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Community structure of fishes attracted to shallow water fish aggregation devices off South Carolina, U.S.A.

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Synopsis

Twenty-two fish aggregation devices were deployed in 14 m of water off South Carolina. Species composition and abundance were determined by diver visual census on eight occasions from May through November, 1985. A total of 21 families and 36 species of fishes was observed at 121 stations. Pelagic fishes dominated the fauna with a 99.3% relative abundance, and *Decapterus punctatus* accounted for 97.6% of the individuals. *Caranx crysos, Diplectrum formosum, Decapterus punctatus, Centropristis striata* and *Monacanthus hispidus* were the most frequent species. Total fish abundance, number of species and abundance of four of the six most common species were significantly affected by season. Hurricane activity may have caused a significant drop in pelagic fish abundance at the FADs in July. No significant correlations among species abundances were found after removal of season and FAD type effects. Spatial zonation and seasonal occurrence patterns suggest some competition among pelagic fishes. Several factors that regulate FAD faunal abundance and composition are hypothesized, including: juvenile fish availability, availability of shelter, availability of adequate food resources, interspecific and intraspecific competition, severe sea conditions, and sporadic intrusions of large predatory fishes. It is hypothesized that the abundances of benthic and pelagic FAD fishes are correlated and that there is a direct or indirect energetic link between shallow water pelagic and benthic fish assemblages near FADs.

Introduction

Associations of fishes with seaweeds and many kinds of flotsam have been widely reported in the literature (Mortensen 1917, Uda 1933, Gooding & Magnuson 1967, Hunter & Mitchell 1967, Hunter 1968, Dooley 1972, Yesaki 1977). Fishermen have exploited this behavior by seeking out and actively fishing around flotsam, seaweeds, and whales (Uda 1933, Uda & Tukusi 1934, Gooding & Magnuson 1967, Yesaki 1977). Recently the importance of flotsam in commercial tuna fisheries was discussed by Greenblatt (1979) and Park (1984).

Unfortunately, catches around flotsam and similar natural sources of fish aggregations all depend on chance encounters by fishermen. To improve their chances of finding fish, fishermen learned that they could make their own 'flotsam' and numerous economically important fisheries developed around the world (Hardenberg 1950, Westenberg 1953, Kojima 1956, 1960a, 1966b, Matsumoto et al. 1981, de Sylva 1982, Myatt & Myatt 1982, Shomura

& Matsumoto 1982, Floyd & Pauly 1984, Myatt 1985). Today these man-made flotsam have become known as fish aggregation devices (usually referred to as FADs or F.A.D.s) because they apparently aggregate fishes which would otherwise be scattered over large expanses of water.

FADs were first introduced into the United States in the 1970s (Myatt & Myatt 1982), where two fundamentally different oceanic and coastal FAD fisheries have since become established. In Hawaii a large scale commercial and recreational fishery for oceanic pelagics, such as tuna and dolphin, has been successfully developed using various types of large raft-like FADs deployed in up to 1829 m (1000 fm) of water (Matsumoto et al. 1981, Shomura & Matsumoto 1982, Samples & Sproul 1985). In South Carolina small mid-water FADs are used in the state's shallow coastal waters (Hammond et al. 1977, Myatt & Myatt 1982, Myatt 1985). The nearshore South Carolina recreational fishery targets coastal pelagic fishes such as king mackerel, *Scomberomorus cavalla*, and is operated in 14 m–30 m of water from 5 km to 50 km offshore. The concept of deploying up to several hundred small FADs in long 'trolling alleys' was developed in South Carolina (Hammond et al. 1977, Myatt & Myatt 1982, Myatt 1985). Since 1983 over 1400 mid-water FADs have been deployed on 13 artificial reefs in South Carolina (M. Bell, Artificial Reef Coordinator, SCWMRD, Charleston, South Carolina, personal communication). Trolling alleys are used as primary artificial reefs or to supplement and enhance bottom reef materials.

There were two main objectives of this FAD study. The first objective was to use FADs as a tool to examine the hypothesis that fishes associate with flotsam in order to avoid predation. The hypothesis that the abundance of fishes associated with FADs is a function of the degree of shelter (indicated by FAD size) provided by the structure was specifically addressed in a previous paper (Rountree 1989). This paper focuses on the second goal of the study which was to describe the faunal composition, abundance and seasonality of fishes associated with the mid-water FADs used in the South Carolina fishery. Additionally, a hypothetical model of the trophic structure of the FAD assemblage is presented and its implications to the aggregation versus production enhancement debate (Bohnsack & Sutherland 1985) is discussed.

Materials and methods

The study site was located in 14 m of water about 23 km northeast of Charleston, South Carolina, within the permitted grounds of Capers Artificial Reef (32°45.20'N, 79°34.15'W). The area was characterized by a flat sandy bottom, lacking live bottom reef habitat, with the nearest artificial bottom relief located more than 1 km southeast.

The streamer-type FADs used in this study were modeled after the FADs used in the South Carolina artificial reef program (see Rountree 1989 for a complete description). The structure consisted of three components: the FAD, the mooring line and the anchor (Fig. 7). The FAD was made up of a float and one or more subunits. Each subunit consisted of a 154 mm long piece of 57 mm diameter PVC pipe to which were attached twelve 1.5 m long black plastic streamers. Three different FAD sizes were made by varying the number of subunits comprising the FAD (i.e., one, two or four subunits) in order to test for the importance of FAD size to fish recruitment. Each FAD size was replicated six times for a total of 18 structures. In addition, some observations were also made on four parasol-type FADs (see Rountree 1989) for general comparisons with the streamer-type structure.

On 15 May 1985 the 18 streamer-type FADs were deployed in a randomized block configuration in two 300 m long rows. FADs were spaced at 30 m intervals along a rope line attached to the FAD anchors. The four parasol-type FADs were added to the end of the rope grid two weeks later. FADs were censused by following the rope grid from station to station (see Rountree 1989). Visibility about the FADs ranged from 5 to 7 m, but was sometimes less around the FAD anchors. All fishes within visible range of the FADs and FAD anchors were censused. Infrequently, when schools extended beyond visible range of the FAD, divers censused them by moving out until all fishes associated with the FAD could be observed. Benthic fishes associated with the FAD anchors were not surveyed during one census.

To examine faunal changes through time, the FADs were visually censused eight times over a seven month period from May through November. The experimental design, therefore, included a day factor where each treatment level represented the age of the FAD expressed as the number of days elapsed from the time of deployment to the time of census. The experimental design used in this study calls for a statistical analysis using a 3-way Model-I ANOVA (Sokal & Rohlf 1981) in which there are three FAD size treatments, eight day treatments (i.e., eight censuses representing temporal levels within time of year) and six FAD size treatment blocks (resulting from the randomized block spatial configuration). The analysis was conducted on original data and on log (x + 0.5) transformed data for each of the 14 most frequently occurring species, for total number of pelagic and benthic fish and for number of species. Results based on rank transformations used to conservatively test the FAD size effect, for reasons previously outlined (Rountree 1989), agreed well with results based on the log transformation for the day effect so only the latter is presented. Univariate analysis of the residuals confirmed the appropriateness of the log (x + 0.5) transformation.

A total of 121 fish counts were made. Eighty-nine counts were on streamer type FADs. The remaining counts were made on the parasol type FADs and on damaged streamer FADs. Due to differences in soak time, deployment configuration and other confounding problems, the parasol-type FADs and other damaged structures could not be used in the ANOVA and only the 89 streamer FAD observations were used. The Least Significant Difference (LSD) means comparison was used to determine differences among day means, for variables exhibiting a significant overall day effect in the ANOVA.

An opportunity to compare faunal abundance and occurrence between single concrete block structures and streamer FAD anchors was provided by the loss of the FAD from the anchor at some of the stations. Since there were no significant differences among the three sizes of streamer FADs for any of the anchor-associated faunal components (Rountree 1989), all observations at the streamer type FAD anchors were pooled (N = 76) and compared to observations at the concrete blocks (N = 11). Because benthic fishes were not recorded during one census, only data from seven censuses were used in this analysis. A 2-way ANOVA with structure type (two levels) and day (seven levels) main effects was used to compare number of fish and number of species between the blocks and anchors. Additionally, frequency analysis (chi-square) was used to compare the occurrence of fauna between the two types of block structures.

Cluster analysis based on the Jaccard (presence/absence) and Bray-Curtis (abundance) similarity indices (Clifford & Stephenson 1975, Boesch 1977) was used to characterize the fauna attracted to the FADs. Due to unequal sample sizes, the Bray-Curtis index was standardized by station totals. A flexible sorting strategy was used so that the Jaccard similarity was constrained between 1 and − 1 (Clifford & Stephenson 1975). Only those species occurring in at least 5% of the samples were used to compute the similarity indices. The analyses were based on data pooled for the 89 streamer FAD, 12 parasol FAD and 11 concrete block faunal counts combined (N = 106 non-zero stations). Because of the close agreement between the Jaccard and Bray-Curtis analyses, only the Jaccard will be presented.

Interspecific relationships were examined using Spearman rank correlations. However, because the effects of FAD type and census day strongly influenced the correlations, correlations among species were high. To remove the effects of FAD type, census day and station location (treatment block), partial correlation coefficients derived from the error matrix in a multiple analysis of variance were used. Partial correlation coefficients between species and other variables were determined by employing the MANOVA option in the 3-way ANOVA described above using the Generalized Linear Models (GLM) procedure of the Statistical Analysis System (SAS Institute Inc. 1982).

The manner in which fish made use of the FADs was examined by a study of the behavior and spatial distribution of fishes around the FADs. The frequency and density of a species or species group within a matrix of square meter cells around the FAD were calculated. A 2-dimensional matrix was used to represent the area up current and down current of a composite FAD. For example, a school of forty fish might have been observed to occupy an area ranging from 1 to 3 m up current of the FAD and 3 to 5 m above the bottom. Assuming all the fish lie within a plane parallel to the current and passing through the FAD (i.e., compressing the 3-dimensional school into 2-dimensions), the school would be said to occupy a 4 m^2 area with a density of 10 fish m^{-2}. A frequency of one and density of ten would then be assigned to each of four cells in a matrix representing the area in which the fish were observed. This procedure was repeated for each observation and then matrix addition was used to obtain a final matrix of fish frequency and number within each square meter around a composite FAD based on pooled streamer FAD observations. Percent frequency and density contour plots of fish distribution around a composite FAD could then be obtained by dividing each matrix element by the sample size. Contours were compiled for total fish, total fish excluding *Decapterus punctatus* and for the six most common fish species.

