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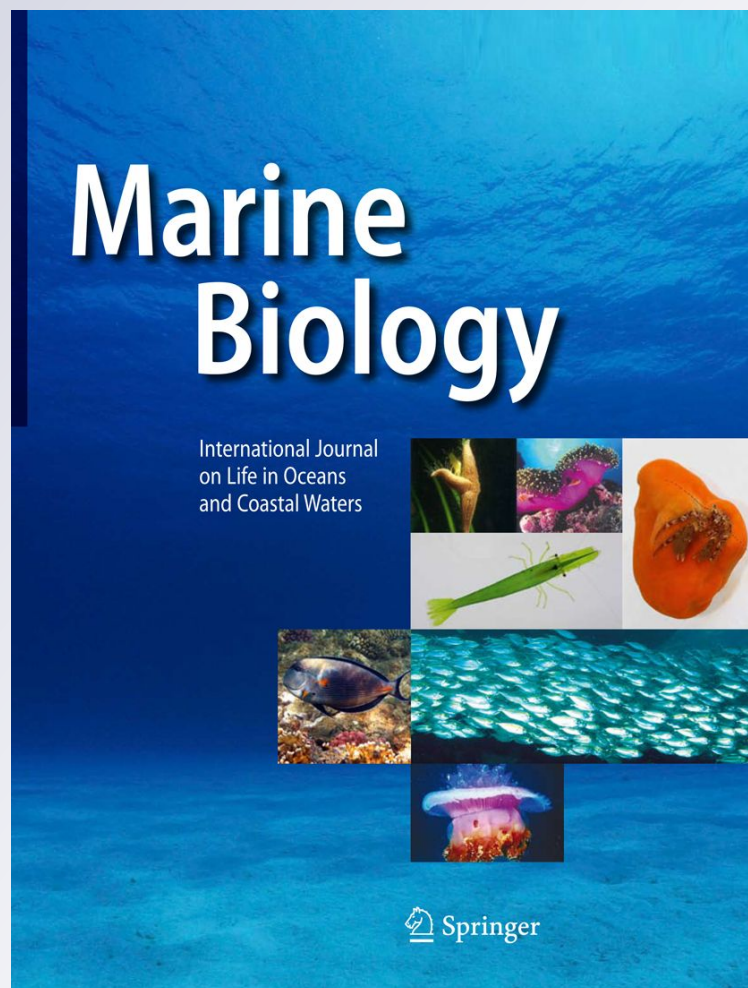
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Predator biomass, prey density, and species composition effects on group size in recruit coral reef fishes

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Abstract Group incidence and size are described for recruit parrotfishes, wrasses, and damselfishes on Hawaiian reefs over 3 years (2006–2008) at sites spanning the archipelago (20–28°N, 155–177°W). Coral-poor and coral-rich areas were surveyed at sites with both low (Hawaii Island) and high (Midway Atoll) predator densities, facilitating examination of relations among predator and recruit densities, habitat, and group metrics. Predator and recruit densities varied spatially and temporally, with a sixfold range in total recruit densities among years. Group (≥ 2 recruits) metrics varied with time and tracked predator and

recruit densities and the proportion of schooling species. Groups often included heterospecifics whose proportion increased with group size. A non-saturating relationship between group size and recruit density suggests that the anti-predator benefits of aggregation exceeded competitive costs. Grouping behavior may have overarching importance for recruit survival—even at high recruit densities—and merits further study on Hawaiian reefs and elsewhere.

Introduction

Habitat selection by fishes on tropical coral reefs is related to the availability of coral and other shelter resources that provide safe havens from predation (reviewed by Wilson et al. 2006). Predator density also importantly influences the density and distribution of prey fishes (Overholtzer-McLeod 2004 and references therein). This is especially true for recruit (recently settled) reef fishes (Garpe and Ohman 2003, 2007) that are at greater risk of predation because of their smaller and more vulnerable body sizes (Munday and Jones 1998) and inexperience in avoiding reef-based predators (Almany and Webster 2006). The anti-predator benefits of schools and aggregations of prey individuals are certainly recognized (Hobson 1978; Webster and Almany 2002; Sandin and Pacala 2005). However, the relative competitive costs in individual growth versus anti-predation benefits in survival of grouping remain unresolved for recruit reef fishes (Booth 2004; White and Warner 2007a, b) and for organisms in general (Hamner and Parrish 1997; Krause and Ruxton 2002). If the formation and maintenance of groups by an organism is density dependent (Fretwell and Lucas 1970; Shepherd and Litvak 2004), the incidence of groups of two or more individuals should, by chance

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alone, increase with density. The average number of individuals present in groups, however, should reach an asymptote at which the costs just offset the benefits of aggregation (Krause and Ruxton 2002), despite the potential advantage for solitary prey to avoid predator detection or predator-switching behavior and a Type III functional response (Murdoch 1977).

Descriptions of fine-scale spatial distributions and aggregative behaviors are generally lacking for juvenile fishes on coral reefs. Habitat relations and aggregative behaviors have been described for recruit surgeonfishes (Acanthuridae) on fringing reefs of leeward Hawaii Island (DeMartini and Anderson 2007) and for the older juveniles and adults of Hawaiian reef fishes elsewhere in the main Hawaiian Islands (MHI) (Friedlander and Parrish 1998; Friedlander et al. 2003). Here, we describe (1) the incidence and size (number of individuals) of groups (of two or more within 10 cm of one another and orienting together) formed by juvenile wrasses (Labridae), parrotfishes (Scaridae), and damselfishes (Pomacentridae), and (2) the relative influence of predator density, recruit density, and recruit species composition on group metrics at sites bracketing the Hawaiian Archipelago over three successive years.

