Abstract—Fishes are widely known to aggregate around floating objects, including flotsam and fish aggregating devices (FADs). The numbers and diversity of juvenile fishes that associated with floating objects in the nearshore waters of the eastern tropical Pacific were recording by using FADs as an experimental tool. The effects of fish removal, FAD size, and the presence or absence of a fouling community at the FAD over a period of days, and the presence of prior recruits over a period of hours were evaluated by using a series of experiments. The removal of FAD-associated fish assemblages had a significant effect on the number of the dominant species (*Abudefduf troschelii*) in the following day's assemblage compared to FADs where the previous day's assemblage was undisturbed; there was no experimental effect on combined species totals. Fishes do, however, discriminate among floating objects, forming larger, more species-rich assemblages around large FADs compared to small ones. Fishes also formed larger assemblages around FADs possessing a fouling biota versus FADs without a fouling biota, although this effect was also closely tied to temporal factors. FADs enriched with fish accumulated additional recruits more quickly than FADs that were not enriched with fish and therefore the presence of prior recruits had a strong, positive effect on subsequent recruitment. These results suggest that fish recruitment to floating objects is deliberate rather than haphazard or accidental and they support the hypothesis that flotsam plays a role in the interrelationship between environment and some juvenile fishes. These results are relevant to the use of FADs for fisheries, but emphasize that further research is necessary for applied interests.

Marine fish assemblages associated with fish aggregating devices (FADs): effects of fish removal, FAD size, fouling communities, and prior recruits

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Fishes associate with floating objects in nearly all oceans of the world (Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Klima and Wickham, 1971; Crawford and Jorgenson, 1993; Kingsford, 1993; Druce and Kingsford, 1995; Massuti et al., 1998; Hampton and Bailey, 1999; Parin and Fedoryako, 1999). Fishes also gather around fish aggregating devices (FADs), floating objects deployed to concentrate target species or bait fishes and improve the catch for artisanal, sport, or commercial fisheries. The physical attributes of a floating object, such as a FAD, may affect the ability of potential fish recruits to locate the floating object or may affect the adaptive advantages of associating with that object (or both)—a topic that has been addressed in numerous prior studies (e.g. Hunter and Mitchell, 1968; Wickham et al., 1973; Wickham and Russell, 1974; Fedoryako, 1989; Rountree, 1989; Safran, 1990; Safran and Omori, 1990; Friedlander et al., 1994; Hall et al., 1999b). However, the present study is apparently the first to address empirically the effects of disturbance, fouling communities, and prior recruits by examining both the number and the diversity of fishes that aggregate around FADs. In addition, this study addresses the effect of FAD size, a factor well represented in prior studies but frequently confounded by temporal or design issues. FADs are widely used to enhance sport and commercial fisheries, but are expensive to build, deploy, and maintain; therefore better information about the effects of FAD size and fouling could aid design efforts. Given the bycatch associated with the FAD fishery for tuna in the eastern tropical Pacific (Hall et al., 2000), for example, we need a better understanding of how fishes use FADs in order to manage fisheries for FAD-associated species (Lennert-Cody and Hall, 2000). Finally, careful study of how differing characteristics of floating objects affect fish recruitment may provide important clues regarding the adaptive significance of fish associations with flotsam and drift algae—a phenomenon widely noted but poorly understood.

Prior research has suggested that rates of immigration and fish removal from FADs similar to those seen in the present study were high from one day to the next (Nelson, 1999), and Wickham and Russell (1974) reported that midwater FADs, which were fished daily, produced a larger cumulative catch than mid-water FADs, which were undisturbed during the same period and then fished once at the end of the conclusion of the study. I tested the hypothesis that, over time, the size and diversity of FAD-associated fish assemblages are reduced by the repeated removal of these fishes compared with undisturbed assemblages. Effective management or use of FADs deployed for fisheries purposes and an understanding of the ecological relationship between flotsam and fishes associated with flotsam will depend in part on patterns of immigration and loss to fish assemblages.

There have been numerous attempts to equate flotsam structure (size, complexity, orientation, etc.) with the number of associated fishes (e.g. Hunter and Mitchell, 1968; Dooley, 1972; Wickham et al., 1973; Wickham and Russell, 1974; Rountree, 1989; Druce and Kingsford, 1995), but the results have been equivocal, except when the analysis was restricted to a single species (e.g. *Histrio histrio*, Dooley, 1972; *Decapterus punctatus*, Rountree, 1989). Huge aggregations have been associated with very small objects—IATTC (Inter-American Tropical Tuna Commission) records include a report of 55 metric tons of mostly yellowfin tuna (*Thunnus albacares*) fished from beneath a 1-m length of floating polypropylene rope (Hall et al., 1999b); therefore, despite the intuitive appeal, there is no clear reason to expect that size of FAD *per se* is an important factor in determining the size of associated assemblages. Thus, object size remains an unresolved problem in understanding flotsam-associated communities. If there are optimal FAD sizes, these may be species specific, and economical FAD design depends upon controlled experiments in the field.

Fouling organisms (sessile invertebrates and algae that colonize flotsam) are believed to have a strong, positive effect on the subsequent recruitment and retention of fishes by commercial fishermen (Gaertmer and Medina-Gaertner, 1999; Hall et al., 1999a; Hallier and Parajua, 1999; Suzuki, 1999). However, prior to the results presented here, there appear to have been no controlled tests of the hypothesis that the presence of fouling organisms enhances fish recruitment to a floating object. I also compared the numbers and diversity of fishes associated with FADs that are equipped with artificial (lead weight) fish versus FADs without these artificial fish. The latter experiment was intended to determine the importance of prior recruits to subsequent patterns of recruitment. To test a similar hypothesis over the short term (hours versus days) and using living fish instead of painted models, I also compared recruitment to FADs enriched with real fish (juvenile *Abudefduf troschelii*) to unenriched FADs.

I tested the hypothesis that each of these factors would affect the number of fishes associated with FADs (combined and individual species), as well as the species diversity of FAD-associated fish assemblages. Both the size of these FAD-associated fish assemblages and their species diversity provide insight on recruitment processes and the use of floating objects by fishes. Although the association of fishes with floating objects has been well documented, very little is known regarding the behavioral and ecological processes behind these assemblages. The results reported in the present study provide new information on the role of flotsam and FAD characteristics in determining the number and diversity of these assemblages, and some clues towards
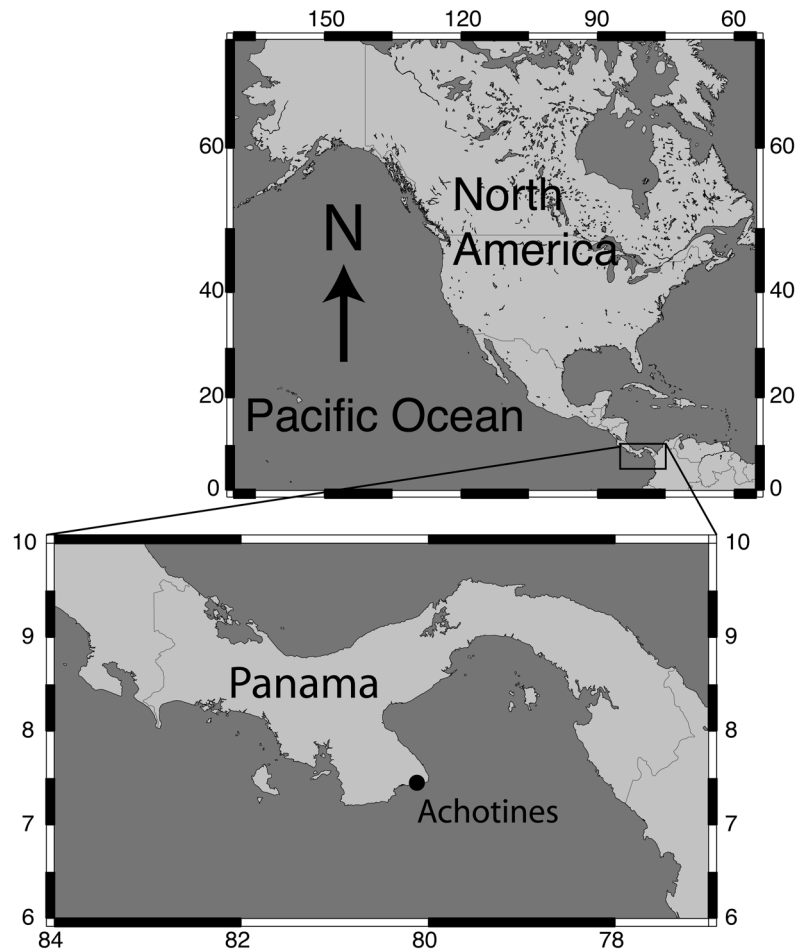

Figure 1

Location of the study site at Achotines, Panama, Central America.

understanding why and how fishes aggregate beneath floating objects.

