Persistent spatial patterns of recruitment in a guild of Hawaiian coral reef fishes

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ABSTRACT: We herein describe a long-term (22 consecutive yr, 1990 to 2011) time series of recruitment surveys for a guild of coral-sheltering fishes at 7 to 12 sites along a 26 km section of the west coast of Hawaii Island. For arc-eye hawkfish, the numerically dominant species, recruitment (defined as the contribution of young-of-year to the benthic population within several months after settlement from the water column) varied 7-fold among years averaged over sites. Nonetheless, recruitment also differed spatially, with sites along the Kohala Peninsula comprising a high recruitment group. Spatial differences were persistent (some sites predictably low, others predictably high) and generally lacked demonstrable variation over time. Complementary empirical data suggested that post-settlement processes (predation, interspecific competition) also affected recruitment. A dispersal model combined with currents from an oceanic circulation model (Hybrid Coordinate Ocean Model, HYCOM) was used to simulate the spatial patterns of settlement by larvae released throughout the main Hawaiian Islands. These simulations generally agreed with observed spatial patterns of recruitment. Greater recruitment was also predicted near geomorphological features (headlands) on Hawaii Island most influenced by the flow of surface eddy currents generated by prevailing E-NE trade winds. Empirical data and simulations together suggest that the headlands of west Hawaii Island likely enhance recruitment by intercepting or concentrating larvae at greater rates, but that post-settlement processes dampen variations in settlement. We suggest that habitat geomorphology should be considered in the criteria used to select sites for no-take Marine Protected Areas at Hawaii Island.

KEY WORDS: Planktonic dispersal · Larval transport · Pre- vs. post-settlement processes · *Paracirrhites arcatus* · Cirrhitidae · Headland · Currents · Hawaii Island

INTRODUCTION

Many factors influence the magnitude, spatial patterns, and timing of the settlement of planktonic marine fish and invertebrate larvae (Doherty 2002). Likewise, many additional factors such as the productivity of benthic prey and intra- and interspecific competition and predation on benthic young-of-year (YOY) can affect the settlement of larvae and their subsequent recruitment to benthic populations on tropical coral as well as temperate reefs (Jones 1991). Included among the many physical and biological factors potentially involved prior to settlement are the dynamics of planktonic nutrient availability and the influences of primary and secondary planktonic production and predation on larval growth and mortality (Hixon & Webster 2002); tidal and ocean currents and wind-generated waves that transport and disperse larvae as plankton (Cowen & Sponaugle 2009, DeMartini et al. 2009); and ontogenetic

changes in the swimming capabilities of larvae as they affect dispersion and transport (Leis 2006, 2010). Habitat geomorphology as the cause of localized retention versus enhanced dispersion and transport of larvae by currents remains among the most complex and least understood factors influencing larval settlement on coral reefs (Sponaugle et al. 2002). Examples of both retention (e.g. Swearer et al. 1999, 2002) and transport (Cowen 2002) exist, but the relative importance of the interactions between water movements and geomorphology as causes of potential retention versus dispersion is, with few exceptions (Caselle & Warner 1996), poorly understood. Our understanding of the effects of habitat geomorphology must increase if we are to better appreciate the prevalence and significance of reseeding, especially as it influences the selection of sites for marine reserves (Warner et al. 2000).

We herein describe the spatial and temporal patterns of recruitment in a guild of coral-sheltering reef fishes along the leeward (west) coast of Hawaii Island in the Hawaiian Archipelago, a coastline of fringing coral reefs exposed — to varying extents diurnally, seasonally, and inter-annually — to onshore wind-generated waves, swells produced by northern storms (Friedlander et al. 2005), and by eddy currents generated by prevailing E-NE trade winds (Jia et al. 2011). We also evaluate several possible post-settlement factors (intra-specific facilitation, interspecific competition, and predation) by exploring possible relations between the magnitude of recruitment of arc-eye hawkfish *Paracirrhites arcatus* (the numerically dominant species) and the incidence of coral-sharing by recruits and later-stage resident fish, interspecific aggression, and a ratio estimator of combined mortality and growth rates of resident fish. We further evaluate observed recruitment by comparing it with simulated dispersal of planktonic larvae, generated using spatial and temporal input parameters that approximate those of the arc-eye hawkfish. In conclusion, we discuss the overall implications of our empirical observations and modeling results, emphasizing our evidence for the relative extent that physical features like headlands create lees for self-seeding or otherwise enhance recruitment by intercepting or concentrating larvae that have been produced at (and transported from) elsewhere. We suggest that geomorphological habitat features like headlands be considered when selecting sites for marine protected areas (MPAs).

