ASSOCIATION OF FISHES WITH FISH AGGREGATION DEVICES: EFFECTS OF STRUCTURE SIZE ON FISH ABUNDANCE

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ABSTRACT

The hypothesis that the abundance of fishes associated with fish aggregation devices (FADs) is a function of the degree of shelter provided by the structure was tested by comparing recruitment to three sizes of mid-water FADs. Each treatment was replicated six times and the eighteen FADs were deployed in a randomized block array in 14 m of water in the Atlantic Ocean off South Carolina. A total of thirteen species of fishes was observed to associate with the FADs. Eighty-nine FADs were censused in eight surveys from May through November 1985. The fauna associated with the FADs was very similar to published reports of fauna associated with *Sargassum* spp. and jellyfish, suggesting similar origins and causes of these associations. *Decapterus punctatus* was the most frequently occurring (70%) and abundant species ($\bar{x} = 576$ fish/FAD). The total number of fishes and number of *D. punctatus* per FAD exhibited a significant linear FAD size effect (P = 0.0272, 0.001, respectively). Associations with drifting objects may allow prey fishes which have habituated to an object to escape predation by capitalizing on a reflexive avoidance of the object by a pursuing predator.

With the growing importance of flotsam and fish aggregation devices (FADs) to commercial fisheries, scientific investigation into the causes of associations of fishes with drifting materials has rapidly increased in recent years (see reviews by Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Dooley, 1972; de Sylva, 1982; Myatt and Myatt, 1982; Rountree, 1987). Numerous hypotheses have been advanced to explain the association and, although more than one hypothesis may be true, the most widely held hypothesis is that fishes utilize floating materials in some manner which gives them protection from predators. Protection might be obtained in several ways: through direct shelter provided by the materials or structure (Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Mitchell and Hunter, 1970; Dooley, 1972; Wickham et al., 1973; Wickham and Russell, 1974; Hastings et al., 1976; Kulczychi et al., 1981; Murray et al., 1985); through camouflage and mimicry (Mortensen, 1917; Breder, 1942; 1946; 1949; Randall and Randall, 1960); or through an unexplained mechanism of interference with a predator's ability to capture prey (Gooding and Magnuson, 1967; Mitchell and Hunter, 1970; Wickham et al., 1973; Wickham and Russell, 1974). It has also been suggested that floating objects provide protection by making the silhouette of associated fishes difficult to see against the dark backdrop of the structure (M. Bell, SCWMRD, pers. comm.), or by protecting a school's blind zone from approach by predators (Soemarto, 1960). Most of these observations (with the exception of a few special cases of mimicry, Breder, 1942; 1946; 1949; Randall and Randall, 1960) are speculations based on circumstantial evidence without supporting data or arguments. In fresh water, shade provided by the object has been suggested to provide a protective advantage to associated fishes (Helfman, 1979; 1981). A few authors have remained skeptical of the importance of shelter to the maintenance of the association of fishes with drift materials or FADs (Mortensen, 1917; Westenberg, 1953; Brandt, 1960; Klemm, 1984).

Field observations on the behavior exhibited by associated fishes in the presence of predators does lend some support to the protection hypothesis. When threat-

ened many fishes have been observed to congregate close to the structure and in some cases to actively use an object as a barrier between themselves and a potential predator (Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Mitchell and Hunter, 1970: Wickham et al., 1973; Wickham and Russell, 1974; McIlwain and Lukens, 1978). Observations of predator behavior around floatsam and FADs are conflicting, but indicate that some species may not successfully prey on fishes which are spatially closely associated with drifting objects (Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Hunter, 1968; Potthoff, 1969; Wickham, 1972; Wickham et al., 1973; Wickham and Russell, 1974; Anonymous, 1980; Matsumoto et al., 1981). In addition, the limited gut content data available does not support the hypothesis that large predators associated with FADs depend on prey fishes associated with FADs as a food source (Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Kojima, 1967; Brock, 1985). The only direct study of predator success on flotsam associated fishes was conducted by Mitchell and Hunter (1970) who found that the presence of drifting kelp significantly reduced predator success in the laboratory.

If some fishes are utilizing flotsam and FADs for shelter from predators, then characteristics of the structure such as volume, size, type of material or structural complexity might influence their attractiveness to fishes. Attempts to determine the effect of these characteristics on the attraction of fishes have produced varied, mostly negative, results. Studies of flotsam have not demonstrated a significant correlation between the number of fish and the volume or biomass of flotsam (Ida et al., 1967; Dooley, 1972). Hunter and Mitchell (1967) did report a correlation of flotsam size to the number of fishes, but they did not provide supporting statistics and they later rejected their conclusions (Hunter and Mitchell, 1968). Dooley (1972) could not demonstrate a significant relationship between total biomass of fishes and biomass of sargassum, but he did report a significant positive correlation for *Histrio histrio* and *Stephanolepis* (=Monacanthus) hispidus.