Results

Twenty-one families and 36 species of fishes were observed at the 121 stations censused (Table 1). Fourteen species were represented by a single occurrence. The most frequently observed families were Carangidae with seven species; and Serranidae with six species. In addition, the octopus, *Octopus vulgaris*, and three species of crabs, *Menippe mercenaria, Portunus* sp. and an unidentified majid, were observed. Ten species of fishes associated only with the FAD and 23 species associated only with the FAD anchor. Round scad, *Decapterus punctatus*, yellow jack, *Caranx bartholomaei*, and planehead filefish, *Monacanthus hispidus*, associated with both the FAD anchor and the FAD (Table 1). At the streamer-type FADs, six of the top ten fishes by percent occurrence (Table 2), *Decapterus punctatus, Caranx crysos, Monacanthus hispidus, Caranx bartholomaei, Seriola* sp. and *Seriola zonata* associated primarily with the FAD. The other four top-ten fishes associated with the anchor and consisted of the serranids, *Diplectrum formosum, Centropristis striata*, and *Centropristis ocyurus*, and the blenny *Hypleurochilus geminatus*.

Most common species of fishes attracted to the structures were represented by juveniles with only an occasional adult. The only common species which were represented largely by sub-adult and adult individuals were the round scad, *Decapterus punctatus*, and the scup, *Stenotomus chrysops*. The only adult gamefish observed were the Atlantic spadefish, *Chaetodipterus faber*, and the sheepshead, *Archosargus probatocephalus*. A school of three cobia, *Rachycentron canadum* (about 100 cm T.L.) were the only large piscivores observed. Frequent visits by piscivores were suggested, however, by the large wounds which were observed on numerous individuals of *Decapterus punctatus, Seriola* sp., *Caranx bartholomaei*, and *Caranx crysos*.

Pelagic fish dominated the fish fauna at the streamer FADs with a 99.3% relative abundance. *Decapterus punctatus* accounted for 97.6% of the fauna. Excluding *D. punctatus*, pelagic fish still dominated, accounding for 70% of the fauna (Fig. 1). *Caranx crysos* occurred at 44% of the stations (Table 2) and was the second most abundant fish with an average of 7.1 fish FAD^{-1}. This species made up about 1% of the total fauna but accounted for 43% of the fauna after removing *D. punctatus*. *Diplectrum formosum* was the dominant benthic fish accounting for 11% of the total fauna after excluding *D. punctatus*. Although *Stenotomus chrysops* accounted for 8% of the faunal abundance, it only occurred at 6% of the streamer FAD anchors. *Centropristis striata*, however, occurred at 55% of the streamer FAD anchors, but because it occurred as a solitary individual 88% of the time, it accounted for only 3% of the total faunal abundance with *D. punctatus* removed.

The fauna of anchors of destroyed FADs (i.e., a single concrete block without a FAD) was significantly more depauperate than that associated with FAD anchors (Table 3). Twenty-one species of benthic fishes were observed associated with the streamer FAD anchors (Table 1), with an average

Table 1. Species associated with FADs and/or with the FAD anchors and life history stages observed.

Family Species	Associated with anchor	Associated with FAD	Juvenile	Adult or sub-adult
Congridae				
Conger oceanicus	*			*
Clupeidae				
Sardinella aurita		*		*
Batrachoididae				
Opsanus tau	*			*
Antennariidae				
Antennarius sp.	*			*
Gadidae				
Urophycis sp.	*			*
Syngnathidae				
Hippocampus erectus	*			*
Syngnathus sp.	*			*
Serranidae				
Centropristis ocyurus	*		*	
Centropristis striata	*		*	
Diplectrum formosum	*		*	
Epinephelus morio	*		*	
Mycteroperca microlepis	*		*	
Serranus subligarius	*		*	
Grammistidae				
Rypticus sp.	*		*	
Priacanthidae				
Priacanthus cruentatus	*		*	
Rachycentridae				
Rachycentron canadum		*		*
Carangidae				
Caranx bartholomaei	*	*	*	
Caranx crysos		*	*	
Caranx ruber		*	*	
Decapterus punctatus	*	*	*	*
Seriola zonata		*	*	
Seriola sp.		*	*	
Trachurus lathami		*		*
Lutjanidae				
Lutjanus sp.	*		*	
Haemulidae				
Haemulon aurolineatum	*		*	
Sparidae				
Archosargus probatocephalus	*			*
Stenotomus chrysops	*			*
Sciaenidae				
Equetus acuminatus	*		*	
Ephippidae				
Chaetodipterus faber		*		*
Pomacanthidae				
Holacanthus sp.	*		*	
Labridae				
Halichoeres sp.	*		*	
Blenniidae				
Hypleurochilus geminatus	*		*	*
Balistidae				
Aluterus monoceros		*		*
Aluterus scriptus		*		*
Monacanthus hispidus	*	*	*	
Diodontidae				
Chilomycterus schoepfi	*			*

of 2.1 species anchor^{-1} and 5.7 fish anchor^{-1} (Table 3). A total of only two fish species was observed at the concrete blocks with a significantly lower average of 0.4 fish species and 0.5 fish block^{-1}. Fishes were absent from concrete blocks significantly more frequently (73%) than at FAD anchors (8%, Table 3). *Diplectrum formosum* was the only common fish species observed at the concrete blocks, but it was significantly more abundant at the FAD anchors (Table 3). Although *D. formosum* occurred more frequently at the FAD anchors than at the blocks, the difference was not significant ($p = 0.057$).

Cluster analysis based on the Jaccard similarity among the species at the 106 pooled stations resulted in three species groups (Fig. 2). Group-I includes eight of the ten most frequently occurring species. This group was further divided into subgroups A and B with group-IB most common in early summer. Group-IA species occurred fairly constantly over much of the study period and FAD types. Group-II species were a heterogeneous assemblage that occurred mainly from mid-summer to early fall and were more frequent (and abundant) at the parasol FADs (especially *Equetus acuminatus, Stenotomus chrysops* and *Seriola* sp.). In Group-III the three pelagic species, *Seriola zonata, Caranx ruber* and *C. bartholomaei*, were united by frequent co-occurrence early in the study (May-June) before they disappeared in July. *Caranx bartholomaei*, however, reappeared in the late fall and was united with the other common fall species, *Octopus vulgaris* and *Chaetodipterus faber*.

Although some species pairs co-occurred frequently (Table 4), log transformed abundances among the six most common fish species (Table 5) were not significantly correlated. However, the number of *C. striata* and total number of bottom fish excluding *C. striata* exhibited a nearly significant negative correlation ($r = -0.415$, $p = 0.0689$). Several variables were significantly correlated with species number.

Changes in species composition and abundance over the study period indicate a strong seasonality (Table 6). The average number of species per FAD was significantly affected by census day and exhibited a peak on day 55 (Fig. 3). The mean number of pelagic species and benthic species were nearly equal and exhibited similar significant temporal trends. The mean number of bottom fish peaked on day 55 and then declined through the fall, while the

Table 2. Mean number (SD) and percent frequency of the ten most common fishes and two most common invertebrates observed at the streamer FADs.

Species	Percent frequency	Mean (SD)
Fishes		
Decapterus punctatus	67.7	576 (1267)
*Diplectrum formosum**	57.9	2.1 (3.4)
*Centropristis striata**	55.3	0.6 (0.6)
Caranx crysos	43.8	7.1 (13.0)
Monacanthus hispidus	40.4	1.1 (3.4)
Caranx bartholomaei	29.2	1.7 (4.5)
*Centropristis ocyurus**	19.7	0.2 (0.6)
*Hypleurochilus geminatus**	14.5	0.3 (0.9)
Seriola sp.	11.2	1.2 (5.1)
Seriola zonata	7.9	0.1 (0.3)
Invertebrates		
*Menippe mercenaria**	27.6	0.3 (0.5)
*Octopus vulgaris**	15.8	0.2 (0.4)

Sample size N = 89

* Sample size N = 76

* Benthic species were not censused during one dive.

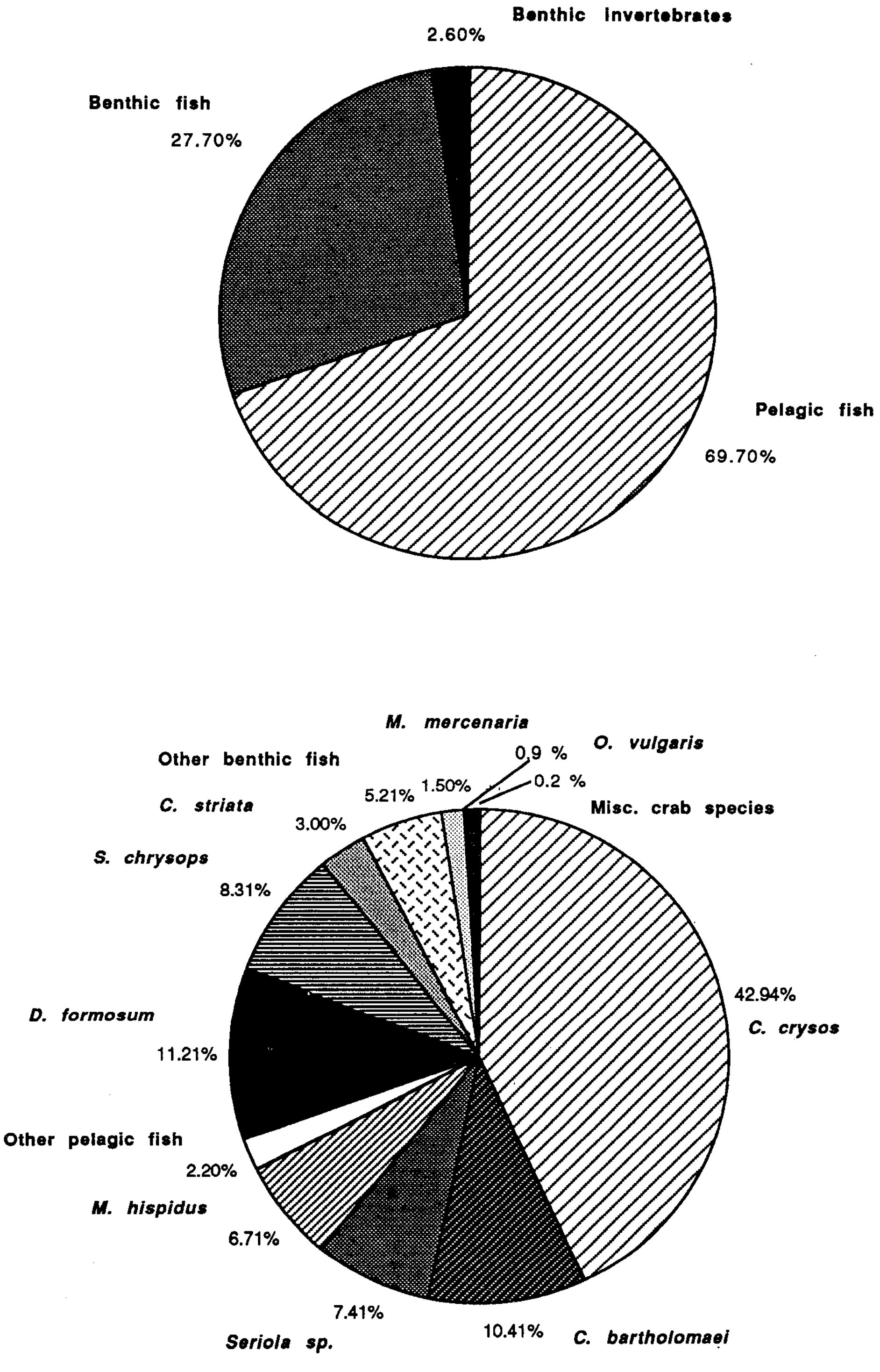

Fig. 1. Relative abundance of pelagic and benthic faunal assemblages (upper pie chart) and of the most abundant species (lower pie chart) observed at streamer FADs (N = 89). Note, because of the overwhelming dominance of *Decapterus punctatus* (97.6% relative abundance) the relative abundances used in these figures were calculated with *D. punctatus* excluded.

