12%). Other important major taxa were: Polychaeta, which accounted for 2.77% of the individuals and 12 taxa (22%), and Gastropoda, which accounted for 1.79% of the individuals and nine taxa (17%). The 10 dominant taxa consisted of 91.5% of the individual abundance of the dominant taxa used in CANCECORR. Five crustacean taxa (*Corophium* spp., 31.72%; *Balanus reticulatus*, 16.07%; *Stenothoe minuta*, 14.14%; *Erichthonius brasiliensis*, 8.75%; *Leptochelia rapax*, 2.41%; and *Podocerus brasiliensis*, 0.62%) represented 73.71% of the individuals. Two bivalves, one bryozoan, and one polychaete accounted for 17.6%, 0.9%, and 0.8% of the individuals, respectively.

Number of taxa: The mean number of taxa per settling plate was lowest (7.8) during the first, Nov. 1987, sampling period (Fig. 1A). There was a general increase in the mean number of taxa per plate (with a slight decrease in Feb.) until June, when the highest mean number of taxa was recorded (36.6). The mean number of taxa declined dramati-

cally in Aug. (14.8) but increased to 28.6 and 28.4 in Sept. and Oct. respectively.

Number of individuals: The mean number of individuals per settling plate was low in Nov. 1987, Dec. 1987, and Aug. 1988 (170.9, 147.6, and 186.3, respectively). The mean number of individuals increased from the the initial deployment to attain a peak of 4,848 in June (Fig. 1B). There was a dramatic drop in the number of individuals per plate after June, and this lower abundance persisted for the remaining months of the study.

Species diversity ( $H'$ ): The lowest mean species diversity ( $H'$ ) per settling plate was recorded in Feb. (0.74), and the highest was recorded in Sept. (2.46). There was a trend for species diversity to increase from the initial Nov. 1987 sampling period to the end of sampling in Oct. 1988. However, species diversity among the epifaunal samples increased gradually from Nov. 1987 until Jan. 1988 and decreased sharply in Feb., while individual abundance increased. This decrease in  $H'$  and concomitant rise in abundance was due to heavy recruitment of the barnacle *B. reticulatus* (Table 3). Species diversity of epifauna collected in March was twice that of Feb., yet there was an average of about 1,000 fewer individual organisms per plate in March. Differential recruitment of the barnacle most probably influenced this result. Statistical measures for the samples collected in April, May, and June reflected colonization. During this period, the reef assemblage was colonized by over 5,000 individuals per 706.5-cm<sup>2</sup> settling plate. Species diversity decreased, while both taxa and individual abundance increased from April to June. The summer-early fall seasons indicated an interesting pattern, in which individual abundance declined 85% in Aug. through Oct. from its peak in June, while