Attempts to determine the effects of FAD structure on fish attraction have also produced conflicting results, possibly due to inadequate experimental design. Studies have indicated that there is no correlation between the size, shape and color of an object and the number of fish attracted (Hunter and Mitchell, 1968; Wickham, 1972; Wickham et al., 1973; Wickham and Russell, 1974). In a study of freshwater FADs, Helfman (1979) concluded that the total number and density of fishes were positively correlated with FAD surface area and that the amount of shade provided by the structure was the cause of this correlation. Unfortunately, none of these investigations employed replicated FAD types in their experimental designs and their conclusions are cautioned. Klima and Wickham (1971) conducted the only study on the effect of FAD type which made use of replication in the experimental design. It was found that simple structures (elongated threesided tent shaped structures) usually attracted much greater numbers of fish than complex structures (similar structures with vertical openings in the sides), but because water depth and FAD type were confounded in their experimental design, their results should be viewed with caution. In addition, Klima and Wickham (1971) made no attempt to look at the effects of FAD complexity on individual species.

Past experimental studies have suffered primarily from a lack of adequate treatment replication and small sample sizes because of the logistical difficulties of offshore experiments with FADs. For this reason, the primary goal of this study was to test the hypothesis that the standing crop of fishes associated with a FAD is a function of the degree of cover provided by the FAD. A second goal was to study the faunal composition of fishes attracted to the small, shallow water FADs

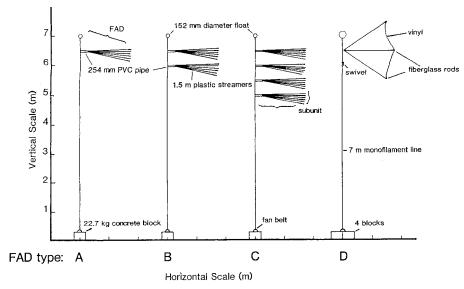


Figure 1. Scale drawing of the FAD type treatment (A, B, and C), and the FAD type D structures, used in this study.

used in the South Carolina recreational fishery (Myatt, 1985). Information on faunal composition and fish behavior will be presented in a separate paper (Rountree, in review¹).

MATERIALS AND METHODS

To test the hypothesis that fish abundance is a function of the amount of shelter provided by a FAD, it was assumed that the amount of potential shelter provided by a FAD is related to the surface complexity of the structure. It was reasoned that structures with many crevices and hiding spaces should support a larger number of fishes than structures with fewer hiding places. If fish abundance was found to respond positively to increasing amounts of cover, the protection hypothesis would be supported. Three FAD types with increasing amounts of potential shelter were used as treatments. The structures used in this study consisted of three components: the FAD, the mooring line and the anchor (Fig. 1). FADs consisted of a float and a set of subunits. The different levels of cover used for each FAD type treatment were made by varying the number of subunits comprising the FAD; FAD type A had one subunit and a 0.5 m vertical profile, type B had two subunits and a 1.0 m vertical profile, and type C had four subunits and a 2.0 m vertical profile. The subunits consisted of a 154 mm length of 57 mm diameter PVC pipe to which were attached twelve 1.5 m black plastic straps (13 mm width), referred to as streamers (Fig. 1). Each FAD was buoyed by a 152 mm diameter float (9 kg lift at the surface) and was anchored with a single 22.7 kg concrete block. Unfortunately, I later realized that the amount of cover, vertical profile, area and volume of the FAD types were confounded in this design. Fortunately, these factors were increased in the same proportion among treatment levels (i.e., vertical profile levels were 0.5, 1.0, and 2.0 m, while levels of the amount of cover represented by number of subunits were 1, 2, and 4). Since these factors are each a measure of FAD "size," the treatment levels can be considered levels of FAD size. The experimental design is structured to allow the a-priori test of polynomial contrasts on fish response to FAD size. With three treatment levels it is possible to test linear and quadratic treatment effects in addition to the overall FAD type effect (Hicks, 1982).

A fourth FAD type, designated type D, was also used in this study, but was not included in the experimental design because these type FADs were structurally dissimilar to the other FAD types and, therefore, they could not be considered a treatment (Fig. 1). In addition these FADs were deployed

¹ Rountree, R. Community structure of fishes attracted to shallow water fish aggregation devices off South Carolina. Environ. Biol. Fish. In review.

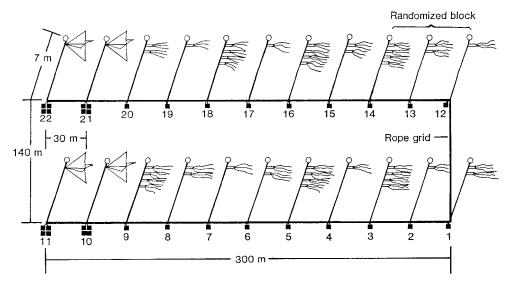


Figure 2. Experimental design and configuration of FAD type treatments used in this study. Numerals designate station numbers.

about two weeks later than the other FAD types. For these reasons FAD type D will not be discussed in this paper.

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). Although the site was located on the artificial reef grounds, it was characterized by a flat, featureless sandy bottom which lacked the invertebrate species characteristic of live bottom communities in the region (e.g., sponges and soft corals). The nearest bottom relief was located more than 1.0 km southeast (except for the remains of 18 FADs located about 250 m southeast of the study area, which were abandoned after most of the structures were destroyed in storms during earlier experimental trials), thus my results were not biased by proximity to artificial reef materials.