mean number of pelagic fish excluding *D. punctatus* fluctuated widely (Fig. 4). *Decapterus punctatus* abundances were highly significantly affected by census day with mean abundance peaking at 3186 fish FAD^{-1} on day 100 in August. However, *D. punctatus* was present at 100% of the stations throughout the summer and early fall except on day 91 (Fig. 5). Both the abundance and frequency of *D. formosum* rose from a low on day 8 to a peak on day 55 and then declined through the rest of the study. *Caranx crysos* abundances fluctuated widely throughout the study, but peaked in October on day 159 before dropping to zero in November on day 194 (Fig. 4). The percent frequency of *C. crysos*, however, quickly rose to a peak of 79% on day 55 in July and then fluctuated between 64% and 72% over most of the summer and fall except for day 91 (Fig. 5). *Caranx bartholomaei* occurred most frequently and abundantly only during the cooler periods at the beginning and end of the study when *C. crysos* was virtually absent. However, a few young-of-the-year *C. bartholomaei* were observed on day 100 (14%) when drifting sargassum was common in the study area.

After Hurricane Bob passed through the study area in July, the total number of species and the frequency and abundance of many of the pelagic species dropped sharply on day 91 (Table 6, Fig. 3, 4, 5).

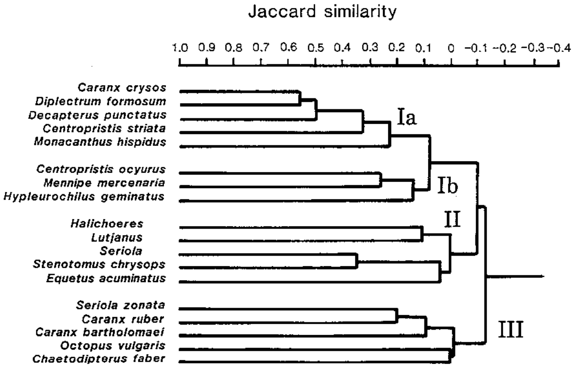

Fig. 2. Dendrogram resulting from inverse cluster analysis using the Jaccard similarity index based on presence/absence of species occurring in at least 5% of the observations. The analysis was based on data pooled for the 89 streamer FADs, 12 parasol FADs and 11 concrete block stations combined (N = 106 non-zero stations).

Total fishes, including *D. punctatus*, tended to be distributed more to the up current side of both the anchor and the FAD with highest occurrence around the anchor and within one meter below the FAD float. For data compiled over all streamer FAD censuses (N = 88 non-zero stations) fishes utilized a total area of 119 m^2 and averaged 12.2

Table 3. Summary data comparing benthic fauna found associated with concrete blocks without FADs to fauna associated with the concrete block anchors of streamer FADs.

	Concrete blocks		Streamer FAD anchors		Test for difference	
	Percent frequency	$\bar{x}$ ($S_{\bar{x}}$)	Percent frequency	$\bar{x}$ ($S_{\bar{x}}$)	χ^2	ANOVA
Zero species	45.5		5.3		***	
Zero fish species	72.7		7.9		***	
Diplectrum formosum	27.3	0.4 (0.2)	57.9	2.2 (0.4)	ns$^+$	**
Halichoeres sp.	9.1	0.1 (0.1)	3.9	0.1 (0.1)	ns	ns
Octopus vulgaris	27.3	0.3 (0.1)	15.8	0.2 (0.1)	ns	ns
Menippe mercenaria	9.1	0.1 (0.1)	27.6	0.3 (0.1)	ns	ns
Total no. bottom fish		0.5 (0.2)		5.7 (1.2)		***
No. fish species		0.4 (0.2)		2.1 (0.1)		***
Total fish species		2		21		
Sample size		11		76		

* = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$
$^+$ $p = 0.057$

Table 4. Percent co-occurrence of fishes, *Octopus vulgaris* and *Menippe mercenaria* observed at the streamer FADs (n = 89).

Species no. Species Species no.:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 *Caranx crysos*	–	60	55	37	29	28	20	20	5	13	22	21	7	5	8	10	8	2
2 *Diplectrum formosum*		–	49	43	38	30	18	20	7	11	20	17	9	2	7	11	9	0
3 *Decapterus punctatus*			–	37	38	22	13	16	8	10	16	16	21	6	5	5	7	5
4 *Centropristis striata*				–	21	33	8	7	5	5	14	11	12	5	5	7	8	5
5 *Monacanthus hispidus*					–	16	25	21	11	11	21	7	9	2	3	5	3	8
6 *Menippe mercenaria*						–	25	7	0	8	14	0	9	8	9	13	9	0
7 *Centropristis ocyurus*							–	14	0	18	9	0	5	5	13	0	0	0
8 *Seriola* sp.								–	25	23	17	0	0	6	0	0	0	0
9 *Stenotomus chrysops*									–	0	0	0	0	0	14	11	0	0
10 *Caranx ruber*										–	6	0	0	8	0	0	0	0
11 *Hypleurochilus geminatus*											–	5	3	0	0	7	0	0
12 *Octopus vulgaris*												–	9	0	0	0	7	0
13 *Caranx bartholomaei*													–	18	0	0	3	7
14 *Seriola zonata*														–	0	0	0	0
15 *Halichoeres* sp.															–	14	0	0
16 *Lutjanus* sp.																–	0	0
17 *Epinephelus morio*																	–	0
18 *Chaetodipterus faber*																		–

(± 8.5) m^2 station^{-1}. With *D. punctatus* removed from the analysis, fishes utilized a total of 65 m^2 and averaged 8.1 (± 5.6) m^2 station^{-1} (N = 87 non-zero stations, Fig. 6a). Fishes occurred most frequently (79% of the stations) within an area of 1 m^2 up and down current of the anchor, followed by an area of 1 m^2 up and down current of the float and first subunit of the FAD (54–58% of the stations, Fig. 6a). Average densities of fishes (excluding *D. punctatus*) around the streamer FADs were highest around the anchor (1.51–2.00 fish m^{-2}, Fig. 6b). Excluding *D. punctatus*, fishes utilized an area equally distributed up current and down current of the structure, but tendend to be more numerous down current (Fig. 6).

The most abundant species, *D. punctatus*, oc-

Table 5. Selected partial correlations from a partial correlations matrix derived from the error matrix obtained in a 3-way MANOVA on streamer FAD observations.

Species/variable	Bottom species	Pelagic species	Total species
Decapterus punctatus	– 0.173	0.234	– 0.095
Diplectrum formosum	0.369	0.042	0.292
Centropristis striata	– 0.255	– 0.266	– 0.309
Caranx crysos	0.209	0.351	0.390
Monacanthus hispidus	0.472*	0.219	0.466*
Caranx bartholomaei	0.189	0.632**	0.481*
Total no. bottom fish	0.689***	0.243	0.595**
Total no. pelagic fish (minus *D. punctatus*)	0.266	0.602**	0.611**
Total no. pelagic fish	0.037	0.472*	0.213
Total no. fish (minus *D. punctatus*)	0.462*	0.565**	0.709***
Total no. fish	0.173	0.406	0.278
No. bottom species		0.161	0.785***
No. pelagic species	0.161		0.704***

N = 76, DF = 18, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$

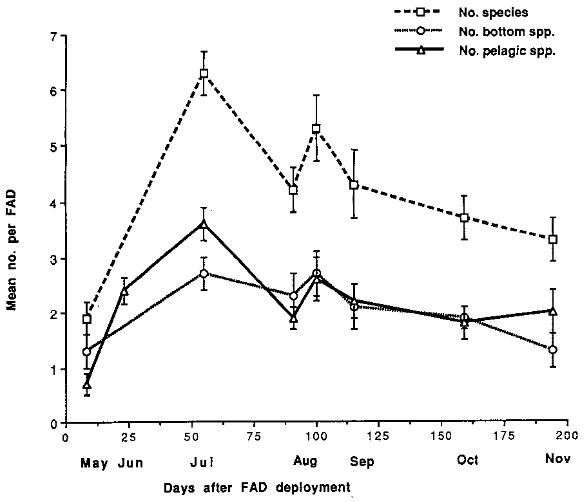

Fig. 3. Mean number (standard error) of pelagic, bottom and total fish species per streamer FAD plotted against census day (i.e., days elapsed between the time of FAD deployment and the time of census, N = 89).

curred most frequently and in greatest numbers at a point level with, and 1–2 m up current of the FAD (30–39% contour and 30–39.9 fish m^{-2} contours in Fig. 6c and 6d, respectively). *Decapterus punctatus* was usually observed to be actively feeding on plankton while associated with the FAD, however, occasionally small, compact schools were observed in an apparently inactive state near the bottom, up current of the FAD anchor (10–19% contour 3–4 m up current of the FAD anchor in Fig. 6c). *Decapterus punctatus* utilized a total area of 117 m^2 with an average of 10.1 ($\pm$5.8) m^2 $station^{-1}$ (N = 61 non-zero stations, Fig. 6).