Materials and methods

Study site and FAD construction

All research was conducted between July and October 1997 on the Pacific coast of Panama, Central America, from the Inter-American Tropical Tuna Commission laboratory at Achotines, near the tip of the Azuero Peninsula (Fig. 1). Experimental FADs were constructed of three tuna purse-seine buoys lashed together and anchored to the substrate with a 25-kg cast concrete block unless otherwise noted (Fig. 2). The length of the anchor lines allowed the FADs to rest at the surface at all tidal heights. Each buoy was roughly 25 cm in cross sectional diameter, and approximately 35 cm in length. The FADs were detachable from their moorings by detaching a large (2 m diameter) loop on the anchor line that held a 2-kg line weight (Fig. 2). This design allowed me to change FADs for another treatment. The FAD arrays were deployed nearshore (within 1.5 km;

Fig. 3) and in shallow water (14–25 m). The FAD treatments were not assigned randomly to FAD positions; instead, I assigned treatments uniformly across the FAD array because the total number of FADs was relatively low (8–10) and, given the small number of experimental units, in order to reduce the possibility that the results be confounded by positional effects.

The anchored FADs were spaced approximately 100 m apart. The maximum horizontal underwater visibility measured was 27 m, and typically averaged much less. Assuming that vision was the principal means by which fishes located these objects, it is therefore highly unlikely that fishes treated the FAD array as a single "object" or moved from FAD to FAD within the array. I believe that it was unlikely that any fish transferred from one FAD to another for the following reasons. 1) The horizontal underwater visibility was always much less than the distance between FADs. 2) Observations suggest that short-term, daytime fidelity was high; once a fish associated with a floating object, it was unlikely to leave that object during the day (Nelson, 1999). 3) Crossing an open stretch of water for another floating object (presumably within detection range) entails a potential risk for a fish. Moser et al. (1998) did note that the larger juveniles and adult fishes associated with floating *Sargassum* showed little apparent fidelity to this habitat and would move between their research boats, floating observation equipment, and the *Sargassum* habitat. However, the fishes that were observed to move between these floating objects were juvenile carangids between 10 and 20 cm in length (Moser et al., 1998), whereas the fishes in the present study were generally much smaller and presumably less vagile.

Longshore currents ran roughly west to east through the experimental area, and rarely in the reverse (Fig. 3). I recorded an estimate of current direction using an underwater compass and the angle of the FAD anchor lines. This estimate represented the sum of the forces due to windage on the FAD buoys and currents.

Censusing FADS

FAD-associated fish assemblages were censused by direct visual observation by divers using mask and snorkel. Most other studies of fish assemblages associated with floating material have employed nets or quantitative fishing methods for sampling purposes (e.g. Kojima, 1960; Dooley, 1972; Kingsford, 1992, 1995), but Hunter and Mitchell (1968) compared data from net captures, automated photography and direct visual observations and found that the visual observations agreed well with the other methods, and provided behavioral information not available with the other methods. In my study, a FAD was approached by swimming
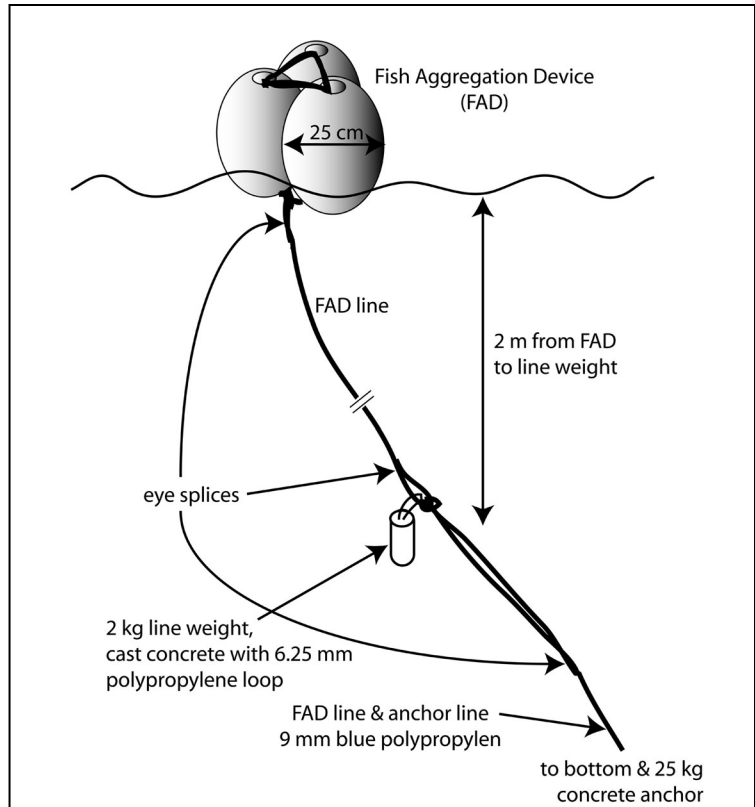

Figure 2
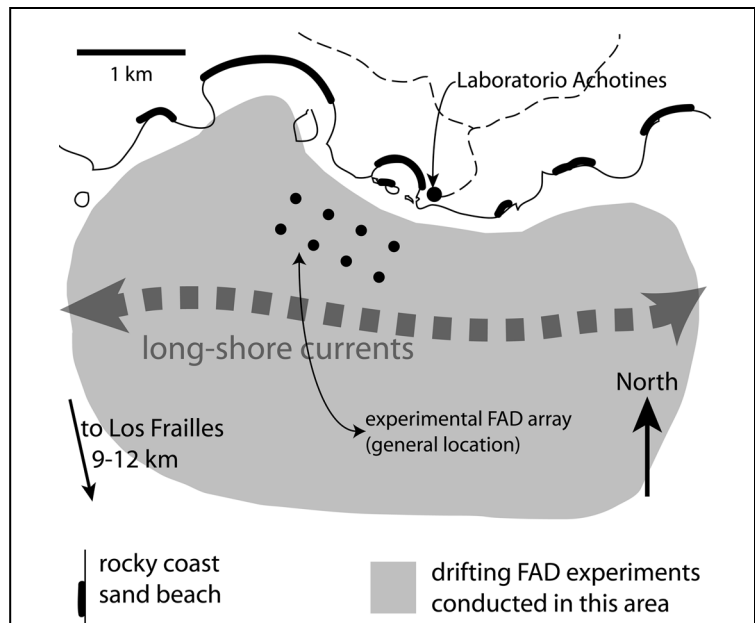Design of detachable fish aggregating devices (FADs) used in the present study.

Figure 3
Coastline and general location of experiments and observations. The laboratory (Laboratorio Achotines) is located at approximately 7°5′N lat, 80°10′W long.

slowly and quietly at the surface from a distance of at least 12 m. All fishes associated (defined below) with the floating object were counted and identified; therefore the statistical unit in all of the experiments described below was a single FAD-associated assemblage of fishes at a given date and time. Horizontal underwater visibility, measured with a Secchi disk, was always sufficient to allow the identification of species and to count individual fishes from a minimum distance of 2 meters.

Any fish observed within 2 m of a FAD was considered to be "FAD-associated." Very few fishes were observed outside of this range, and with rare exceptions, fishes responded to the approach of an observer first by swimming towards the observer and then by moving closer to the FAD, rather than away from it. Different species of fishes used the space around and below the FAD differently, as both Gooding and Magnuson (1967) and Hunter and Mitchell (1967) described, but the juvenile fishes that predominated in the present study were unambiguous regarding their relationship to the FADs. After fishes resumed their prior positions in relation to a FAD, continued observations of these fishes revealed that there was no inclination to abandon that FAD. The appearance of potential predators invariably resulted in a tightening of the spatial distribution around the FAD.

When the experiment required the capture of FAD-associated fishes, I used a smaller (1.1×1.3 m) version of the diver-operated liftnet described by McCleneghan and Houk (1978). Captured fishes were preserved for further studies, held in grow-out facilities in the laboratory to verify species identification, or released 1.5 km down-current over rocky reef habitat to ensure that they had effectively been removed from the FAD array.

Diversity calculations

Measurements of species diversity provided a means of monitoring treatment effects on the composition of FAD-associated assemblages. I measured species diversity using species richness (S, the raw number of species observed), and the Brillouin index (HB). S is simple and widely used, but increases with sample size, and, where sample sizes are unequal, HB provides a less biased measure of diversity (Magurran, 1988). In addition, HB was chosen over one of the more commonly used information theory indices (e.g. the Shannon-Wiener index) because 1) FAD-associated assemblages are not a random sample of potential recruits (different species vary in their attraction to floating objects) and 2) each of these assemblages was completely censused—not sampled (Magurran, 1988, and references therein).

