Influences of wind-wave exposure on the distribution and density of recruit reef fishes at Kure and Pearl and Hermes Atolls, Northwestern Hawaiian Islands

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Abstract This paper describes the results of a field survey designed to test the prediction that the density of benthic juveniles of shallow-reef fishes is greater on wind-wave “exposed” sectors of a pair of isolated oceanic atolls (Kure, Pearl and Hermes) at the far

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northwestern end of the Hawaiian Islands, an archipelago in which east-northeasterly trade winds dominate onshore water flow and transport by surface currents. The densities of recruits (juveniles ≤ 5 cm total length) were higher overall on windward versus leeward sectors of carbonate rock-rubble back reefs at both atolls, and the pattern was stronger for smaller (likely younger, more recently settled) recruits of four of the five most abundant species and the remainder pooled as an “Other” taxon. The windward-leeward disparity was four-fold greater at Pearl Hermes (the atoll with a three-fold longer perimeter) than at Kure. Resident predator biomass also was correlated with recruit densities, but habitat (benthic substratum) effects were generally weak. The distribution and abundance of recruits and juveniles of the primarily endemic reef fishes on shallow back reefs at these atolls appear partly influenced by relative rates of water flow over windward vs. leeward sectors of barrier reef and by the size, shape, and orientation of habitat parcels that filter out postlarval fishes with relatively weak swimming capabilities like labroids. Whole-reef geomorphology as well as fine-scale habitat heterogeneity and rugosity should be considered among the suite of many factors used to interpret observed spatial patterns of post-settlement juvenile fish distribution at atolls and perhaps some other tropical reefs.

Keywords Reef fish recruitment · Labroids · Larval dispersal · Wind transport · Post-settlement factors · Habitat selection · Piscivory

Introduction

The mostly uninhabited low islands of the Northwestern Hawaiian Islands (NWHI) comprise an extensive series of reefs, banks and atolls that represent the most northern and western two-thirds of the 2,000-km-long Hawaiian Archipelago. Three atolls (Kure, Midway, and Pearl and Hermes), separated by 100- to 150-km from their nearest neighbor, are situated at the extreme northwestern end of the NWHI (Fig. 1). All three are classic atolls, with fore reef separated from back reef and patch reefs, the latter within a semi-enclosed lagoon having at least one major pass. The three atolls are either located at (Kure) or near the “Darwin Point” (Grigg 1982) at which coral accretion is balanced by erosion and subsidence. Coral cover is sparse and substratum is dominated by carbonate rock, carbonate rubble (especially on back reefs within lagoons), and macroalgae (Vroom et al. 2006). Habitat structure is relatively simple compared to coral species-rich equatorial reefs in the Indo-Pacific (Vroom et al. 2006).

Fish faunas of the far NWHI atolls are dominated by labroids (labrids, scarids) and allied pomacentrids (DeMartini 2004), many species of which are endemic (DeMartini and Friedlander 2004). Their recruits settle onto reefs from the water column after relatively brief (several weeks in pomacentrids to several months in labroids) pelagic larval durations as small (typically 1- to 2-cm total length; Victor 1987) and morphologically unspecialized post-larvae with swim-

ming capabilities that are weak relative to other, larger and morphologically specialized taxa like acanthurids and chaetodontids (Leis and McCormick 2002). Hawaiian endemics in general are weak dispersers that exhibit significant genetic metapopulation structure (Eble et al. 2009).

Wave-sheltered back reefs and patch reefs are prime recruitment and nursery habitats at these NWHI atolls (DeMartini 2004). The densities of adult labroids and most other reef fishes are generally greater on atoll fore reefs than inside their lagoons (DeMartini et al. 2002); and it is likely that most spawning activity occurs on the fore reef (and in passes) and that larger pools of competent (ready-to-settle) post-larvae occur in fore reef waters outside of these atolls, as at most atolls elsewhere (Leis 1994). Most larvae recruiting to back reefs and patch reefs within these atoll lagoons must be entering the lagoons over the barrier reef, and environmental factors influencing the occurrence and intensity of this transport must importantly effect the spatial distributions of recruits.

Peak settlement occurs episodically during the summer for reef fishes throughout the Hawaiian Archipelago (Walsh 1987; DeMartini and Friedlander 2004). Summer is when northwesterly swells generated by North Pacific storms are least frequent and smallest in Hawaii and nearshore reefs are then least turbulent (Friedlander et al. 2005) and provide the most wave-sheltered environments for juvenile reef fishes. East-northeasterly trade winds that blow from northeast to southwest dominate Ekman flow during the summer in Hawaii (Firing and Brainard 2006). All of the mostly small-bodied (DeMartini and Friedlander 2004), endemic fishes of Hawaii are site-attached as benthic juveniles and adults and have small home ranges (Ross 1986; DeMartini 1998); hence, most dispersal is by planktonic eggs and pelagic larvae-juveniles.