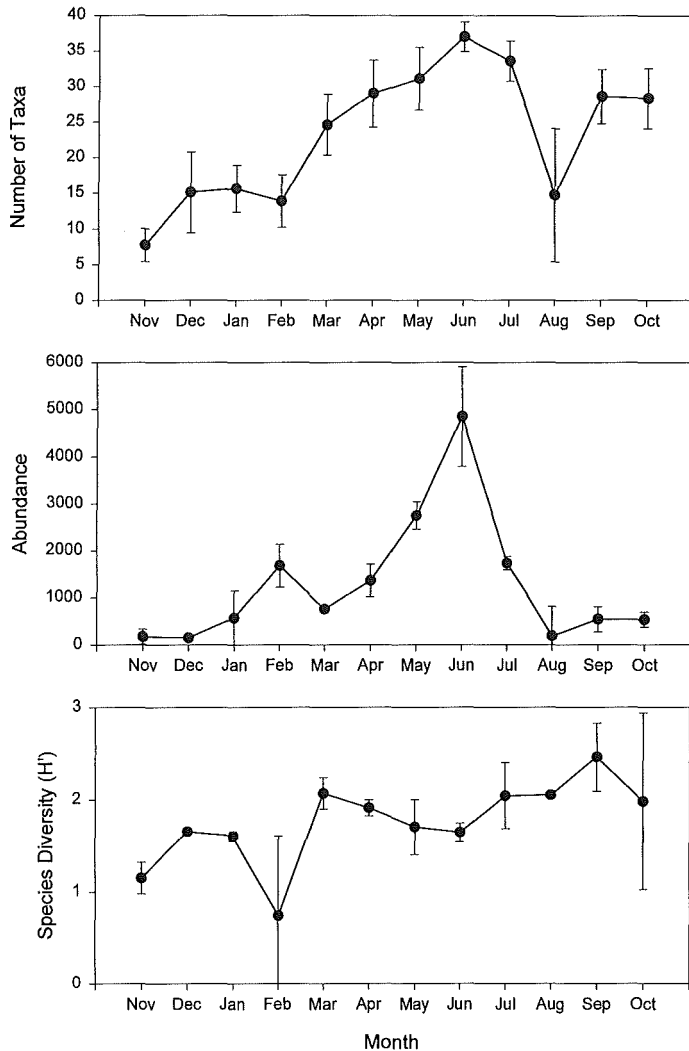


Fig. 1. (A) Number of taxa, (B) total abundance, and (C) species diversity by month per disk recovered from the modular artificial reef in Choctawhatchee Bay.

the number of taxa and species diversity continued to increase. The highest species diversity was recorded in Sept. This coincided with a tropical storm which passed through the northeast Gulf of Mexico between the Aug. and Sept. sampling episodes.

*Coverage.*—There was a general tendency for coverage (as measured by the mean monthly percent coverage per settling plate) to increase from the outset of the reef group deployment in Oct. 1987 to the end of the study period in Oct. 1988 (Fig. 2A). The lowest mean percentage of cover was 6.6% in Nov. 1987 and the highest was 96.7% during the last sampling period in Oct. 1988. Coverage increased initially

to about 80% in Feb. and stayed high (i.e., above 75%) for the remainder of the study period. There was a wide range of values recorded for coverage during Aug. Foraging activity by sea urchins on selected disks most likely contributed to this variation in coverage. The epifaunal assemblage was nearly completely removed on some disks (two with values as low as 12% and 24%), whereas other disks (two with 99% coverage) showed no evidence of foraging by sea urchins.

Coverage fluctuated due to colonization by *B. reticulatus* from March through May. Variation in coverage among the sampling plates during June and July was minimal. This period was also recognized as the season when arbo-



TABLE 3. Monthly total abundance data matrix of the Choctawatchee Bay artificial reef epifauna compiled from the canonical correlation analyses. Matrix rows in decreasing order of their canonical variate scores.

Taxa	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.
Nematoda			1	26	45	158	214	87	11	4	2	18
<i>Balanus reticulatus</i>	204	192	2,096	10,840	995	123	832	832	955	65	233	334
Terebellidae					133	167	85	36	2	3	11	4
Turbellaria	10		217	287	60	11	26	59	24			20
<i>Stenothoe minuta</i>	9		123	235	1,487	3,898	4,842	805	1,284	2	43	
Arborescent bryozoans	0.4	3.5	24.3	68.2	168.9	2,077	284	200.8	108.9	14.3	34.8	73.1
<i>Luconacia</i> (cf.) <i>incerta</i>	7	11	200	27	204	74	54	16	3	1	7	1
Opheliidae		1			47	18	50	6				
<i>Argopecten gibbus</i>		2	1	3	12	3	4	2	2		1	
Holothuriidae					17	26	27	7				
<i>Barbatia candida</i>	1	12	22	126	95	146	345	345	247	25	69	59
<i>Erichthonius brasiliensis</i>	1,211	400	916	1,518	951	532	1,970	399	1,242	841	606	427
Serpullidae		33	12	89	117	37	41	12	34	6	102	72
Nudibranchs	5	37	33	19	47	109	66	34	1	3	1	7
<i>Musculus lateralis</i>		3	1	2	43	62	185	97	99	11	21	
<i>Turbo castaneus</i>					10	3					5	
<i>Chione grus</i>		9	26	193	524	1,411	6,892	6,892	4,591	327	393	86
Sabellidae			12	1	12	10	10	12	3	2	6	3
<i>Paracaprella</i> sp.					67	41	50	23	13	2	2	10
<i>Corophium</i> spp.	141	432	526	1,093	798	4,135	7,892	17,558	3,877	202	650	2,134
<i>Erichsonella attenuata</i>		1				3	3	12				
Rhyncocoela		13	2	1	4	14	44	12	13		8	2
Phyllococidae	1		2		7	30	82	69	32	17	9	1
Spionidae					37	24	59	43	31	4	15	23
<i>Styela plicata</i>		115	0.1	3	314	8.2	8.6	171.7	21.5	2		0.1
<i>Paracaprella tenuis</i>	92		246	50	44	60		2	10			11
Xanthidae		4			9	2	1	9	3	2	7	3
<i>Crepidula</i> sp.		1		2	3	8	14	21	19	2	2	6
<i>Paracaprella pusilla</i>	4	116	92		1							
Ophiuroidea								22	1			12

TABLE 3. Continued.