HB is calculated as

$$HB = \frac{\ln N! - \sum \ln n_i!}{N},$$

where N = the total number of fishes of all species observed; and
n_i = the number of individuals within the ith species (Magurran, 1988).

Statistical analyses

I used a two-way repeated measures ANOVA (α=0.05) to test for treatment differences, differences among observation dates and evidence of treatment-by-sample interaction for assemblage sizes (no. of fish(es)), species richness (S) and species diversity (HB). Because individual species differed in their relative abundance and had different ecological requirements, there was the potential for the dominant species to bias comparisons of experimental treatments where assemblage size (a combinination of all species) was used. For all experiments except for the recruit-enriched experiment, I repeated the statistical analyses twice: once using the number of sergeant major damselfish (*Abudefduf troschelii*) only and again using all fishes combined but with *A. troschelii* removed. For the artificial fish experiment where rainbow runner (*Elagatis bipinnulata*) were particularly abundant, I ran separate analyses for *A. troschelii* alone, *E. bipinnulata* alone, and for all species minus the numbers of *A. troschelii*. When no fishes were present at a FAD, HB was undefined; the "missing" data were replaced according to the procedures of Zar (1996) and the degrees of freedom were reduced accordingly.

Fish-removal experiments

Observations on similar FADs during a previous field season at the same location suggested that the turnover rate of fish associated with anchored FADs is high, especially when the initial assemblage is large, but that some recognizable individuals did persist from day-to-day (Nelson, 1999). If immigration and emigration rates were as high as suspected, FADs cleared of fish on a daily basis should not differ significantly from undisturbed FADs in their mean assemblage size or in the average number of species associated with these FADs. Wickham and Russell (1974) compared the catches of bait fishes associated with FADs subject to daily purse-seine sets versus those allowed to "soak" undisturbed for three days prior to a single purse-seine set and concluded that sufficient emigration and immigration occurred on a daily basis to remove any appreciable effect of daily removals. I sought to address similar questions, but by using a different system (juvenile reef fishes versus bait fishes).

To test these hypotheses, I deployed eight identical FADs on 30 June 1997 in two lines of four FADs each, oriented roughly parallel to shore (Figs. 2 and 3). Fishes associated with all eight FADs were counted and identified on a daily basis, beginning 3 July 1997. Alternate FADs were cleared of all fish, following the daily counts; the remaining FADs were left undisturbed in such a way as to distribute the treatments evenly among the FAD array. After three consecutive days of these observations (series 1), the treatments were reversed, and previously undisturbed FADs were cleared, and those that had been cleared regularly were left undisturbed (series 2). The treatments were reversed in an attempt to control for possible positional effects of the FADs. However, the two series were necessarily run consecutively, not concurrently; therefore treatment position was confounded by sample date. I used a 2 (cleared vs.
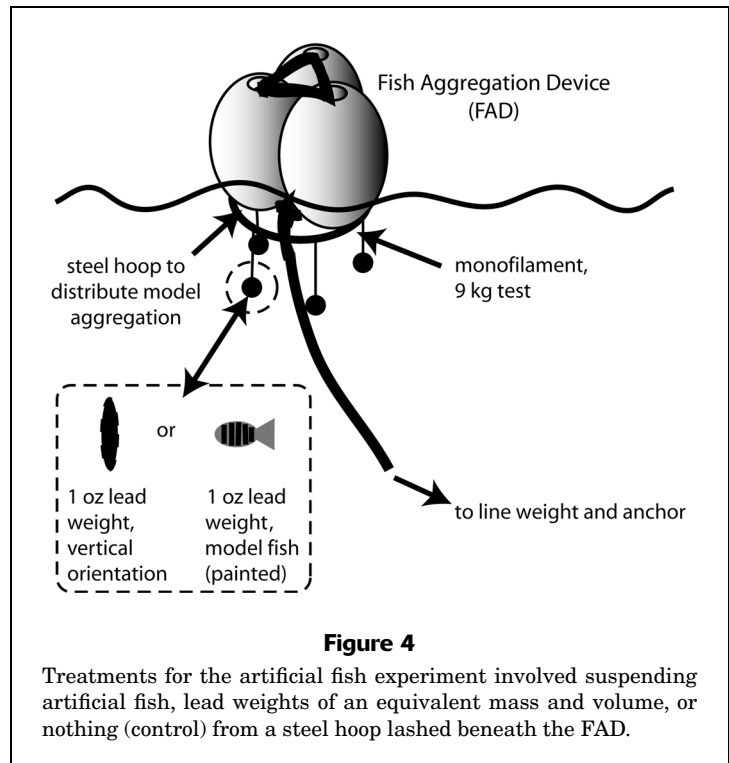
undisturbed) by 2 (first series vs. second series) by 6 (sample date) model and I used a repeated measures ANOVA (repeated on sample date) on the following dependent variables: assemblage size (total no. of fishes), species richness (S), and HB. I repeated analyses of assemblage-size effects looking at the number of *A. troschelii* only, and the total number of fishes minus the number of *A. troschelii*.

FAD size

To determine the effect of FAD size on the associated assemblage size and diversity, I compared FAD-associated fish assemblages between triple-size FADs and single FADs. An existing anchored array of eight FADs (two lines parallel to the coast of four FADs each, Fig. 3) was cleared of fishes on 24 July 1997. As the fish were removed from the FADs, each FAD was replaced with a fresh (i.e. clean and unfouled) single or triple-size FAD, placed at alternating positions. The single FADs were constructed as described above and in Figure 2; the triple-size FADs were identical to the single FADs, except that they consisted of nine, rather than three, purse-seine buoys lashed together and had the effect of nearly tripling the wetted surface area (although inner buoys are less exposed than outer ones) and the volume of the FAD, and of increasing the maximum linear dimension of the FAD by a factor of two. Treatments were not reversed for this or subsequent experiments because sample date appeared to be the major factor determining assemblage size for any species, based on the previous experiment. Note that in each of these experiments, except for the recruit-enrichment experiment that used drifting FADs, treatments were assigned uniformly throughout the FAD arrays so that onshore, offshore, or longshore biases in recruitment due to oceanographic processes would not confound the results. Fishes at all FADs were counted and identified on three dates (26, 28, and 30 July 1997), each observation separated from the next by 48 hours. No fish were collected, with the exception of one balistid, taken from the array on 26 July because it was the first of that species to be observed associated with a FAD. Data were analyzed for experimental effects on total assemblage size, species diversity (S and HB), the number of *A. troschelii,* and total number of fishes minus the number of *A. troschelii*.

Presence of absence of a fouling community

To determine whether the presence of a fouling community on a floating object affected the associated fish assemblage, I compared FAD-associated assemblage sizes and species richness between fouled and unfouled (control) FADs. Control FADs were scrubbed of all fouling organisms. Fouled FADs had been deployed for a minimum of 14 days (range: 14–22 days) in the study area, and had accumulated fouling that completely covered the wetted surface of the FAD with gooseneck barnacles (*Lepas* sp.), hydroids, and bryozoans. Grapsid crabs and polychaete worms (*Amphimone vagans*)

Figure 4

Treatments for the artificial fish experiment involved suspending artificial fish, lead weights of an equivalent mass and volume, or nothing (control) from a steel hoop lashed beneath the FAD.

were also intermittent associates of fouled FADs. Control and fouled FADs were deployed on 8 September 1997 in an alternating array of eight buoys, with four FADs per treatment (layout and spatial distribution of treatments follow that of the FAD size experiment). All fishes were cleared from FAD positions prior to deploying the FADs, and data collection commenced 24 hours later. Data were collected on four consecutive days (9, 10, 11, and 12 September 1997) and analyzed for experimental effects on total assemblage size, species diversity (S and HB), the number of *A. troschelii*, the number of *E. bipinnulata*, and total number of fishes minus the number of *A. troschelii*.

Artificial fish experiment

I tested the hypothesis that potential recruits would distinguish between FADs with an "assemblage" of artificial fish suspended beneath them, FADs with an "assemblage" of suspended material equal to the artificial fish in size but not resembling fish in appearance, and control FADs without anything suspended beneath them (Fig. 4). I constructed artificial fish from 31.25-g lead fishing weights. These weights were flattened, tear-drop–shaped objects, painted a dull yellow with black bars to resemble juvenile *Abudefduf troschelii* and suspended, by using monofilament (20 lb. test) and a steel hoop, beneath the "artificial fish FADs" (Fig. 4). I suspended oblong 31.25-g lead fishing weights beneath "weighted FADs," and the control FADs had only a steel hoop beneath each (Fig. 4). These FADs were deployed in an anchored array, and the various treatments were distributed in an alternating pattern throughout the array. FAD positions were cleared of fishes,

Table 1

Fish species and life history stages observed at all experimental FADs (combined data) with relative importance by frequency and abundance. 1 = coastal pelagic species; 2 = substrate-associated species; and 3 = possible flotsam specialists. J = juvenile; A = adult.

