

## HABITAT ASSOCIATIONS AND AGGREGATION OF RECRUIT FISHES ON HAWAIIAN CORAL REEFS

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### ABSTRACT

Associations with structural habitat complexity and the aggregation of individuals lessen the risk of predation, and both are commonly observed for recently settled fishes on coral reefs. On reefs fringing Hawaii Island, such recruits of many fishes, particularly two species of surgeonfishes, exhibited strong affinities for branching finger coral (*Porites compressa* Dana, 1846), the most structurally complex coral available in the relatively low-diversity assemblage of Hawaiian reef corals. Recruits of these species also aggregated with conspecific and heterospecific recruits as they associated with this coral. That recruits of reef fishes take refuge in the best available shelter, however, is not a novel observation. More noteworthy is the frequent co-occurrence of recruits with other recruits of the same and other species. Our observations suggest that small juvenile reef fishes aggregate near preferred coral habitat and perhaps also with one another independently of habitat per se, the latter a phenomenon that has been generally overlooked by researchers focusing on evidence for density-dependent negative interactions within juvenile reef fishes. Because interactions between habitat structure and aggregative behaviors have the potential to importantly modify the survivorship of recruits that may influence year-class strength, they merit further study.

The distributions of adult reef fishes, like the adults of most other organisms, are primarily related to the distribution of food and mating opportunities. The distributions of juvenile reef fishes, however, are more proximally related to the distribution of structurally complex habitats and other factors that directly influence survival under intense predation (Shulman, 1985; Hixon, 1991; Caley and St. John, 1996; Nemeth, 1998; Almany and Webster, 2006). Safe havens from predators provided by habitat features have been documented by many studies (e.g., Carr and Hixon, 1995; Beukers and Jones, 1997; Carr et al., 2002; Webster, 2002), and the anti-predator benefits of schools and less structured aggregations of individuals are also clear (Hobson, 1978; Webster and Almany, 2002; Sandin and Pacala, 2005). Surprisingly few studies, however, have described the undoubtedly complex interplay between refuging and group behaviors for organisms in general (Krause and Ruxton, 2002) and for juvenile reef fishes in particular.

Numerous studies have evaluated relations between the distribution, abundance, and diversity of fishes and live coral cover on shallow tropical reefs (reviewed by Wilson et al., 2006), often with an emphasis on relations of recently settled recruit stages (Tolimieri, 1998; Jones et al., 2004). It is generally accepted that structurally complex coral reefs provide biologically important physical structure in the form of shelter holes and habitat for prey including small fishes (Caley and St. John, 1996). In this study, we describe the interrelated sheltering and aggregating behavior of recruits (benthic juveniles < 2 mo old) of fishes commonly encountered on the fringing coral reefs of the Big Island of Hawaii (Hawaii Island) in the Main Hawaiian Islands (MHI), along with implications for reef fishes throughout the archipelago and elsewhere.

## MATERIALS AND METHODS

**STUDY AREA.**—Surveys of fishes and habitats were conducted using SCUBA in 8–13 m depths at three locations spanning 25 km, each within extensive continuous fringing reefs and representative of wave exposures on the leeward coast of northwest Hawaii Island: Point at End-of-the-Road, Puako Beach Drive (Location 1: exposed), Holoholokai Beach Park (Location 2: partially exposed), Mahukona (Location 3: protected). Both recruit fishes and habitat were surveyed during a 19-d period from 23 May to 10 June 2005. Supplemental surveys of recruit-habitat associations were conducted biweekly to monthly at Location 3 through mid-October 2005.

**SURVEY PROTOCOLS.**—The densities of recruits and other small-bodied fishes were estimated using 50-m<sup>2</sup> belt transects (25-m long × 2-m wide) within 1.0–1.5 ha areas at each location. The starting points and bearings of transects were chosen haphazardly following minimal criteria (> 50% consolidated substratum and a constant depth ± 1 m). Eight to ten transects were surveyed per location. Fish were tallied by species or lowest taxon and size (1-cm total length [TL] for individuals ≤ 10 cm TL) encountered as the transect line was laid. Fishes were classified as either recruits (≤ 5 cm TL) or as older (≥ 6 cm TL) juveniles. Two acanthurids—the goldring surgeonfish, *Ctenochaetus strigosus* (Bennett, 1828), endemic to the Hawaiian Islands and Johnston Atoll (Randall and Clements, 2001), and the yellow tang, *Zebrasoma flavescens* (Bennett, 1828), a species broadly distributed throughout the tropical central Pacific—were targeted for special consideration because of their abundance at the time surveys were conducted. Each species settles from the plankton at ~3 cm TL beginning in late May–early June and continuing throughout the summer on leeward Hawaii Island (Walsh, 1987; E. DeMartini, unpubl. data).