Taxa	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.
<i>Dulichelia</i> (cf.) <i>appendiculata</i>					5		3	4	11		6	
Actinaria						1	3	5				3
<i>Mitrella lunata</i>		2	1		7	50	30	66	89	10	21	22
Polychaeta	25	13	6		1							
<i>Elasmopsis levis</i>		39			3	11	46	158	246	19	44	2
<i>Podocerus brasiliensis</i>	2	57	81	10	4		14	277	219	7	63	29
<i>Aplysia</i> sp.	2	1					2	17	2	4	1	
Polynoidae							9	15	7	11	10	3
Eucinidae					3						9	3
Hesionidae							1				16	1
<i>Leptochelia rapax</i>	3	14	30	4	10	142	105	1,020	859		370	234
Nereidae		25	5	4	44	67	263	149	134	83	125	179
<i>Cerithiopsis</i> spp.							9	9	27	23	59	12
Megalopa		1	1				3	30	15	4	21	9
<i>Membranipora</i> sp.				1.03	12.01			21.14			55.57	28.43
<i>Anomia simplex</i>							1	3	17	2	205	
Syllidae		1				55	56	69	115	120	100	41
<i>Terebra</i> sp.		1							11	19	42	2
<i>Cerithium ebureum</i>											5	10
Pycnogonida							6	1	104	3	105	155
<i>Gitanopsis laguna</i>	8	22	11		1				1	3		66
<i>Cantharus</i> sp.									5	4		13
<i>Brachidontes exustus</i>											35	45
<i>Crassostrea virginica</i>									131	34	234	155

TABLE 4. Canonical variate scores of the environmental variables from the Choctawhatchee Bay artificial reef. Underlined scores indicate high loadings.

Environmental variable	Axis 1	Axis 2	Axis 3
Surface area	0.1440	0.1710	<u>0.8891</u>
Absolute time from noon	-0.0300	0.1020	<u>-0.5400</u>
Equatorial moon position	<u>0.7830</u>	<u>0.4320</u>	<u>-0.1130</u>
Salinity	<u>0.5283</u>	-0.1600	0.0102
Temperature	<u>-0.4955</u>	<u>0.7230</u>	0.1294
Disk height	<u>-0.1703</u>	<u>-0.0300</u>	-0.0400

rescent bryozoan colonies initially decreased and were replaced by new colonies of other spatial competitors. Epifaunal coverage decreased due to live portions of the arborescent bryozoans breaking off from their main stalks, leaving extensive networks of holdfasts in July and Aug.

ganisms predominated the epifaunal assemblage of the settling plates, sessile organisms were few, and no sedentary organisms were recorded (Fig. 2B). In Feb. there was a notable increase in the relative number of sessile organisms, corresponding to a simultaneous reduction in motile epifauna. Subsequent to this exchange in relative abundances between motile and sessile organisms in Feb., there was a reversal in relative abundance of these two

*Percent abundance of epifaunal functional groups.*—At the outset of this study, motile or-