Methods

Study areas

Carbonate coral rock and rubble platforms are prevalent on wave-sheltered shores landward of fringing reefs in the MHI and on back reefs at low island atolls in the Northwestern Hawaiian Islands (NWHI). Surveys of the fishes of these habitats were conducted using SCUBA and by snorkeling in 1–3-m depths at two sites each at one island and one atoll: (1) on the wave-protected leeward coast of Hawaii Island in the MHI and (2) on the sheltered back reef at Midway Atoll, 1,750 km up-chain of Hawaii Island, at the extreme opposite end of the archipelago in the NWHI. The fundamental basis for choosing these two locations is their strikingly different densities of predators on recruit reef fishes (Friedlander and DeMartini 2002). Predator-rich Midway Atoll has abundant predatory reef fishes typical of the northernmost atolls of the NWHI (DeMartini and Friedlander 2004), whereas predator-poor reef fish populations on shallow reefs at Hawaii Island, as at other human-populated MHI, are depressed by overfishing (Friedlander and DeMartini 2002; Williams et al. 2008). In selecting Midway Atoll and Hawaii Island, we reasonably assumed that other potential, temporally and spatially varying oceanographic factors (e.g., larval transport and levels of planktonic productivity: Polovina and Howell 2005) had

little effect on the group metrics of benthic recruits compared to the post-settlement effects of predator and recruit densities and the composition of recruits.

The two sites surveyed on the fringing reef of Hawaii Island are about 10-km apart and differ primarily in wave exposure and related substratum characteristics—“coral-rich” and “coral-poor” at the more and less wave-sheltered site, respectively. The two sites surveyed on the back reef at Midway Atoll are separated by about 5 km and similarly differ in wave exposure and coral cover (DeMartini et al. 2010). Each of the four sites are rectangular plots, with dimensions of about 100 m × 1,000–1,500 m (10–15 ha), nested within much larger tracts of continuous reef. All sites were surveyed during June–July periods of 2006 and 2007 and during late May–early August 2008. Our survey design thus allowed us to explicitly evaluate the combined influences of predator and recruit densities on the incidence and size of groups of recruits both spatially and temporally.

Survey protocols

The densities of recruits and fish predators were estimated using 50-m-long transects distributed throughout the sites. The starting points and bearings of transects were chosen haphazardly each year following minimal criteria (>50% consolidated substratum and a constant depth ±1 m). Predators were tallied within a 4-m-wide strip (200 m² area) as the transect line was initially laid; after a several-minute pause, recruit fishes were tallied within a 2-m-wide strip (100 m² area) on a return swim back to the starting point. The 12–20 transects conducted at each site in each year totaled about 1,200–2,000 m² for recruits and 2,400–4,000 m² for predators; thus, the areal extents of transects were small relative to the total areas of the reef plots in which they were situated. We, therefore, were unlikely to encounter the same individuals of older-stage fish in subsequent years. Our intention was to survey over a broad array of varying predator biomass, recruit density, and recruit species composition (at two extremes in coral habitat quality) to describe the influences of these variables on group metrics. The testing of site and year effects per se on predator biomass and recruit density was not our primary goal; had it been so, we would have surveyed a larger number of sites distributed throughout the archipelago.

Fish were tallied by species or lowest taxon (Randall 2007) and body size (cm total length, TL). Predators (≥10 cm) and recruits (≤5 cm) were recorded in 5- and 1-cm size classes, respectively. Recruits were later classified as either a “schooling” species or not (Table 1) based on whether their respective adults commonly occur in social groups. Although such a match in sociality between recruits and adults would be inaccurate for reef fishes in general, it is appropriate for the species whose recruits

were observed in this study (E. DeMartini, unpublished data). Species of recruits were also classified as preferring either rugose corals or other substrata, including non-rugose corals (see DeMartini et al. 2010). The predators of recruit Hawaiian reef fishes are best characterized by reef-resident species, including one species (the saddle wrasse *Thalassoma duperrey*) that concurrently settles to the study reefs. We considered all reef-resident (i.e., not coastal pelagic) species of reef fishes 10–50 cm TL as predators if they were either known (e.g., see Parrish et al. 1986) or morphologically capable of preying on 1–5-cm fish (DeMartini et al. 2009). Twelve, 19–20, and 18–20 transects were surveyed for predators and recruits at sites in 2006, 2007, and 2008, respectively. Recruits were also surveyed on 19–20 transects at each of the two Hawaii Island sites in May–June 2009 and again in May–July 2010 to provide a longer-term perspective of natural variation in recruit densities at this location.

The percentage cover of coral and other major substratum types was estimated along the transect lines. Six major substratum categories were distinguished (dead coral limestone, coral rubble, macroalgae, two types of living coral, and sand; DeMartini et al. 2010). Live corals were classified into two functional types—rugose (digitate-branched, discrete) and non-rugose (prostrate, encrusting)—that differ importantly as recruitment habitat among fish

species in Hawaii (DeMartini et al. 2010). Percentage cover of each of the six substrata was estimated visually within each quadrat (DeMartini and Anderson 2007).