To assess coral habitat, the percentage cover of major coral taxa and other predominant substratum types were recorded using 1-m<sup>2</sup> quadrats. The major corals included four taxa ranging in structural complexity from prostrate (lobe coral, *Porites lobata* Dana, 1846 and *Montipora* spp.), to digitate (finger coral, *Porites compressa* Dana, 1846) and discrete (cauliflower coral, *Pocillopora meandrina* Dana, 1846). The two additional major substratum types were coral limestone with short (< 1-cm high) turf algae, and sand. Percentage cover of each of the six substrata was estimated visually; accuracy was evaluated previously by comparing visual estimates with a random-point-contact method (Dethier et al., 1993). Within each quadrat, a rugosity index ratio of conforming-to-straight line distance (Risk, 1972; Andrews and Anderson, 2004) was determined using a 1.25 cm-link chain laid over the substratum.

Three 1-m<sup>2</sup> reference quadrats, positioned randomly along each transect line, and six 1-m<sup>2</sup> target quadrats, centered on recruits of target species haphazardly encountered within 5 m of each transect line, were surveyed for coral cover and rugosity. Prior to the placement of target quadrats, individual recruits were sighted from a distance of 1.5–3 m. Once recruits were sighted, the species, number, and size (cm TL) of fish were recorded, along with the distance from the target individual to the closest substratum type (cm), and the median distance (cm) to other recruits in a “group” (defined as one or more individuals ≤ 10 cm TL of the same or other species present within 10 cm of the target individual). Any aggressive acts also were noted. Target quadrats were then placed over the substratum, centered on the exact point at which the recruit(s) were first sighted; 1-m<sup>2</sup> quadrats were sufficient in area because recruit ambits were typically ≤ 50 cm. Additional data on proximity to substratum type and median distance among aggregated fishes were collected on supplemental dives dedicated to finding individuals of target species both shoreward (to 5-m depth) and seaward (to 16 m) of transected areas at Location 3. The latter dives were necessary to augment the number of recruit sightings. All estimates of distances to substratum and among recruits were made as previously described. Supplemental observations were limited to one site (Location 3) because of limited personnel and easier access.

**STATISTICAL ANALYSIS.**—Standard parametric (Sokal and Rohlf, 1981) and nonparametric (Siegel and Castellan, 1988) tests were used, with choice based on the metric and its case-

specific sampling distribution. Variance heterogeneity was evaluated using Cochran's C test (Underwood, 1997). Except where noted, the variances in densities of fish became homogeneous after log-transformation. Recruit-habitat relations and recruit aggregations were evaluated using several categorical analyses. Contingency, goodness-of-fit, and heterogeneity Chi-square and G-tests (Sokal and Rohlf, 1981) were used, as appropriate, if contrasts lacked a response variable. Logistic regression was used if a response variable was clearly distinguishable among the explanatory variables (Allison, 1999). We assumed that the expected numbers of singleton and grouped recruits followed a Poisson distribution, and we compared their observed frequencies against this expectation. Poisson regression (Allison, 1999; proc GENMOD: SAS, 2000) was used to test whether the number of recruits in a group was predictably related to the proximity of the substratum. Sokal and Rohlf's (1981, p 779) statistic was used for combining probabilities resulting from analogous tests. The Bonferroni correction ( $p_{crit} = 100 \alpha / m \%$ ), where  $m$  = number of comparisons; Manly, 1991) was used to adjust P-values wherever multiple testing was unavoidable. Interaction effects in factorial ANOVAs and G-tests were not listed if non-significant.

## RESULTS

**HABITAT CHARACTERISTICS.**—The percentage cover of each major type of substratum was equivalently estimated visually and by using random-point contacts (matched-pair t-tests, all  $P > 0.24$ ). Error in estimation by eye was considered negligible, ranging from  $< 1\%$ – $3\%$  among substratum types, and substratum cover was estimated visually thereafter. Live coral cover (mean  $\pm$  SE:  $64.3 \pm 0.9\%$  of total cover) was equivalent among locations, with turf-covered, dead coral limestone ( $30.2 \pm 1.6\%$ ) and sand ( $5.5 \pm 0.7\%$ ) constituting the remainder. Lobe coral and other prostrate corals such as *Montipora* spp. dominated (mean =  $44.4 \pm 4.1\%$ ), with finger coral constituting most of the remaining cover (mean =  $18.1 \pm 0.6\%$ ). Prostrate corals and finger coral generally co-occurred in a patchwork mosaic of species at the scale of a  $1\text{-m}^2$  quadrat. Based on 30 reference quadrats at each location, these two coral growth forms co-occurred within 69 of 90 quadrats surveyed.