No.	Species	Family	Stage	Frequency (%)	Abundance (%)
1	*Abudefduf troschelii*[2]	Pomacentridae	J	34.1	81.4
2	*Elagatis bipinnulata*[1]	Carangidae	J	16.9	8.1
3	*Polydactylus approximans*[2]	Polynemidae	J	6.4	1.8
4	*Mugil* sp. [2]	Mugilidae	J	6.4	1.3
5	*Lutjanus argentiventris*[2]	Lutjanidae	J	6.4	1.1
6	*Epinephelus panamensis*[2]	Serranidae	J	3.4	0.5
7	*Hoplopagrus guntheri*[2]	Lutjanidae	J	3.2	0.5
8	*Canthidermis maculatus*[1]	Balistidae	J	2.8	0.4
9	*Gnathanodon speciosus*[2]	Carangidae	J	1.5	0.2
10	*Alectis ciliaris*[1]	Carangidae	J		
11	*Caranx caninus*[1]	Carangidae	J		
12	*Caranx caballus*[1]	Carangidae	J	14.7	3.9
13	*Caranx vinctus*[1]	Carangidae	J	(nos. 10–14)	
14	*Seriola peruana*[1]	Carangidae	J		
15	*Tylosaurus acus pacificus*[1]	Belonidae	A		
16	*T. crocodilus fodiator*[1]	Belonidae	A		
17	*Fistularia commersonii*[2]	Fistulariidae	J		
18	*Syngnathus auliscus*[2]	Syngnathidae	J		
19	*Lobotes pacificus*[3]	Lobotidae	J and A		
20	*Mulloidichthys dentatus*[2]	Mullidae	J	4.1	0.7
21	*Sectator ocyurus*[3]	Kyphosidae	A	(nos. 15–26)	
22	*Parapsettus panamensis*[2]	Ephippidae	J		
23	*Hypsoblennius breviceps*[2]	Blenniidae	?		
24	goby (unidentified) [2]	Gobiidae	?		
25	*Aluterus scriptus*[2,3]	Balistidae	J and A		
26	*Balistes polylepis*[2]	Balistidae	J		
	26 species	16 families		100	100

and treatment FADs were deployed on 24 September 1997. FADs were monitored daily as described above, from 25 September through 3 October 1997 (sampling days=9). Data were analyzed for experimental effects on total assemblage size, species diversity (*S* and *HB*), number of *A. troschelii*, number of *E. bipinnulata*, and total number of fishes minus the number of *A. troschelii*.

Recruit-enriched vs. nonenriched FADs

I tested the hypothesis that the presence of prior recruits (juvenile sergeant major damselfish, *Abudefduf troschelii*) would have a positive effect on subsequent recruitment to a FAD. I used *A. troschelii* because these were the most important species associated with FADs by frequency and abundance (Table 1). It is possible that the selection of a particular species as the prior recruit might affect the subsequent recruitment of the same or different species (via intra- or interspecific competition for example), but I had no basis for predicting the direction of such effects.

Given the strong day-to-day changes in assemblage sizes, this test required frequent, short-interval observations of the experimental FADs. I used drifting, rather than anchored, FADs to provide a more realistic (and conservative) test of the effect. (Drifting objects should result in fewer chance encounters by potential fish recruits carried by currents through a fixed FAD array, but anchored FADs are much easier to track for longer experiments.) I deployed four drifting FADs (constructed from 3 buoys—the "single" size) in the stippled area indicated in Figure 3. Two of these FADs were enriched with nine *A. troschelii* per FAD, previously collected from anchored FADs and released in close proximity to drifting FADs immediately after deployment. The two control FADs received no sergeant majors to start. Both groups were checked immediately following deployment to verify that the fish had associated with the experimental FADs and to check against quick recruitment to the control FADs. To minimize the potential transfer of fish with the boat, I accelerated sharply when leaving a FAD enriched with sergeant majors and when checking

the FADs, entered the water from the boat a minimum of 10 m from each FAD.

The FADs were deployed from an inflatable boat at 50-m intervals in a roughly linear array, and checked at hourly intervals. The FADs did not maintain their initial spatial arrangement, but I did not move any FAD once the drift began unless FAD-to-FAD distance had been reduced to less than 10 m. In this instance, I moved one or more FADs to a minimum FAD-to-FAD distance of 50 m after checking for any FAD-associated fishes. In none of these instances were any FAD-associated fishes observed. I monitored the drift for four hours; deteriorating weather and fading light, however, did not permit additional observations.

I used linear regression to test the hypothesis that the number of FAD-associated fishes changed over time for the enriched FADs and for the nonenriched FADs. I used a *t*-test to compare the slopes of the two regression models and to test the hypothesis that the treatments accumulated fish at different rates.

Results

Twenty-six species of fishes from 16 families were recorded, including species associated with reef, soft bottom, and coastal pelagic habitats as adults (Table 1). Only juvenile specimens were observed clearly associated with FADs, with the exception of *Aluterus scriptus* and *Lobotes pacificus*, of which both juvenile and adult forms were observed in close, continuous proximity to the FADs. Two needlefish species (*Tylosaurus acus pacificus* and *T. crocodilus fodiator*) appeared occasionally in close proximity to the FADs, but they were not clearly associated with the FADs. An adult *Lobotes pacificus* (tripletail) was observed once and a single adult *Aluterus scriptus* (scrawled filefish) were observed on three separate instances. Horizontal underwater visibility averaged 13.4 m (±1.7 SE) for all sampling days combined.

Juvenile sergeant major damselfish (*Abudefduf troschelii*) were the dominant species by frequency of occurrence and numerical abundance (Table 1) for all experiments. The damselfish was followed in rank overall by juvenile rainbow runner (*Elagatis bipinnulata*), although this species was observed with the FADs only during the fouling and model fish experiments. Juvenile threadfin (*Polydactylus approximans*), mullet (*Mugil* sp.), and yellow snapper (*Lutjanus argentiventris*) were equally frequent but differed slightly in abundance (*P. approximans*>*Mugil* sp.>*L. argentiventris*; Table 1). The latter pattern was consistent across all experiments. Specimens from a suite of juvenile carangids (excluding *E. bipinnulata*) were also observed frequently.

Fish-removal experiments

Sample date, series, and treatment combined to have a significant effect on *A. troschelii* abundance (three way interaction, *P*=0.03), but there was no clear pattern; the remaining species (combined species less numbers of *A. troschelii*) were influenced by sample date (date by series
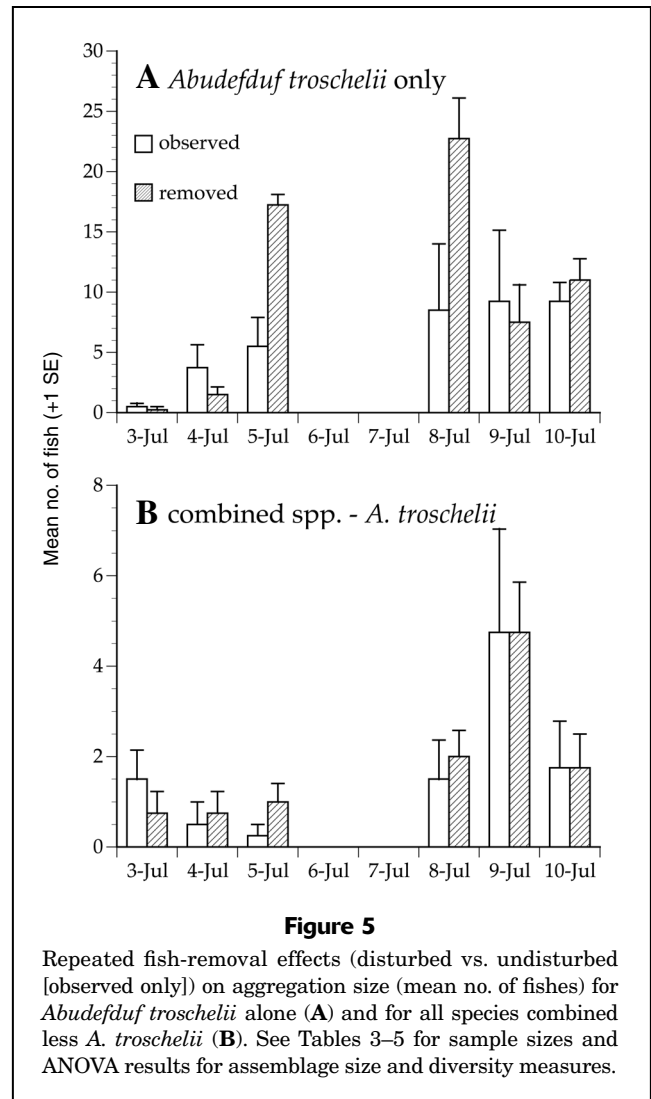

Figure 5

Repeated fish-removal effects (disturbed vs. undisturbed [observed only]) on aggregation size (mean no. of fishes) for *Abudefduf troschelii* alone (**A**) and for all species combined less *A. troschelii* (**B**). See Tables 3–5 for sample sizes and ANOVA results for assemblage size and diversity measures.

interaction, *P*<0.01) but not by treatment (*P*=0.73, Table 2, Fig. 5). Measures of diversity varied between series (series: *S*, *P*<0.01; HB, *P*=0.01) but were unaffected by treatment. Thus, fish removal or fish disturbance may contribute to assemblage sizes for individual species (e.g. *A. troschelii*), but, in the present study, the total number of combined species was unaffected.