Habitat availability was assessed using reference quadrats: five to ten 1-m² quadrats positioned randomly along each transect line were surveyed for benthic cover (DeMartini and Anderson 2007). Habitat use was based on the proximity of recruits to benthic substrata, with proximity to substrata noted for a haphazard subset of the recruits encountered on transects. Recruits were sighted from a distance of 1.5–3 m; when first sighted, the species, number, and body length of that recruit and any other recruits present with it in a “group” (defined as two or more recruits of the same or different species within 10 cm of the focal recruit and orienting together) were recorded; encounters also included sightings of single recruits. The type of benthic substratum nearest to the recruit or group of recruits was noted.

Statistical analysis

Predator lengths were converted to biomass using species-specific allometric length–weight relationships derived from specimens collected in the Hawaiian Archipelago (Friedlander and DeMartini 2002). The product of individual weights and numerical densities was used to

Table 1 Alphabetical list of major taxa ($\geq 1\%$ of total) of recruit reef fishes by species name

Scientific name	Common name	Preference	Sociality	Abundance range (%)
<i>Abudefduf vaiigiensis</i> and <i>A. abdominalis</i>	Indo-Pacific and Hawaiian sergeant major damselfishes	No	Schooling	0–24.0
<i>Chromis ovalis</i>	Oval chromis damselfish	No	Schooling	0–3.3
<i>Chlorurus perspicillatus</i>	Spectacled parrotfish	Yes	Schooling	0–11.7
<i>Chlorurus spilurus</i>	Pacific bullethead parrotfish	Yes	Schooling	0–49.5
<i>Chromis vanderbilti</i>	Blackfin chromis damselfish	No	Schooling	0–20.5
<i>Coris venusta</i>	Elegant coris wrasse	No	Non-schooling	0–9.4
<i>Dascyllus albisella</i>	Hawaiian dascyllus (domino) damselfish	Yes	Schooling	0–10.4
<i>Gomphosus varius</i>	Bird wrasse	Yes	Non-schooling	0–5.8
<i>Halichoeres ornatus</i>	Ornate wrasse	No	Non-schooling	0–2.9
<i>Macropharyngodon geoffroy</i>	Snubnose wrasse	No	Non-schooling	0–6.6
<i>Plectroglyphidodon imparipennis</i>	Bright-eye damselfish	No	Non-schooling	0–3.5
<i>Scarus dubius</i>	Regal parrotfish	Yes	Schooling	0–11.8
<i>Scarus psittacus</i>	Palenose parrotfish	Yes	Schooling	0–45.9
<i>Stethojulis balteata</i>	Belted wrasse	No	Non-schooling	4.8–71.5
<i>Stegastes marginatus</i>	Hawaiian Gregory damselfish	No	Non-schooling	0–8.5
<i>Thalassoma duperrey</i>	Saddle wrasse	Yes	Non-schooling	1.9–42.8
All major species as percentage of total recruits				97.8

Habitat preference for rugose corals (yes, no) based on resource selection function (Manly et al. 2002; see DeMartini et al. 2010). Sociality (schooling, non-schooling) of recruits of each species is also noted. Abundance range represents the varying proportions that the species contributed to total recruit counts among the 12 site-years (i.e., at each of the four sites in each of the 3 years). Endemic species (Randall 2007; Randall and Rocha 2009) are noted in bold

estimate biomass by species. Comparisons of substratum cover and fish densities used standard parametric and nonparametric univariate tests, with choice based on the metric and its case-specific sampling distribution. Variance heterogeneity was evaluated using Cochran's C test (Underwood 1997). Log-transformed data were used in all parametric analyses of densities; if the variances of estimates still differed greatly following log transformation, the significance level of the test was specified more conservatively (Underwood 1997) at $P = 0.001$. Substratum percentage cover estimates were arcsine square-root transformed prior to analyses. The Bonferroni correction ($p_{\text{crit}} = 100 \alpha/m\%$), where m = number of comparisons (Manly 1991) was used to adjust P values wherever multiple testing was done. Interaction effects in factorial ANOVAs were not considered if non-significant.

Our primary means of analysis was multiple regression, although we first used ANOVA to explore the effects of year and site (two sites within each location) on group size (number of individuals in group) and on each of our explanatory variables using a fixed 2-way nested design (Proc GLM; SAS Institute Inc. 2006). We conducted preliminary ANOVAs because the likely complex relations among factors for potential use as explanatory variables in multiple regressions should first be evaluated temporally and spatially. In our study, the effects of time (year) and space (location, site-within-location) on fish densities and habitat composition facilitate interpretation of the influences of the explanatory variables that were used in our multiple regressions describing group metrics. Results of the preliminary ANOVAs are provided in the electronic supplementary material.

The explanatory variables were predator biomass density, total recruit numerical density, the proportions of individuals that were schooling species and that preferred rugose corals within recruit encounters, and the proportion of heterospecific groups (i.e., the fraction of groups containing individuals of more than one species). Predator biomass and recruit density arguably represent the two most important factors (predation and competition) influencing the distribution of recruits in groups. The other variables were chosen a priori as likely to explain most of the remaining variation in the numbers of individuals present in groups. The variable proportion schooling, for example, was appropriate because propensity to aggregate clearly influences group formation, species differ in their propensity to aggregate (Table 1), and because the relative contribution of species varied greatly among the survey sites and over time (Table 1).