On 15 May 1985 a total of 18 treatment type FADs were placed in a randomized block configuration with six blocks containing one of each FAD type treatment (Fig. 2). FADs were attached at 30 m intervals along a rope grid which could be followed by divers while conducting a census. The 30 m spacing between FADs was chosen largely because of logistical constraints, but as the distance was more than four times the maximum visibility of 7 m it is unlikely that fishes moved between stations. Fishes which venture beyond visual range of one of the small FADs used in this study are unlikely to be able to find their way back along the featureless sand bottom. However, fishes may have been able to move from one FAD to the next by following the grid line. Even if some species were found to move against the entire FAD array, strong differences in abundance among FAD types would still support the protection hypothesis.

The randomized block design was used to account for variation due to a number of related factors involving location effects and temporal effects. Variation in the number of fish per station due to FAD location can result from specific location effects (e.g., water depth, habitat, etc.) or from differences in the likelihood of fish encountering a FAD due to its position relative to other FADs. For example, if FADs are placed in a long line connected with a rope, units located towards the middle of the line might have higher numbers of fish if fish move from one unit to another by following the rope line. This design also accounts for any bias which might result from the movement of fishes between the abandoned FADs and the new FAD array (though such movement was unlikely, except by random chance). Temporal sources of variation can also arise from the order in which FADs are censused. These sources might include tidal effects, diel behavior effects, and behavior effects invoked by the presence of divers. Fishes might follow divers from one station to the next so that the last FAD censused would have abnormally high numbers. Grouping the treatments randomly within blocks along the grid line (Fig. 2) effectively controls for both these types of spatial and temporal sources of variation.

To increase the sample size, and to examine faunal changes through time, the FADs were visually censused eight times over a period of 7 months. The experimental design, therefore, included a day

Days elapsed from FAD deployment									
FAD type	8	23	55	91	100	115	159	194	_ Type totals
A	5	3	5	5	3	5	5	4	35
В	5	3	5	4	2	4	5	1	29
Ċ	6	3	4	2	2	2	3	3	25
Ď	Ō	2	3	3	1	3	0	0	12
Month:	May	June	July	Aug.	Aug.	Sept.	Oct.	Nov.	

Table 1. Sample sizes for FAD type by day number

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 three-way model-I ANOVA (Sokal and Rohlf, 1981) in which there are three FAD type treatments, eight day treatments and six FAD type treatment blocks. In addition, orthogonal linear and quadratic contrasts could be tested independently of the overall FAD type effect. A rank transformation was made by ranking variates within FAD type treatment blocks, so that rank values ranged from one to three. Because many of the blocks contained missing cells, due to the loss of FADs and incomplete sampling, inferences based on the statistical analysis of the randomized block design were questionable. For this reason, data were also analyzed by means of a two-way ANOVA with FAD type and day factors, ignoring blocks. Rank transformations for this test were made by ranking the data within day (census). This more conservative test was compared to the above test and used to help determine if computational errors due to missing cells invalidated the three-way ANOVA. If the two-way and three-way ANOVAs agreed, then the three-way ANOVA could be safely used despite the large number of missing values.

Rank transformations (see Conover and Iman, 1976; Conover, 1980) were used because counts of fishes were not normally distributed and species exhibited different types of distributions; ranks could be compared among days (census) even though the abundance of fishes was highly dependent on time of year; and ranking within a census reduces error due to inconsistent diver estimation of fish abundance at FADs among days. As suggested by Conover and Iman (1976) unranked data were also analyzed for comparison with the ranked data analysis. Rank transformations were preferred over the more commonly used log transformations because rank data reduce the impact of measurement error in counting large numbers of fish underwater (however, results using log-transformed data were consistent with both rank transformed and original data).

These statistical tests were performed on the number of species, total number of fishes per station, and the total number of fishes per station excluding *Decapterus punctatus* (because of the numerical dominance of *D. punctatus*). Analysis including and excluding benthic species was performed because in the shallow water of the study area, it was not always clear whether a species should be recorded as associating with the FAD or with the anchor for a particular observation. In addition, it was found that the abundance of bottom fishes may be affected by the abundance of pelagic fishes associated with the FAD (Rountree, in review¹). Analysis for each of the 14 most frequently observed species (including some benthic species) were also performed, but only *D. punctatus* will be discussed here (for other species see Rountree, 1987).

A total of 121 counts was made in eight censuses over a 7-month period from May through November, 1985. Eighty-nine counts were on FAD types A, B and C. The remaining counts were made on structure type D and on damaged treatment type FADs which could not be used in the statistical analysis of the treatment effect. The FADs were visually censused after the structures had been located with the aid of Loran-C coordinates and a search by a team of Scuba divers. Visibility about the FADs ranged from 5 to 7 m. All fishes within this radius were counted. In addition, when large schools were present, an area extending 5-7 m up current of the school was also censused to ensure that all fishes were counted. Actual sample sizes by day and FAD type are given in Table 1.