MATERIALS AND METHODS

Study sites

Sites were shallow (1 to 5 m deep) fringing reef habitats spread over 26 km of the west coast of Hawaii Island, within the populated windward main Hawaiian Islands (MHI) (Fig. 1). All sites are semi-exposed to onshore wind waves during most afternoons and to seasonal (October to April) northwest storm swell (Friedlander et al. 2005). At the depths studied, all sites were dominated (>90% of all live coral cover) by cauliflower coral *Pocillopora meandrina*, a branching species with discrete colonies. This coral occupies a substantial proportion of consolidated lava rock substrate at all study sites. Twelve sites total were studied for differing lengths of time during the overall period of 1990–2011: 7 'Core' sites were censused (see
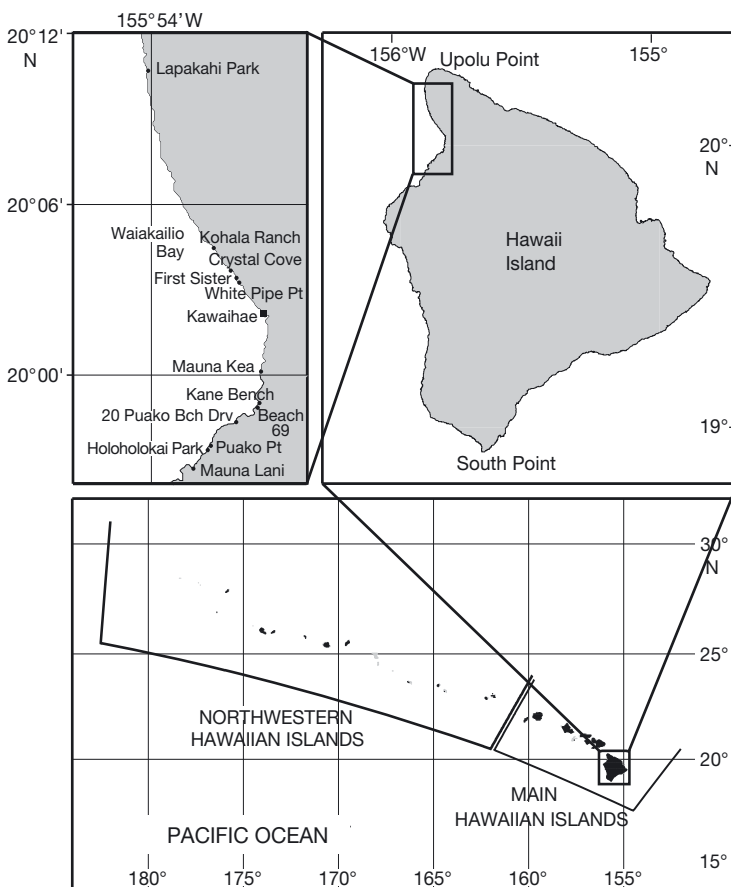

Fig. 1. Hawaiian Archipelago showing Hawaii Island and sites on the North-South Kohala coast of west Hawaii Island at which recruitment censuses were conducted during 1990–2011

below) quarterly or more frequently during the first decade; these plus 5 'Other' sites were censused once yearly in summer (July to September) starting in 2000–2002. The boundaries of census sites were delimited by prominent subtidal and shoreline habitat features.