Types of coral cover differed strongly between reference and target quadrats but only weakly among locations. Cover of finger coral was 50% greater within target quadrats than in reference quadrats (Fig. 1) but there was no detectable a posteriori location effect (Two-way ANOVA—quadrat type:  $F_{1,52} = 5.41$ ,  $P = 0.024$ ; location:  $F_{2,52} = 3.27$ ,  $P \geq 0.05$ ). Cover of prostrate corals (mainly lobe coral) did not differ between quadrat types or among locations. Percentage cover afforded by discrete colonies of cauliflower coral was negligible at the study locations (mean =  $1.8 \pm 0.5$ ), did not differ between quadrat types, but was greater at Location 1 than the other locations (Two-way ANOVA—quadrat type:  $F_{1,52} = 1.36$ ,  $P = 0.25$ ; location:  $F_{2,52} = 6.54$ ,  $P = 0.003$ ).

Substratum rugosity differed among locations and between target and reference quadrats (Two-way ANOVA—quadrat type:  $F_{1,52} = 5.4$ ,  $P = 0.025$ ; location:  $F_{2,52} = 12.8$ ,  $P < 0.001$ ). Rugosity was 24% greater at Locations 2 and 3 and  $\sim 10\%$  greater in target vs reference quadrats (Fig. 1). Rugosity was generally correlated with percentage cover of finger coral for both quadrat types at all locations ( $r = 0.55$ – $0.81$ ,  $n = 8$ – $10$  quadrats per location and quadrat type,  $P = 0.01$ – $0.10$ ;  $\chi^2 = -2 \sum \ln p = 39.7$ ,  $df = 12$ ,  $P < 0.001$ ; Sokal and Rohlf, 1981; Fig. 1). The percentage cover of prostrate and cauliflower corals were unrelated to rugosity.

**RELATIVE ABUNDANCE OF RECRUITS AND OLDER FISHES.**—Goldring surgeonfish (21%) and yellow tang (12%) together accounted for about one-third of 628 older ju-

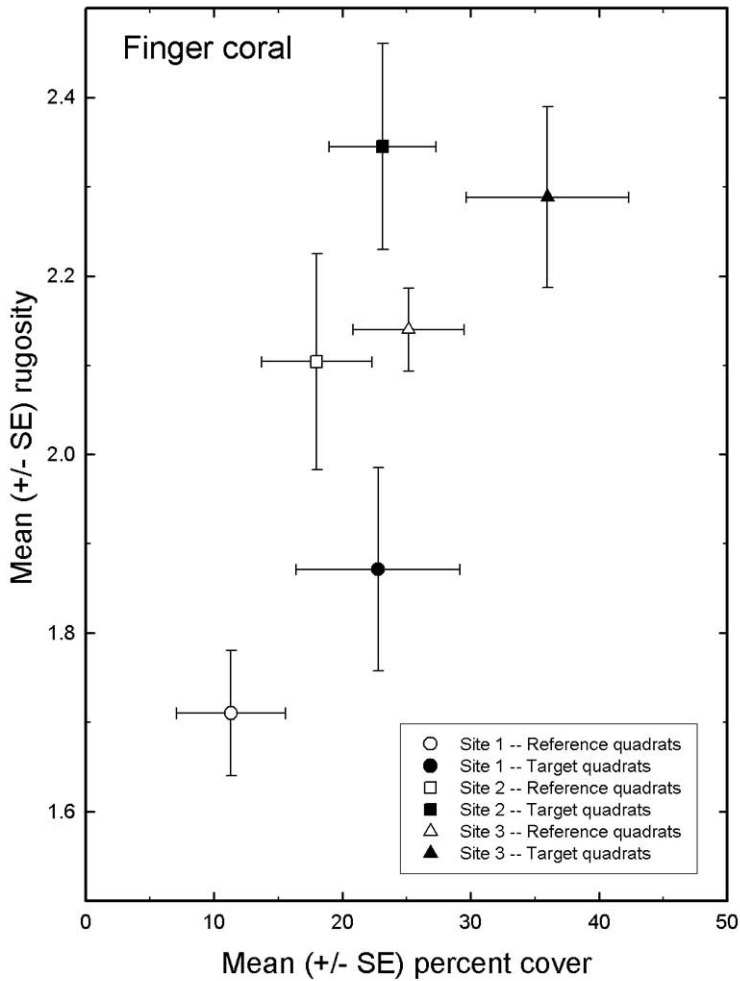


Figure 1. Relationship between percentage cover of finger coral *Porites compressa* and rugosity for each quadrat type at each of the three study locations (distinguished by different symbols as noted on figure). Mean values are based on 8, 10, and 10 transects at Locations 1, 2, and 3, respectively.

venile-adult fish of 33 species encountered on transects. These two species, however, totaled nearly one-half of the 94 recruits of 13 species, including herbivores and micro-carnivores, present on transects (Table 1). Goldrings and yellow tangs together accounted for over 92% of all recruits present in target quadrats during the main study and subsequent surveys. Densities of recruits on transects were low ( $4.0 \pm 0.72$  fish  $50 \text{ m}^{-2}$ ) and indistinguishable among the three locations for either species. The statistical power of these tests, however, was low ( $1-\beta = 0.65$  and  $0.4$ , for goldrings and yellow tangs, respectively), so possible location effects were considered in exploring relations between habitat and recruit aggregation.