FAD size

Abudefduf troschelii was strongly affected by a combination of treatment and sample date (date by treatment interaction, *P*=0.03, Table 3, Fig. 6). Results from the remaining species combined were comparable with larger total numbers at the larger FADs, although not statistically significant (treatment, *P*=0.07). Although both measures of diversity (*S* and HB) suggested that the treatment may have had a positive effect on diversity (*S*, treatment, *P*=0.02), species richness was positively correlated with sample size. HB, a diversity measure comparatively unaf-

Table 2

Repeated measures ANOVA results (cleared FADs vs. undisturbed FADs, $n_1=n_2=12$) in fish-removal experiment.

Dependent variable	Factor(s)	F	df	P	$1-\beta$
Number of fishes	treatment	0.12	1, 12	0.73	0.06
(all species combined)	series	35.3	1, 12	<0.01	>0.99
	treatment × series	0.64	1, 12	0.44	0.11
	date	5.53	2, 24	0.01	0.81
	date × series	48.5	2, 24	<0.01	>0.99
	date × treatment	3.22	2, 24	0.06	0.55
	3-way interaction	0.06	2, 24	0.94	0.06
Number of fish	treatment	16.7	1, 12	<0.01	0.97
(*A. troschelii* only)	series	5.92	1, 12	0.03	0.61
	treatment × series	0.27	1, 12	0.61	0.08
	date	3.10	2, 24	0.06	0.53
	date × series	7.71	2, 24	<0.01	0.93
	date × treatment	2.95	2, 24	0.07	0.51
	3-way interaction	4.24	2, 24	0.03	0.69
Number of fishes	treatment	0.05	1, 12	0.82	0.06
(all spp. minus *A. troschelii*)	series	13.3	1, 12	<0.01	0.93
	treatment × series	0.01	1, 12	0.94	0.05
	date	2.93	2, 24	0.07	0.51
	date × series	4.06	2, 24	0.03	0.66
	date × treatment	0.07	2, 24	0.93	0.06
	3-way interaction	0.31	2, 24	0.74	0.09
Species richness (*S*)	treatment	0.63	1, 12	0.44	0.11
	series	11.8	1, 12	<0.01	0.90
	treatment × series	0.63	1, 12	0.44	0.11
	date	0.43	2, 24	0.66	0.11
	date × series	0.63	2, 24	0.54	0.14
	date × treatment	0.69	2, 24	0.51	0.15
	3-way interaction	2.08	2, 24	0.37	0.37
Species diversity *(HB)[1]*	treatment	1.05	1, 10	0.33	0.15
	series	8.79	1, 10	0.01	0.79
	treatment × series	0.54	1, 10	0.48	0.10
	date	1.43	2, 22	0.26	0.27
	date × series	2.80	2, 22	0.08	0.49
	date × treatment	0.12	2, 22	0.12	0.07
	3-way interaction	0.61	2, 22	0.55	0.14

[1] Missing data were replaced according to the directions in Zar (1996), and the degrees of freedom were reduced accordingly. "3-way interaction" refers to interactions between treatment, series, and dates.

fected by sample size (Magurran, 1988), was marginally nonsignificant (HB, treatment, P=0.07, Table 3).

Presence or absence of a fouling community

Treatment and sample date combined to have a significant effect on the number of *A. troschelii* (date by treatment interaction, *P*<0.01)—an effect contributing to the similar significant interaction effect for all species combined (Fig. 7, Table 4). Although the mean numbers of fish(es) were consistently higher at fouled FADs for *E. bipinnulata* alone and for all species minus *A. troschelii*, the only significant main effects were due to sample date (Table 4, Fig. 7). Spe-

cies diversity (HB), though not richness (*S*), was significantly affected by sample date (*P*=0.02).

Artificial fish experiment

Experimental treatments (FADs with model fish, with lead weights or with nothing, Fig. 4) had no effect on any measured parameter—combined species, *A. troschelii* alone, *E. bipinnulata* alone, combined species less *A. troschelii*, species richness and diversity (Fig. 8, Table 5). All measures were significantly affected (*P*<0.01) by sample date except for *E. bipinnulata* alone (date, *P*=0.48). Although individual FADs varied in the number of associated *E. bipinnulata*,

Table 3
FAD-size effects and repeated measures ANOVA results (single FADs vs. triple-size FADs, $n_1=n_2=12$).

Dependent variable	Factor(s)	F	df	P	$1-\beta$
Number of of fishes	treatment	24.1	1, 6	<0.01	0.99
(all species combined)	date	10.7	2, 12	<0.01	0.97
	date × treatment	2.56	2, 12	0.12	0.41
Number of fish	treatment	10.9	1, 6	0.02	0.79
(*A. troschelii* only)	date	18.2	2, 12	<0.01	>0.99
	date × treatment	4.55	2, 12	0.03	0.66
Number of fishes	treatment	4.84	1, 6	0.07	0.45
(all spp–*A. troschelii*)	date	0.42	2, 12	0.67	0.10
	date × treatment	0.29	2, 12	0.75	0.09
Species richness (S)	treatment	11.3	1, 6	0.02	0.81
	date	0.38	2, 12	0.69	0.10
	date × treatment	0.38	2, 12	0.69	0.10
Species diversity (HB)	treatment	5.00	1, 6	0.07	0.46
	date	3.39	2, 12	0.07	0.52
	date × treatment	0.40	2, 12	0.68	0.10

these numbers were strikingly constant across sample date and, to a lesser extent, across treatments (Fig. 8).

Recruit-enriched vs. nonenriched FADs

Enriched FADs showed significantly higher rates of recruitment than nonenriched FADs: the regression line for the enriched FADs had a significant slope ($F_{(1,8)}=20.76$, $P<0.01$), but the regression line for the nonenriched FADs did not ($F_{(1,8)}=2.29$, $P=0.17$; Fig. 6). All additional fish were juvenile sergeant major damselfish, *Abudefduf troschelii*. These slopes are significantly different ($t=3.05$, 2 tailed test, $v=6$, $P=0.02$; Fig. 9); enriched FADs accumulated fish at a significantly higher rate (2.5 fish per hour) than did nonenriched FADs that accumulated fish at a rate of 0.1 fish per hour. Horizontal underwater visibility was 15 m at the beginning of the experiment.