Census protocols

All observations were made by the senior author while snorkeling and free-diving during daylight hours. Observations were made during censuses of fixed-area plots of reef that ranged in area from about 1000 to 3000 m^2; censuses were timed, and times were site-specific and proportional to area (from 50 to 150 min). The near 2-dimensionality of the study sites at the depths surveyed enabled effective search by 1-way zig-zag swim. Six species (4 cirrhitid hawkfishes and 2 salariine blenniids), comprising >99% of all of the fish that shelter in and near cauliflower corals at this depth along semi-exposed Hawaiian shorelines (E. DeMartini unpubl. data) were censused. These species are of minor or at most secondary (arc-eye and blackside hawkfishes) importance to the west Hawaii ornamental fishery; and reported catches of arc-eyes have consistently been <0.1% of the estimated numbers of this species present at collecting depths off west Hawaii (W. J. Walsh and S. Cotton, State of Hawaii Department of Land & Natural Resources, Division of Aquatic Resources pers. comm.). Fish were identified to species (Randall 2007) and tallied by body size (nearest cm total length, TL). Body lengths were estimated visually at a distance of 1 to 2 m; length estimates were periodically checked against benthic features and referenced against a ruled measure (DeMartini & Donaldson 1996). All fish observed occupying a colony of cauliflower coral were tallied by species and by the number and body lengths of individuals. Instances where other major benthic substrata (encrusting corals, dead coral-lava rock) were used as 'perches' (DeMartini 1996) were also recorded, as were the total (including unoccupied) numbers of suitably sized (≥15 cm diameter: DeMartini 1996) cauliflower coral colonies present in census areas. The identities and body sizes of fishes engaged in agonistic interactions (chasing bouts) were also noted during the timed censuses, as was relative dominance (identities of aggressor and aggressee). Densities of cauliflower coral were estimated from counts made each census within the fixed-area plots.

Data derivations and statistical analyses

Differences in overall densities among species, and size distributions within species, required the use of a standardized recruitment metric for our evaluation of among-species patterns. For each census, site, and species, a 'Recruit Index' (RI) was derived, using a ratio of the sum of all early YOY standardized by the sum of resident individuals tallied, as RI = 100 × (N_1 ≤ 4 cm / N_2 ≥ 5 cm), where fish ≤4 cm TL were defined as 'recruits' to the benthic population and fish ≥5 cm TL were considered post-recruit 'residents'. Evaluation of size-frequency plots indicated that arc-eye hawkfish ≤4 cm TL were half-yr-old or younger. For arc-eye hawkfish, we further evaluated temporal recruitment patterns based on the estimated densities of recruits, recruit densities standardized by long-term (22 yr) average recruit density at the regional scale (over all Core Sites), and both lagged and unlagged metrics based on the residuals of recruit densities regressed on resident densities. Densities of recruit and resident fish were estimated as the respective numbers of individuals tallied on each census divided by the area of the censused plot. Relations between log-transformed resident and recruit densities were evaluated using Proc AUTOREG in PC SAS v. 9.1.3 (SAS Institute 2006). Nonparametric regression (SAS Proc GAM) was used to relate each of the various recruit metrics to census date and evaluate temporal patterns. Spline curves, based on moving averages of the last 3 values, were fit using SAS Proc LOESS to visualize fits of the nonparametric regressions. To evaluate whether resident arc-eye hawkfish facilitated recruitment of conspecifics, the relative numbers of recruit and resident fish that co-habited colonies of cauliflower corals were compared using contingency chi-square (Zar 1984). The electivity or preference (relative use versus availability) of cauliflower coral and other substrata were evaluated using a Manly et al. (2002) resource selection function (RSF). Aggression among conspecific arc-eyes and other species was evaluated using goodness-of-fit chi-square (Zar 1984). Other standard statistical procedures including 1-way nonparametric (Kruskal-Wallis, K–W) ANOVA (SAS Proc NPAR1WAY), parametric ANCOVA (SAS Proc GLM), and rank correlation (SAS Proc CORR) were used, as appropriate, to evaluate temporal and spatial effects on the RI and among the post-settlement factors listed in the next paragraph.