RELATION BETWEEN HABITATS AND GROUPS.—Comparisons of reference and target quadrats indicated that recruits of goldring surgeonfish and yellow tang occurred within close proximity of finger coral more frequently than expected based

on the cover of finger coral ( $2 \times 2$  G-test–substrate: maximum likelihood [ML]  $\chi^2 = 95.3$ , 1 df,  $P < 0.0001$ ; Fig. 2). The two species differed, however, in the strength of their relationship with finger coral ( $2 \times 2$  G-test–species  $\times$  substrate: ML  $\chi^2 = 66.2$ , 1 df,  $P < 0.0001$ ). The relationship between recruit yellow tang and finger coral was overwhelming (occurrence with finger coral = 89% of all sightings), whereas that for goldrings was positive but not nearly as strong (55% occurrence with finger coral). Overall electivities for finger coral were  $\sim$  five- and three-fold for the recruits of yellow tangs and goldrings, respectively.

Recruits occurred singly in a majority of encounters but nonetheless grouped with one or more (to as many as five) recruit and older juvenile individuals  $\leq 10$  cm TL of the same and other species of reef fishes in about one-third of all sightings (Table 1, Fig. 3A–D). About three-fourths of the groups involved one or both target species only, and about one-fourth of all cases were mixed-species groups that involved one target species individual and one or more individuals of the other nine species (Table 1), with as many as four non-target species in a single association. Groups were present in 29 of 89 target quadrats and for 125 of 429 sightings of target species during the study. No aggressive interactions were observed among recruits in any group, and recruits typically oriented towards, and often swam together with, one another.

Groups were related to coral habitat type. Observations of target recruits within quadrats and during supplemental sightings indicated that finger coral was the closest substratum in most cases (Fig. 4). More importantly, finger coral was more fre-

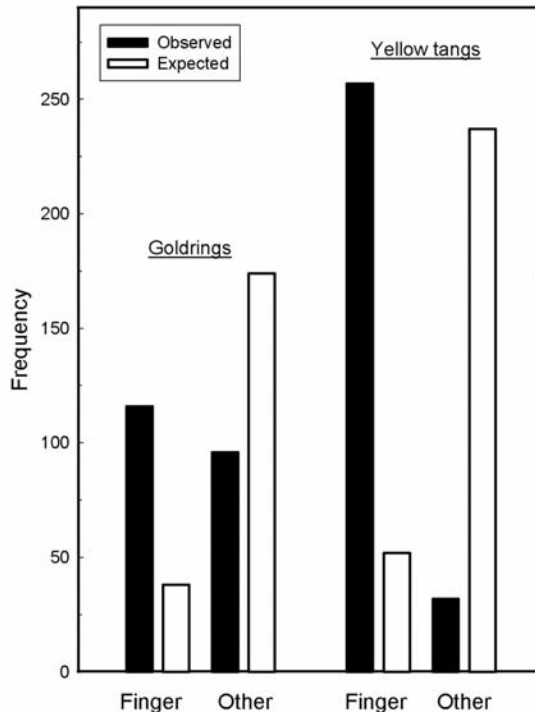


Figure 2. Observed and expected incidence of closest proximity to finger coral (vs other substrates) in target and reference quadrats, respectively, for recruits of goldring surgeonfish *Ctenochaetus strigosus* and yellow tang *Zebrasoma flavescens*. Data for the three study locations were pooled.