Discussion

FAD size, the presence of a fouling community, and the presence of prior recruits all had positive effects on the size of FAD-associated assemblages, although the latter factor was assessed over a period of hours, whereas the former were assessed over days. The repeated removal of an existing assemblage also had significant effects due at least partially to treatment, but in all of these analyses sample date appeared to play the largest role in determining the numbers of fish(es) at these FADs. The presence of artificial fish or comparable-size weights did not significantly affect assemblage sizes. There was little support for the hypothesis that any of these factors might affect the species diversity of these assemblages; only species richness was significantly increased along with an increase in FAD size and this result may be an effect of assemblage size rather than object characteristics. Where treatment effects did significantly affect the numbers of fishes, their effects
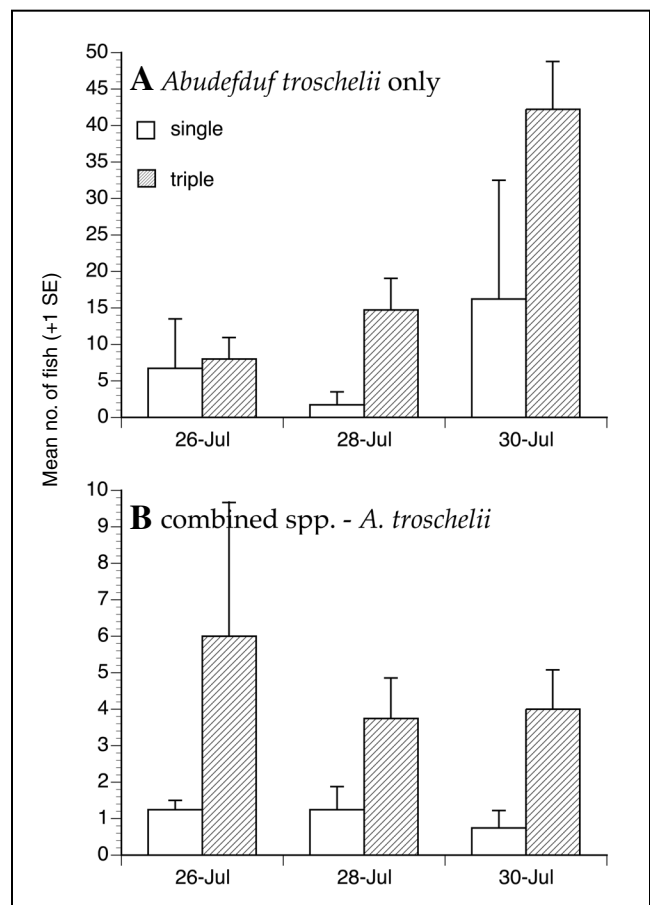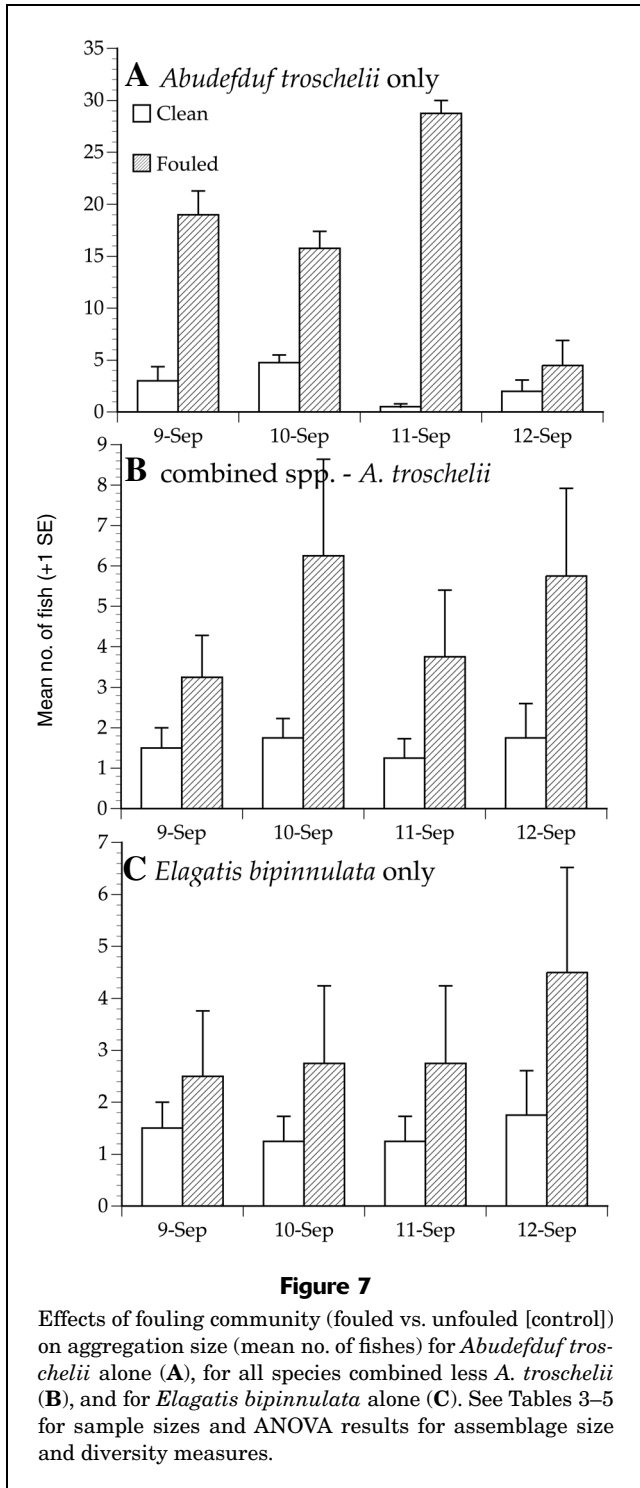

Figure 6
FAD-size effects (single FADs vs. triple-size FADs) on aggregation size (mean no. of fishes) for *Abudefduf troschelii* alone (**A**) and for all species combined less *A. troschelii* (**B**). See Tables 3–5 for sample sizes and ANOVA results for assemblage size and diversity measures.

Figure 7

Effects of fouling community (fouled vs. unfouled [control]) on aggregation size (mean no. of fishes) for *Abudefduf troschelii* alone (**A**), for all species combined less *A. troschelii* (**B**), and for *Elagatis bipinnulata* alone (**C**). See Tables 3–5 for sample sizes and ANOVA results for assemblage size and diversity measures.

Figure 8

Artificial-fish effects (empty [control] FADs, FADs with weights, versus FADs with artificial fish) on aggregation size (mean no. of fishes) for *Abudefduf troschelii* alone (**A**), for all species combined less *A. troschelii* (**B**), and for *Elagatis bipinnulata* alone (**C**). See Tables 3–5 for sample sizes and ANOVA results for assemblage size and diversity measures.

on *Abudefduf troschelii* were generally the strongest. It is not clear whether this is a species-specific effect or if these results are due to the fact that *A. troschelii* was the most numerically important species.

The absence of a significant treatment main effect in the fish-removal experiments suggests that recruitment and loss from these anchored FADs is sufficiently rapid so that
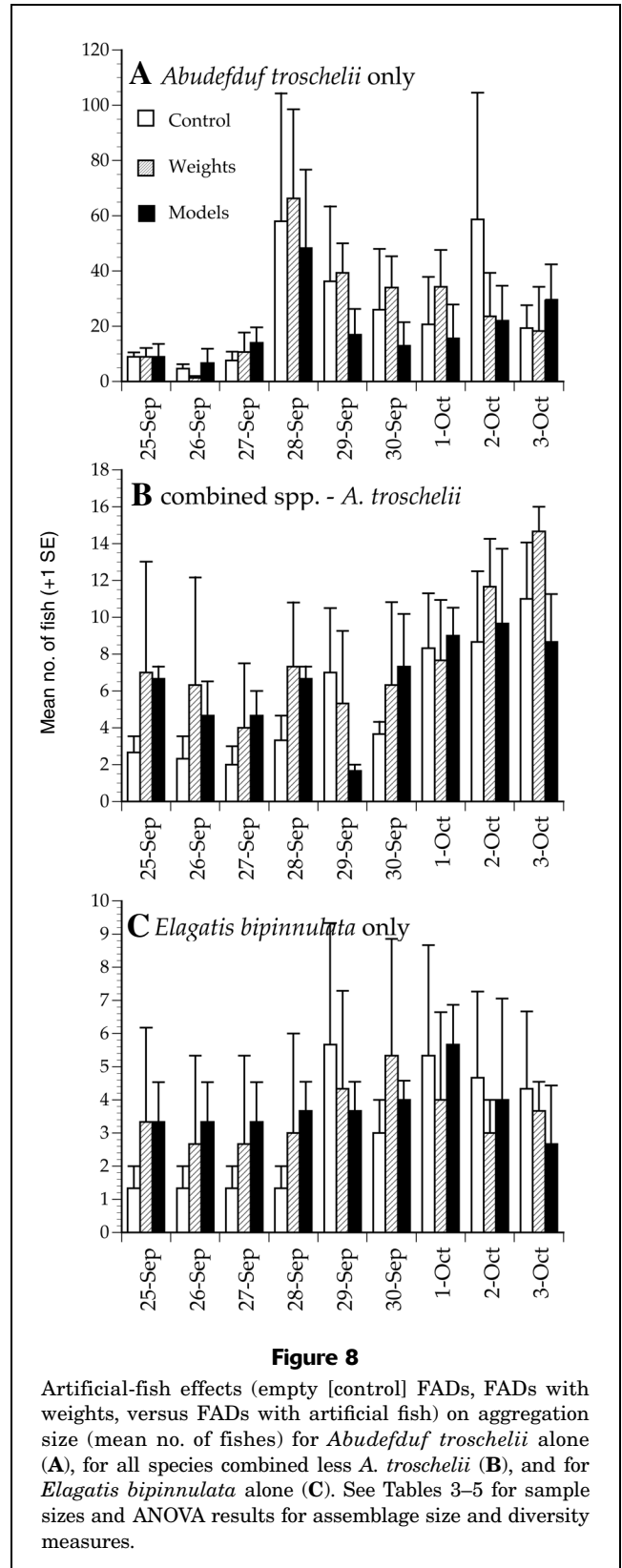
the complete removal of all fishes on a daily basis has no effect on the next day's assemblage size or diversity. These

Table 4

Repeated measures ANOVA results (absence of fouling community vs. presence of a fouling community, $n_1=n_2=16$) in fouling community experiment.