A composite figure made from the two highest frequency and highest density contours for the six most common species depicts the spatial distribution of fishes at a 'typical' streamer FAD (Fig. 7). Typically the jacks, *C. crysos* and *C. bartholomaei*, remained closer to the FAD than *D. punctatus* and when either species co-occurred with *D. punctatus* they usually were found down current. However, *C. crysos* and *C. bartholomaei* rarely co-occurred at the same station (6.6% co-occurrence, Table 4). All three of these species were often observed feeding on plankton. *Monacanthus hispidus* was intimately associated with the shelter of the FAD and anchor, and often was observed feeding on the fouling organisms of the FAD. *Centropristis striata*

Table 6. Significance of day of census for the abundance of the six most common fishes, total fishes and number of species from the 3-way Model-I ANOVA on log transformed data. Within a variable days with the same letter are not significantly different (LDS means comparison, p < 0.05).

Species	Day of census								Overall day effect (p =)
	8	23	55	91	100	115	159	194	
Decapterus punctatus	D	B	A	C	A	A	C	D	0.0001
*Diplectrum formosum**	D	–	A	AB	AB	BC	BC	CD	0.0013
*Centropristis striata**									0.0724 NS
Caranx crysos	C	C	A	BC	A	AB	A	C	0.0028
Monacanthus hispidus									0.7270 NS
Caranx bartholomaei	B	A	C	C	BC	C	BC	A	0.0001
Total no. bottom fish*	D	–	A	BC	AB	C	CD	D	0.0001
Total no. pelagic fish (minus *D. punctatus*)	E	BCD	A	DE	AB	CD	AB	ABC	0.0002
Total no. pelagic fish	F	C	AB	DE	A	B	D	E	0.0001
Total no. fish (minus *D. punctatus*)	E	DE	A	CD	AB	CD	AB	BC	0.0001
Total no. fish	F	C	AB	DE	A	B	DE	E	0.0001
No. bottom species*	C	–	A	A	A	AB	AB	BC	0.0217
No. pelagic species	C	AB	A	B	AB	B	B	B	0.0001
Total no. species*	D	–	A	BC	AB	BC	C	C	0.0001

* N = 76, all others N = 89

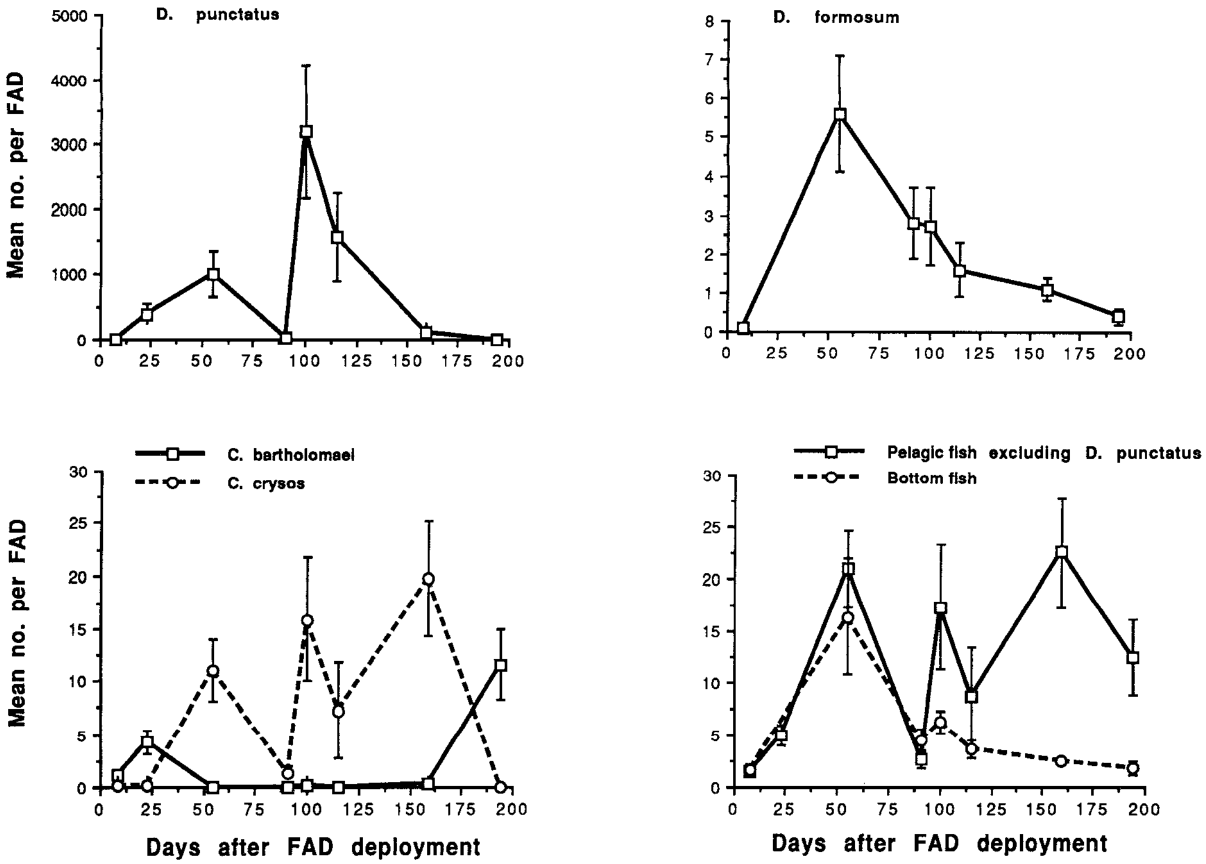

Fig. 4. Seasonal abundance patterns of selected fish species and of the total number of bottom fish and total number of pelagic fish, excluding *D. punctatus*. Mean number of fish per streamer FAD, with standard error bars, is plotted against census day.

and *Diplectrum formosum* associated with the anchor (Fig. 7). Although *D. formosum* was frequently observed in the sand around the FAD anchor, *C. striata* was usually observed resting upon or inside of the anchor. *Diplectrum formosum* and smaller individuals of *C. striata* often approached the divers and could be observed feeding on materials disturbed from the sediment by diver movements. Larger individuals of *C. striata* usually ignored the divers and could not be driven from the shelter of the block even with vigorous agitation by the divers.

Orientation to the grid rope may have made fish movement between stations possible. *Centropristis striata, M. hispidus* and *Mycteroperca microlepis* were observed to orient to the rope grid line when more than a meter from the anchor. On two occasions individuals of rare species were assumed to have moved between stations by following the rope grid line. A red grouper, *Epinephelus morio*, was first observed at station number seven on day 91 and again on days 100 and 115 (24 days elapsed) before it was sighted at the adjacent station number eight on day 154 (total of 63 days elapsed). Similarly a frogfish, *Antennarius* sp., was observed at station nine on day 100 and at the adjacent station number ten on day 115.

Discussion

Most of the species observed in this study did not occur in sizes large enough to directly contribute to the recreational fishery, except for *Archosargus probatocephalus* and *Chaetodipterus faber*. However, FADs are used mainly to attract baitfishes

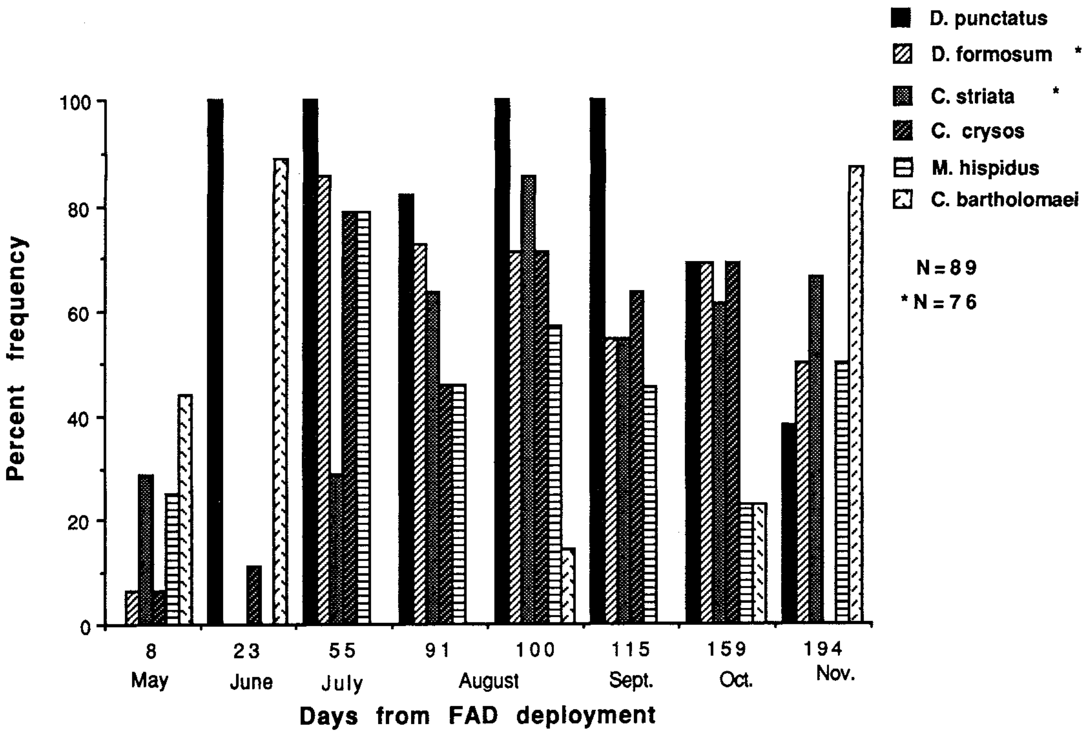

Fig. 5. Percent occurrence of the six most common fishes observed at the streamer FADs by day of census.

which, in turn, are thought to attract the important pelagic gamefishes into the general area (M. Bell personal communication). Trolling alleys in South Carolina are typically made up of 100 FADs scattered along a 0.8–1.6 km alley. The mean number of fishes observed at the FADs during the peak period of August can be used to extrapolate an estimated peak standing crop of 320900 fish in a typical trolling alley. I have little doubt that such large aggregations of fish would have an important impact on the pelagic predators sought after in the fishery. The lack of observations of large predator species at the FADs during SCUBA censuses in this study may be due in part to poor visibility, however, species such as *Rachycentron canadum, Seriola dumerili*, and *Sphyraena barracuda* would almost certainly have been observed if present. Other species which tend to avoid divers and which are transient visitors at the FADs (sensu Gooding & Magnuson 1967), such as *Scomberomorus cavalla* and *S. maculatus*, may not have been adequately censused. In fact, an earlier study of FADs in South Carolina found greater catch per unit effort for pelagic gamefishes (*S. cavalla* and *S. maculatus*) at a trolling alley compared to control areas (Hammond et al. 1977).