Since initial observations indicated persistently strong spatial differences in observed recruitment, we also explored whether the ratio of mortality rate

to growth rate (*M/K*; Wetherall et al. 1987) was related to recruit and coral metrics for arc-eye hawkfish. In part because predation is typically size-dependent, both mortality and growth are post-settlement factors that have potentially great influence on recruitment to benthic reef fish populations (Jones 1991, Hixon & Webster 2002, Hixon & Jones 2005). We assumed that *M/K* for resident fish was a valid proxy for the *M/K* of YOY between settlement and recruitment at a site and compared relative *M/K* rates of fully recruited (≥6–7 cm TL) resident arc-eyes at the 7 Core sites during 1990–2011, and at the 5 Other sites during 2000/02–2011. Analyses used data for all years pooled at each site, but were restricted to summer censuses to control for possible bias resulting from census efforts that differed among sites during fall-spring. At each site, we used length-specific abundances to estimate *M/K* by first fitting the relationship between the natural logarithm of abundance and cm-length class (Wetherall et al. 1987) using simple least-squares regression. We then re-ran the regression using predicted values of ln(abundance-at-length) to appropriately weight the length classes (Maceina & Bettoli 1998). A median count value among sites for fish measuring 6–7 cm was used to standardize intercepts. The specific prediction tested was that sites at which arc-eyes differed in resident mortality or growth should differ in *M/K*, i.e. plots for fish at sites experiencing greater rates of lengthspecific decline should exhibit steeper negative slopes than those for fish at sites with lower mortality or slower growth rates.

We further estimated the grand mean densities of resident arc-eyes as the mean of all summer density estimates (numbers 100 m^{-2}) at each site. Grand mean densities of *Pocillopora meandrina* coral were similarly derived and expressed. Finally, we compared *M/K*, RI, and resident arc-eye and coral colony densities using nonparametric correlation.

Simulation modeling

A biased random-walk dispersal model (similar to that of Polovina et al. 1999), combined with currents from an oceanic circulation model (Hybrid Coordinate Ocean Model, HYCOM; Bleck 2002) was used to simulate dispersal of the planktonic eggs and larvae of arc-eye hawkfish (unlike blenniids that spawn demersally, cirrhitids are pelagic spawners: Kadota et al. 2010) using input data for the summers of 2009, 2010, and 2011. High resolution current data were available for these 3 years only. For the description of

surface current velocities along west Hawaii Island, we used data for the entire flow field extending between Upolu Point in the north and South Point (Fig. 1) at a spatial resolution of 0.04 degrees and averaged within the uppermost mixed layer at 0 to 50 m depths. These depths were selected because the larvae of cirrhitids and salariine blenniids occur primarily at shallow (<20 to 40 m) depths within the upper-mixed layer off Oahu (Boehlert & Mundy 1996). Dispersal simulations were used to estimate the settlement destinations of eggs and larvae released from sites distributed among 5 km sectors along coastlines of all of the MHI, including the 160 km extent of the west coast of Hawaii Island between Upolu Point and South Point (Fig. 1). Virtual propagules were released at the shoreline (1 m isobath) but were not considered viable if they did not enter the flow field at a distance of 0.5 km offshore, because we lacked finer spatial resolution within the flow-field of our model. A planktonic larval duration of 45 d was defined for competent larvae of arc-eye hawkfish that settle (from the water column into coral shelter as miniature benthic fish), at a mean size of 2 to 2.5 cm TL and an age of 1 to 2 mo based on observed timing of peak spawning and settlement (E. DeMartini unpubl. data). We released 500 propagules each day from each of 302 sectors (sector length = 5 km) spanning coastlines of the entire MHI from Kauai to Hawaii Island during each of the three 3 mo (May to July) spawning seasons, and tallied settlers during the respective mid-June through mid-September settlement period (see 'Temporal patterns of recruitment' in Results). The larval dispersal simulation was repeated 5 times and evaluated for consistency. Specifically, the potential effects of the multiple releases, sector, and year on numbers of settlers were evaluated by 3-way *G*-tests (Proc CATMOD, SAS Institute 2006; Zar 1984). No swimming ability was assumed prior to Day 45, when larvae were assumed competent and capable of successfully settling at the nearest coast if at that time they were within 5 km distance of a coastline. We chose this conservative definition of a distance that is indicative of likely successful settlement (distances of 5 to 9 km or more have been used by others: e.g. Paris et al. 2007) because settlers are certainly capable swimmers based on their morphology, and because the ontogeny of swimming capabilities is unknown for cirrhitids and salariine blenniids (with the lone exception of *Salarius patzneri*: Fisher 2005) during the larval phase. Moreover, the ontogeny of swimming behavior differs greatly among the larvae of even closely related species of reef fishes (Leis 2010).