Temporal and spatial patterns of group incidence were first evaluated using G tests on frequencies. Because of the likely positive correlations among many explanatory variables, we then explored the use of residual/sequential

regression to generate and evaluate variables that avoided multicollinearity (Graham 2003). We first replaced the variable predator biomass with residuals derived from regressing it on the correlated variable recruit density. Because both predator biomass and its residuals were correlated with the variable proportion schooling, we next derived the residuals of the predator biomass residuals regressed on the proportion of schooling recruits—the latter being the regressor with greatest influence on group size (Graham 2003; see “Results”). Two other explanatory variables (proportion of rugose coral-preferring recruits, proportion of heterospecific groups) also were cross-correlated with the proportion schooling and with each other; these were regressed against proportion schooling to derive the remaining residuals that were used in all subsequent analyses. Residuals were examined for trends; all of those used lacked significant trend when regressed against the other explanatory variables. Finally, we pooled transects across years and locations and used stepwise multiple, logistic and least-squares regression to evaluate the relative importance of the potential predictor variables. Both forward selection and backward deletion were evaluated at $P = 0.05$ using stepwise multiple regression. The final stepwise selection model was checked against possible alternative models generated using backward selection, Mallows' (C_p) selection, and maximum R^2 improvement selection (SAS Institute Inc. 2006). Evaluation of the final regression model was based on Mallows' C_p and Akaike's Information Criterion (AIC) to ensure that the final model explained the most variance with the fewest variables. Tolerance and variance inflation factors (VIF: unacceptably large if >10 ; Der and Everitt 2009) were examined to complete our regression diagnostics. Maximum likelihood (ML) chi-square statistics were used to evaluate the complementary topic of proportional representation of taxa within groups. Spearman's rank correlation (r_s) was used to compare group size with recruit density with the assumption of linearity relaxed.

Results

Densities of predators and prey

The numerical and biomass densities of total resident predators ranged from two- to fourfold greater at unfished Midway Atoll versus fished Hawaii Island (Supplement 1, Fig. S1). Differences were especially large for predator biomass because of the larger average body sizes of predators at Midway. Hawaiian endemic species of wrasses, parrotfishes, and damselfishes constituted most recruits (Table 1). Mean densities of total recruits (all species pooled) varied over sixfold among the three years studied

(Supplement 2, Fig. S2). At Hawaii Island, estimated densities of total recruits in 2009 and 2010 were less than those in 2007–2008 (Supplement 2).

Collinear relations among densities and other variables

Because the percentage cover of total and rugose live coral did not differ temporally despite spatial variation (Anderson et al., in prep.), habitat availability at each site was constant during 2006–2008, which allowed us to pool data over years at each site when evaluating the effects of other variables on grouping behavior. Our experimental design and opportunity each contributed to surveys that intercepted a broad range of habitat availability, predator density, and recruit density. Sufficient variation in these factors facilitated multiple regression analyses of their effects on the group metrics of recruits.

Group size was strongly correlated with each of the five potential explanatory variables (Table 2), even though predator and recruit densities differed unpredictably among years and sites (Supplements 1, 2). Group size was positively correlated with recruit density but negatively correlated with predator biomass (Table 2). The biomass density of total resident predators (including saddle wrasse) was uncorrelated with total recruit density (Table 2); predator biomass density and recruit numerical density remained uncorrelated ($r = -0.05$, $P = 0.42$) if the saddle wrasse was excluded from estimates of predator biomass. All subsequent analyses used the residuals of total predator biomass density (including saddle wrasse) regressed on total recruit density as our proxy of predation risk to preserve the potentially important contribution to predation by larger saddle wrasse. Interestingly, total recruit density was not correlated with any of the other explanatory variables. Of the latter, the three recruit-composition variables (proportions of schooling, heterospecific, and rugose coral-preferring recruits) varied without pattern among sites and years (Supplement 3, Fig. S3; Supplement 4, Fig. S4).

Before residuals were derived for use in multiple regressions on group size, the original data of all the three of the recruit-composition variables were positively correlated with one another (Supplement 5, Fig. S5m–o), although generally less so than each was with group size (Table 2). After the residuals of predator biomass and the proportion heterospecific and proportion rugose coral-preferring recruit variables were regressed on the proportion of schooling recruits, most resulting residuals became completely uncorrelated. The lone exceptions were the proportion rugose coral-preferring and proportion heterospecific variables, which remained weakly related ($r = 0.14$, $P = 0.04$).

The degree of collinearity among all potential regressors did not invalidate inferences based on stepwise multiple regression, because the appropriate residuals were used. As a result, the tolerance and VIF of all predictor variables were acceptably low at <1.0 and <1.02 , respectively.

Group occurrence and number

Spatial and temporal patterns of group size were most efficiently evaluated based on the relative incidence of singletons versus groups of 2 and ≥ 3 individuals; using this classification, group size differed among years and sites within locations (two-way G test: both $P < 0.0001$). Larger groups were prevalent at the Hawaii Island coral-rich site, especially in later years of greater recruit density, and singletons were generally prevalent in all surveys at Midway Atoll (Fig. 1). Group size ranged upwards to an observed maximum of 50 individuals of as many as six different species. The median number of recruits present per group was 1 in most years and at most sites except in 2006 at Hawaii Island (coral-poor: 1.5, coral-rich: 2.25) and in 2007 at Hawaii Island (coral-rich site: 4.0; Fig. 1). Group size modes were 1 for all sites in all years except the Hawaii Island coral-rich site in 2007, for which the mode was 2 (Fig. 1). Mean group sizes ranged from a minimum of 1.5 individuals at both Midway Atoll sites in 2006 to a

Table 2 Pearson product-moment correlation coefficients (r) of pairwise relations among mean group size and five explanatory variables ($n = 203$ transects across sites and years)

	Predator biomass ^a	Recruit density	Proportion schooling	Proportion heterospecific	Proportion rugose coral-preferring
Mean group size	-0.34	+0.35	+0.70	+0.59	+0.51
Predator biomass ^a	–	-0.17	-0.23	-0.24	-0.31
Recruit density		–	+0.13	+0.09	-0.04
Proportion schooling			–	+0.42	+0.63
Proportion heterospecific				–	+0.39

Correlations significant at $P < 0.001$ are noted in bold

^a Biomass density of total resident predators (all species including saddle wrasse)

maximum of almost 7 individuals at the Hawaii Island coral-rich site in 2007, and differed both temporally (year: $F_{(2,195)} = 6.5, P = 0.002$) and spatially (site-within-location: $F_{(2,195)} = 49.0, P < 0.0001$; location: $F_{(1,195)} = 85.3, P < 0.0001$). Group sizes generally increased in later years at most sites (Fig. 1).