RESULTS

Of the thirteen pelagic species which associated with the FADs (Table 2), only *D. punctatus* was significantly affected by the FAD size treatment. *D. punctatus* was the most frequently occurring (70%) and abundant species (Table 2). The mean number of *D. punctatus* per FAD increased with increasing FAD size (Table 2). The difference in the number of *D. punctatus* per FAD among the treatments was especially evident during several dives made early in the study (May and



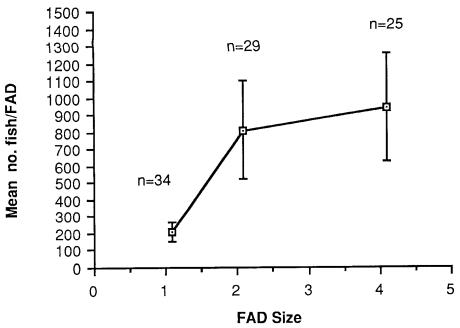


Figure 3. Mean number (bars are errors of the means) of *Decapterus punctatus* per FAD plotted against FAD size (size 1 = FAD type A, 2 = type B, 4 = type C).

June) when abundances differed by an order of magnitude among the treatments (Fig. 3). These differences were not as obvious later in the study, but FAD type A tended to have lower numbers throughout the study (Fig. 4). Good agreement among the ANOVA tests performed indicates that the three-way ANOVA on the randomized block design was valid despite numerous missing cells. All ANOVAs resulted in a significant FAD type linear effect. The two-way ANOVA on the original data tended to be the most conservative test while the three-way ANOVA on data ranked within treatment block tended to result in higher significance levels (P = 0.0421, P = 0.001 for the FAD type linear contrast for the two-way and three-way ANOVAs, respectively). The overall FAD type effect was significant only for the three-way design if all data (N = 89) were included, but with one outlier removed all ANOVAs resulted in a highly significant overall FAD type effect (P = 0.0012 for the more conservative two-way ANOVA).

The total number of fishes, with and without benthic species, also exhibited a significant linear FAD type effect (Table 2). However, if *D. punctatus* was excluded from the total, the FAD type effect was not significant. The number of species per station was also not significantly affected by FAD type, although there was a tendency for more species to be present at FAD type A (Table 2).

Fishes associated with the FAD tended to remain very close to the structure and typically could not be frightened away even by vigorous attempts by divers. On a number of occasions fishes were observed to remain with a damaged FAD which was being moved across the bottom by divers. The FAD associated fishes did not display fright behavior until closely approached by a diver. When frightened, D. punctatus, C. crysos, C. bartholomaei and other schooling species would

Decapterus punctatus

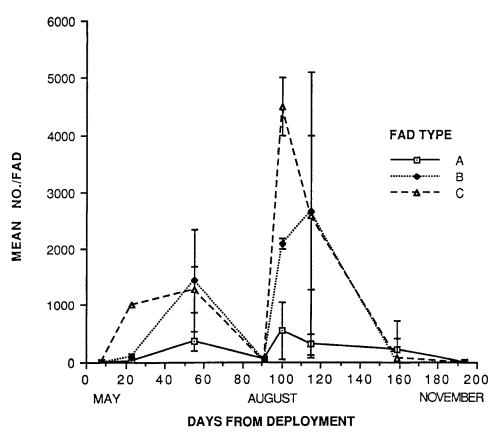


Figure 4. Mean number (bars are errors of the means) of *Decapterus punctatus* per FAD plotted against census day for each FAD type.

form a tightly packed school around the FAD. The frightened school would then move in quick darts all around the FAD and up and down the mooring line, but would not move more than a few meters away from the FAD and line. Normally these fishes were observed within a few meters up current of the FAD in a loose feeding formation when undisturbed. Three transient individuals of *Rachycentron canadum* (observed on a single occasion) were the only large piscivorous predators recorded during this study. Frequently observed lacerations on the schooling species were the only other evidence of visits by predators.

DISCUSSION

The significant linear response of *D. punctatus* to FAD size supports the hypothesis that this species utilizes FADs as shelter from predators. Although abundances of the other schooling species did not significantly differ among FAD types, they exhibited behavior similar to *D. punctatus*. More frequent sampling during the peak abundance periods of these highly seasonal species are needed to clarify the effect of FAD size on their abundance. The behavior and feeding habits of *D. punctatus* do not support the hypothesis that the effect of FAD size results from

Table 2. Mean number and standard deviation of fishes per station by FAD type

Species	FAD type A	FAD type B	FAD type C	Pooled	FAD type effect	Linear effect
Decapterus punctatus	171 ± 325	771 ± 1,564	901 ± 1,560	576 ± 1,267	**	***
Caranx crysos	8.3 ± 14.3	4.9 ± 9.7	7.8 ± 14.6	7.1 ± 13.0		
Caranx bartholomaei	1.4 ± 3.6	0.7 ± 1.8	3.4 ± 7.0	1.7 ± 4.5		
Seriola sp.	0.9 ± 3.1	0.9 ± 3.8	2.0 ± 8.1	1.2 ± 5.1		
Monacanthus hispidus	1.5 ± 5.1	0.6 ± 1.1	1.2 ± 1.8	1.1 ± 3.4		
Seriola zonata	0.1 ± 0.4	0.7 ± 0.3	0.1 ± 0.4	0.1 ± 0.4		
Caranx ruber	0.0 ± 0.2	0.1 ± 0.3	0.1 ± 0.3	0.1 ± 0.3		
Chaetodipterus faber	0.0 ± 0.0	0.2 ± 1.1	0.1 ± 0.5	0.1 ± 0.7		
Rachycentron canadum	0.0 ± 0.0	0.1 ± 0.6	0.0 ± 0.0	0.0 ± 0.3		
Aluterus sp.	0.0 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1		
Aluterus scriptus	0.0 ± 0.0	0.0 ± 0.2	0.0 ± 0.0	0.0 ± 0.1		
Aluterus monoceros	0.0 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1		
Sardinella aurita	0.0 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1		
Total no. bottom fish	5.0 ± 5.6	6.0 ± 14.1	6.3 ± 11.6	5.7 ± 10.5		
Total no. pelagic fish						
(minus D. punctatus)	12.2 ± 15.0	7.5 ± 10.3	14.4 ± 16.4	11.3 ± 14.2		
Total no. pelagic fish	183 ± 325	$778 \pm 1,564$	$916 \pm 1,564$	$588 \pm 1,271$		*
Total no. fish	188 ± 325	$783 \pm 1,571$	$921 \pm 1,564$	$592 \pm 1,271$	*	*
No. bottom species	2.5 ± 1.2	1.7 ± 1.0	1.8 ± 1.0	2.1 ± 1.4		
No. pelagic species	2.2 ± 1.3	2.0 ± 1.1	2.1 ± 1.4	2.1 ± 1.2		
Total no. species	4.7 ± 2.0	3.7 ± 1.6	3.8 ± 7.0	4.1 ± 2.0		