RESULTS

Use of cauliflower coral by the coral-sheltering guild

Three of the hawkfishes and 1 blenny species strongly elected cauliflower coral versus other available benthic substrata (Table 1). All 4 hawkfish species and both blennies, however, occupied colonies of cauliflower coral to some extent as recruits or resident fish. One species — the stocky hawkfish or po`opa`a *Cirrhitus pinnulatus* — was the only exception for which the use of coral by recruits could not be evaluated because no likely recruits (no individuals ≤10 cm TL) were observed. Arc-eye hawkfish dominated numerically (>92% of all fish; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m485p165_supp.pdf). Only rarely (in 4% of 62 625 sightings of arc-eyes in coral heads) were groups of 2, 3, or, very rarely, 4 individuals seen cohabiting the same coral colony. However, 1 or more recruits were present with 1 or more resident conspecific arc-eyes in a disproportionately high number of instances (>8% of 2500 groups; contingency $\chi^2 = 87.5$; df = 1, p < 0.0001). More than 1 species occupied a single coral colony in only 50 instances; arc-eyes were present in such colonies in proportion to their relative abundance (46 cases, one-way goodness-of-fit $\chi^2 <$ 0.003; df = 1, p > 0.9). Overall occupancy of cauliflower coral colonies by this guild of fishes was low

and variable (on average 1 occupied coral for every 1 to 5 dozen unoccupied coral colonies, depending on site).

The density of cauliflower coral was positively correlated with the densities of both recruit (Spearman's rank correlation, $r_S = +0.76$, p = 0.004) and resident ($r_S = +0.89$, p < 0.0001) arc-eye hawkfish for all sites and years pooled. Coral densities differed among all 12 sites (1-way K–W ANOVA, $\chi^2 = 115.2$; df = 11, p < 0.0001), including some of the 7 Core sites ($\chi^2 = 29.8$; df = 6, p < 0.0001). The density of cauliflower corals of suitable shelter size generally increased from about the mid-1990s until 2001 (grow-out of 1993 coral recruits after substrate disturbance by Hurricane Iniki in September 1992: E. DeMartini unpubl. data) and declined thereafter (nonparametric regression, p < 0.0001). Grand mean percent cover of cauliflower coral was 18%, with site means ranging from 14 to 25%.

Temporal patterns of fish recruitment

There was a general seasonality to recruitment, even though some reproduction apparently occurs throughout the year. There was a pervasive, recurrent pattern of greater RIs during summer, both for arc-eye hawkfish (+29%; maximum likelihood [ML] $\chi^2 = 32.7$, df = 1, p < 0.0001) and for the aggregate of the other cirrhitids and 2 blenniids (+34%;

Table 1. Summary statistics for the use and availability of, and electivity (preference) for cauliflower coral *Pocillopora meandrina* or other benthic substrata (if preferred), for the recruits and residents pooled of arc-eye hawkfish and each of 5 other species of coral-sheltering fishes observed at the North Kohala (west Hawaii Island) sites during 1990–2011

Species	% use[a] of cauliflower coral	Preferred substratum	% use[a] of other preferred substrata	Electivity[c]	p-value
Arc-eye hawkfish *Paracirrhites arcatus*	61 860/64 193 = 96.4	Cauliflower coral	n/a[b]	5.27	<0.0001
Blackside hawkfish *Paracirrhites forsteri*	1053/1503 = 70.1	Cauliflower coral	n/a[b]	3.88	<0.0001
Redbarred hawkfish *Cirrhitops fasciatus*	112/379 = 60.7	Cauliflower coral	n/a[b]	1.70	<0.0001
Stocky hawkfish *Cirrhitus pinnulatus*	13/168 = 7.7	Limestone	80.4	1.37	<0.0001
Scarface blenny *Cirripectes vanderbilti*	181/1293 = 14.0	Encrusting coral	24.6	1.13	0.05 > p > 0.01
		Limestone	61.2	1.06	0.001 > p > 0.01
Leopard blenny *Exallias brevis*	328/427 = 76.5	Cauliflower coral	n/a[b]	4.18	<0.0001

[a]Substratum use: 'perch' occupied by an individual fish when first encountered on a given survey; % use defined as the proportion of the specific substratum occupied relative to the total number of substratum occupancies tallied for the species.