In this study we describe the influences of wind-wave exposure on the distribution and abundance of newly recruited reef fishes. Patterns are described using in situ diver-surveys conducted over several weeks of a summertime period in windward and leeward sectors of shallow back reefs at Kure and Pearl and Hermes atolls. Prior surveys at Kure had suggested that recruit fish abundances are greater on windward vs. leeward sectors of the back reef in late summer (Walsh et al. 2002). The specific predictions

Fig. 1 Map of the Northwestern Hawaiian Islands showing major islands, reefs, and atolls. Kure (KUR), Midway, and Pearl and Hermes (PHR) Atolls are indicated by arrows

we tested in our study were: (1) recruit densities should be higher on sheltered back reefs adjacent to wind-wave “exposed” (windward) sectors of the atolls experiencing greater water transport; (2) such patterns should be magnified for smaller, younger recruits that have settled more recently; and (3) we should observe prior detected patterns again at Kure and, if spatially general, these should be further observable at Pearl and Hermes. In conclusion, implications of the observed spatial patterns are discussed in terms of dispersal among reef fish metapopulations in the NWHI and throughout the Hawaiian Archipelago.

Materials and methods

Study area

Surveys of fishes and habitats were conducted using SCUBA in 1–5 m depths along back reefs at Kure (KUR; 28.42° N, 178.33° W) and Pearl and Hermes (PHR; 27.83° N, 175.83° W) atolls. Oceanic waters flow into and exit the lagoons of these atolls through passes, although most water flows into the lagoons of these NWHI atolls, and many other atolls and reefs elsewhere (Callaghan et al. 2006; Coronado et al. 2007), across their barrier reefs (R. Hoeke, NOAA Fisheries, Pac. Islands Fish. Sci. Center, personal communication). The major difference between KUR and PHR is size: KUR has a diameter of 10 km whereas the major (northeast to southwest) and minor axes of PHR are 32 and 20 km, respectively. The two atolls thus differ somewhat in shape: KUR is roughly circular while PHR is more elliptical in outline. Stations (surveyed sites) spanned the entire back reef perimeter at each atoll—distances of 23 and 65 km, respectively (Fig. 2). Surveys at KUR were conducted at 30 stations during a 5-d period from 24 to 28 July 2007, and at PHR at 58 stations during 11 days from 29 July to 8 August 2007.

Survey protocols

Densities of predators on recruits and the availabilities of corals and other habitats (two post-settlement factors that might confound the effects of pre-settlement transport and recruit settlement) were concurrently assessed with recruit densities. Surveys

consisted of standard 45-min dives. At each station, 2, 50-m long strip (belt) transects were surveyed; each of two divers (BJZ, RCB) surveyed one of the two transects, set parallel to each other along 1- to 3-m deep isobaths. Divers operated at least 5-m apart (lateral underwater visibility always exceeded 5 m and averaged 10 m) and alternated between reef crest and lagoon sides of the back reef to distribute possible observer biases and microhabitat variations in species composition and abundance equally between divers. At each station, each diver first counted the numbers of fish predators of recruits encountered along a 50-m long×4-m wide strip (200-m² area) as the transect line was laid and then swam back along the laid line, recording the numbers of recruit fishes encountered within a 50-m long×2-m wide strip (100 m²). Larger juvenile and adult (≥10-cm TL) predators were tallied by species and 5-cm length-class. Recruits (≤5-cm TL, including those of predators) were tallied by lowest recognizable taxon or species (Randall 2007) and 1-cm TL length-class. Predators of recruits were defined as all moderate-sized (10–40 cm) reef fishes either known (e.g., see Parrish et al. 1986) or morphologically capable of consuming 1–5 cm long fishes.

To assess benthic habitat, the percentage cover of major coral taxa and other predominant types of substrata were described using a line point intercept (LPI) method (Nadon and Stirling 2007). Intercept points were equally spaced at 50-cm intervals (100 points per 50-m line, 200 total points per station). Live corals were recorded by genus-species or major growth form. Growth forms ranged in structural complexity from prostrate (lobe coral *Porites lobata*, *Montipora* spp., *Leptastrea* spp.) to discrete and branched like *Pocillopora* spp. Digitate corals (e.g., finger coral *Porites compressa*) were rare. Discrete-branching and digitate growth forms were post-classified as “rugose” and prostrate corals as “non-rugose”; taxa were pooled for analyses within coral growth form. Erect fleshy algae (macroalgae >1-cm tall), consolidated carbonate rock (dead coral) with short (<1-cm high) turf algae, unconsolidated (easily moveable by hand), carbonate rubble (>1 cm particle diameter), and sand (<1 cm diameter) were the other recorded substratum types. Percentage cover of each of these six substrata was estimated at each station based on the 200 total points. Prior to the surveys described herein, EED conducted a test comparing