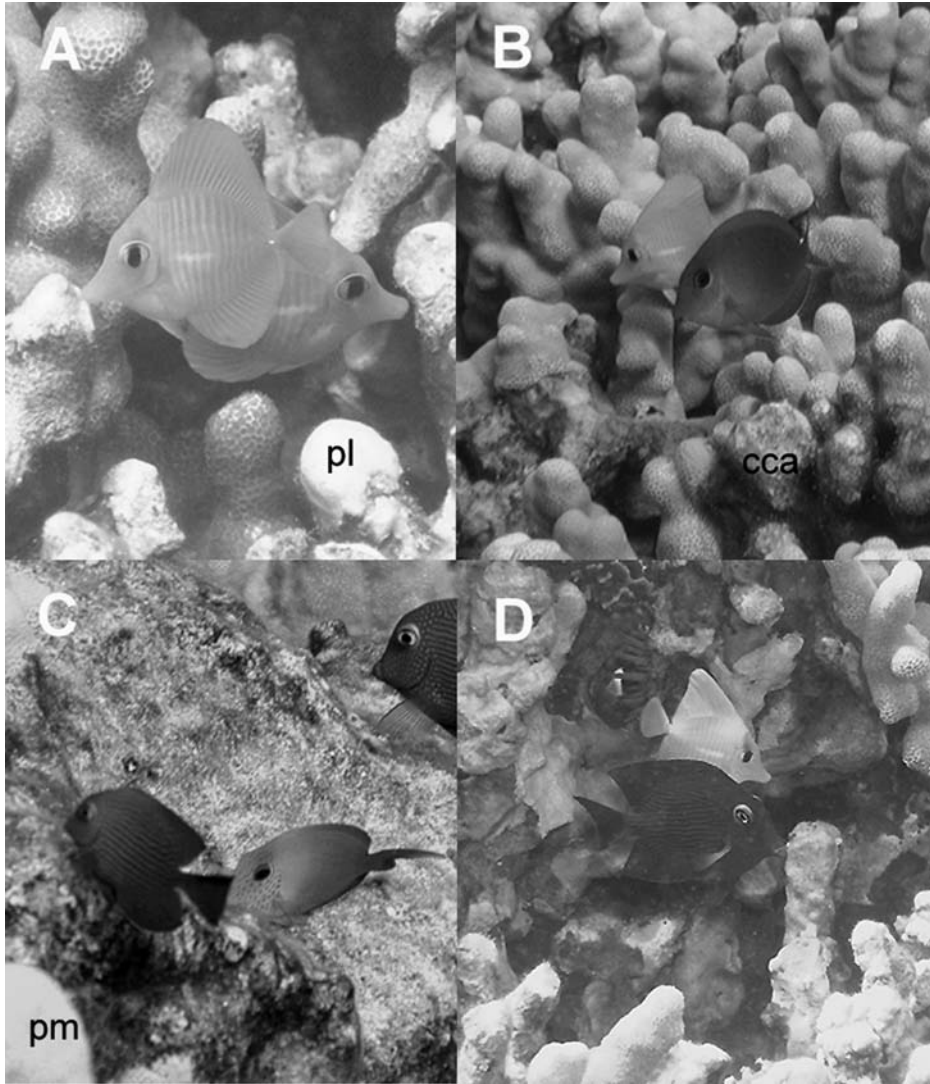


Figure 3. Photographs of various recruit aggregations: (A) two yellow tang *Zebrasoma flavescens* (3 and 4 cm total length), (B) yellow tang (4 cm) with brown surgeonfish *Acanthurus nigrofuscus* (8 cm), (C) goldring surgeonfish *Ctenochaetus strigosus* (4 cm) with brown surgeonfish (6 cm), (D) yellow tang (3 cm) with goldring surgeonfish (5 cm). In (A) finger coral *Porites compressa* (labeled pc) comprises all living coral except the small colony of lobe coral *Porites lobata* (pl) growing on a dead branch of finger coral in the lower right. In (B) all cover is living finger coral except for the crustose coralline algae (cca) growing over dead finger coral at the bottom of photograph. In (C) the substratum is turf algal-covered, weathered limestone except for part of a cauliflower coral *Pocillopora meandrina* colony (pm) in the bottom left. In (D) the substratum behind the pair of fish is cca-covered limestone, with living finger coral at the top and bottom right and along the bottom of the photo.

quently the closest substratum when recruits were aggregated (83%) vs singletons (71%;  $2 \times 2$  contingency  $\chi^2 = 6.55$ ,  $P < 0.02$ ; Fig. 4). The number of groups with  $\geq 2$  recruits occurred more frequently than expected based on the total numbers of recruits sighted and an assumed Poisson distribution of the numbers expected closest to finger coral vs other substrata (goodness of fit Chi-square tests; all  $P < 0.0001$ ). The