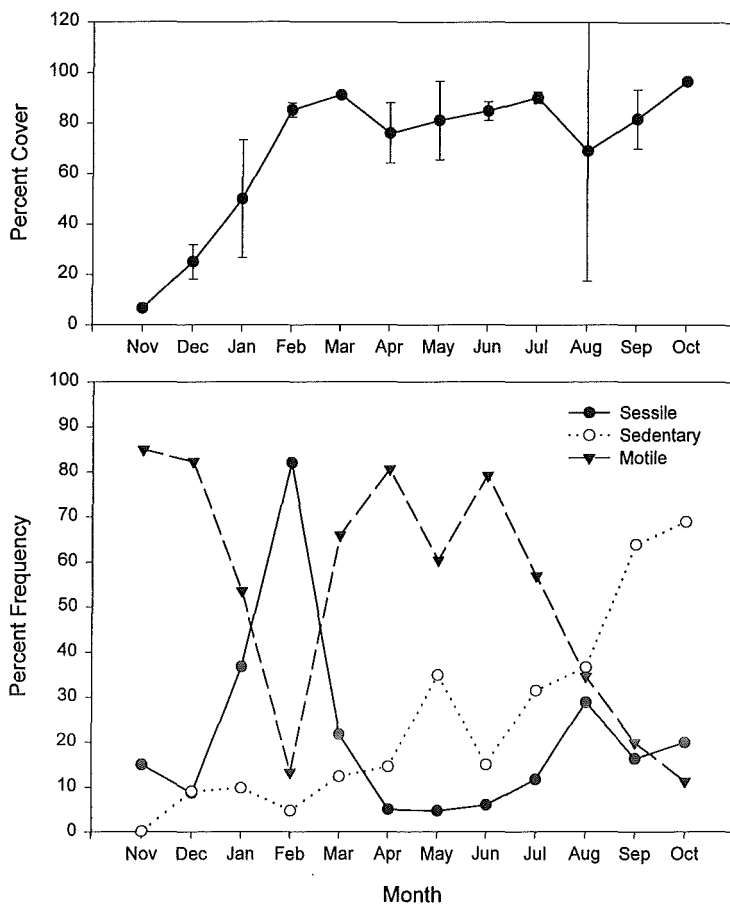


Fig. 2. (A) percent cover and (B) percent frequency of sessile, sedentary, and motile functional groups by month per disk from the modular artificial reef in Choctawhatchee Bay.

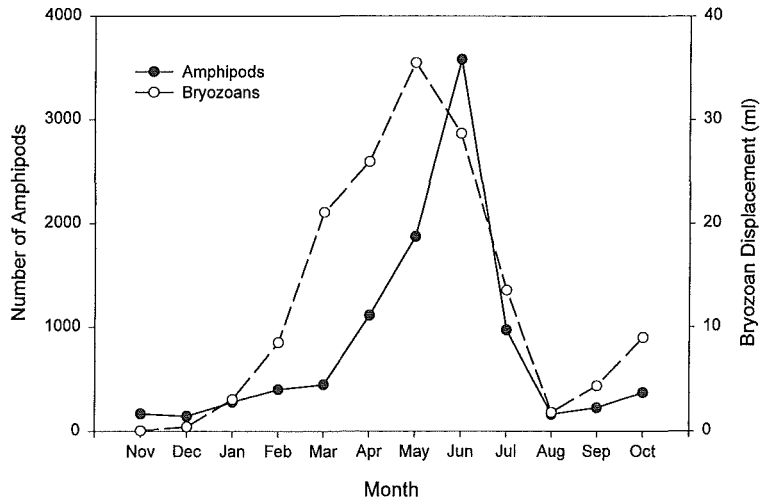


Fig. 3. Number of amphipods and the volumetric displacement of arborescent bryozoans by month per disk from the modular artificial reef in Choctawhatchee Bay.

functional groups in March. Thus, as temperatures in the bay became warmer, the plates were covered with a higher percentage of motile forms. Overall, there was a general trend toward an increase in sedentary epifauna throughout the study period. The sedentary functional group attained its highest relative abundance in Oct. Along with this relative increase in sedentary organisms, there was a concomitant decrease in the relative abundance of motile epifauna. After their peak in Feb., sessile organisms never regained prominence on the reef.

*Temporal changes in taxa abundance.*—There were noticeable changes in abundances of certain taxa that could be due to either seasonal or successional factors (Table 3). To demonstrate the seasonal changes typified by taxa, we examined monthly abundances of amphipods and arborescent bryozoans more closely (Fig. 3). Arborescent bryozoan colonies collected in Nov. 1987 to May 1988 exhibited an increase in mass (as measured by displacement) on the settling plates. The potential habitat complexity of the plates apparently increased as a result of an increase in this portion of the sessile epifauna. It is likely that, as microhabitat complexity increased, species composition and abundance of amphipod epifauna also increased. Plates collected after July showed a decrease in arborescent bryozoans, with a concomitant decrease in amphipod abundance. The reduction in microhabitat complexity may have affected amphipod abundance.