^{*} indicates $P \le 0.05$, ** indicates $P \le 0.01$, *** indicates $P \le 0.001$.

an increased food availability at the FAD, since FAD size has no influence on their plankton food source. Observations of the schooling behavior and spatial distribution of *D. punctatus* around the FADs support Soemarto's (1960) suggestion that FADs protect a school's down stream blind zone (Rountree, in prep.). It has been suggested that the general absence of planktivorous fishes in the water column over sand bottoms during the day is related to a lack of shelter and the threat of predators since planktivorous fishes, directing their attentions to the water column, would be vulnerable to attack by predators from the rear (Hobson, 1968; 1979; Hobson and Chess, 1986). Feeding up current of a FAD may reduce vulnerability to predators and allow *D. punctatus* to spend more time feeding. Association with FADs, therefore, may increase feeding efficiencies of planktivorous fishes as well as providing them with protection from predators.

Fishes associated with FADs in this study did not appear to move freely among stations. Their behavior indicated a strong attachment to an individual FAD. Most of the fishes observed were planktivores which spent much of their time in a relatively fixed school configuration up current of the FAD while feeding (Rountree, in review¹). Movement between stations would interfere with feeding activities and, because of the small FAD size and low visibility, would probably not be possible unless fishes followed the grid line. There is probably little incentive for such movements by planktivorous fishes during the daylight feeding hours, though movement over longer time periods is more likely. In this study fishes did not even move between FADs positioned within a few meters of each other by storm activities, but associated only with the up-current structure.

Piscivorous species, on the other hand, might be more likely to move between stations in search of prey. Because of the visibility constraints, large predators which might have occurred beyond the census area around a FAD may not have been adequately censused. However, most of the large predators which might be

expected in the shallow waters of the study site are species which tend to maintain a close association with structure and which are attracted to divers (e.g., Seriola dumerili, Sphyraena barracuda, and Rachycentron canadum). If present, these species would almost certainly have been observed. Large predators may not have been attracted to the FADs because the small structures probably did not support an adequate food supply for them (Sphyraena barracuda has been observed associated with much larger FADs which have been more recently placed on the nearby artificial reef; M. Bell, SCWMRD, pers. comm.).

Although FADs and free-drifting materials such as flotsam and drift weeds appear to be very different systems at first glance, their species compositions are very similar. In fact, the association of fishes with FADs may result from a preadaptation of many pelagic fishes to opportunistically associate with a variety of drifting materials including living organisms such as Sargassum spp. and jellyfishes. Hunter and Mitchell (1967) suggested that the various associations of fishes with flotsam and with other living animals (e.g., jellyfish, sharks, whales, turtles, etc.) may be related behaviors. Russian researchers carried this idea further and discussed the importance of association with floating debris, drift weeds, Sargassum spp., whales, etc. to epipelagic and neustonic fishes (Besednov, 1960; Parin, 1968; Zaitsev, 1971). Many fishes known to associate with jellyfish (see review by Mansueti, 1963) have also been reported to associate with Sargassum spp. and other drifting seaweeds, as well as with FADs and flotsam. A trend for larger individuals of a species to associate with FADs than with drifting flotsam may occur because some juvenile fishes might have difficulty maintaining contact with a FAD moored in a strong current (Kojima, 1960; Gooding and Magnuson, 1967).

A strong similarity of the fish fauna associated with FADs in this study (and in others) to fish fauna associated with Sargassum spp. is apparent. Numbers of species observed with Sargassum spp. and other seaweeds tend to be higher than the number associated with FADs (See Dooley, 1972 for review). This trend may result from the large number of highly specialized species which have adapted to drifting sea weeds such as Sargassum spp. Pelagic species observed associating with FADs in this study that are known to associate with Sargassum spp. include: Caranx bartholomaei, Caranx ruber, Decapterus punctatus (Dooley, 1972), Caranx crysos (Berry, 1959; Dooley, 1972; Bortone et al., 1977; Johnson, 1978a), Aluterus spp., Monacanthus hispidus (Weis, 1968; Fine, 1970; Dooley, 1972; Bortone et al., 1977; Johnson, 1978b), Seriola sp. and Seriola zonata (Dooley, 1972; Bortone et al., 1977; Johnson, 1978a). All seven species of carangids observed around FADs in the present study are considered moderate to close associates of Sargassum spp. (Dooley, 1972). In fact, 10 of the 13 species of fishes (excluding Sardinella aurita, Rachycentron canadum, and Chaetodipterus faber) which I observed associating with FADs are known to be moderate to close associates with Sargassum spp. (sensu Dooley, 1972).