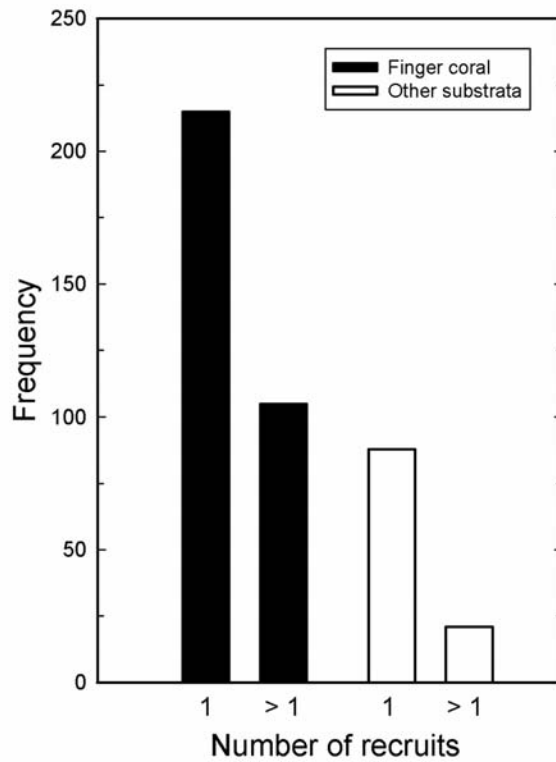


Figure 4. Frequency occurrence of finger coral vs other substrata as the substratum closest to recruits (all species and locations pooled) for cases in which recruits occurred singly or in groups of > 1 fish.

departure from random expectations increased for progressively larger groups of 2, 3, and  $\geq 4$  recruits (heterogeneity  $\chi^2 = 22.8$ ; 2 df;  $P < 0.0001$ ; Fig. 5). The occurrence of a group was 128% more likely than a single recruit if finger coral was the closest substratum (logistic regression;  $\ln(p/1 - p) = -1.72 + 0.826 \cdot \text{finger coral}$ ; odds ratio = 2.283, 95% C.I. = 1.217–4.284;  $P = 0.01$ ). The number of recruits present in a group was a positive function of whether or not finger coral was the closest substratum (Poisson regression corrected for overdispersion;  $P = 0.013$ ; Fig. 5).

We also observed that groups and type of substratum were related to the distances of recruits to the closest substratum and to each other. Target recruits occurred on average about 3-cm (mean = 3, median = 2, range = 1–10 cm) from the closest substratum when first observed, and distance to substratum was influenced by type of substratum. Distance from fish to the substratum was closer when finger coral was the closest substratum but was unrelated to location (Two-way ANOVA, substratum:  $F_{1,484} = 6.87$ ,  $P < 0.01$ ; location:  $F_{2,484} = 0.34$ ,  $P = 0.71$ ).

Target recruits averaged about 6 cm apart from others in groups (mean = 7, median = 5, range = 3–10 cm). Distance to the substratum relative to the distance separating recruits also was dependent on the type of substratum (ANCOVA—distance to other recruits  $\times$  substratum type:  $F_{1,128} = 4.71$ ,  $P = 0.03$ ). The distance to other recruits in a group was less at closer distances to the substratum when finger coral was the closest substratum ( $r = 0.35$ ,  $n = 85$  target sightings,  $P < 0.001$ ) but was unrelated when the closest substratum was not finger coral ( $r = -0.14$ ,  $n = 17$  sightings,  $P = 0.60$ ; Fig. 6).

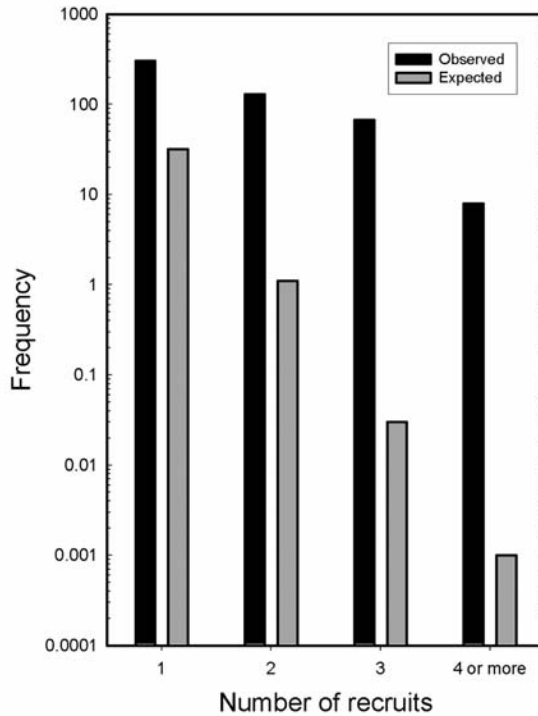


Figure 5. Observed incidence of multiple (2, 3, and  $\geq 4$ ) recruits grouped with one another in target quadrats and supplemental fish sightings vs expected frequencies of recruits distributed among finger coral and other substrata in a Poisson (random) distribution.

## DISCUSSION

**RECRUIT-HABITAT RELATIONSHIPS.**—Recruits of the two target species were strongly associated with finger coral habitat. The observed association of recruits with finger coral might reflect active habitat selection at settlement or the passive result of poorer survival of recruits associated with other substrata. Of course, the relative importance of habitat selection and post-settlement differential survival should be distinguished whenever possible to understand the processes responsible for these patterns.