Fig. 2 Chart of **a** Kure and **b** Pearl and Hermes Atolls, Northwestern Hawaiian Islands, showing survey locations. Stations are labeled by wind-wave exposure (W = windward, L = Leeward). Numerical densities ($N \cdot 100 \text{ m}^{-2}$) of total recruit fishes ($\leq 5 \text{ cm}$ total length, TL) are indicated by pie diagram opposite each location. Each recruit pie diagram is partitioned into SMALL ($\leq 2 \text{ cm}$ TL) and LARGE (3–5 cm TL) size-classes separately for saddle wrasse *Thalassoma duperrey* and a compound “All Remaining” recruit taxon excluding saddle wrasse. Locations of passes are indicated by arrows. Note different scales in (a) and (b)

substrate percent cover estimates between matched plot (multiple 1-m² quadrats) and plotless LPI methods on 50-m transects at several reefs in the main Hawaiian Islands that provided a broad range of substrate types and coral morphologies. Mean percent cover estimates were indistinguishable between methods

(*t*-tests: all $P > 0.2$) and the LPI method was unbiased (least squares regression of plot on plotless methods: slopes = 0.82–1.06; all $P > 0.01$ ns—see “[Statistical Analysis](#)”) for all major substratum categories.

The initial station surveyed at each atoll was located randomly. Subsequent stations were spaced

approximately 0.5 (KUR) and 0.7 km (PHR) apart so as to extend the survey area along the entire back reef perimeter of the respective atoll. Stations were sited haphazardly based on minimal criteria (>50% reef substrata and a constant depth ± 1 m for the entire transect). Global Positioning System positions of stations were plotted on charts and classified (before any biological data were analyzed) as either “windward” or “leeward” exposure depending on whether the station position fell into one of two, roughly equal-sized sectors falling on either side of an imaginary northwest-southeast line bisecting the respective atoll.

Statistical analysis

Conventional parametric and nonparametric tests (Sokal and Rohlf 1981; Siegel and Castellan 1988) were used to compare habitat characteristics and recruit density patterns between wind-wave exposures and atolls and to relate densities between size-stages of recruits and between recruits and larger juveniles-adults at individual stations. Choice of the specific test was based on characteristics of the particular metric and its case-specific sampling distribution. Predator biomass density and a habitat index were used as covariates in analysis of covariance (ANCOVA) to statistically control for possible predation and habitat effects that might obscure transport influences of recruit distribution and abundance. Predator biomass was estimated by multiplying size class-specific counts and weights derived using length-weight relations (FishBase). The covariate chosen to index habitat was the simple difference between the two most important substrate types (carbonate rock/rubble and erect fleshy algae) identified by principal component analysis (PCA) of substrate composition (proc PRINCOMP; SAS Institute Inc. 2004). Variance heterogeneity was evaluated using Cochran’s C test (Underwood 1997). Parametric analyses were used only after variances of density and substratum percent cover estimates had been made homogeneous after log- and arcsine-square root-transformation, respectively. 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 unavoidable. Interaction effects in analysis of variance (ANOVA) and ANCOVA are not listed if insignificant.

Results

Habitat characteristics

Percentage live coral cover was low, with a mean of 6.8% ($SE \pm 0.9$), and equivalent at the two atolls and for windward and leeward exposures (2-way ANOVA—atoll effect: $F_{1,84}=0.3$, $P=0.57$; exposure effect: $F_{1,84}=0.1$, $P=0.80$). Rugose coral cover represented one-third to one-half of all live coral. Rugose coral cover differed between atolls at the back reef scale (2-way ANOVA—atoll: $F_{1,84}=4.8$, $P=0.03$) but the magnitude of this difference was trivial (<2% greater cover; 3.8% at KUR vs. 2.1% at PHR). Carbonate rock with a mean of 36% ($SE \pm 2$) and fleshy macroalgae at 32% ($SE \pm 2$) co-dominated benthic cover and did not differ between exposure sectors or atolls ($P=0.21$ – 0.55). Rubble constituted most of the remainder at 15% ($SE \pm 1$). Sand at 9% ($SE \pm 1$) was the only substratum other than rugose coral that appeared to differ spatially. Sand cover was nominally 1% greater in the windward sector at PHR (8%; 2-way ANOVA—exposure: $F_{1,84}=4.2$, $P=0.04$ ns). However, unlike rugose coral, sand did not differ overall between atolls (2-way ANOVA—atoll: $F_{1,84}=0.2$, $P=0.69$).