Many of the species of fishes which were observed at the FADs are also known to associate with jellyfish. Mansueti (1963) reviewed the literature of fish-jellyfish associations and cited records of most of the pelagic species I observed around FADs as associating with jellyfish. Since Mansueti's (1963) review, *Caranx crysos* (Böhlke and Chaplin, 1968), *Caranx* sp. (Phillips et al., 1969; Phillips, 1971), *Caranx bartholomaei* (Rountree, 1983), *Monacanthus hispidus* (Phillips et al., 1969; Phillips, 1971; Rountree, 1983) and *Seriola zonata* (Johnson, 1978a) have also been reported as associating with jellyfish.

The genus *Decapterus* includes many species which are prominent in FAD-based fisheries around the world (Hardenberg, 1950; Westenberg, 1953; Soemarto,

1960; Brandt, 1960; Ogren, 1974; Wickham, 1972; Matsumoto et al., 1981). These fishes are also often collected with drift weeds and other flotsam (Hirosaki, 1960; Hunter and Mitchell, 1967; Dooley, 1972). Many members of this genus then, apparently have become adapted to opportunistically associate with a variety of drifting materials and the association with FADs is probably an extension of this behavior.

Although the abundance of D. punctatus increased with increasing size, its behavior did not immediately suggest a correlation of abundance to shelter because schools usually occupied a relatively stationary position while feeding on zooplankton some distance up current of the FAD. However, when frightened by divers, D. punctatus usually moved closer and formed a compact, highly mobile, school around the FAD. The importance of FAD size might come into play, then, only when the school is threatened. Insight into a possible advantage of this behavior can be found in observations on schooling behavior and predatory tactics discussed by Radakov (1973). It was noted that many predators herd schooled fish to the surface or into shallow water where restricted movements impair avoidance maneuvers and minimize the advantage of schooling. Zaitsev (1971) also discussed problems in predator avoidance faced by schooling and solitary fishes living near the surface layer of the ocean. Many solitary predators are known to hunt by rushing into a school of fish, not so much in an attempt to snatch a fish, but rather to confuse the school and drive off some individuals which could then be chased down and captured (Radakov, 1973). Floating objects might function, then, to aid schooling fishes to maintain the school integrity by preventing predators from splintering the school by repeated lunges into it.

Association of fishes with floating objects may tend to inhibit or reduce the effectiveness of predatory tactics. Predators might be reluctant to lunge into a school associated with a floating object for fear of collision. A simple reflex response to a visual stimulus might cause the predator to veer slightly or slow down momentarily, allowing the prey to escape. Such a reflexive avoidance of an object might account for the frequent reports of poor predator success on fishes crowding closely around FADs (Gooding and Magnuson, 1967; Mitchell and Hunter, 1970; Wickham et al., 1973; Wickham and Russell, 1974). Habituation to a specific object might enable the prey fish to avoid the same reflex response, thereby gaining an advantage over the predator. The importance of habituation may account for the apparent reluctance of fishes to leave an object for which they have established an association for a new object placed nearby (Hunter and Mitchell, 1967). Some predators, however, may have specialized to prey on flotsam associated fishes (e.g., Histrio histrio, Lobotes surinamensis, the sea snake Pelamis platurus, and perhaps Coryphaena hippurus; Breder, 1946; 1949; Hunter and Mitchell, 1967; Dooley, 1972).

Characteristics that optimize the number of fishes which can crowd around the object should have an important influence on the standing crop of fishes. Long vertically oriented objects would allow a larger school to crowd around the object than short thick objects, or long horizontally oriented floating objects. Some support for this idea comes from reports that vertically floating objects such as logs are thought to be more effective than horizontally floating objects in FAD/flotsam fisheries (Inoue et al., 1968; Waldvogel, 1978; Matsumoto et al., 1981). An analysis of the spatial distribution and schooling behavior of *D. punctatus* about the FADs supports the hypothesis that the vertical profile of the FAD was the most important factor affecting fish abundance in this study (Rountree, in prep.). This mechanism of utilizing an object to prevent predators from disrupting a schooling formation through a reflexive avoidance response by the predator

may explain the linear response of fish abundance to FAD size observed in this study.

The value of using controlled experimental designs in the study of marine habitat ecology is clearly evident from this study. Implications of results and conclusions drawn from this study demonstrate the need for more controlled field research on the use of structure by fishes. This study also demonstrates that replicated small scale structures can be an effective alternative to large scale artificial reefs in the study of habitat use by fishes.