Factors influencing incidence and size of groups

Three of the five potential explanatory variables significantly influenced the relative frequency of occurrence of singletons versus groups of ≥ 2 individuals based on step-wise multiple logistic regression. Group incidence was

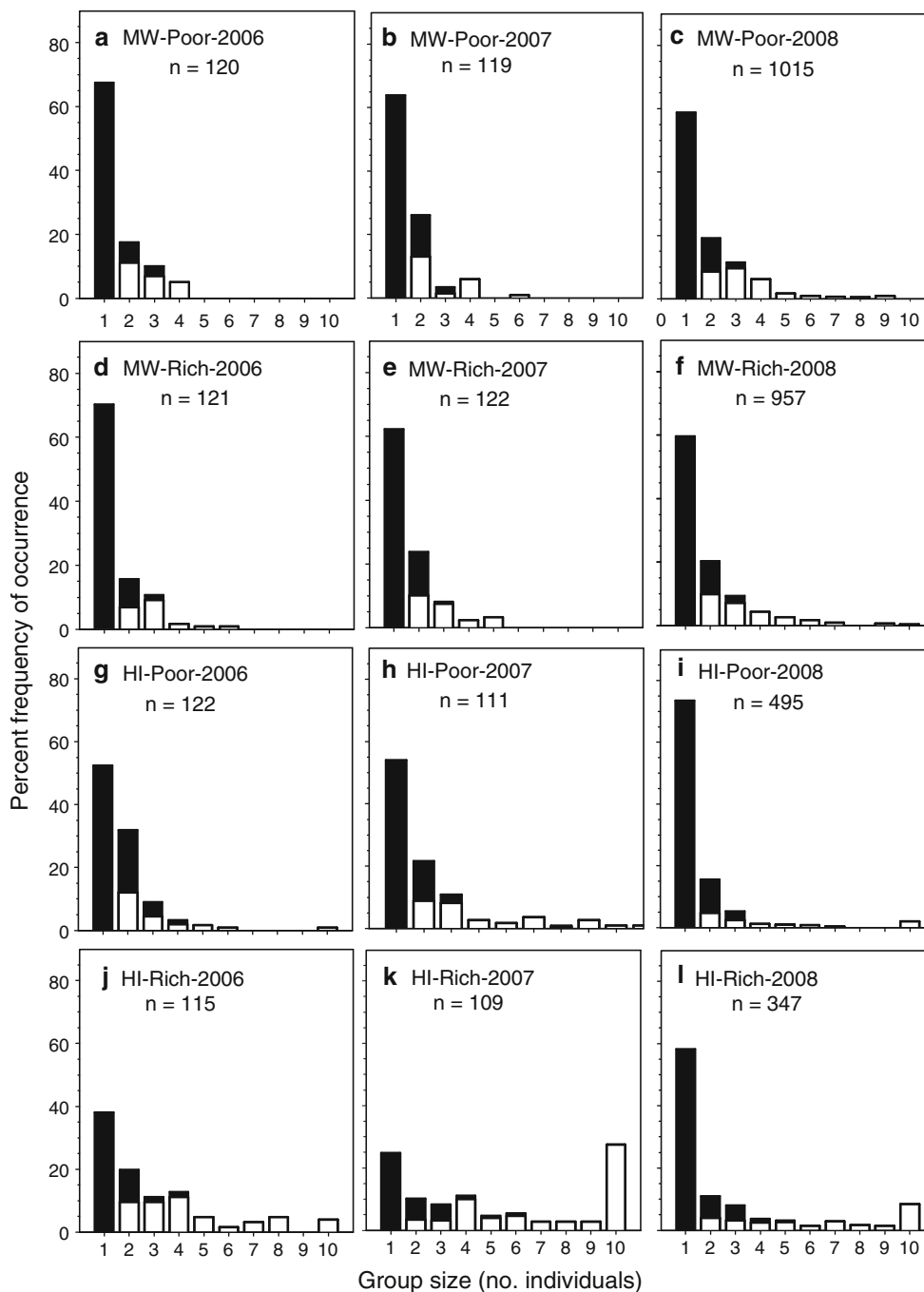


Fig. 1 Percentage frequency distribution of singletons versus groups of recruits of various sizes (filled bars) at each of the four sites in each of 3 years (2006–2008). Proportion of heterospecific groups (groups

comprising more than one species) is indicated by unfilled area within each bar. The largest group size indicates ≥ 10 individuals

Table 3 Results of stepwise multiple (a) logistic regression relating group incidence (relative frequency occurrence of groups of ≥ 2 individuals versus singletons) to four potential explanatory variables (predator biomass density, total recruit density, the proportion of

individuals present in groups that are schooling species, and the proportion that prefer rugose coral), and (b) least-squares (LS) regression relating mean group size to five potential explanatory variables (including proportion of heterospecific groups)