FADs in trolling alleys in South Carolina are much more closely spaced than FADs in this study (personal observation). Such close spacing may result in large transitory predators treating the alley as one large artificial reef rather than treating each FAD as a separate island reef. Although single FADs of the type used in this study may not attract prey fishes in sufficient abundances to attract larger predators, many closely spaced FADs may support bait fish populations in numbers great enough to attract transient predators such as *S. cavalla* and *S. maculatus*.

There were strong differences in the fish fauna observed associated with the FADs and the fauna of sandy bottom in the South Atlantic Bight. I observed only four of the 14 numerically dominant demersal fishes collected over sandy bottom during the summer months in the 9–18 m depth zone of the South Atlantic Bight (Wenner et al. 1979). However, the three dominant species *Stenotomus acu-*

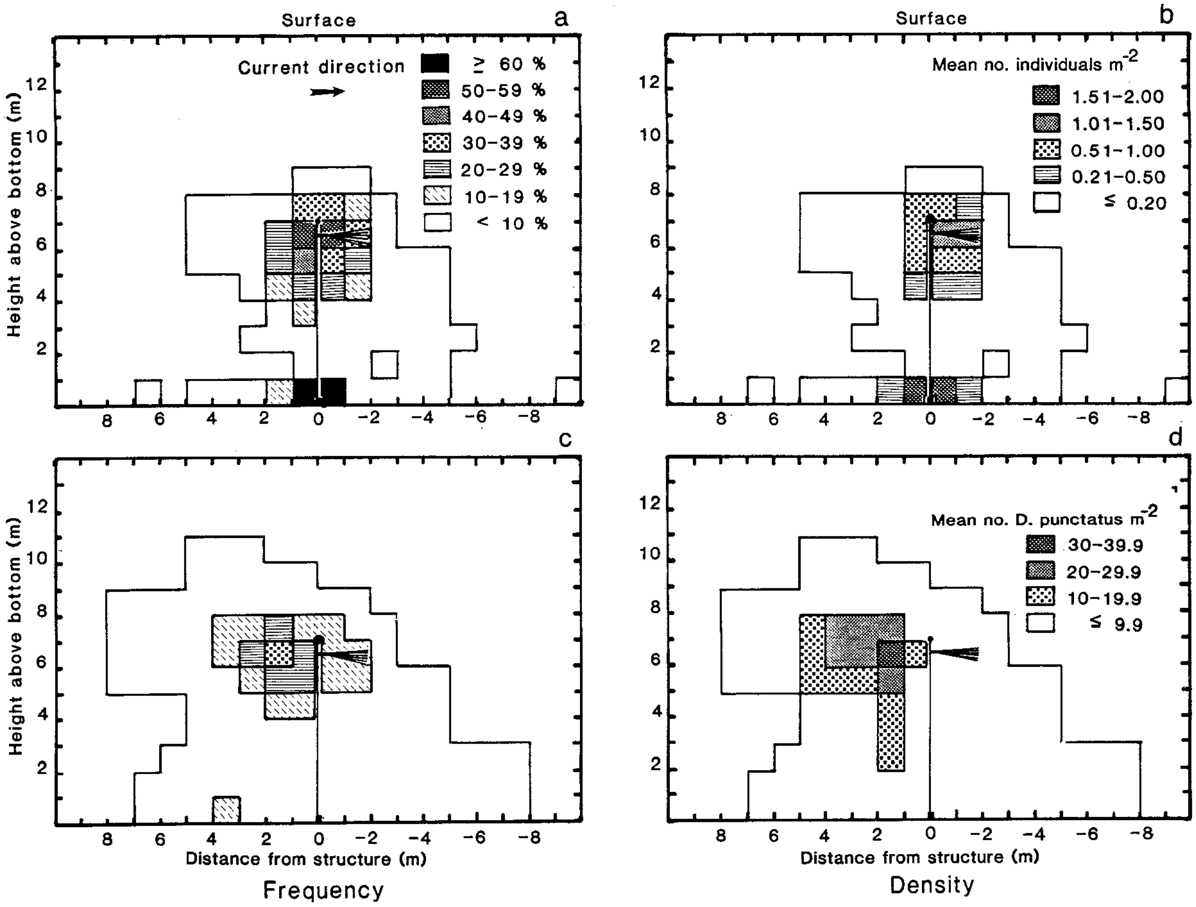

Fig. 6. Percent frequency and density contours for total fish, excluding *D. punctatus*, and for *D. punctatus* (N = 89, Fig. a, b, c, and d respectively).

leatus (= *chrysops*), *Stephanolepis* (= *Monacanthus*) *hispidus* and *Diplectrum formosum* reported by Wenner et al. (1979) were also among the most important fishes observed at the FADs (Fig. 1). These and other demersal species observed at the FADs are, however, also characteristic of live bottom (sponge-coral) areas (Wenner 1983, Sedberry & Van Dolah 1984) and of shallow water artificial reefs in the South Atlantic Bight (Buchanan 1973, Buchanan et al. 1974, Parker et al. 1979, Steimle & Ogren 1982, Lindquist et al. 1985). Although the pelagic fauna associated with the FADs exhibit their strongest similarities with flotsam and *Sargassum* fauna (Rountree 1989), they were also representative of dominant species taken over sandy bottom (Wenner et al. 1979, 1980). Generally, the total fauna associated with the FADs was more characteristic of communities associated with live bottom and hard substrate than the truly sand bottom communities.

Decapterus punctatus, the most common and abundant species observed at the FADs (Table 2, Fig. 4), is one of the most abundant coastal pelagic species in the South Atlantic Bight (Wenner et al. 1979, 1980, Hales 1987). *Decapterus punctatus* has been described as a close associate of *Sargassum* spp. (Dooley 1972) and as one of the most abundant species observed around FADs in the Gulf of Mexico (Klima & Wickham 1971, Wickham et al. 1973, Ogren 1974, Wickham & Russell 1974). Hammond et al. (1977) also observed *D. punctatus* as common around FADs in South Carolina. Murray et al. (1987), however, reported *D. punctatus* as infrequent and occurring in low abundance around FADs during the summer in 7 m of water off North Carolina. However, *Decapterus punctatus* is known to exhibit spatial segregation with depth by size class and is thought to undergo seasonal inshore-offshore migrations (Hales 1987). Therefore, the absence of *D. punctatus* around FADs in North Carolina was probably due to the proximity to shore of the study site as the species has been observed in abundance around FADs placed in deeper water nearby (Stephan & Lindquist 1989).

The blue runner, *Caranx crysos*, the second most abundant species observed in this study (Table 2, Fig. 4) has been commonly reported to associate with FADs (Klima & Whickham 1971, Wickham et al. 1973, Wickham & Russell 1974, Murray et al. 1987). Juvenile *C. crysos* have also been described as *Sargassum* spp. associates (Berry 1959, Dooley 1972, Bortone et al. 1977, Johnson 1978). Dooley (1972) reported that blue runner occurred in relatively low abundance with *Sargassum* spp. from March through June, in high abundance in June and July and were uncommon after November, agreeing well with the seasonality observed around FADs in South Carolina (Fig. 4, 5). Murray et al. (1987) reported that *C. crysos* did not appear around FADs in North Carolina until early June, while I observed small numbers as early as late May (Fig. 5). More recently Stephen & Lindquist (1989) report a similar seasonal distribution of *C. crysos* at FADs off North Carolina.

According to existing literature, larvae and juveniles of *C. crysos* occur with strongest affinity within the Gulf Stream and offshore waters of the southeastern United States and remain offshore until reaching a size of from 80 mm to 100 mm SL (McKenney et al. 1958, Berry 1959, Johnson 1978, Goodwin & Finucane 1985). Fish over 80 mm SL begin moving into the inshore waters in July and may move back offshore after November (Berry 1959, Johnson 1978). The sudden disappearance of *C. crysos* around FADs in November (Fig. 4, 5) was probably a result of such offshore migration.

Caranx bartholomaei observed in this study exhibited a bimodal seasonal distribution occurring during the cooler months (excluding the few very small juveniles observed in August). Although I observed the species in small numbers during May and June off South Carolina (Fig. 4, 5), Murray et al. (1987) did not report *C. bartholomaei* around FADs off North Carolina during that period. More recently, *C. bartholomaei* has been observed in small numbers at FADs off North Carolina (Stephan & Lindquist 1989). The lack of previous *C. bartholomaei* records in FAD studies in the western Atlantic and Gulf of Mexico was probably be-

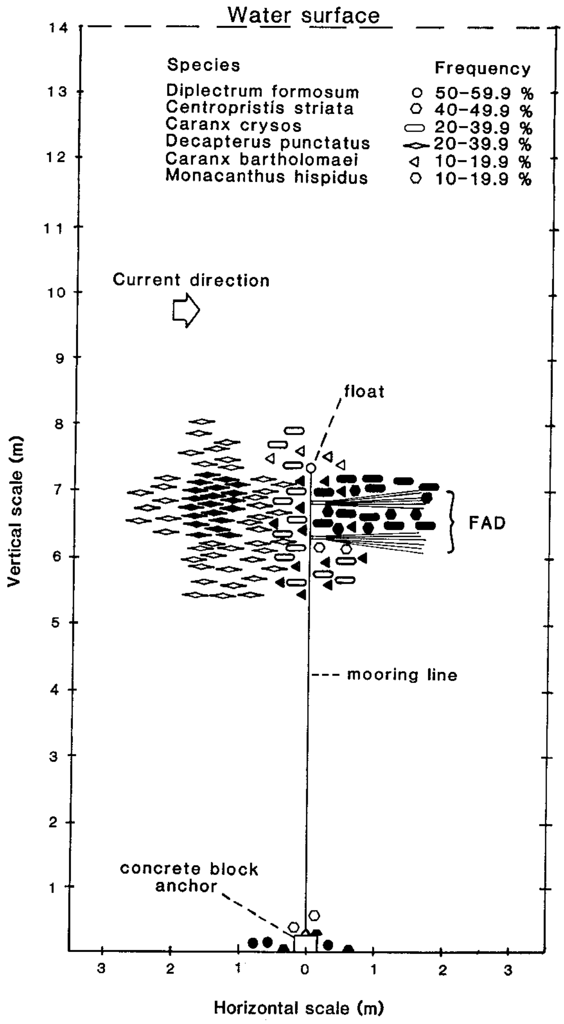

Fig. 7. Spatial distribution of fishes at a sterotype streamer FAD derived by overlaying the two highest frequency and highest density contours for the six most common fishes observed at the FADs (N = 89). Open symbols define the most frequent spatial distribution of each species, while darkened symbols define the area of greatest density for each species.

cause these studies were carried out during the summer (Klima & Wickham 1971, Wickham et al. 1973, Wickham & Russell 1974, Murray et al. 1987).