Benthic habitats of windward and leeward exposures at the two atolls could be succinctly characterized by the first two principal components in PCA. Carbonate substrata (rock plus rubble) and erect fleshy algae, the substrata that together represented 82–87% of all benthic cover, were negatively correlated with one another and dominated both PC1 and PC2. The first two principal components together explained from 92 to 97% of total habitat variance for the four atoll-exposure combinations.

Densities of larger juvenile-adult predators

More than 98% (by number) of all larger (≥ 10 cm TL) predatory fishes observed were resident species as defined by DeMartini et al. (2005). Relatively large-bodied, transient piscivores were rare but dominated overall predator biomass. Transient piscivores were excluded from all following analyses because they inordinately influenced the precision of predator biomass estimates and because recruit-sized fishes do not contribute appreciably to the diet of large carangids that dominate transient piscivore biomass in

the NWHI (DeMartini et al. 2005). All resident and transient predatory fishes that were encountered are listed in Appendix A of the [Electronic Supplementary Material](#).

Most resident predators were wrasses (labrids), and these were dominated (in numbers: 60%, biomass: 27%) by the ubiquitous saddle wrasse *Thalassoma duperrey*, one of the most abundantly recruiting species. The old woman wrasse *Thalassoma ballieui* ranked second highest in biomass among resident predators (22–24% at the two atolls). Saddle wrasse and one other labrid—the elegant coris (*Coris venusta*)—were the only resident predators whose recruits contributed nontrivially to total recruit counts at the time of our surveys. These two “recruiting” species represented about two-thirds of all resident predators by number (6.0 ± 0.3 [SE] individuals $\cdot$ 100 m⁻²) and one-third of all resident predator biomass. Cannibalism might obscure positive numerical population responses between recruits and larger juvenile and adult conspecifics; hence, resident predator biomass was partitioned into the two recruiting species and a complementary “non-recruiting” taxon of all other resident predator taxa. The biomass of recruiting predators was 60% greater at KUR vs. PHR (187 vs. 117 g $\cdot$ 100 m⁻²; 2-way ANOVA—atoll: $F_{1,84}=7.2$, $P<0.009$) but was unaffected by exposure (2-way ANOVA—exposure: $P=0.68$). Non-recruiting predator biomass did not differ between atolls or between exposures (2-way ANOVA—atoll: $P=0.18$; exposure: $P=0.15$). Correlations between biomass of non-recruiting predators and numbers of recruits were positive at each atoll for SMALL recruits (1–2 cm TL, likely younger—more recently settled) but not LARGE recruits (3–5 cm TL, likely older—less recently settled), and significantly so for SMALL recruits at KUR ($r_s=0.37$, $P=0.04$, Fig. 3).

Species composition and densities of recruit fishes

Five species of Hawaiian endemics (four labrids, one scarid; Fig. 4) consistently represented >90% of all recruit fishes encountered within exposure sectors at the atolls, with a single species, the belted wrasse *Stethojulis balteata*, contributing 60% to total recruit numbers (Fig. 5). An “Other” taxon of remaining species (excluding the Top 5 species) made up 4.3% and 5.7% of the remaining recruits tallied at KUR and PHR, respectively (Figs. 5a, b). A grand total of 31

Fig. 3 Scatterplot of correlations between the biomass densities of larger juveniles-adults (≥ 10 cm TL) of non-recruiting species of resident predators and the numerical densities of SMALL (≤ 2 cm TL) and LARGE (3–5 cm TL) recruits of all taxa at **a** KUR and **b** PHR. Non-recruiting resident predators exclude two species of wrasses (saddle and elegant coris) well represented in the recruit counts (22% and 5% of all recruits, respectively). (See Appendix A in [Electronic Supplementary Material](#) for list of all predator species)

species of recruits were surveyed (Appendix B in [Electronic Supplementary Material](#)), with 11 additional species encountered at PHR (27 species total), the more extensively surveyed atoll, vs. KUR (19 species total, with only 3 unique to KUR).

Wind-wave exposure pervasively influenced recruit densities but effects differed among species and somewhat between the two atolls (Table 1). Although relations with exposure were generally similar for both SMALL and LARGE recruits of respective taxa, patterns were stronger for SMALL recruits and this paper hereafter focuses on the SMALL size-class (Table 1). The densities of SMALL recruits were everywhere similar except for leeward PHR, where they were relatively low for each of four of the Top 5