(a) Logistic regression effect	Order variable entered	Estimate \pm SE	Odds ratio	df	Maximum likelihood chi-square	$P > X^2$
Intercept		-2.017 \pm 0.35		1	32.8	<0.0001
Proportion schooling	1	1.448 \pm 0.19	4.253	1	57.5	<0.0001
Predator biomass	2	-0.214 \pm 0.08	0.807	1	24.8	<0.0001
Recruit density	3	0.384 \pm 0.09	1.467	1	16.9	<0.0001
Prop. rugose coral-pref.	4				0.49	0.48
(b) LS regression effect	Order variable entered	Partial R^2	Model R^2	C_p	F	$P > F$
Intercept					19.5	<0.0001
Proportion schooling	1	0.495	0.495	134.9	196.8	<0.0001
Proportion heterospecific	2	0.080	0.574	84.1	37.5	<0.0001
Recruit density	3	0.066	0.640	42.8	36.2	<0.0001
Predator biomass	4	0.060	0.700	5.5	39.2	<0.0001
Prop. rugose coral-pref.	5	0.002	0.702	6.0	1.5	0.23

Mallows' C_p statistic is also noted. All regressions are based on 203 transects surveyed at the four sites over 3 years. Probabilities of significant effects are noted in bold

positively related to the proportion of schooling recruits and recruit density but negatively related to predator biomass density (Table 3a). The proportion of schooling recruits, recruit density, and predator biomass density together accounted for all of the explained variation in group incidence (Table 3a). The proportion of recruits preferring rugose corals did not explain variation in group incidence and the proportion of heterospecific groups, although a strong influence on group size (see below), did not have a clearly interpretable effect on group incidence (Table 3a) and was disregarded.

A disproportionate number of recruits and relatively more heterospecific groups of recruits consisted of wrasses, other microcarnivores, and herbivores as opposed to carnivores (including <3-cm-long parrotfishes: Bellwood 1988), and herbivores separately (3×3 G test; recruits: $ML X^2_4 = 502.7$, $P < 0.0001$, Fig. 2a; groups: $ML X^2_4 = 85.4$, $P < 0.0001$, Supplement 6, Fig. S6a). The numbers of recruits of mixed benthivorous wrasses and planktivorous damselfishes also were over-represented compared to the numbers of individuals in heterospecific groups composed of benthivores or planktivores only ($ML X^2_4 = 77.2$, $P < 0.0001$, Fig. 2b). Evidence for a greater proportion of groups consisting of mixed benthivores and planktivores was suggestive ($ML X^2_4 = 11.8$, $P < 0.02$, Supplement 6, Fig. S6b).

Group size was significantly ($P \leq 0.001$) influenced by the residuals of all of the potential explanatory variables, including the proportions of schooling species and

heterospecifics present in groups, except for the proportion of recruits present that preferred rugose corals (Table 3b). Based on stepwise multiple regression, group size was positively related to the proportion of schooling recruits and to recruit density, but negatively related to predator biomass (Table 3b; Fig. 3). Group sizes were greatest when recruit densities were greatest (Fig. 4). Non-saturating positive relationships between group size and recruit density were observed at each of the four study sites (all $P \leq 0.002$) and collectively at the four sites pooled ($r_s = 0.39$, $P < 0.0001$; Fig. 4).

Given the limitations in interpreting the effect of heterospecifics on group incidence, it is important to note that group size also was strongly (positively) related to the proportion of heterospecific groups (Table 3b; Fig. 1). The proportion of recruits preferring rugose corals did not explain additional variation in group size (Table 3b), although group size (and recruit density) tended to be higher at the coral-rich sites of Hawaii Island (Fig. 1; Supplement 2, Fig. S2). The proportions of schooling recruits and heterospecific groups, recruit density, and predator biomass altogether explained $\sim 70\%$ of total variance in group size (Table 3b); this 4-predictor model also was the most efficient, having the lowest AIC (-817). Stepwise and backward selection, Mallows' (C_p) selection, and Maximum R^2 improvement selection all converged on the same suite of four predictor variables, thus confirming the robustness of our analyses.

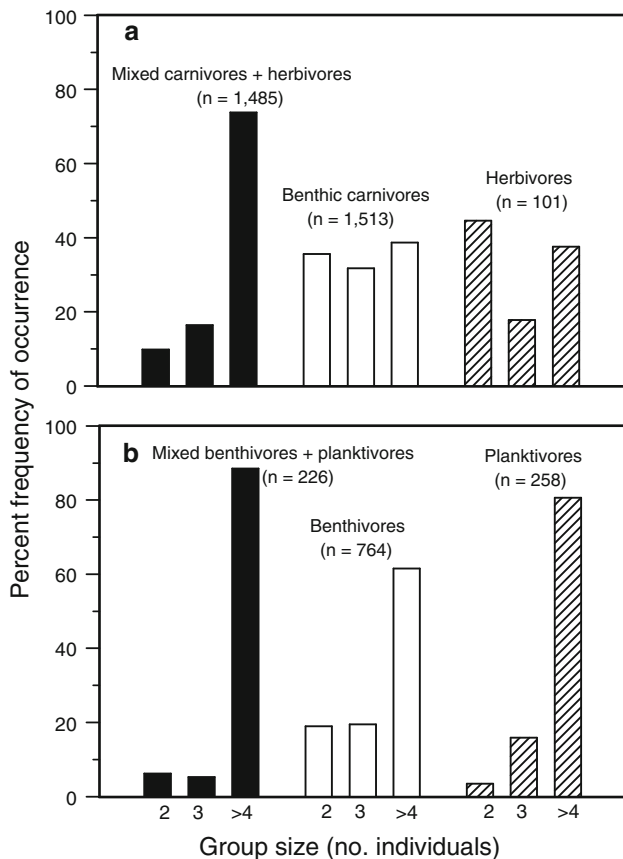


Fig. 2 Relative frequency occurrence (number of individuals) of groups of recruit reef fishes composed of **a** mixed carnivores and herbivores, carnivores only, and herbivores only; and **b** mixed benthic carnivores (benthivores) and planktivores, benthivores only, and planktivores only, in groups of 2, 3, or >4 recruits