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LITERATURE CITED

- Anonymous. 1980. Report on fish aggregation devices workshop. U.S. Dept. Commerce NOAA, NMFS Honolulu Laboratory, Southwest Fisheries Center. 17 pp.
- Berry, F. H. 1959. Young jack crevalles (*Caranx* species) of the southeastern Atlantic coast of the United States. Fish. Bull. Fish Wildl. Serv. U.S. 59(152): 417–535.
- Besednov, L. N. 1960. Some data on the ichthyofauna of the Pacific Ocean flotsam. Trudy Inst. Okeanol. (Trans. from Russian by W. van Campen Bureau of Commercial Fisheries, Honolulu, Hawaii.) 41: 192–197.
- Böhlke, J. É. and C. C. G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingston Publ. Co., Wynnewood, Pennsylvania. 771 pp.
- Bortone, S. A., P. A. Hastings and S. B. Collard. 1977. The pelagic-Sargassum ichthyofauna of the eastern Gulf of Mexico. Northeast Gulf Sci. 1(2): 60-67.
- Brandt, A., von. 1960. Fishing methods in world sardine fisheries. *In* H. Rosa, Jr. and G. Murphy, eds. Proceedings of world scientific meetings on the biology of sardines and related species. Rome. Vol. II. Subject Synopsis No. 3: 563–623.
- Breder, C. M., Jr. 1942. On the behavior of young *Oligoplites saurus* (Bloch and Schneider). Copeia 1942: 267.
- 1946. An analysis of the deceptive resemblances of fishes to plant parts, with critical remarks on protective coloration, mimicry and adaptation. Bull. Bingham Oceanogr. Collect. Yale Univ. 10(2): 1-49.
- _____. 1949. On the behavior of young Lobotes surinamensis. Copeia 1949: 237-242.
- Brock, R. E. 1985. Preliminary study of the feeding habits of pelagic fish around Hawaiian fish aggregation devices or can fish aggregation devices enhance local fisheries production? Bull. Mar. Sci. 37: 40-49.
- Conover, W. J. 1980. Practical nonparametric statistics, 2nd ed. John Wiley and Sons, Inc., New York, 493 pp.
- and R. L. Iman. 1976. On some alternative procedures using ranks for the analysis of experimental designs. Communications in Statistics A5(14): 1348-1368.
- 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(March): 1–32.
- Fine, M. L. 1970. Faunal variation on pelagic sargassum. Mar. Biol. 7: 112-122.
- Gooding, R. M. and J. J. Magnuson. 1967. Significance of a drifting object to pelagic fishes. Pacific Sci. 21: 486-497.

- 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., L. H. Ogren and M. T. Mabry. 1976. Observations of the fish fauna associated with offshore platforms in the northeastern Gulf of Mexico. Fish. Bull. 74: 387–402.
- Helfman, G. S. 1979. Fish attraction to floating objects in lakes. Pages 49–57 in D. L. Johnson and R. A. Stein, eds. Response of fish to habitat structure in standing water. North Central Division AFS Special Publication No. 6, 77 pp.
- ——. 1981. The advantage to fishes of hovering in shade. Copeia 1981: 392–400.
- Hicks, C. R. 1982. Fundamental concepts in the design of experiments, 3rd ed. Holt, Rinehart and Winston, New York. 425 pp.
- Hirosaki, Y. 1960. Some ecological observations of fishes in Sagami Bay appearing together with the drifting seaweeds. J. Fac. Sci. Hokkaido Univ. Ser. 6. 14: 435–442.
- Hobson, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Bur. Sport Fish. Wildl. Res. Rept. 73: 1-92.
- ——. 1979. Interactions between piscivorous fishes and their prey. Pages 231–242 in H. Clepper, ed. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.
- —— and S. R. Chess. 1986. Relationships among fishes and their prey in a nearshore sand community off southern California. Environ. Biol. Fishes 17: 201–226.
- Hunter, J. R. 1968. Fishes beneath flotsam. Sea Frontiers 14: 280-288.
- and C. T. Mitchell. 1967. Association of fishes with flotsam in the offshore waters of Central America. Fish. Bull. 66: 13–29.
- ----- and -----. 1968. Field experiments on the attraction of pelagic fish to floating objects. S. Cons. Perm. in Explor. Mer. 31: 427-434.
- Ida, Y., Y. Hiyama and T. Kusaka. 1967. Study of fishes gathering around floating seaweed. I. Abundance and species composition. Bull. Jap. Soc. Sci. Fish. 33: 923–929.
- Inoue, M., R. Amano, Y. Iwasaki and M. Yamantio. 1968. Studies on environments alluring shipjack and other tunas. II. On the driftwoods accompanied by skipjack and tunas. Bull. Jap. Soc. Sci. Fish. 34: 283–387.
- Johnson, G. D. 1978a. Development of fishes of the Mid-Atlantic Bight. IV. Carangidae through Ephippidae. U.S. Fish. Wildl. Serv., Biol. Servs. Prog., FWS/OBS-71/12. 314 pp.
- ——. 1978b. Development of fishes of the Mid-Atlantic Bight. VI. Stromateidae through Ogcocephalidae. U.S. Fish. Wildl. Serv., Biol. Servs. Prog., FWS/OBS-78/12. 416 pp.
- Klemm, R. 1984. Big island tuna conference: more questions than answers. MAKAI: "towards the Sea." University of Hawaii Sea Grant Program 6(8): 1–4.
- Klima, E. F. and D. A. Wickham. 1971. Attraction of coastal pelagic fish with artificial structures. Tran. Am. Fish. Soc. 100: 86–99.
- Kojima, S. 1960. 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.
- ——. 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.
- Kulczychi, G. R., R. W. Virnstein and W. F. Nelson. 1981. The relationship between fish abundance and algal biomass in a seagrass-drift algae community. Estuarine Coastal Shelf Sci. 12: 341–347.
- 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 and D. C. Aasted. 1981. Anchored fish aggregating devices in Hawaiian waters. Mar. Fish. Rev. 43: 1-13.
- McIlwain, J. D. and R. R. Lukens. 1978. Artificial reef enhancement utilizing midwater attraction devices. Pages 33–34 in D. Y. Aska, ed. Artificial reefs in Florida. State Univ. System of Florida, Sea Grant Program. Report No. 24. 68 pp.
- Mitchell, C. T. and J. R. Hunter. 1970. Fishes associated with drifting kelp, *Macrocystis pyrifera*, off the coast of southern California and northern Baja California. Calif. Fish and Game 56: 288–297
- 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 Naturchist. Forem. 69: 57–96, ill.
- Murray, J., D. Lindquist, D. Griffith and J. Howe. 1985. The use of midwater fish aggregation devices to attract marine fishes at two North Carolina fishing piers. Working paper 85-1, UNC Sea Grant College Program, 105 1911 Building, North Carolina State University, Raleigh, North Carolina 27650. 53 pp.
- Myatt, D. O. 1985. Midwater fish attractors. Chapter 10, Pages 303–315 in F. M. D'Itri, ed. Artificial reefs: marine and freshwater applications. Lewis Publishers, Inc., Chelsea, Michigan. 589 pp.