Fig. 4 Photographs of the top-ranked species of recruit fishes in surveys: **a** belted wrasse *Stethojulis balteata*, **b** saddle wrasse *Thalassoma duperrey*, **c** Hawaiian gregory damselfish *Stegastes marginatus* (representing 35% of the Other taxon), **d** snubnose wrasse *Macropharyngodon geoffroy*, **e** elegant coris wrasse *Coris venusta*, and **f** regal parrotfish *Scarus dubius*. Photo credits—J. Johnson: a,c; EED: b,d,e; J. Leung: f, layout, and formatting for final production

species plus the 3rd ranked Other taxon (Table 1). The endemic Hawaiian gregory (*Stegastes marginatus*) contributed 74% and 30% to SMALL Other recruits at KUR and PHR, respectively, and was more than one-third less abundant at leeward vs. windward PHR. Twelve of the fifteen species of SMALL Other recruits at PHR were less abundant in leeward vs. windward sectors (Wilcoxon matched-pairs signed-ranks test; $T=19$, $0.025 > P > 0.01$). As a result of lower densities at leeward PHR, recruit densities tended to be higher overall at KUR vs. PHR (Table 1). The exception was saddle wrasse, the 2nd-ranked recruit species, whose densities were higher at PHR and trended greater leeward (Table 1).

Predator biomass and habitat covariates variably influenced the effects of exposure and atoll on recruit densities, depending on species and taxon, but nowhere did they overshadow the primary effects of exposure and atoll (Table 1). The biomass of non-recruiting resident predators tended to be more

influential than habitat represented by the carbonate rock/rubble-algae difference. The correlations were positive wherever recruit densities were significantly or suggestively correlated with the biomass of non-recruiting resident predators (Table 1). The two covariates were themselves correlated: predator biomass was positively related to the carbonate rock/rubble-algae difference (Spearman's rank correlation: $r_s=+0.32$ and $P=0.09$, $r_s=+0.56$ and $P<0.0001$, $r_s=+0.50$ and $P<0.0001$ for KUR, PHR, and both atolls pooled, respectively). Interactions between covariates (Table 1) reflect the greater strength of the correlation at PHR vs. KUR.

Correlations between conspecific life-stages

Most observed relations between the densities of SMALL and LARGE recruits matched by station were positive, and many significantly so (Table 2). Correlations between the densities of recruits and

Fig. 5 Bar histograms depicting the densities of total recruits surveyed and of each of the Top 5 species plus the compound Other taxon, between windward and leeward exposure sectors at **a** Kure and **b** Pearl and Hermes Atolls. The Top 5 species and Other taxon are ranked based on overall numerical density at both atolls and ordered from *left to right* by descending density and labeled by scientific name acronym (STBA: belted wrasse; THDU: saddle wrasse; Other; MAGE: snubnose wrasse; COVE: elegant coris wrasse; SCDU: regal parrotfish). See Fig. 4 caption for scientific names. Bar designations are partitioned into SMALL (≤ 2 cm TL; hollow) and LARGE (3–5 cm TL; diagonal lines) recruits. Vertical lines indicate $+ 2$ SE of the mean density of recruits of all sizes

larger juvenile-adult conspecifics also were positive and significant for saddle wrasse and elegant coris, the two resident predators that were nontrivially represented in the recruit counts (Table 2). The overall spatial correlation between the densities of SMALL and LARGE recruits was positive at each atoll (KUR: $r_s = +0.47$, $P < 0.01$; PHR: $r_s = +0.59$, $P < 0.0001$; Fig. 6).

Discussion

Wind-wave exposure appears to have had a pervasive influence on recruit distributions and densities in our

study. However, several other key issues (influences of habitat and predators, correlations between the densities of recruits and older juvenile and adult conspecifics) must first be considered to put interpretations of wind-wave exposure in proper context.

Influences of benthic habitat and predators

Habitat composition and distribution likely did not strongly influence the distribution and abundance of recruits at KUR and PHR back reefs because substrate composition was similar throughout exposure sectors at both atolls. Carbonate rock and algae predominated regardless of exposure or atoll. Rugose substrata like corals (DeMartini and Anderson 2007) contributed little to overall benthic cover at both atoll back reefs.

That the few observed correlations between habitat and fish density involved resident predators rather than recruits suggests that spatial variations in carbonate rock/rubble and algae were influencing the distributions of secondary predators more so than their prey. Resident predators as well as herbivores are the prey of apex predators like transient carangids (DeMartini et al. 2005), and habitat features also provide shelter from predation for larger-bodied prey.

Predator density was correlated with recruit distribution and density for some recruit and predator taxa. The positive correlations between the densities of recruits and non-recruiting predators suggest either that predators were concentrating at places where prey were abundant (Connell 1996) or that numerical population responses were lagged over years of poor recruitment for some species (see below). Correlations between recruits and predators also were positive for species of predators that were recruiting (saddle wrasse and elegant coris), introducing the possibility that the correlations for recruiting species might represent more than just predator attraction.