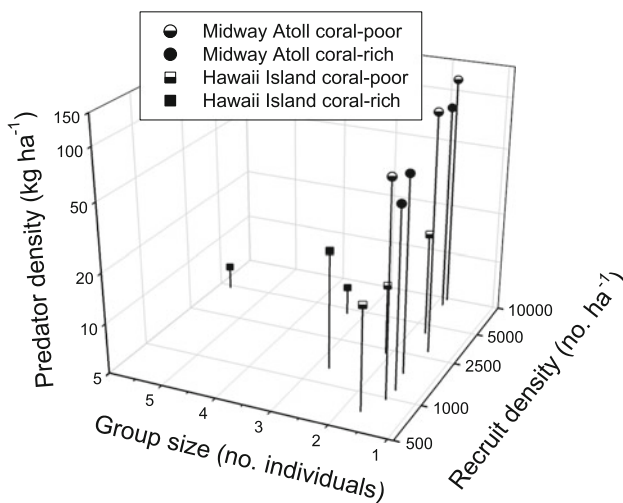


Fig. 3 Scatterplot of mean group size, total predator biomass density, and total recruit density at each of the four sites during each of the 3 years (2006–2008). Note \log_{10} scales for predator biomass and recruit density

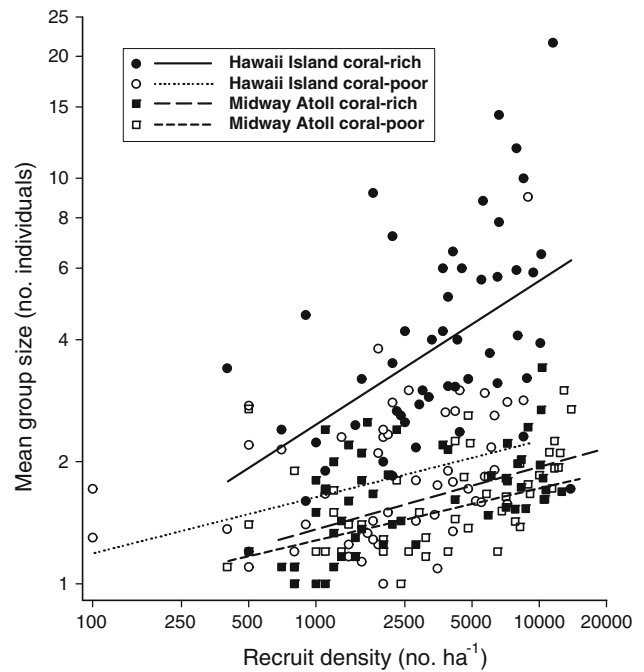


Fig. 4 Relationship between group size and recruit density ($n = 203$ transects) surveyed at each and all of the four sites over 3 years (2006–2008). Note the \log_{10} scale for both axes and the absence of asymptote in group size at the highest recruit densities observed collectively or at any of the four sites

Discussion

Factors influencing recruit density

The functional structure of rugose coral substrata importantly influences the distribution and abundance of recruit fishes (Luckhurst and Luckhurst 1978; Garpe and Ohman 2003, 2007; Brooks et al. 2007; DeMartini and Anderson 2007; Holbrook et al. 2008; Wilson et al. 2008; DeMartini et al. 2010). Species that prefer such complex substrata often occur more abundantly in habitats in which these substrata are prevalent. Social factors, nonetheless, often importantly modify (Gardiner and Jones 2010) or, as in this study, override the effects of habitat on recruit distribution and abundance, and the complementary “habitat” afforded by other prey in an aggregation might at such times provide preferred shelter. Recruit densities also will be higher if greater proportions of numerically abundant schooling species are settling at the time, or if numerous species are undergoing settlement concurrently. Many factors simultaneously influence the dynamics of juvenile reef fishes (Jones 1991), and predator and recruit densities often interact in complex fashion to varying extents (White 2007; Stallings 2008; DeMartini et al. 2009).

Aggregations of juvenile fishes

Group formation is clearly a function of density. By chance alone, groups must occur more frequently at higher densities (Krause and Ruxton 2002). Thus, the greater incidence of groups that we observed in subsequent years is to be expected, given the higher densities observed over time. Group size clearly is further influenced positively by the proportional composition of schooling species and by the number of species settling to reefs. Thus, the perceived occurrence of “year-class” strength can be misleading if based on total recruit densities alone. Our observations illustrate that annual variation in the relative abundances of schooling and non-schooling species and the degree of overlap in timing of settlement can influence perceptions of variation in year-class strength.