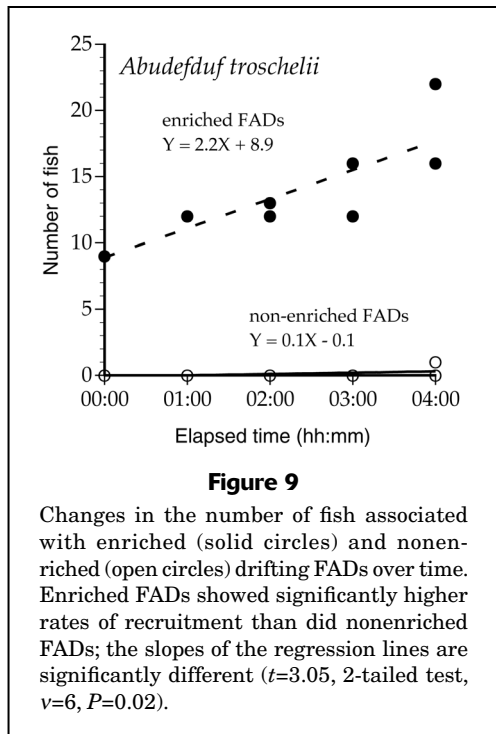| Dependent variable	Factor(s)	F	df	P	$1-\beta$
Number of fishes	treatment	39.8	1, 6	<0.01	0.99
(all species combined)	date	24.4	3, 18	<0.01	0.97
	date × treatment	33.5	3, 18	<0.01	0.41
Number of fish	treatment	165	1, 6	<0.01	>0.99
(*A. troschelii* only)	sate	19.7	3, 18	<0.01	>0.99
	date × treatment	25.2	3, 18	<0.01	>0.99
Number of fish	treatment	1.06	1, 6	0.34	0.14
(*E. bipinnulata* only)	date	4.89	3, 18	0.01	0.84
	date × treatment	2.15	3,18	0.13	0.45
Number of fishes	treatment	3.01	1, 6	0.13	0.30
(all spp.–minus *A. troschelii*)	date	3.88	3, 18	0.03	0.73
	date × treatment	2.27	3, 18	0.12	0.47
Species richness (*S*)	treatment	2.49	1, 6	0.17	0.26
	date	3.00	3, 18	0.06	0.60
	date × treatment	0.60	3, 18	0.62	0.15
Species diversity (HB)	treatment	1.74	1, 6	0.23	0.19
	date	4.35	3, 18	0.02	0.79
	date × treatment	1.91	3, 18	0.16	0.40

Table 5

Repeated measures ANOVA results (control [no weights and no artificial fish] vs. weights and vs. artificial fish, $n_1=n_2=n_3=27$) in the artificial fish experiment.

Dependent variable	Factor(s)	F	df	P	$1-\beta$
Number of fishes	treatment	0.13	2, 6	0.88	0.06
(all species combined)	date	3.52	8, 48	<0.01	0.97
	date × treatment	0.37	8, 48	0.98	0.20
Number of fish	treatment	0.12	2, 6	0.89	0.06
(*A. troschelii* only)	date	3.34	8, 48	<0.01	0.95
	date × treatment	0.41	8, 48	0.97	0.22
Number of fishes	treatment	0.29	2, 6	0.76	0.08
(all spp. minus *A. troschelii*)	date	4.82	8, 48	<0.01	>0.99
	date × treatment	0.73	8, 48	0.75	0.41
Number of fish	treatment	0.05	2, 6	0.95	0.06
(*E. bipinnulata* only)	date	0.95	8, 48	0.48	0.38
	date × treatment	0.36	8, 48	0.94	0.20
Species richness (*S*)	treatment	0.41	2, 6	0.68	0.10
	date	9.87	8, 48	<0.01	>0.99
	date × treatment	0.90	8, 48	0.58	0.50
Species diversity (HB)[1]	treatment	0.13	2, 5	0.88	0.06
	date	4.44	8, 47	<0.01	0.99
	date × treatment	1.00	8, 47	0.45	0.56

[1] Missing data were replaced according to the directions in Zar (1996), and the degrees of freedom were reduced accordingly.

results are consistent with those obtained by Wickham and Russell (1974). A similar result would occur if these FADs had a predictable carrying capacity and recruitment was sufficiently rapid that removal of the assemblage was followed by its replacement before the next observation. However, assemblage sizes within treatments varied widely from one day's observations to the next; therefore recruitment, rather than carrying capacity, seems to determine assemblage size.

Figure 9

Changes in the number of fish associated with enriched (solid circles) and nonenriched (open circles) drifting FADs over time. Enriched FADs showed significantly higher rates of recruitment than did nonenriched FADs; the slopes of the regression lines are significantly different (t=3.05, 2-tailed test, v=6, P=0.02).

There appears to be insufficient time or stability for such factors as competition or predation to influence the size or diversity of these FAD-associated fish assemblages. Despite these results, individual fish do remain with a specific FAD for days: On at least five separate occasions associated with some of the other experiments described in this paper, individuals recognizable by scars and bite marks were sighted repeatedly as many as six days after the initial observation (Nelson, unpubl. data). Although the FADs and the associated fishes described in the present study are not directly comparable to FADs and fishes targeted in fisheries-scale operations, these experiments are among the first controlled efforts at understanding the effects of disturbance or fishing for FAD-associated assemblages.

The average assemblage size for all experiments and treatments varied considerably, often significantly, over time (Tables 2–5). Significant interaction effects between sample date and FAD treatments may be indicative of day-to-day recruitment fluctuations, dependent upon recruitment variability. A significant interaction may result when these effects are large and are in evidence regardless of the experimental treatment (i.e. occur in concert across treatments). Significant sample date effects (and series effects in the fish-removal experiment, Table 2) are likely a result of temporal fluctuations in the numbers of fishes available to recruit to the FADs.

Note that the two series in the fish-removal experiment differed not only in which FADs were given a particular treatment (positional effects), but also in time—the two series were necessarily run consecutively, not concurrently. I believe, however, it to be unlikely that positional effects influenced any of the results reported in the present study: treatments were assigned to FADs within the arrays in such a way as to ensure that inshore, offshore, or longshore positions were equally weighted among treatments. Significant series main effects, independent of additional factors, were found only for species richness and diversity (*HB*)—a result I attribute to changes in the availability of potential recruit species. Temporal patterns of juvenile reef fish recruitment are often variable and may be affected by such factors as spawning periodicity (Love et al., 1990), variable predation (Nelson, 2001), or changing physical oceanographic processes (Doherty, 1991; Levin, 1994; Kingsford and Finn, 1997). Rountree (1989), also, found that the mean numbers of the most abundant species observed around a FAD array off South Carolina varied widely during FAD deployment, albeit over a much longer time period (nearly 200 days). Thus, differences in assemblage size and diversity over time are not unexpected.

FAD size had significant, positive effects on assemblage size and species richness. Although tripling the FAD size resulted in a nearly threefold increase in the number of associated fishes (combined species), the response may not be linear. (Note, however, that Rountree (1989) demonstrated that the number of *Decapterus punctatus* associated with midwater FADs exhibited a significant, positive linear response to FAD size.) Further research will be necessary to resolve the effect of FAD size on numbers of aggregating fishes. Also of interest is the significant increase in species richness attributable to increased FAD size. Bortone et al. (1977) suggested that species diversity may be a function of "clump size" for *Sargassum*-associated fish assemblages, and Moser et al. (1998) found greater numbers of fish species under large (10–20 m diameter) mats of floating *Sargassum* than they did under smaller clumps (<1 m diameter) or in open water. However, the changes in species richness from this experiment could well be an effect of assemblage size; treatment effects on species diversity measured using the Brillouin index (*HB*) were marginally nonsignificant (Table 3, P=0.07). Significant sample date differences in treatment and evenness are due to large fluctuations in the abundance of the dominant species, *Abudefduf troschelii*, ranging at the triple-size FADs from 1 to 55 individuals over the course of 11 days.

Fishes were five times more numerous on average at fouled FADs than they were at comparable FADs lacking fouling organisms, but measures of diversity showed no significant treatment effect (Table 4). There was a significant interaction between treatment and sample date for the present experiment (Table 4) that may have been due to fluctuations in assemblage sizes among sample dates across both FAD treatments. The species composition of these assemblages was similar to that of other experiments, except that *Elagatis bipinnulata* were regularly observed: *Abudefduf troschelii* were the dominant species by abundance, followed by *E. bipinnulata*, and *Mugil* sp. All were small, young-of-the-year fishes (the largest *E. bipinnulata* individuals reached approximately 80 mm SL) and seemed not to be feeding on the larger invertebrates forming much of the colonizing community. During casual observations of FAD-associated fishes, I observed fish feeding on plankton carried past the FADs, but no physical contact with the FAD or fouling organisms. Ibrahim et al.