The loss of arborescent bryozoans was ac-

companied by replacement of the amphipod assemblage with gastropods. This can be observed in the contribution that gastropods made to the sedentary functional group after July (Fig. 2B; Table 3). Thus, as the motile assemblage decreased, there was a concomitant increase in the sedentary group dominated by gastropods.

*Assemblage structure.*—The statistical models examined taxa abundances from 95 epifaunal settling plates to determine their best linear fit in relation to six environmental variables (i.e., bottom temperature, bottom salinity, equatorial moon position, ATFN, surface area, and vertical disk height above substrate). Compass orientation was not significant to the model and was removed from the analysis. A multiple linear regression model predicting Shannon-Weaver species diversity ( $H'$ ) indices from the settling plates was also constructed. However, it had no significant relationship with the independent variables measured here.

Before using canonical correlation analysis (CANCORR) to determine the specific relationships between independent and dependent variables, it is necessary to determine if the overall independent and dependent data matrices are significantly associated. Using several multivariate statistical tests (i.e., Wilk's lambda, Pillai's trace, Hotelling-Lawley trace, and Roy's greatest root), we noted a significant ( $P < 0.05$ ) relationship between these two matrices.

CANCORR was subsequently used to determine which of the dependent variables were

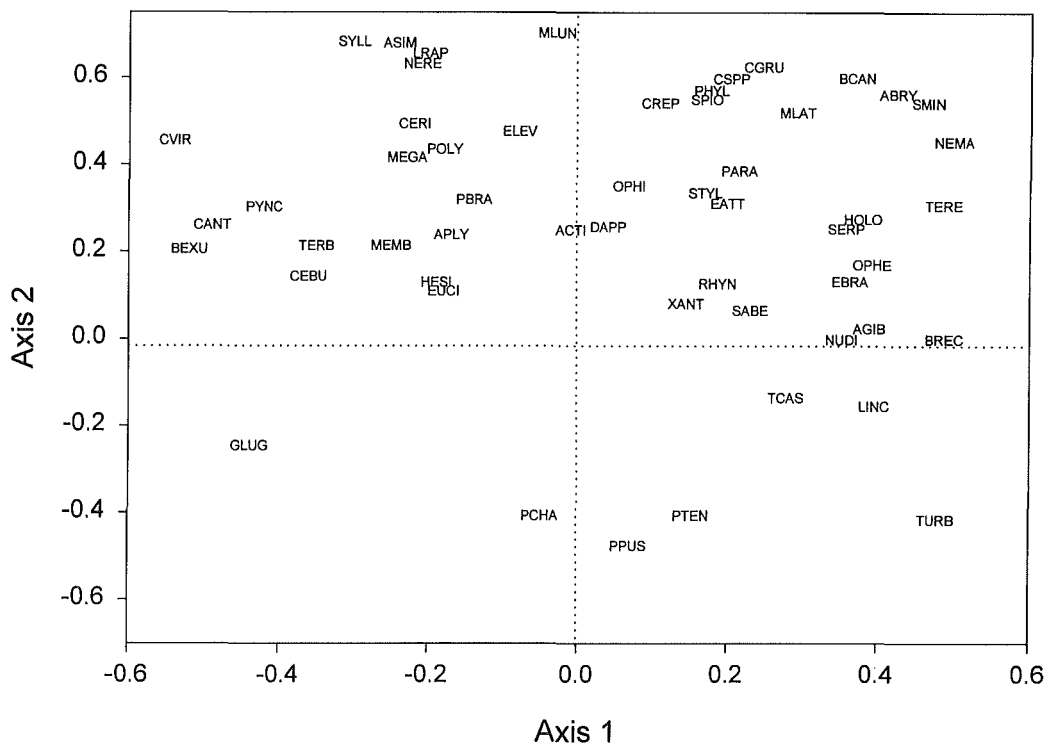


Fig. 4. Scatter diagram of the taxa (taxa abbreviations as per Table 2) on the first two canonical correspondence axes.

associated with the independent environmental variables. The eigenvalue and the percent variance contribution for the first canonical correlation axis were 35.36% and 48.41%, respectively. Environmental variables that had the highest canonical variance scores on Axis 1 were equatorial moon position (0.78), salinity (0.53), and temperature (-0.50) (see Table 4).