Group formation clearly can be advantageous to individuals of schooling conspecifics that share physical and behavioral characteristics (Hobson 1978). But perhaps the most intriguing aspect of the recruit reef fish aggregations we observed is the frequent occurrence of heterospecific associations. A sizeable number of groups encountered comprised more than a single species, and heterospecifics were, as expected, represented more in larger groups. Because the resource requirements of heterospecifics should overlap less than those of conspecifics, juveniles of mixed species that associate should also experience less competition for food (Bonin et al. 2009) than similarly sized groups of conspecifics only. The benefit-to-cost ratio of aggregating should be greater still among heterospecifics that occupy different trophic levels or feeding guilds. It is intriguing that we observed a disproportionately large number of mixed-species groups of recruits composed of microcarnivores and herbivores and of benthivorous wrasses and planktivorous damselfishes. This implies that competitive costs within groups are further reduced for heterospecifics having less dietary overlap. Whether a selective basis exists for mixed-species group formation by Hawaiian labroid and pomacentrid recruits is unknown; further research is needed to determine whether groupings reflect co-evolved mutualisms or facultative associations. Possible mutualisms of recruit wrasses and parrotfishes have been observed on the Australian Great Barrier Reef (Green 1994).

Published documentation of the species composition and relative frequency occurrence of various species within multi-species associations of juvenile reef fishes are rare (e.g., Stephens and Zerba 1981; Overholtzer and Motta 2000; DeMartini and Anderson 2007). To our knowledge, comparisons of group metrics between reefs and regions that differ in the densities of recruits do not exist; and such studies are necessary to further quantify how density and the prevalence of mixed-species groups are related.

The strength of the relations between habitats and recruit associations, as well as the strength of the relations among individuals in the associations, should vary with the densities of recruits, with the intensity of predation on recruits, and with interactions between them (Hixon and Webster 2002; DeMartini and Anderson 2007). Although descriptive statistics alone cannot adequately quantify the relative importance of predation and competition among recruits as they influence group size, our results indicate that both factors were likely important during our study. The potentially complex, likely mixed positive and negative (White and Warner 2007a, b), density-dependent interactions among newly settled reef fishes are poorly understood and remain to be fully explored at all spatial scales. By providing information on the incidence and species composition of groups of juvenile Hawaiian reef fishes, our study indicates the need for further experimental examination of temporal and spatial patterns of aggregation (especially heterospecific associations) for juvenile reef fishes elsewhere (e.g., Anderson et al. 2007; Lecchini et al. 2007) that are necessary to identify the mechanisms causing grouping behavior.

Concentration, density dependence, or both?

Primarily, as a result of concurrent settlement by multiple species that tended to school, recruits aggregated to the greatest extent at times when recruit densities were extremely high. This fundamental observation was unexpected, because it runs counter to the prediction (Krause and Ruxton 2002) that the number of individuals within groups should not continue to increase monotonically with density without reaching an upper bound. A fundamental precept of the ideal-free distribution (Fretwell and Lucas 1970; Shepherd and Litvak 2004) is that organisms should distribute themselves among all available habitats (including those less- as well as more-preferred) in such a way that individual fitness (survival and growth in this case) is maximized. Our data suggest that the potential anti-predator benefits of aggregation exceeded the potential competitive costs of aggregating, even at the highest densities we encountered. Theoretically, a complex interplay exists between vigilance and the prey-dilution effect in reducing mortality by group formation (Beauchamp and Ruxton 2007). If so, we should have observed a stronger response (disproportionately greater increase in mean group size at higher recruit densities at predator-rich sites like Midway Atoll, where recruit group sizes are usually small), and this is exactly what we observed over 3 years. This observation, coupled with the generally inverse relation we documented between recruit density and predator biomass, is consistent with an interpretation that cropping by predators at Midway was impeding group formation by recruit prey despite

aggregative behavior by prey to reduce their per capita mortality (Anderson 2001). Attraction of piscivorous fishes to dense patches of prey, however, can also produce positive relationships, at least in the short term before cropping reduces prey densities (Stewart and Jones 2001).

Of course, the key unknown in our study is whether the numbers of recruits present in groups would continue to climb or asymptote at some higher recruit density within the range of natural density fluctuation. Do our observations suggest a lack of density-dependent habitat selection (ideal-free distribution)? This is impossible for us to fully evaluate. However, observations made over a 12-year period on the back reef at Midway Atoll (in 1993 and yearly from 1995 to 2002; DeMartini 2004; DeMartini and Friedlander 2004) indicate that recruit densities in 2008 were within the upper range of naturally occurring values. Subsequent estimates of recruit densities at the two Hawaii Island sites in 2009 and 2010 further indicate that recruitment magnitudes lower than those observed in 2008 are more common at the two Hawaii Island sites. We suggest that observed mean recruit densities that varied nearly sixfold among the 3 years likely represent a large proportion of the range in natural recruitment variation within assemblages of Hawaiian reef fishes; therefore, our data should have enabled us to detect a saturating relationship. Year-class fluctuations of many species of temperate marine fish, however, range upwards to one order of magnitude (e.g., Hennemuth et al. 1980), so we caution that we might not have intercepted the very rare, exceptional event that might produce an asymptotic group size–density relationship despite the absence of density-dependent responses most of the time (Strong 1986).

Long-term, quantitative time series of recruit density like ours provide important information despite their descriptive nature. Multi-year field experiments, coupled with modeling of linked experimental results and time series observations, would be required to fully explore the interrelations among recruit density, grouping, habitat preference, density-dependent predation, and recruit survivorship (White et al. 2010). All of these factors might at times interact to importantly influence year-class strength and related population dynamics, and they should be priority topics for further study.

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