[b]n/a: other substrata are not preferred.

[c]Electivity ('preference') of a substratum based on the ratios of use versus availability (defined as the cover of a substratum as a percentage of total cover of all benthic substrata) over all sites; i.e. for each species, defined as the relative proportion of substratum-specific occupancies versus the proportion of total benthic cover represented by that specific substratum, expressed as a resource selection function (RSF; Manly et al. 2002)
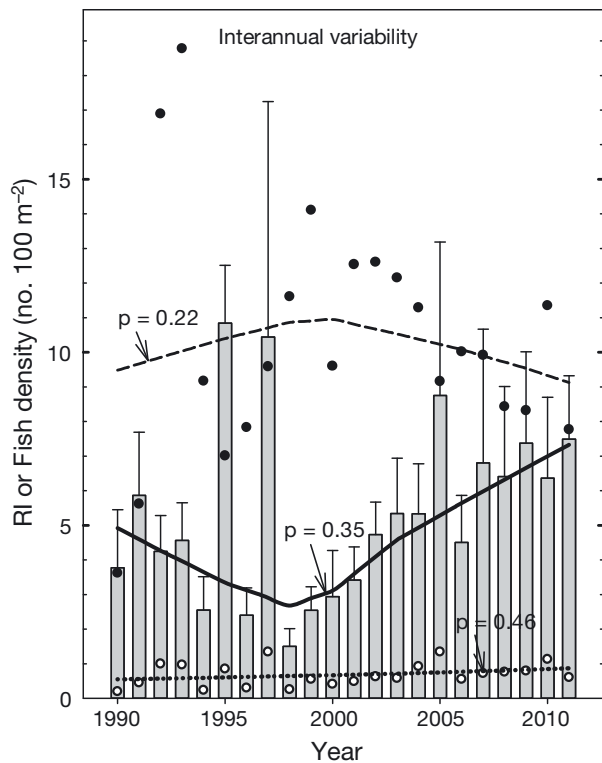
Fig. 2. *Paracirrhites arcatus.* Interannual variability in esti-
mated mean (+SE) recruit index (RI, histograms and solid
trend line), mean recruit densities (hollow circles and dotted
trend line), and resident densities (filled circles and dashed
trend line) at the pooled 7 Core Sites, North-South Kohala
Coast, west Hawaii Island, that were monitored during 1990
through 2011. SEs of the RI based on a constant n = 7 sites
surveyed in each year. Trend lines for the RI, recruit densi-
ties, and resident densities were LOESS-fitted using Proc
GAM nonparametric regression. Regressions with apparent
but insignificant (Bonferroni-corrected: p < 0.05/3 < 0.0167)
trend are labeled by p-value, where p-values indicate the
probability of Type I error

ML χ^2 = 4.7, df = 1, p < 0.015) (see Fig. S2 in the
Supplement at www.int-res.com/articles/suppl/m485
p165_supp.pdf).

Recruitment of arc-eye hawkfish varied inter-
annually but without a significant long-term trend
(Fig. 2). There were no detectable annual differ-
ences in arc-eye recruitment, based on summer
censuses spanning all 22 years at the 7 Core Sites
pooled (1-way K–W ANOVA, year effect on RI: χ^2 =
29.3, df = 21, p > 0.10). Recruitment appeared high-
est (RI > 10) in the summers of 1995 and 1997 and
lowest (<3.0) during all other years during the sec-
ond-half of the 1990s, but the overall temporal trend
in the RI was statistically insignificant (nonparamet-
ric regression, p = 0.35; Fig. 2) despite an apparent
7-fold variation over all 22 years at the 7 Core Sites.

This index varied less (15% of the max.), however,
when averaged over these 7 sites during the last 3
years of the time series (2009–2011) for which cur-
rent data were available to simulate settlement.
Arc-eye recruitment gauged by recruit density like-
wise varied an apparent 7-fold (nonparametric
regression: p = 0.46; Fig. 2) among all years, but
<50% during the last 3 years at the 7 sites. Results
were consistent whether based on the RI, directly
on recruit density, or based on the residuals of
lagged recruit versus resident densities because of
the generally high correlation among metrics (all
p < 0.001). Since results using recruit densities and
the residuals from regressions of recruit versus resi-
dent arc-eye densities generally agreed with those
using the RI, we henceforth report RI values only
unless results using the other metrics differed quali-
tatively or further specification was otherwise
necessary.