The matrix eigenvalue and percent variance contribution for the second canonical axis was 19.07% and 26.11%, respectively. Temperature and equatorial moon position had the two highest canonical variate scores (0.72 and 0.43, respectively) of environmental variables that contributed to positions of the taxon axis loadings on Axis 2. The third canonical axis eigenvalue and the percent variance contribution were calculated at 8.33% and 11.40%, respectively. Reef module surface area and ATFN had the highest canonical variate scores for Axis 3 (0.89 and -0.54, respectively). The cumulative variance associated with the first three canonical axes was 85.92%.

The spatial arrangement of individual taxa on the canonical variate axes is a resultant measure of the effect of environmental vari-

ables on each taxa and the associated effect of taxa on each other. The resultant taxa groupings depicted in Figure 4 are based on their correlation with the environmental variables and their associations with other members of the associated epibenthic artificial reef assemblage.

Taxa with high positive canonical variate scores on Axis 1 (Fig. 4) were chiefly early colonizers to the reef system and represented 92.5% of the total number of individuals. These early colonizers were those species that colonized and were resident on the reef from Nov. 1987 to June 1988. Out of the 31 early colonizing taxa, 11 were crustaceans comprising 70.2% of the total faunal abundance, five were bivalves comprising 17.6%, seven were polychaetes at 1.3%, two were gastropods at 0.8%, and six were miscellaneous taxa at 2.4%. The functional group structure for these early colonizers were chiefly comprised of motile organisms. Thus, motile organisms accounted for 58.5% of the early colonizers, sedentary taxa for 17.9%, and sessile taxa for 16.0%. The sessile functional group was characterized by four taxa that may have been spatial competitors; for example, arborescent bryozoans, a barna-

cle (*B. reticulatus*), serpulid polychaetes, and the tunicate, *Stylea plicata*. Many early colonizing taxa associated closely with arborescent bryozoan colonies. Among these were four bivalves species (*Chione grus*, *Barbatia candida*, *Musculus lateralis*, and *Argopecten gibbus*) which were found to attach readily to the arborescent bryozoan fronds. *Musculus lateralis*, *B. candida*, and *C. grus* built extensive byssal string baskets in branches of arborescent bryozoans on which tube-dwelling amphipods (*Corophium* spp. and *E. brasiliensis*) built their tubes. The amphipods *Corophium* spp., *S. minuta*, and *E. brasiliensis* and an isopod, *Erichsonella attenuata*, were also closely associated with the arborescent bryozoans. *Stenothoe minuta* and *Luconacia* (cf.) *incerta* were the most abundant free-living amphipods in the assemblage and were also associated with early colonizers. Amphipods were numerically dominated by tubicolous forms, specifically *Corophium* spp., which represented 31.3% of individual abundance.

Twenty-three taxa loaded negatively on Axis 1 and are considered later colonizers to this estuarine reef group. These taxa included: five crustaceans comprising 3.6% of the total abundance, six gastropods at 0.8%, six polychaetes at 1.4%, three bivalves at 1.2%, and three miscellaneous taxa at 0.4%. The functional group structure for later colonizers includes: 13 motile taxa comprising 5.3% of the total late colonists, seven sedentary taxa at 0.9%, and three sessile taxa at 1.3%. Taxa loading lower on the first canonical correlation axis were also delineated by spatial competitors, which colonized in late summer (i.e., *Crassostrea virginica*, *Brachidontes exustus*, *Membranipora* spp., and *Anomia simplex*). Gastropods were represented chiefly in the late colonizing portion of the assemblage. The predacious gastropods (*Cantharus* sp., *Mitrella lunata*, and *Terebra* sp.) were collected in late summer (July–Aug.) and early fall months (Sept.–Oct.) of the study. *Bittium* sp., *Cerithium ebureum*, *Cerithium* sp., and *Aplysia* spp. can also be considered late summer colonizers (Table 3).

Taxa loadings on Axis 2 (Fig. 4) were more highly correlated with temperature and equatorial moon position than any other environmental variables examined herein. No obvious trends were identified by the alignment of taxa along this axis. However, motile epifaunal organisms were more broadly distributed along Axis 2, suggesting that they were less restricted, as a group, by environmental features associated with this axis.