In our study, the goal was to determine habitat associations of post-settlement recruits only. The apparently obligate relationship between juvenile yellow tang and finger coral has been known for many years, but has only recently been documented (Tissot et al., 2004). Young-of-the-year (YOY) yellow tang both shelter within the branches of finger coral and browse algae from the dead basal surface, undoubtedly facilitated by the apical growth of this coral species (Hobson et al., 1995). At least for yellow tang, finger coral appears to provide an important feeding as well as sheltering substratum. Our results further reinforce prior findings that finger coral also provides key recruitment habitat for goldring surgeonfish and several other species on the leeward coast of Hawaii Island (Tissot et al., 2004). A prior study (DeMartini, 2004) suggests that this might also be true for young-of-year juveniles of many

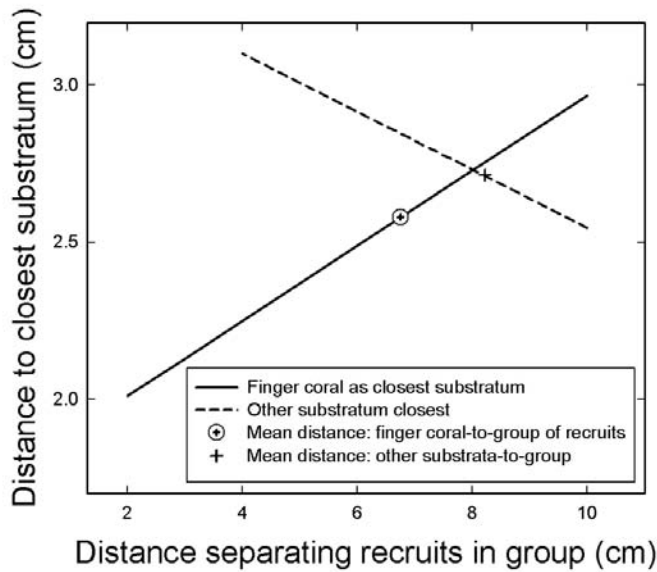


Figure 6. ANCOVA results showing relations between inter-individual distance within groups of recruits and distance to closest substratum when the latter was finger coral vs other substrata. The regression (indicated by solid line) for finger coral was significant ( $P < 0.001$ ) but that for other substrata (dashed trend line) was not ( $P = 0.60$ ).

species on patch reefs within atoll lagoons in the Northwestern Hawaiian Islands (NWHI) and likely elsewhere on wave-protected reefs throughout the archipelago.

Our observations illustrate a key characteristic of finger coral as habitat for recruit fishes. Although total coral cover did not differ among the three study locations, functional shelter as cover provided by finger coral was seemingly greater in the more rugose, complex stands of finger coral present at more wave-protected Locations 2 and 3. Finger coral is relatively sensitive to wave disturbance and more developed stands occur in more wave-sheltered environments (Grigg, 1983). Rugosity differed more strongly among locations than the percentage cover of finger coral, and more complex interstices (measured as greater rugosity) in the more developed stands of this coral may provide higher quality habitat for recruits. The suggestively higher densities of recruits in the most rugose stands of finger coral at Location 3 are consistent with this interpretation. The effects of habitat structure and other possible influences of recruit abundance that are confounded with it in wave-sheltered environments, including rates of settler delivery by currents and the abundance and availability of the prey of recruits, can be further decoupled by field experimentation. The strong attraction of recruits and other small-bodied fishes for branching coral habitats has been widely documented (e.g., Luckhurst and Luckhurst, 1978; Kawasaki et al., 2003), but so too has their affinity for wave-sheltered environments, for a variety of possible reasons (Adams and Ebersole, 2002).

Our results also underscore the importance of interactions between habitat association and group behavior. One possible explanation for the shorter distances to the substratum and between individuals when recruits were grouped near finger coral is simultaneous shelter-seeking behavior. Another, non-mutually exclusive possibility is that the risk of predation for surgeonfishes and other algivores when aggregated

is lowered such that more time may be spent grazing algae (Overholtzer and Motta, 2000) from the dead basal surfaces of finger coral. The inverse relation between vigilance and feeding rates has been described elsewhere for associations of juvenile and other small-bodied fishes on coral reefs (Wolf, 1987; Sakai and Kohda, 1995).

**AGGREGATION OF JUVENILE FISHES.**—Recruits showed a strong affinity for one another as well as finger coral. Our analyses documented that groups of greater numbers of recruit individuals, including heterospecific herbivores and microcarnivores, occurred progressively more frequently than expected based on a random distribution, suggesting either that recruits were positively attracted to, and associating with, one another or that they were aggregating at especially preferred, high quality sites within finger coral habitat. Properly scaled field experiments manipulating and monitoring recruits and coral habitat would be necessary to discriminate between these two possibilities.