Spatial and species-specific patterns of recruitment

Observed recruitment levels were low and variable
among sites for all fishes in the guild, with RIs aver-
aging 3.7% over all sites pooled and ranging >5-fold
from 1.6 to 8.9% among sites for arc-eye hawkfish
(Table 2). Among species, RIs ranged from an aver-
age min. of 2.6% for leopard blenny to an average
max. of 11.4% for scarface blenny. Variability was
especially pronounced if censuses during all periods
of the year, including the 'Other' (fall-spring) period,
were included. For example, a unique recruitment
spike in arc-eye hawkfish was encountered at the 20
Puako Beach Drive site in late September 1997 (RI =
78; see Fig. S3 in the Supplement at www.int-res.
com/articles/suppl/m485p165_supp.pdf).

Recruitment levels differed for arc-eye hawkfish
among the 7 Core sites (1-way K–W ANOVA, site
effect on RI: χ^2 = 63.5, df = 6, p < 0.0001). Long-term
mean densities of recruit arc-eyes varied >30-fold
among sites, from 0.07 to 2.2 recruits 100 m^{-2}. Resi-
dent and recruit abundances were highly correlated
over all years at all sites (r^2 = 0.77 to 0.99, all p <
0.005), with a numerical response by residents best
described by a lag of 1 yr (Durbin-Watson D = 0.99,
positive first-order autocorrelation = 0.34, p = 0.003).
Recruitment of this species in the general Kawaihae
region was relatively low, whereas recruitment at
the 3 North Kohala sites was relatively high. Of the
latter, only the Crystal Cove and Kohala Ranch sites
near the North-South Kohala border exhibited
strong, monotonically increasing RIs over time — but

Table 2. *Paracirrhites arcatus*. Summary statistics for recruit indices (RI), the slopes of length-specific abundances regressed on length-class (mortality/growth ratios, *M/K*); densities of resident fish; and densities of cauliflower coral, based on censuses, by site and period of study. Data are mean ± SE. Site names are cross-referenced by number and ordered (1 to 12) from upcoast (northwest) to downcoast (south) along the North and South Kohala Coast of west Hawaii Island. Sample size (n) based on the number of summers censused at the site for RI, resident fish densities, and for coral densities but based on least-squares regression of ln abundance vs. length class for *M/K* (n = 8)

Site	Coordinates (°N, °W)	Study period	RI[a] (n)	(M/K)[b] (n = 8)	Fish density[c]	Coral density[d]
(1) Lapakahi MLCD	20.17823, 155.90098	1990–2011	8.39 ± 1.21 (22)	−0.997 ± 0.050	14 ± 1.3	294 ± 33
(2) Kohala Ranch Cove	20.07443, 155.86065	1990–2011	7.20 ± 1.24 (22)	−1.107 ± 0.086	3 ± 0.3	159 ± 26
(3) Crystal Cove	20.06113, 155.84933	1990–2011	8.88 ± 1.39 (22)	−1.078 ± 0.061	28 ± 2.6	858 ± 123
(4) First Sister	20.05656, 155.84450	2000–2011	2.62 ± 0.52 (12)	−1.018 ± 0.051	22. ± 3.3	810 ± 50
(5) White Pipe Point	20.05569, 155.84401	2001–2011	4.66 ± 1.26 (11)	−0.982 ± 0.046	32 ± 5.2	1279 ± 68
(6) Mauna Kea	20.00219, 155.82767	2001–2011	3.91 ± 0.61 (11)	−0.850 ± 0.071	14 ± 0.7	532 ± 48
(7) Kanekanaka Bench	19.98315, 155.82914	1990–2011	1.64 ± 0.40 (22)	−0.663 ± 0.061	4 ± 0.2	169 ± 11
(8) Beach 69	19.98161, 155.82914	1990–2011	2.48 ± 0.50 (22)	−0.780 ± 0.056	3 ± 0.2	168 ± 14
(9) 20 Puako Beach Drive	19.97208, 155.84191	1990–2011	6.53 ± 2.26 (22)	−1.054 ± 0.101	15 ± 1.3	252 ± 30
(10) Puako End-of-Road	19.95857, 155.85850	1990–2011	2.49 ± 0.66 (22)	−0.973 ± 0.067	4 ± 0.5	69 ± 7
(11) Holoholokai Beach Park	19.95607, 155.86097	2000–2011	3.35 ± 0.67 (12)	−1.060 ± 0.076	31 ± 4.9	607 ± 61
(12) Mauna Lani	19.94391, 155.87321	2002–2011	5.81 ± 1.08 (10)	−0.976 ± 0.067	3 ± 0.3	155 ± 15