## DISCUSSION

*Functional group associations.*—Defining functional groups involves categorizing species by their competitive mechanisms and motility (Woodin and Jackson, 1979). Epifaunal assemblages contain three motility functional groups: sessile, sedentary, and motile. Sessile organisms attach firmly to substrates using morphological adaptations that help stabilize the biomass on the physical structure of a reef. Many sessile species are resilient to harsh environmental conditions, whereas sedentary organisms display limited movement and are less resilient to environmental conditions. Together, they represent a loose assemblage that move little between reefs. Motile epifauna move freely and are greatly affected by environmental conditions. The highly motile nature of this group facilitates their movement into or out of a reef system. Each of these functional groups plays a role in determining the assemblage structure of the epifauna associated with an artificial reef.

Sessile and sedentary functional groups have been used to describe successional processes in other studies (Dayton, 1971; Sutherland, 1974; Sutherland and Karlson, 1977). The reason for the focus on these functional groups has chiefly been because they are large, conspicuous, and easy to identify and quantify (Osman, 1982). Their relative ease of manipulation has allowed their use as model assemblages for testing ecological hypotheses concerning competition and predation (Paine, 1966; Osman, 1977; Russ, 1980). However, research has been hindered by the difficult and time-consuming tasks of identifying and quantifying assemblages of motile invertebrates (amphipods, isopods, and polychaetes). The only simultaneous examination of all three epifaunal groups in a single study was by Ardizzone et al. (1989).

Early colonists were clearly dominated by the motile functional group, and late colonizers were dominated by the sedentary functional group. The assemblage structure began to change in June and was most evident by Oct. 1988. This change could be attributed to the loss of habitat complexity represented by arborescent bryozoans. In July, arborescent bryozoan abundance began to decline, perhaps permitting other spatial competitors to colonize the reef. The apparent loss and replacement of arborescent bryozoans was also observed in the coverage measured for the epifauna. The reduction in arborescent bryozoans produced new unutilized space which was col-

onized by sedentary and motile functional groups.

Russ (1980) investigated the effects of microhabitat complexity on predatory success of fishes on epifauna. He noted that artificial bryozoan plates reduced the predatory efficiency of fishes on epifaunal assemblages. In our study, arborescent bryozoans were most abundant in May. Amphipods increased in June, probably because the carrying capacity of the plate habitat had increased along with arborescent bryozoans. Amphipods subsequently decreased, with the decrease in the bryozoans in Aug., to a level similar to that observed in winter. This concomitant decrease in bryozoan abundance might have been affected by 1) the sea urchins (*Arbacia punctulata* and *Lytechinus variegatus*) foraging on the reef groups and 2) the mechanical failure of the arborescent bryozoan holdfasts. The arborescent bryozoans seemed to have a positive effect on abundance and diversity of other epifauna as well. Arborescent bryozoans are not the only epifaunal organisms positively associated with the increase in motile epifaunal abundance. Osman (1982) found that species diversity increased four to six times on settling plates that contained a complex microhabitat generated from exoskeletons of previous sessile organisms. Spatial heterogeneity has been identified by Pianka (1988) as one of the ten mechanisms that influence species diversity. Arborescent bryozoans may add an additional dimension to the reef surface. Anything that reduces or eliminates this added dimension can have profound effects on the assemblage structure. Dean (1981) noted that changes in the relative amount of microstructure available was unaffected by the presence of spatial competitors in the epifaunal assemblage on a reef in an estuary.

*Environmental association.*—We determined that equatorial moon position was one of the most influential variables in the model. As equatorial moon position is somewhat synonymous with tides. One possible explanation for the dominance of this variable is the high percentage of organisms in the motile functional group. In fact, 82.4% of all individuals (63.9% motile and 18.5% sedentary) were organisms that had some degree of motility and could respond to tidal changes. Relatively motile organisms may have an advantage over non-motile organisms under changing conditions.