Very little is known of the ecology of *C. bartholomaei*, but the larvae and juveniles are thought to occur mainly in offshore currents with adults uncommonly found in inshore waters (Berry 1959, Johnson 1978). Young juveniles, however, have been reported as associates of jellyfish (Fowler 1945, Berry 1959, Mansueti 1963, Johnson 1978) and with *Sargassum* spp. (Berry 1959, Fine 1970, Bortone et al. 1977, Johnson 1978). The occurrence of the very young juveniles at the FADs in August (Fig. 5) corresponded with the presence of large amounts of *Sargassum* spp. in the surface waters of the study area during that time. Therefore, these individuals were probably strays from offshore which were carried into the shallow inshore waters of the study site with the drifting *Sargassum*.

The abundance of most of the FAD fauna was significantly affected by census day (Table 6, Fig. 4). Differences in faunal composition and abundance among census days could result from successional and/or seasonal effects. However, it is known that seasonal changes frequently swamp out succession changes on artificial reefs (Hastings 1979, Lukens 1981, Bohnsack & Sutherland 1985, Lindquist et al. 1985). Although, succession may have occurred to some degree at the FADs, seasonal inshore-offshore movement patterns and seasonally regulated juvenile fish availability were apparently the most important factors determining FAD species composition and abundance. Since juveniles dominated the FAD fauna, much of this effect was probably a reflection of juvenile recruitment dynamics in the study region. *Decapterus punctatus* (Hales 1987), *Diplectrum formosum* (Darcey 1985), *Centropristis striata* (Waltz et al. 1979), and *Caranx crysos* (Berry 1959, Goodwin & Finucane 1985) are thought to exhibit some sort of seasonal segregation in depth distribution by size, indicating inshore-offshore migrations. The seasonal occurrence of many of the less common species, such as *Menippe mercenaria, Octopus vulgaris, Mycteroperca microlepis, Archosargus probatocephalus*, etc., were also probably related to inshore-offshore movements. Stephan & Lindquist (1989) also report that seasonal inshore-offshore migrations of nearshore fishes probably account for the seasonal differences in fish composition at FADs off North Carolina. The abundance and composition of fauna at the FADs was most strongly a reflection of juvenile fish availability due to a combination of seasonal spawning and seasonal movement patterns.

Weather conditions apparently affected the abundance of fishes at the FADs. The effects of Hurricane Bob probably resulted in the diminished abundance of pelagic fishes at the FADs (Table 6). Interestingly, the effects on *Decapterus punctatus* (Rountree 1989) and other pelagic species were greatest at the larger FADs. Although larger FADs normally attracted significantly greater numbers of fishes than smaller FADs, the trend was reversed on day 91 when larger FADs exhibited the lowest abundances (Rountree 1989). This suggests that heavy surge conditions adversely affect the ability of pelagic fishes to maintain their orientation to the FADs and can occasionally disrupt shallow water communities.

The large number of rare species observed at the FADs indicates that sporadic intrusions of larger fishes, especially of predators (like *Opsanus tau, Antennarius* sp., *Epinephelus morio, Mycteroperca microlepis, Rachycentron canadum*) may have an important impact on the community structure of FADs. Occasional denuding of fishes at FADs by the intrusion of predators would increase variation among stations and make interpretation of community structure analysis more difficult.

Competition for planktonic food resources may have been an important determinant of the pelagic FAD fauna composition. *Decapterus punctatus* is known to be a planktivore and feeds largely on copepods (Dooley 1972, Hales 1987). Similarly, I have observed *C. crysos* actively feeding on plankton and the species has been reported to feed on planktonic copepods and other zooplankton (McKenney et al. 1958, Dooley 1972). I am unaware of any published reports on feeding by juvenile *C. bartholomaei*, but I have observed the species actively feeding on plankton while associated with the FADs. Recent studies have shown that planktivorous fishes can measurably reduce the concentration of plankton in the water (Kingsford & MacDiarmid 1988, Hamner et al. 1988). In fact, Hamner et al. (1988) found that planktivorous fishes can deplete most of the plankton from the water up current of coral reefs. This suggests that there may be competition for plankton food resources among pelagic FAD associated fishes. In such an event the species which positions itself furthest up current of the FAD would have the competitive advantage. Both *C. bartholomaei* and *C. crysos* occupied a position directly around the FAD and down current of *D. punctatus* (Fig. 7). When extremely abundant, *D. punctatus* may severely deplete the plankton food resource before it reaches *C. bartholomaei* or *C. crysos* resulting in increased competition between these species for a limited food resource.

The spatial position occupied by fishes around FADs is also governed by predator avoidance behavior (Rountree 1989). Large schools of fish may be less dependent on FADs for shelter and could then afford to move farther up current of the shelter to obtain better food resources than small schools. In fact, the behavior of *D. punctatus* supports this idea (Rountree unpublished). Species, such as *C. bartholomaei* and *C. crysos*, occurring at the FADs in smaller numbers may, however, be forced to choose a less than optimal feeding position because of their greater need for protective shelter.

Although the blue runner co-occurred with *D. punctatus* frequently, the yellowjack co-occurred with *D. punctatus* only 21% of the time and only 7% of the time with *C. crysos* (Table 4). Given the nearly complete overlap of the spatial distributions of *C. bartholomaei* and *C. crysos* (Fig. 7) and their strikingly opposite temporal abundance and frequency patterns (Fig. 4, 5), interspecific competition is suggested. Specifically, *C. bartholomaei* may not be able to compete with *C. crysos* for a limited plankton food resource in the presence of *D. punctatus*. Simple differences in the seasonal occurrence of these species does not completely account for this apparent competition because the two species rarely co-occurred at the same station (Table 4) despite both occurring at the FADs during censuses in May, June and October (Fig. 5). Further studies with FADs promise to help elucidate the role of such hypothetical competitive interactions in shaping nearshore fish communites.

Other than seasonal availability, three main factors may be hypothesized to have governed the attraction of bottom fish to the FADs: (1) the availability of shelter, (2) the availability of food, (3) larval settlement channel (sensu Beets 1989). Although there were strong indications of competition for shelter within the concrete blocks anchoring FADs, the otherwise identical concrete block structures lacking FADs were significantly depauperate (Table 3), indicating that shelter alone was not enough to attract many bottom fish species. The presence of the FAD may have increased the attractiveness of the concrete block anchor to bottom fishes directly by providing a settlement channel for fish larvae (Beets 1989) or indirectly by enhancing the food resources available to the bottom fishes associated with the FAD anchor.

FAD enhanced settlement of larvae to the concrete blocks was suggested by the presence of some very small juveniles of rare species (e.g., *Lutjanus* sp. and *Holacanthus* sp.). However, most common bottom species occurred as older juveniles indicating recruitment through bottom movements, perhaps enhanced through orientation to the grid rope (e.g., *M. microlepis, C. striata*, and *D. formosum*). The apparent movement of *Antennarius* sp. and *Epinephelus morio* between adjacent FADs, and the frequently observed behavioral orientation of *C. striata* and *M. microlepis* to the grid rope, supports this hypothesis. It is the opinion of this author that most bottom fish recruitment to the FADs occurred through movements of young juveniles and adults along the ocean floor. However, because of the length of time between censuses, the settlement channel hypothesis can not be ruled out.

Food resources available to the bottom fish may have been enhanced by the presence of pelagic schooling fishes at the FADs or by the occurrence of organic fallout from fouling organisms growing on the FADs. This hypothesis is supported by the observations that the abundance of bottom fish at the FADs was found to increase with increasing

FAD size (though not significantly), while the abundance of pelagic fish exhibited a significant linear response to FAD size (Rountree 1989) suggesting that bottom fish abundance may be influenced by pelagic fish abundance. In addition, larger FADs provided more area for fouling organisms and, hence, may have resulted in greater amounts of organic fallout from the fouling community.

Several factors further support a hypothetical link between pelagic fish and bottom fish. The absence of *C. striata* and significantly lower abundance of *D. formosum* at the concrete blocks (Table 3), and the grouping of these species together with *M. hispidus, D. punctatus* and *C. crysos* in the cluster analysis (Fig. 2) indicates that some sort of community interactions may be taking place among these benthic and pelagic fishes. The pelagic species *C. crysos* and bottom species *D. formosum* were the most frequently co-occurring species pair (Table 4). *Decapterus punctatus* and *D. formosum* also co-occurred frequently (Table 4). By abundance the two schooling species *Seriola* sp. (pelagic) and *S. chrysops* (bottom) were most similar (Bray-Curtis similarity index of 0.572). Additionally, *M. hispidus* was significantly correlated with number of bottom species (Table 5).

Schools of resident fishes have been suggested to increase secondary productivity of certain benthic communities by a transfer of nutrients obtained while feeding in other habitats to the benthic communities through the accumulation of organic materials in fecal deposits (Bray et al. 1981, Meyer et al. 1983, Meyer & Schultz 1985a, 1985b). Similarly, pelagic species such as *D. punctatus*, by feeding on plankton and depositing feces on the bottom near the FADs, may increase the attractiveness of the FAD anchors to bottom fishes. Although much of this organic rain may be swept away from the FAD site by water currents, some portion may reach the FAD in the vicinity of the anchor. Movements of the pelagic fishes including frequent visits to the bottom around the anchor and occasional resting periods on the bottom up current of the anchor (Fig. 6c) may substantially increase the amount of organic fallout reaching the bottom near the FAD anchor.

Although the importance of organic rain is well known in deep sea literature (e.g., Bruun 1957, Smith 1977), the transfer of energy from the water column to the benthic community by pelagic fish in shallow water has received little attention (Jurkevics unpublished M.S. thesis, Bray et al. 1981, Robertson 1982, Bray & Miller 1985). Jurkevics (unpublished), found that fecal material may reach the benthos in sufficient amounts to significantly affect community distributions in kelp forests. Particulate material collected in bottom traps in a kelp forest were comprised of 7–51% fish feces. Robertson (1982) found interspecific coprophagy to be common on Pacific coral reefs and that some fish species consumed the feces of zooplanktivorous fishes with which they associated. The extremely dominant pelagic component of the FAD fauna (99.3% relative abundance, Fig. 1) may generate sufficient organic fallout to increase benthic secondary production enough to support the much less abundant bottom fish fauna. Organic fallout resulting from uneaten fish carcasses and fish debris left by piscivorous predators may also provide an important supplement to bottom fish diets. Observations of demersal fishes feeding on materials kicked up from the sand by diver activity suggests that some form of food was available immediately around the FAD anchor.