Within-species relationships

The generally positive correlations between the densities of SMALL and LARGE recruits and between SMALL recruits and larger juvenile and adult conspecifics might represent lagged numerical responses by juvenile-adult segments of populations resulting from localized concentrations of recruits (Adams and Ebersole 2004). The first author has never observed agonistic behaviors among recruits or

Table 1 ANCOVA results of the effects of wind-wave exposure (W = windward, L = leeward) and atoll (KUR = Kure, PHR = Pearl and Hermes), on the numerical densities of the SMALL size-class of each of the a.–f. Top 5 ranked species plus the compound Other taxon and g. their aggregate excluding saddle wrasse. The two covariates evaluated are “non-recruiting” predator biomass and a habitat metric of the simple difference between the arcsine-square

root-transformed proportion cover of carbonate rock/rubble and erect fleshy algae. Densities were log (x+1)-transformed prior to analyses. Covariates and higher-order terms are retained in final model and specified only if significant after penultimate model run ($P < 0.05/m = < 0.05/6 \simeq < 0.01$). Relative magnitude of least square means (back-calculated to original scale) are indicated for a posteriori contrasts

Factor	df	MS	F	Prob>F
SMALL belted wrasse (Model: $F_{3,83}=20.5$, $P<0.0001$, $r^2=0.43$) ^a				
Atoll	1	1.85	21.1	<0.0001
Exposure	1	1.47	16.8	<0.0001
Atoll × exposure	1	1.03	11.7	0.001
Residual	83	0.88		
SMALL saddle wrasse (Model: $F_{2,84}=14.9$, $P<0.001$, $r^2=0.26$) ^b				
Atoll	1	15.46	25.7	<0.0001
Exposure	1	3.03	5.0	0.028 ns
Residual	84	0.60		
SMALL Other taxon (Model: $F_{3,83}=12.8$, $P<0.0001$, $r^2=0.32$) ^{c,d,e}				
Habitat covariate	1	1.09	2.4	0.12
Predator biomass covariate	1	7.54	16.6	0.0001
Exposure	1	2.11	4.7	0.034 ns
Residual	83	0.45		
SMALL snubnose wrasse (Model: $F_{2,84}=6.0$, $P<0.004$, $r^2=0.12$) ^{f,g}				
Habitat covariate × predator biomass covariate interaction	1	6.02	7.1	0.01 ns
Atoll	1	5.01	5.9	0.017 ns
Residual	84	0.85		
SMALL elegant coris wrasse (Model: $F_{3,83}=12.7$, $P<0.0001$, $r^2=0.32$) ^{h,i}				
Habitat covariate × predator biomass covariate interaction	1	24.02	25.8	<0.0001
Atoll	1	4.19	4.5	0.037 ns
Exposure	1	4.14	4.4	0.038 ns
Residual	83	0.93		
SMALL regal parrotfish (Model: $F_{1,85}=12.9$, $P<0.002$, $r^2=0.11$) ^j				
Exposure	1	12.94	10.3	<0.002
Residual	85	1.25		
SMALL Total Recruits less saddle wrasse (Model: $F_{4,82}=17.7$, $P<0.0001$, $r^2=0.46$) ^{k,l}				
Predator biomass covariate	1	0.26	3.9	0.052 ns
Atoll	1	1.16	17.2	<0.0001
Exposure	1	1.19	17.6	<0.0001
Atoll × Exposure	1	0.87	12.8	<0.0006
Residual	82	0.07		

^a a posteriori contrasts: KUR > PHR (+103%) W > L (+88%)

^b a posteriori contrasts: PHR > KUR (+708%) L ≥ W (+140%)

^c LSQR regression: recruit density on habitat metric: $r=+0.31$, $P<0.003$

^d LSQR regression: recruit density on predator biomass: $r=+0.94$, $P<0.0001$

^e a posteriori contrast: W ≥ L (+113%)

^f LSQR regression: recruit density on covariates interaction: $r=+0.06$, $P=0.02$

^g a posteriori contrast: KUR ≥ PHR (+125%)

^h LSQR regression: recruit density on covariates interaction: $r=+0.24$, $P<0.0001$

ⁱ a posteriori contrasts: KUR ≥ PHR (+122%) W ≥ L (+208%)

^j a posteriori contrast: W > L (+719%)

^k LSQR regression: recruit density on predator biomass: $r=+0.26$, $P=0.01$

^l a posteriori contrasts: KUR > PHR (+76%) W > L (+57%)