In selecting independent variables for quantitative ecological research, it is important to choose variables that are orthogonal (i.e., in-

dependent) to each other (Ludwig and Reynolds, 1988). Bottom salinity and temperature are not totally independent of equatorial moon position because of diurnal and seasonal interactions among these hydrographic variables. When equatorial moon positions are at their greatest magnitude of effect, water temperature, salinity, and tidal cycles are all interrelated. Besides invalidating some of the necessary statistical assumptions, the condition of covariation among variables can alter or distort the correlative structure of linear models. The independent variables selected for statistical analysis were analyzed for covariation and selected for their orthogonality. However, the interrelated nature of the hydrographic variables could be responsible for the magnitude of the influence of equatorial moon position in this model.

Another possible explanation for the magnitude of equatorial moon position relationship is Osman's intermediate disturbance hypothesis. Osman (1977) studied the long-term community dynamics of sessile epifauna near Woods Hole, MA, and found that the frequency of destructive disturbance affected species equilibrium and diversity. Presumably, this prevented dominant species from creating single-species assemblages. Here, equatorial moon position does not represent the daily fluctuations of tide levels as a disturbance but does represent the cumulative changes of tidal cycles. It also possibly represents the cumulative change in assemblage structure due to tidal disturbance. The primarily motile epifauna on the artificial reefs in Choctawhatchee Bay could have been reacting to magnitudinal differences in tidal flows between seasons and using them as a behavioral cue that was not evident in a monthly sampling regime (Hobson and Chess, 1986). Baynes and Szmant (1985) also noted the influence of currents on the sessile benthic assemblage structure on artificial reefs.

The recruitment of epifaunal organisms to an assemblage is greatly influenced by seasonality (Sutherland and Karlson, 1977; Schoener and Schoener, 1981; Osman, 1982). The seasonal cycle of this warm temperate reef in Choctawhatchee Bay follows a similar pattern of colonization and assemblage growth observed in most temperate epifaunal communities (e.g., Sutherland, 1974; Osman, 1977, 1982; Schoener and Schoener, 1981). This can be especially noted in the variation in species diversity. The initial colonization of epifauna was observed during the first 4 mo of this study. Total abundance and species diversity all

fluctuated, most probably because of the influx of large numbers of larvae. The next seasonal period (March through June) is notable for the increased numbers of taxa and individuals and for the relatively stable level in species diversity. This suggests the presence of several highly abundant species, but because the diversity was so great, no single species dominated the assemblage. In Sept. and Oct., the total assemblage abundance decreased, but stabilized at a low level when water temperature was reduced.

Overall, the four most significantly associated variables in this analysis were equatorial moon position, temperature, salinity, and reef module surface area. Equatorial moon position, as associated with epifaunal assemblages, has been shown to be important due to the relatively high number of motile organisms and because of its covariation with temperature and salinity (Hobson and Chess, 1986). Surface area was also shown to be an important correlate with spatial competitors and grazers, as identified in the arrangement of taxa on CANCECORR Axis 3. Axis 2 revealed no embedded trends in relation to the arrangement of taxa on the axis. Pimentel (1979) indicated that one of the disadvantages of CANCECORR is the potential for noninformative, noninterpretable or biologically meaningless correlations. To facilitate future studies, evaluations of epifaunal assemblages should be oriented toward functional groups to better understand and decipher the cumulative effects of environmental variables on the total epifaunal reef assemblage.

Bortone et al. (1994) presented information describing the colonization of this same artificial reef group relative to its ichthyofauna and also noted both seasonal and colonization features of the fauna associated with this estuarine reef. Their results closely reflect the observations relative to epifauna reported herein. They noted that temperature, time of day, and tides were among the most important environmental variables associated with variation in the fish assemblage. They also noted that reef-specific features, such as hole size and reef height, seemed to have no effect on the assemblage's structure. Thus, the environmental factors identified as important in influencing the fish assemblage on this artificial reef are the same factors affecting the colonization and succession of the epifauna.

During the past decade, many artificial reef studies have been directed toward testing the hypotheses of whether artificial reefs "attract or produce" biomass (Bohnsack and Suther-

land, 1985). Concomitantly, epifaunal diversity has been linked to the increased spatial heterogeneity of marine habitats. Further study into this mechanism on artificial reefs may reveal important habitat criteria when constructing artificial reefs for the purpose of increasing diversity in the epifauna. Future approaches to addressing the attract vs produce hypotheses should also identify pathways through which the energy moves. They should especially evaluate the potential for energy derived from nonreef sources to that derived from filter-feeding epifauna that encrust on artificial reefs.

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