Alternatively, pelagic and bottom faunal components may be linked by predation of small pelagic fishes by the bottom fishes. However, the dominance of the bottom fauna by small juveniles makes this possibility seem less likely. Most bottom fishes were too small to have preyed on the larger pelagic fishes. Even predators such as *Centropristis striata* were only rarely large enough to have preyed on the pelagic fishes observed at the FADs. If FADs, however, do function as a larval settlement channel (Beets 1989), then such an influx of small fishes may provide a supplemental food resource for larger juveniles which have recruited earlier.

The link between pelagic and benthic fish assemblages around FADs has important implications in the issue of aggregation versus habitat enhancement/productivity by FADs (Bohnsack & Sutherland 1985). Arguments of whether FADs or artificial reefs function to aggregate fish stocks, thereby increasing their vulnerability to fishing pressure, or whether they contribute to fish production and fish stock production (sensu Ricker 1946 and Ivlev 1966 as cited in Allen 1982, Allen 1982) suffer from our poor understanding of interactions between pelagic and benthic assemblages and of what attracts these fish to structure. This study suggests that pelagic fish are attracted to FADs because of enhanced predator avoidance and the consequent increase in feeding efficiency (Rountree 1989, Rountree unpublished). Large aggregations of pelagic fishes may also enhance demersal fish habitat quality by supplementing demersal fish food resources. Enhancement may be both direct, by providing predation and scavenger opportunities, and indirect by enhancing benthic production. If so, then artificial reefs may be effective habitat enhancement and management tools, rather than just fish aggregators.

There were strong indications of intraspecific competition for shelter within the FAD anchors. Fishes (*D. punctatus* excluded) occurred more frequently and densely around the anchor than the FAD (Fig. 6a, b). The stone crab, octopus and many of the bottom fishes exhibited a strong behavioral association with the FAD anchors and appeared to use the holes of the blocks for shelter. Although *Centropristis striata* did frequently share shelter space within a concrete block anchor with other fishes (such as *Mycteroperca microlepis, Epinephelus morio*, and *Centropristis ocyurus* and the stone crab, *Menippe mercenaria*), it rarely shared with conspecifics suggesting that intraspecific competition was strong. A maximum of two *C. striata* was observed at streamer FAD anchors (each anchor having two holes), while up to four individuals of *C. striata* were observed at the parasol FAD anchors (which had four concrete blocks and a total of eight holes), suggesting that crevice space may have been limiting.

In summary, the abundance of most of the FAD fauna was strongly affected by season (Table 6). Seasonal recruitment of young-of-the-year juveniles into the study area reflecting spawning activity and inshore-offshore movement patterns were probably most responsible for this effect. Availability of shelter was probably the second most important factor (Rountree 1989) followed closely by availability of food. Shelter is of little value if an adequate food supply is not available. Thus very few fish were observed at concrete blocks while significantly more occurred at FAD anchors. The hypothetical trophic interactions and energy flow among FAD-associated fishes are summarized in Figure 8. This trophic link between pelagic and benthic FAD communities may result in a correlation between pelagic and benthic fish abundances and account for the fish faunal differences observed between FAD anchors and concrete blocks without FADs. However, FAD enhanced recruitment of larvae to FAD anchors may also contribute to faunal differences between FAD anchors and concrete blocks. Most pelagic FAD fishes feed directly on plankton while others feed on fouling organisms which in turn feed on plankton. A few pelagic fishes, usually transient species, are piscivores (e.g., *Rachycentron canadum*). Both the pelagic fish and fouling communities produce organic fallout which rains down onto the sea floor providing scavenger opportunities and, perhaps increasing benthic secondary production, making the habitat more desirable to juvenile demersal fishes. The habit of some of the pelagic fishes to visit the bottom around the FAD anchor, sometimes forming small 'resting' schools (Fig. 6c, 8i), increases the likelihood for organic rain to reach the bottom around the FAD anchor. Pelagic planktivorous fishes are probably attracted to FADs because of increased feeding efficiency resulting from enhanced predator avoidance while in association with the FAD (Rountree 1989, Rountree unpublished). In addition to these factors, indirect and direct competition for food and space further regulates the faunal composition. Sporadic intrusions of predators or territorial species may also regulate the fauna at specific sites and increase the variability among sites. Localized weather conditions may have a similar disruptive effect.

Further research with FADs and small-scale artificial habitat utilizing replicate structures in a clearly defined experimental design promises to provide insight into the importance of habitat, species availability, competition and other species interactions, in shaping community structure. Studies of

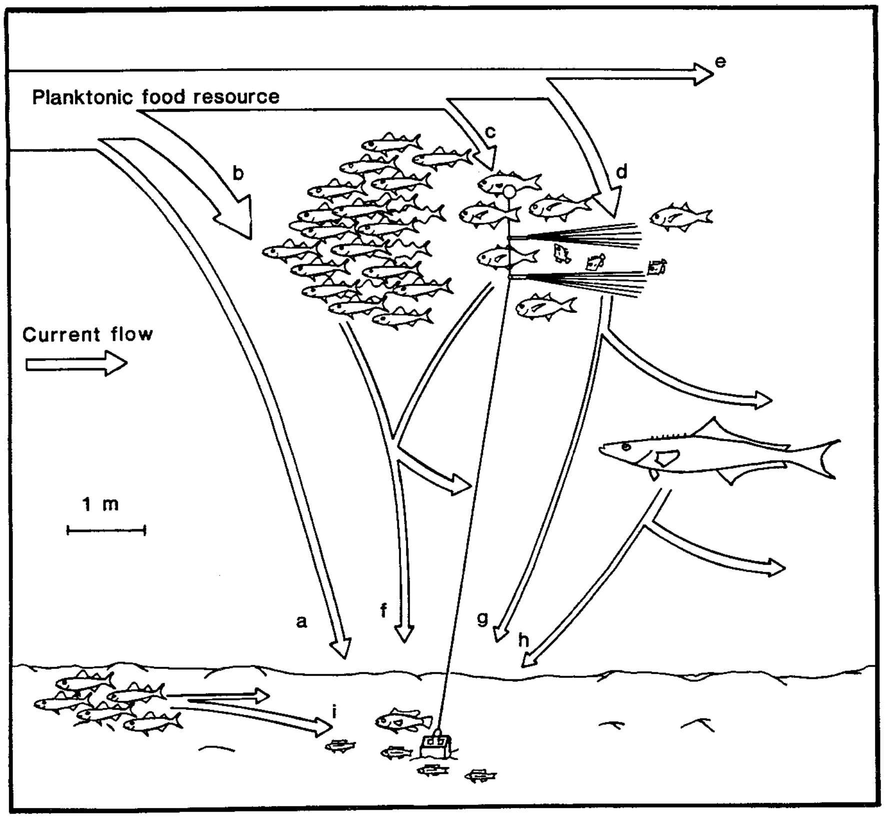

Fig. 8. Hypothetical trophic interactions and energy flow among the FAD community. The FAD and fish positions are illustrated approximately to scale. Fish sizes are exaggerated three to six times. The community is based principally on a planktonic food resource. Arrows indicate the fate of plankton, feces and particulate organic materials. (a) Plankton and plankton fecal materials provide food and nutrients directly to the benthic community. (b) Much of the plankton in the water immediately up current of the FAD is consumed by *Decapterus punctatus*. (c) A portion of the remaining plankton is consumed by *Caranx crysos* and other fishes closely associated with the FAD. (d) Fouling organisms filter out much of the smaller plankton. (e) Plankton which is not consumed by FAD associated organisms. Organic rain from many sources enhances the food and nutrient resources of the benthic community. Much of the organic rain is swept away by currents, but some is deposited on the bottom near the FAD. (f) Fecal materials, uneaten food particles, and occasional fish carcasses from natural mortality, are produced by pelagic fishes. (g) Pseudofeces, feces and other organic litter derived from the fouling community. *Monacanthus hispidus* and other fishes increase this organic litter through cropping and other feeding activities. (h) transient piscivorous predators, such as *Rachycentron canadum*, produce uneaten food debris and fecal materials. (i) small schools of non-feeding *D. punctatus* deposit fecal materials on the bottom near the FAD anchor.

interactions between pelagic and demersal fishes and of the energetic coupling between pelagic and benthic communities are especially promising. Investigations into the influence of species availability and priority effects on community structure can also be examined by deploying FADs at different time intervals and comparing species composition.

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References cited

Allen, L.G. 1982. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. U.S. Fish. Bull. 80: 769–790.

Beets, J. 1989. Experimental evaluation of fish recruitment to combinations of fish aggregation devices and benthic artificial reefs. Bull. Mar. Sci. 44: 973–983.

Berry, F.H. 1959. Young jack crevalles (*Caranx* species) of the southeastern Atlantic coast of the United States. U.S. Fish. Bull. 59: 417–535.

Boesch, D.F. 1977. Application of numerical classification in ecological investigations of water pollution. U.S. Environmental Protection Agency Ecological Research Series EPA-600/3-77-033. 113 pp.

Bohnsack, J.A. & D.L. Sutherland. 1985. Artificial reef research: a review with recommendations for future priorities. Bull. Mar. Sci. 37: 11–39.

Bortone, S.A., P.A. Hastings & S.B. Collard. 1977. The pelagic-*Sargassum* ichthyofauna of the eastern Gulf of Mexico. Northeast Gulf Sci. 1: 60–67.

Bray, R.N. & A.C. Miller. 1985. Planktivorous fishes: their potential as nutrient importers to artificial reefs. Bull. Mar. Sci. 37: 396.

Bray, R.N., A.C. Miller & D.G. Geesey. 1981. The fish connection: a trophic link between planktonic and rock reef communities. Science 214: 204–205.

Bruun, A.F. 1957. Deep sea and abyssal depths. Chapter 22. pp. 641–672. *In:* J.W. Hedgpeth (ed.) Treatise on Marine Ecology and Paleoecology, Volume 1, Ecology, The Geological Society of America, Memoir 67, Washington, D.C.

Buchanan, C.C. 1973. Effects of an artificial habitat on the marine sport fishery and economy of Murrells Inlet, South Carolina. Mar. Fish. Rev. 35: 15–22.

Buchanan, C.C., R.B. Stone & P.O. Parker, Jr. 1974. Effects of artificial reefs on a marine sport fishery off South Carolina. Mar. Fish. Rev. 36: 32–38.

Clifford, H.T. & W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York. 229 pp.

Darcey, G.H. 1985. Synopsis of biological data on the sand perch, *Diplectrum formosum* (Pisces: Serranidae). FAO Fisheries Synopsis No. 143, NOAA Tech. Rep. NMFS 26. 21 pp.

de Sylva, D.P. 1982. Potential for increasing artisanal fisheries production from floating artificial habitats in the Caribbean. Proc. Gulf Carib. Fish Inst. 34: 156–167.