Table 2 Summary of Spearman's non-parametric rank correlations between density estimates ($N \cdot 100 \text{ m}^{-2}$) of a. SMALL and LARGE recruits for each of the Top 5 species of recruits, the 3rd-ranked Other compound taxon, and the aggregate of all recruits excluding saddle wrasse; and of b. the total recruits (both SMALL and LARGE $\leq 5 \text{ cm TL}$) and larger juveniles and adults ($\geq 10 \text{ cm TL}$) of saddle wrasse and elegant coris, two recruiting species of resident predators

a. Densities of SMALL vs. LARGE recruits ($n=87$ stations)		
Species or taxon	Spearman's r_s statistic	Prob $ r_s =0$
Belted wrasse	+0.53	<0.0001
Saddle wrasse	+0.21	0.05 ns
Other	+0.32	0.002
Snubnose wrasse	+0.47	<0.0001
Elegant coris wrasse	+0.78	<0.0001
Regal parrotfish	+0.81	<0.0001
Total minus saddle wrasse	+0.56	<0.0001
b. Densities of recruits (all sizes) vs. larger juveniles and adults ($n=87$ stations)		
Species	Spearman's r_s statistic	Prob $ r_s =0$
Saddle wrasse	+0.43	<0.0001
Elegant coris wrasse	+0.70	<0.0001

between juveniles and adults of these species despite hundreds of hours of underwater observation, although this does not necessarily disprove competition that manifests as slower growth by recruits that aggregate to reduce per capita predation mortality (White and Warner 2007). Only experiments can distinguish among the several, non-mutually exclusive causes of these patterns, which include facilitated settlement, post-settlement attraction, and lagged numerical population responses within and between year-classes.

Effects of wind-wave exposure

Wind-wave exposure appears to have importantly influenced the distribution and abundance of most species of recruit fishes, and of recruit fishes overall, on back reefs at both atolls surveyed. Total SMALL recruits (excluding saddle wrasse) were 15% (ns, but power only 0.2) and 60% lower density in leeward sectors at KUR and PHR, respectively, despite a 40% higher overall density of SMALL recruits of these taxa at KUR. The differences in densities at windward vs. leeward PHR for several of the Top 5 species and Other taxon were nominally large although insignificant because power was low (0.6–0.7) at the species level. The pattern of lower recruit densities in the leeward sector at PHR, although spanning five families, was mostly based on labroids and pomacentrids (10 of the 12 species). The SMALL recruits of all of these high-ranked taxa except for belted wrasse were low in absolute abundance at the time of our

surveys. However, these species should not be considered unimportant contributors to fish population dynamics at these atolls because each of those most abundant as recruits in the present study has been a major component of the assemblage of juvenile and adult fishes at these reefs in the recent past (Table 3).

The opposing patterns for the lone exception among the Top 5 species—saddle wrasse (suggestively higher densities in leeward sectors and a relatively

Fig. 6 Scatterplot of correlations between the numerical densities of SMALL ($\leq 2 \text{ cm TL}$) and LARGE ($3\text{--}5 \text{ cm TL}$) recruit fishes of all taxa at KUR and PHR

Table 3 Rank numerical densities of all (juvenile and older) fishes surveyed in 2000–02 at a. KUR and b. PHR, for each the most abundant species recorded as recruits (this study). Species are ordered by relative recruit density in this study, with Hawaiian gregory damselfish as proxy for the Other compound taxon. Fish species richness was 155 and 174 at KUR and PHR, respectively, in 2000–02. Source: Table 3 and Fig. 2 of DeMartini and Friedlander (2004)

Species	a. KUR	b. PHR
Belted wrasse	5	16
Saddle wrasse	1	1
Hawaiian gregory	3	6
Snubnose wrasse	14	24
Elegant coris wrasse	19	28
Regal parrotfish	13	4

weak correlation between densities of SMALL and LARGE recruits)—are perhaps related to saddle wrasse being the only species abundant both as recruits and as larger juveniles and adults when surveyed. Cannibalism by saddle wrasse (likely, based on its generalist food habits [Randall 2007] and feeding mechanism morphology) would weaken correlations between abundances of its recruit and older stages.

An apparent leeward “recruitment shadow” effect (Jones 1997) was four-fold larger—and significantly so—at PHR, the atoll with the three-fold longer perimeter. It is possible that the spatial extent of leeward back reef at KUR is too small to provide a true lee from the prevailing trade wind-generated flow of surface water currents that deliver most water over the windward barrier reef. Differences in the relative delivery rates of water over windward and leeward barrier reefs provide the most parsimonious explanation for our observed differences in recruit labroid and pomacentrid densities. Physical forcing by geostrophic flows (Cowen 2002) and wind-driven transport (Milicich et al. 1992) obviously can contribute to the settlement process and spatial distribution of recruits, despite the now generally accepted fact that reef fish larvae importantly influence their fine-scale distributions (Leis 2007). Our explanation holds regardless of the relative extents to which replenishment reflects transport from upstream reefs within 100-km distance (Cowen et al. 2006) or local reseeding (Swearer et al. 2002). Our surveys provide the first empirical evidence that the spatial distribution and abundance

of recruits and the larger juveniles and adults of some species of site-attached reef fishes at atolls in the NWHI are likely influenced by the size and perhaps also shape and orientation of habitat parcels which can function as spatial filters. Our description of within-atoll patterns herein appreciably extends the information available on spatial relationships of recruit reef fishes in the NWHI, which until now was limited to general recognition of a latitudinal cline in the density of recruits (DeMartini and Friedlander 2004).