(1996) reported that none of the gut contents from FAD-associated fishes included sessile organisms found on their FADs (fish size ranges included specimens 8–14, 15–99, and ≥100 mm SL—the first two size categories are comparable to the fishes in the present study). Larger, piscivorous fishes do feed at least occassionally on smaller fishes associated with floating objects (Gooding and Magnuson, 1967), but published gut content studies are conflicting. Some suggest that piscivorous species that associate with flotsam rely on other sources of food (e.g. Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Brock, 1985), while others suggest that flotsam- (or algae-) associated fishes form an important food resource for these larger piscivorous fishes (Dooley, 1972; Manooch et al., 1984; Coston-Clements et al., 1991). Morgan et al. (1985) noted the occurrence of at least two members of the *Sargassum*-associated invertebrate fauna among the stomach contents of several species of pelagic fishes. From the perspective of flotsam- or FAD-associated fishes, opportunistic predation by piscivores that do not associate with FADs may be more important than predation by other members of the assemblage. Additional gut content data from juvenile and nonpiscivorous fishes are sorely lacking. I address possible explanations for the results of the present study below.

I recorded no significant treatment effect attributable to differences between FADs with artificial fish, FADs deployed with artificial-fish–sized weights, or control FADs. I attribute significant sample date effects to day-to-day changes in constituent individuals and the fluctuating availability of potential recruits. Numbers of *E. bipinnulata* were strikingly constant across treatments and sample dates in this experiment (Table 5, Fig. 8) and in the fouling experiment (Fig. 7) and seemed to indicate an apparently unusual characteristic of this species—individuals remaining associated with a given FAD for multiple days. Although the experiment was intended to distinguish between FADs with prior recruits versus FADs without prior recruits, the lack of a significant treatment effect does not negate the possibility that potential recruits would distinguish between occupied and unoccupied FADs. The painted artificial fish and lead weights clearly lacked many attributes of living fish. However, comparable numbers of recruits found at all treatments suggest that a change in the structural complexity of the FADs did not affect assemblage size or diversity. Although the addition of four small lead weights (artificial fish were painted and oriented differently but were still lead weights) did not appear to increase appreciably the visible surface area of those FADs, the subsequent experiment with live fishes instead of artificial fish had a dramatic effect on recruitment; therefore sizeable changes in the physical size of a FAD may be necessary to yield a response in fish recruitment. The potential roles of structural complexity and orientation of FADs will be informative areas for future research. Past investigations in these areas (e.g. Hunter and Mitchell, 1968; Klima and Wickham, 1971; Wickham et al., 1973) have provided a useful beginning, but more work is needed.

Although sample sizes were small, the presence of prior *Abudefduf troschelii* "recruits" (enriched FADs) had a significant effect on patterns of subsequent recruitment; this effect contrasted sharply with FADs lacking fish at the start of this experiment (nonenriched FADs). For this species, these results point to a social aspect to these aggregations, and sociality may also be involved in the recruitment of other species, particularly the schooling fishes *Caranx* spp., *Polydactylus approximans,* and *Mugil* spp., as suggested for some scombrids (e.g. Dagorn and Fréon, 1999). The addition of fishes below a FAD may increase recruitment rates by rendering the object more visible, although the artificial fish experiment indicated that simply adding fish-size objects beneath a FAD does not affect recruitment. Comparisons between these two experiments are tenuous, however, because the artificial fish experiment employed anchored FADs observed over a period of days, whereas the enriched FAD experiment used drifting FADs observed over a course of hours.

Why do FAD size, the presence of a fouling community, and the actual presence of prior recruits at a FAD each have the effect of increasing the size and, possibly, the diversity of FAD-associated assemblages of juvenile fishes? The simplest explanation is that these factors contribute to the target strength of the object, increasing the visual, olfactory, or auditory stimulus (or some combination) of the floating object. Larger objects should be easier to find, especially if potential recruits rely on vision to explore their environment. Kellison and Sedberry (1998) found that the fishes associated with mid-water floating structures that were tethered to an artificial reef decreased in abundance over time (193 days), and suggested that the loss in buoyancy associated with the development of a fouling community may have reduced the effective size of these floating objects, accounting for fewer associated fishes (see also Hunter and Mitchell, 1968; Rountree, 1989). To account for the positive effects of a fouling community observed in the present study, it seems reasonable to suppose that fouling organisms may be detected by olfactory means; Sweatman (1988) has shown that some larval fishes use olfactory cues for settlement on reefs. Further experiments, for example experiments controlling for FAD size, odor cues, and visibility of the FADs, are needed to determine why some of these factors exhibit these effects.

Future research on the role of flotsam as shelter from predators and as a conveyance to suitable habitat could yield evolutionary explanations for the attraction to floating objects. For these small fishes, such objects likely represent a shelter from predators (Mitchell and Hunter, 1970). Some species do respond to the approach of an observer by positioning themselves so that the FAD is between them and the observer. Particularly during daylight and crepuscular hours when visually-oriented predators are most active, flotsam may offer refuge in a habitat where there is little alternative refuge. During the day, when onshore winds drive drifting objects towards shallow water, flotsam and drift algae, unlike anchored FADs, may also offer a comparatively safe conveyance to more suitable habitat. Thus, there may be adaptive advantages for juvenile reef fishes in associating with floating objects.

Although the juvenile fishes associated with the FADs used in the present study are not of interest to any fishery, the patterns observed from them may be relevant to FADs

deployed commercially to aggregate fish species at various life history stages. FAD size is clearly relevant to those interested in studying potential improvements to FAD design. Carefully controlled studies on the importance of surface area versus volume and the orientation of FAD structures are needed. The role of a fouling community, too, deserves further investigations. Although a fouling community may weigh down streamers (trailing pieces of buoyant material intended to increase the subsurface of area of a FAD), such a community may also improve recruitment and possibly retention of recruits around a FAD. Finally, the importance of the initial recruits to a floating object should be studied further. Enriching a FAD may increase the speed at which additional fishes are recruited. Improved artificial fish may prove more effective than the items used in the present research. FADs are an important tool in a number of artisanal (small-scale fishery based on traditional methods), sport, and commercial fisheries, especially in tropical waters where FAD fisheries particularly target tunas (Scombridae), jacks (Carangidae), and *Coryphaena* spp. (Galea, 1961; Klima and Wickham, 1971; Beets, 1989; Hilborn and Medley, 1989; Friedlander et al., 1994; Higashi, 1994; Hall et al., 1999b). Due largely to the potential for fisheries enhancement, considerable research has been focused on the importance of floating-object characteristics and the numbers of fishes attracted to such objects; however, the results have been difficult to interpret and are often conflicting (Rountree, 1989; Kingsford, 1993; Druce and Kingsford, 1995). Because log sets in tuna purse-seine fisheries (where fishermen target fish associated with drifting logs or FADs) are associated with high levels of bycatch (Hall, 1998; Lennert-Cody and Hall, 2000), the behavior and ecology of flotsam-associated species is in urgent need of study so that a means of reducing bycatch may be devised.

This study made use of FADs floating at the surface; studies by other researchers have employed similar tools or they have used FADs tethered in mid-water. No one has examined the effects of FAD position in relation to the surface, and the implicit assumption appears to be that there is no biologically significant difference. This assumption has not been tested, although comparisons between data from floating structures, whether at the surface, mid-water, or tethered close to the bottom, are common in the literature. I have made comparisons between my data from surface FADs and results from mid-water FADs (e.g. Wickham and Russell, 1974; Rountree, 1990); such comparisons may be misleading and should be interpreted with caution.

The results from the present study indicate that turnover rates at nearshore anchored FADs are high and that undisturbed FAD assemblages may show little difference in these rates from disturbed FADs. Fishes recruiting to these FADs discriminate among potential floating objects, forming larger, more species-rich assemblages around triple-size FADs than around single FADs. FADs possessing a fouling biota also attract larger (though no more diverse) assemblages than do clean FADs. The latter effect was complicated by temporal fluctuations that overlay these treatment effects, resulting in day-to-day changes in the total numbers of fishes in both treatments (Table 4, Fig. 7). Further, the presence of prior recruits in the enrichment

experiment had a strong effect on subsequent recruitment. Thus, the association of juvenile fishes with floating objects is not a haphazard process, and floating-object characteristics play potentially important roles in fish recruitment to these objects. These results suggest that associating with flotsam may be adaptive, rather than an accidental behavior and support Kingsford's hypothesis (Kingsford, 1993) that floating material is an important environmental component in the relationship between environment and some juvenile fishes.

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