Dooley, J.K. 1972. Fishes associated with the pelagic sargassum complex, with a discussion of the sargassum community. Contributions in Marine Science (Publication of the Institute of Marine Science) Texas University 16: 1–32.

Fine, M.L. 1970. Faunal variation on pelagic sargassum. Mar. Biol. 7: 112–122.

Floyd, J.M. & D. Pauly. 1984. Smaller size tuna around the Philippines – can fish aggregating devices be blamed? Infofish Marketing Digest 5: 25–27.

Fowler, H.W. 1945. A study of the fishes of the southern Piedmont and Coastal Plain. Acad. Nat. Sci. Phila. Monogr. 7. 408 pp.

Gooding, R.M. & J.J. Magnuson. 1967. Significance of a drifting object to pelagic fishes. Pacific Sci. 21: 486–479.

Goodwin, J.M. & J.H. Finucane. 1985. Reproductive biology of blue runner (*Caranx crysos*) from the eastern Gulf of Mexico. Northeast Gulf Sci. 7: 139–146.

Greenblatt, P.R. 1979. Associations of tuna with flotsam in the eastern tropical Pacific. U.S. Fish. Bull. 77: 147–155.

Hales, L.S. 1987. Distribution, abundance, reproduction, food habits, age, and growth of the round scad, *Decapterus punctatus*, in the South Atlantic Bight. U.S. Fish. Bull. 85: 251–268.

Hammond, D.L., D.D. Myatt & D.M. Cupka. 1977. Evaluation of midwater structures as a potential tool in the management of the fisheries resources on South Carolina's artificial fishing reefs. South Carolina Marine Resources Center, Tech. Report No. 15. 19 pp.

Hamner, W.M., M.S. Jones, J.H. Carleton, I.R. Hauri & D. McB. Williams. 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bull. Mar. Sci. 42: 459–479.

Hardenberg, J.D.F. 1950. Development of pelagic fisheries. Proc. Indo-Pac. Fish. Counc., Singapore, 1949, No. 1, sec. IV: 138–143.

Hastings, R.W. 1979. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Bull. Florida State Mus., Biol. Sci. 24: 1–122.

Hunter, J.R. 1968. Fishes beneath flotsam. Sea Frontiers 14: 280–288.

Hunter, J.R. & C.T. Mitchell. 1967. Association of fishes with flotsam in the offshore waters of Central America. U.S. Fish. Bull. 66: 13–29.

Ivlev, V.S. 1966. The biological productivity of waters. J. Fish. Res. Board Can. 23: 1727–1759.

Johnson, G.D. 1978. Development of fishes of the Mid-Atlantic

Bight. IV. Carangidae through Ephippidae. U.S. Fish. Wildl. Serv., Biol. Serv. Prog., FWS/OBS-72/12. 314 pp.

Kingsford, M.J. & A.B. MacDiarmid. 1988. Interactions between planktivorous reef fish and zooplankton in temperate waters. Mar. Ecol. Prog. Ser. 48: 103–117.

Klima, E.F. & D.A. Wickham. 1971. Attraction of coastal pelagic fish with artificial structures. Trans. Amer. Fish. Soc. 100: 86–99.

Kojima, S. 1956. Fishing for dolphins in the western part of the Japan Sea. II. Why do fishes take shelter under floating materials. Bull. Jap. Soc. Sci. Fish. 21: 1049–1052.

Kojima, S. 1960a. Fishing for dolphins in the western part of the Sea of Japan. V. Species of fishes attracted to bamboo rafts. Bull. Jap. Soc. Sci. Fish. 26: 279–382. (Transl. W.G. Van Campen. 1962. Southwest Fisheries Center, NMFS, NOAA, Honolulu).

Kojima, S. 1960b. Fishing for dolphin in the western part of the Sea of Japan. VI. Behaviors of fish gathering around bamboo rafts. Bull. Jap. Soc. Sci. Fish. 26: 383–388.

Kojima, S. 1967. Studies on fishing conditions of the dolphin, *Coryphaena hippurus*, in the western regions of the Sea of Japan-XIII. 'Tsukegi' as a source of food for dolphins. Bull. Jap. Soc. Sci. Fish. 33: 320–324.

Lindquist, D.G., M.V. Ogburg, W.B. Stanley, H.L. Troutman & S.M. Pereira. 1985. Fish utilization patterns on temperate rubble-mound jetties in North Carolina. Bull. Mar. Sci. 37: 244–251.

McKenney, T.W., E.C. Alexander & G.L. Voss. 1958. Early development and larval distribution of the carangid fish, *Caranx crysos* (Mitchill). Bull. Mar. Sci. Gulf Caribb. 8: 167–200.

Mansueti, R. 1963. Symbiotic behavior between small fishes and jellyfishes, with new data on that between the stromateid, *Peprilus alepidotus*, and the scyphomedusa, *Chrysaora quinquecirrha*. Copeia 1963: 40–80.

Matsumoto, W.M., T.K. Kazama & D.C. Aasted. 1981. Anchored fish aggregating devices in Hawaiian waters. Mar. Fish. Rev. 43: 1–13.

Meyer, J.L. & E.T. Schultz. 1985a. Tissue condition and growth rate of corals associated with schooling fish. Limnol. Oceangr. 30: 157–166.

Meyer, J.L. & E.T. Schultz. 1985b. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnol. Oceanogr. 30: 146–156.

Meyer, J.L., E.T. Schultz & G.S. Helfman. 1983. Fish schools: an asset to corals. Science 220: 1047–1049.

Mortensen, T. 1917. Observations on protective adaptation and habits, mainly in marine animals. *In:* Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916. Vidensk. Medd. Dansk Naturhist. Forem. 69: 57–96.

Murray, J., J. Howe, D. Lindquist & D. Griffith. 1987. Using FAD's to attract fish at coastal fishing piers. Mar. Fish. Rev. 49: 143–154.

Myatt, D.O. 1985. Midwater fish attractors. pp. 303–315. *In:* F.M. D'Itri (ed.) Artificial Reefs: Marine and Freshwater Applications, Lewis Publishers, Chelsea.

Myatt, D.O. & E. Myatt. 1982. Midwater fish attractors. pp. 54–71. *In:* 1982 World Record Game Fish, The International Game Fish Association, Fort Lauderdale.

Ogren, L.H. 1974. Midwater structures for enhancing recreational fishing. pp. 65–67. *In:* L. Colunga & R. Stone (ed.) Proceedings of an International Conference on Artificial Reefs, Houston.

Park, S.-W. 1984. On the tuna schools associated with the drift objects or animals in the western equatorial Pacific waters. Bull. Korean Fish. Soc. 17: 47–54.

Parker, R.O. Jr., R.B. Stone & C.C. Buchanan. 1979. Artificial reefs off Murrella inlet, South Carolina. Mar. Fish. Rev. 41: 12–24.

Ricker, W.E. 1946. Production and utilization of fish populations. Ecol. Monogr. 16: 374–391.

Robertson, D.R. 1982. Fish feces and fish food on a Pacific coral reef. Mar. Ecol. Prog. Ser. 7: 253–265.

Rountree, R.A. 1989. Association of fishes with fish aggregation devices: effects of structure size on fish abundance. Bull. Mar. Sci. 44: 960–972.

Samples, K.C. & J.T. Sproul. 1985. Fish aggregating devices and open-access commercial fisheries: a theoretical inquiry. Bull. Mar. Sci. 37: 305–317.

SAS Institute Inc. 1982. SAS User's Guide: Statistics, 1982 edition. SAS Institute Inc. Cary. 584 pp.

Sedberry, G.R. & R.F. Van Dolah. 1984. Demersal fish assemblage associated with hard bottom habitat in the South Atlantic Bight of the U.S.A. Env. Biol. Fish. 11: 241–258.

Shomura, R.S. & W.M. Matsumoto. 1982. Structured flotsam as fish aggregating devices. NOAA Technical Memorandum NMFS October 1982. 9 pp.

Smith, R.L. 1977. Elements of ecology and field biology. Harper & Row Publishers. New York. 497 pp.

Sokal, R.R. & F.J. Rohlf. 1981. Biometry, 2nd ed. W.H. Freeman, San Francisco. 859 pp.

Steimle, F.W., Jr. & L. Ogren. 1982. Food of fish collected on artificial reefs in the New York Bight and off Charleston, South Carolina. Mar. Fish. Rev. 44: 49–52.

Stephan, C.D. & D.G. Lindquist. 1989. A comparative analysis of the fish assemblages associated with old and new shipwrecks and fish aggregating devices in Onslow Bay, North Carolina. Bull. Mar. Sci. 44: 698–717.

Uda, M. 1933. Types of skipjack schools and their fishing qualities: the shoals of 'katuwo' and their angling. Bull. Jap. Soc. Sci. Fish. 2: 107–111. (Transl. by W.G. Van Campen, 1952, U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 83: 68–78).

Uda, M. & Z. Tukusi. 1934. Local variations in the composition of skipjack (*Katsuwonus pelamis*) schools. Bull. Jap. Soc. Sci. Fish. 83: 51–67.

Waltz, W., W.A. Roumillat & P.K. Ashe. 1979. Distribution, age structure, and sex composition of the black sea bass, *Centropristis striata*, sampled along the southeastern coast of the United States. South Carolina Marine Resources Center Tech. Report No. 43. 18 pp.

Wenner, C.A. 1983. Species associations and day-night variability of trawl-caught fishes from the inshore sponge-coral habitat, South Atlantic Bight. U.S. Fish. Bull. 81: 537–552.

Wenner, C.A., C.A. Barans, B.W. Stender & F.H. Berry. 1979. Results of MARMAP otter trawl investigations in the South Atlantic Bight. III. Summer, 1974. South Carolina Marine Resources Center Tech. Report No. 41. 62 pp.

Wenner, C.A., C.A. Barans, B.W. Stender & F.H. Berry. 1980. Result of MARMAP otter trawl investigations in the South Atlantic Bight. V. Summer, 1975. South Carolina Marine Resources Center Tech. Report No. 45. 57 pp.

Westenberg, J. 1953. Acoustical aspects of some Indonesian fisheries. J. Cons. Int. Explor. Mer. 18: 311–325.

Wickham, D.A. & G.M. Russell. 1974. An evaluation of mid-water artificial structures for attracting coastal pelagic fishes. U.S. Fish. Bull. 72: 181–191.

Wickham, D.A., J.W. Watson, Jr. & L.H. Ogren. 1973. The efficiency of midwater artificial structures for attracting pelagic sport fish. Trans. Amer. Fish. Soc. 102: 563–572.

Yesaki, M. 1977. Innovations in harvest of pelagic resources. Mar. Fish. Rev. 39: 14–23.