Few other empirical observations exist with which to test such a habitat filter or recruitment shadow hypothesis (Milicich et al. 1992; Booth et al. 2000). The generally recognized paradigm, largely based on theory (Lobel and Robinson 1986) and either limited empirical data (Lobel and Robinson 1988, but see Boehlert et al. 1992) or mixed oceanographic evidence (reviewed by Cowen 2002), is that downstream eddies on the leeward side of islands are where larvae typically concentrate, rather than that a windward shore might act as a filter against wind-driven transport that thereby reduces the number of potential settlers on a leeward shore (Jones 1997; D’Alessandro et al. 2007). A recent study (Hamilton et al. 2006) described a case in which recently settled recruits of the bluehead wrasse *Thalassoma bifasciatum* were consistently concentrated at certain areas off both windward and leeward shores of St. Croix in the U.S. Virgin islands. Temporally consistent spatial patterns were attributed to a combination of habitat filtering and concentration within gyres (Hamilton et al. 2006).

The fundamentally different geomorphologies of atolls and high islands perhaps affect whether they function as filters or as gyre-inducing barriers to water flow and pelagic transport. The extent to which the windward shores of atolls act as barriers to flow and transport might depend on the development and spatial distribution of higher elevation cays on their windward barrier reefs. Because oceanic water passes over the barrier reefs of atolls to varying (from slight to major) extents, the strength of filtering likely varies among atolls of differing geomorphologies. The potential for formation of downstream eddies and gyres in general might be less at atolls than at high islands of comparable size if high islands act as greater barriers to flow than do atolls through which at least some water passes.

In addition to reef geomorphology, many other spatial and temporal factors must importantly influence whether atolls function as filters or gyre-inducing barriers to flow and larval transport. A variety of local-scale topographic features can importantly modify advection and gyre formation at oceanic islands and coastal reefs (Wolanski and Hamner 1988; Cowen and Castro 1994). Passes at island reefs and atolls also significantly alter patterns of water flow (Wolanski and Hamner 1988). Augmented delivery rates that result from proximity to passes appear unlikely to have influenced recruit distributions in our study (Fig. 2), but stations were not positioned to test this hypothesis. Local tidal and other currents also can modify the outcome of wind-driven transport of ready-to-settle larvae (Kingsford and Choat 1986; Kingsford et al. 2005; Burgess et al. 2007). The magnitude of transport by wind-driven surface currents also can vary with seasonal changes in wind speed and direction (e.g., greater wave setup on the upwind side of reefs during trade wind periods) and can be further modified by seasonal or other temporal and spatial shifts in ocean current patterns, all of which are known to occur in Hawaiian waters (Kobashi and Kawamura 2002; Firing and Brainard 2006). Finally, in an expansive, isolated location like the Hawaiian Islands, the significance of exposure regimes might differ between islands and atolls at the “upstream” vs. “downstream” ends of the archipelago (e.g., the respective windward vs. leeward shores of the Big Island and Kure Atoll).

We caution that our study focused on potential interactions between wind-wave transport, benthic habitat composition, and predation on recruits, and our correlative data clearly cannot distinguish between the results of passive transport and active habitat selection. Other, potentially important factors include hydrography as a cue for active habitat selection by competent larvae (Fulton and Bellwood 2005). We do not imply that choice by settlers for specific flow regimes is not important (although active habitat selection should be more likely for the morphologically specialized, larger-bodied, and stronger swimming settlers of non-labroid species). We also do not imply that the re-seeding of larvae does not occur to some, perhaps appreciable, extents at these atolls. The data are, however, consistent with a greater concentration and/or delivery rate of recruits, especially SMALL individuals closer in time to settlement, at and near windward sectors of these

atolls regardless of whether or not most larvae settle at the same atoll from which they have been produced. The apparent pre-settlement advection effects that we observed cannot be considered necessarily spatially pervasive or temporally consistent, despite the surveys in 2001 by Walsh et al. (2002) that prompted our study. Monitoring of recruitment over many additional years would be needed to determine whether the observed spatial differences are temporally consistent (Tolimieri et al. 1998; Sale et al. 2005). Our observations further suggest that prior settlement events carried over to influence the distribution of LARGE recruits and the larger juveniles and adults of numerous species that are site-attached and have small home ranges once resident. The data on post-settlement mortality needed to test this are lacking, badly needed, and difficult to obtain. The additional observations and experiments that are needed are prerequisite to an understanding of pelagic transport throughout the Hawaiian Archipelago and connectivity among reef-based populations in the NWHI and the MHI.

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