- —— and E. Myatt. 1982. Midwater fish attractors. Pages 54-71 in 1982 World Record Game Fish. The International Game Fish Association, Fort Lauderdale, Florida. 589 pp.
- Ogren, L. H. 1974. Midwater structures for enhancing recreational fishing. Pages 65–67 in L. Colunga and R. Stone, eds. Proceedings of an International Conference on artificial reefs. Houston, Texas. March 20–22, 1974.
- Parin, N. V. 1968. Ichthyofauna of the epipelagic zone. M. Raveh (Transl.), Israel Program for Scientific Translations, IPST No. 5738, United States Department of the Interior, Washington, D.C. 206 pp.
- Phillips, P. J. 1971. The pelagic Cnidaria of the Gulf of Mexico: zoogeography, ecology and systematics. Ph.D. Dissertation. Texas A&M Univ. 212 pp.
- ——, W. D. Burke and E. J. Koener. 1969. Observations on the trophic significance of jellyfishes in Mississippi Sound with quantitative data on the associative behavior of small fishes with medusae. Tran. Amer. Fish. Soc. 98: 703–712.
- Potthoff, T. 1969. Searching for tuna. Comm. Fish. Rev. 31(2): 35-37.
- Radakov, D. V. 1973. Schooling in the ecology of fishes. John Wiley and Sons (Israel Program for Scientific Translations). 173 pp.
- Randall, J. E. and H. A. Randall. 1960. Examples of mimicry and protective resemblance in tropical marine fishes. Bull. Mar. Sci. Gulf Caribb. 10: 444–480.
- Rountree, R. 1983. The ecology of *Stomolophus meleagris* and its fish symbionts. J. Elisha Mitch. Sci. Soc. 99(4): 172. (Abstract)
- . 1987. Ecology of the association of fishes with fish aggregation devices (FADs): importance of structural complexity, with a discussion of the association of fishes with drift materials. MS Thesis, College of Charleston, Charleston, South Carolina. 176 pp.
- Soemarto. 1960. Fish behavior with special reference to pelagic shoaling species: Lajang (*Decapterus* spp.), 8th Proc. Indo-Pacific Fish. Counc. Sec. III: 89–93.
- Sokal, R. R. and F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman and Co., San Francisco. 859 pp.
- Waldvogel, J. 1978. Fishing artificial floating objects. California Sea Grant Marine Advisory Programs Newsletter July 1978: 1–2.
- Weis, J. S. 1968. Fauna associated with pelagic sargassum in the Gulf Stream. Am. Midl. Nat. 80: 554-558.
- Westenberg, J. 1953. Acoustical aspects of some Indonesian fisheries. J. Cons. Int. Explor. Mer. 18: 311–325.
- Wickham, D. 1972. Developments in Mid-water reefs. Pages 7–10 in Proceedings of Sport Fishing Seminar. November 18–19, 1971, Jekyll Is., Ga., Wilmington, N.C., Coastal Plains Center Marine Development Services, Seminar Series 1.
- and G. M. Russell. 1974. An evaluation of mid-water artificial structures for attracting coastal pelagic fishes. Fish. Bull. 72: 181–191.
- J. W. Watson, Jr. and L. H. Ogren. 1973. The efficiency of midwater artificial structures for attracting pelagic sport fish. Trans. Am. Fish. Soc. 102: 563-572.
- Zaitsev, Yu. P. 1971. Marine neustonology. A. Mercado (Transl.). K. A. Vinogradov (ed.). Israel Program for Scientific Translations, IPST NO. 5976, United States Department of the Interior, Washington, D.C. 207 pp.

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