Aggregating behaviors by juvenile fish, although sometimes implicitly recognized (Almany and Webster, 2006), have been conspicuously understudied despite their apparently widespread occurrence on both temperate and tropical reefs. In particular, the aggregation of recently settled reef fishes has been little studied, with the exception of recruitment facilitation or inhibition in which the number of resident recruits is positively or negatively associated with settlement (Sweatman, 1985; Booth, 1992; reviewed by Hixon and Webster, 2002). Most studies of the interactions between recruits and conspecifics have focused on the usually negative interactions between recruits and older juveniles or adults (Shulman et al., 1983; Sweatman, 1985; Jones, 1987; Simpson, 1990). Only a few cases demonstrating post-settlement positive effects resulting from associations of juvenile and other small-bodied reef fishes have been described (Booth and Beretta, 1994; Booth, 1995a,b, 2004; Overholtzer and Motta, 2000; Webster and Almany, 2002; Schmitt and Holbrook, 2003).

Aggregations obviously can range greatly in scale from the schooling of many thousands of individuals at one extreme to simple pairing at the other. Both of the target species, like the other species of associated recruits observed in the present study, were not observed schooling per se (i.e., performing synchronized and polarized swimming; Pitcher, 1986), but juveniles of other benthic fishes do school on Hawaiian reefs. For example, several parrotfishes (*Calotomus* spp., *Chlorurus* spp., *Scarus* spp.), often travel and feed together in schools of hundreds of individuals (E. DeMartini, unpubl. data). Refuge in aggregations numbering many tens of individuals in damselfishes (Booth, 1992, 1995b) to relatively loose associations of a few recruits of other species of surgeonfishes, wrasses, and butterflyfishes (this study) also occurs. Because the importance of shelter and specific associations with habitat varies among species, the strength of the interaction between habitat and aggregation by recruits likely does too.

Aggregating by recruits might be especially prevalent on Hawaiian reefs because of the relatively low densities and extremely patchy spatial and temporal distributions of recruits that result from the extreme isolation of Hawaii (Hourigan and Reese, 1987). In a study specifically designed to monitor densities of juveniles at French Frigate Shoals and Midway Atoll in the NWHI over nearly a decade, the YOY of all primary taxa consistently represented < 20% of the total number of individual fish tallied (DeMartini, 2004). Such values appear strikingly lower than encountered elsewhere (e.g., McFarland et al., 1985). Perhaps the reduced probabilities of locating conspecific individuals at low densities predispose recruits to associate with het-

erospecifics to greater extents in Hawaii. We are unaware, however, of any critical comparisons of the relative incidence of group formation and multi-species association of recruit fishes between reefs and regions that differ in the densities of recruits, and such studies are necessary to determine whether density and the prevalence of mixed-species groups may be related.

The potentially complex, density-dependent interactions among newly settled reef fish remain to be fully explored for recruits at smaller and larger spatial scales. In general, greater densities of fish result in greater per capita mortality of recruits as a result of predation and competition (reviewed by Hixon and Webster, 2002), although this might be less true for densities elevated within mixed-species groups. A recent study (Sandin and Pacala, 2005) indicates that greater mortality at greater density may not always be the case on continuous reef tracts such as those in the present study, although negative effects have been described both for continuous and patch reefs (Carr et al., 2002). The proximate and ultimate factors favoring the formation of groups of recruits seem obvious. However, specific evidence for the negative effects of group associations in the form of density-dependent mortality, especially density-dependent mortality that might involve heterospecifics, is generally lacking (but see Shima, 2001) and deserves further attention. The relations between habitat quality, recruitment, and cryptic density dependence (Shima and Osenberg, 2003) are worth further exploration.

The distribution and abundance of key refuge habitats such as finger coral also need to be evaluated along the entire continuum of spatial scales. The function and importance of habitats are directly influenced by spatial scale, and the strength of recruit-habitat relations is strongly influenced by scale (Tolimieri, 1995; Caselle and Warner, 1996; Andrews and Anderson, 2004). Variation in year-class strength, whether from variation in larval supply or a result of density-dependent post-settlement interactions (Hixon and Webster, 2002), affects the densities of recruits at small spatial scales. In turn, density must modify the relative importance of habitat structure and aggregating behavior in influencing individual survivorship. Descriptive contrasts among reef fish recruit-habitat relationships, densities of recruits, and year-class strength between the near-pristine predator-rich and coral-poor NWHI and the predator-depauperate but coral-rich MHI (Friedlander and DeMartini, 2002) are of potentially great importance. Multi-factorial field manipulations of the densities of recruits and the type and quantity of refuge habitats would be necessary to evaluate the relative importance of habitat and behavior on per capita survivorship (Sale et al., 2005), the persistence and occurrence of recruits in groups (Lecchini et al., 2007), and in this case, the degree to which aggregating recruits are attracted to one another vs mutually orienting to the same highly preferred sites.

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