[a]RI = 100 × (N$_1$ recruit fish ≤4 cm TL / N$_2$ resident fish ≥5 cm TL)

[b]*M/K* = slope of least-squares regression of the natural logarithm of the number of individuals tallied, by cm TL length-class, for all arc-eye hawkfish individuals ≥6–7 cm TL encountered on summer (July to September) surveys during the study period

[c]Fish density = N 100 m^{-2} of resident (≥5 cm TL) arc-eye hawkfish, averaged over all summer (July to September) censuses at the site

[d]Coral density = N colonies 100 m^{-2} bottom area, of cauliflower coral *Pocillopora meandrina* (≥15-cm diameter: DeMartini 1996), throughout all habitat within census plots

only during the second decade (Figs. 3 & 4) — as the numbers of recruit conspecifics increased while the numbers of residents decreased (for site-specific patterns, see Fig. S4 in the Supplement at www.int-res.com/articles/suppl/m485p165_suppl.pdf). Patterns of variations among most of the remaining sites were similar whether examined during the second decade only at all 12 sites (Fig. 3) or over all 22 yr at just the 7 Core sites (Fig. 4). Spatial differences were persistent at the low as well as the high recruitment sites; an increasing trend at the high recruitment sites pooled was not significant overall (accept H_0: no temporal trend, p = 0.16; Fig. 5). We emphasize that there was no evidence that overall recruitment at the high recruitment sites was decreasing over time or that recruitment at the low recruitment sites was generally increasing over time (p = 0.13; Fig. 5).
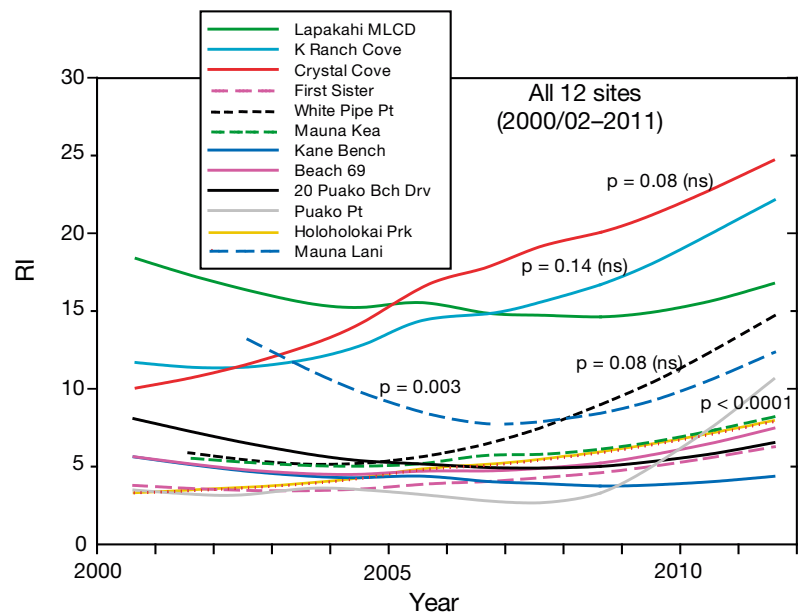

Fig. 3. *Paracirrhites arcatus*. Trend lines of recruit index (RI) during summer (July to September) seasons at each of all 12 sites, North-South Kohala Coast, west Hawaii Island, that were monitored during 2000–02 through 2011. Sites with significant (Bonferroni-corrected: p < 0.004, as 0.05/12) or apparent but insignificant (ns: 0.004 < p < 0.10) trend are labeled by p-value, where p-values indicate the probability of Type I error
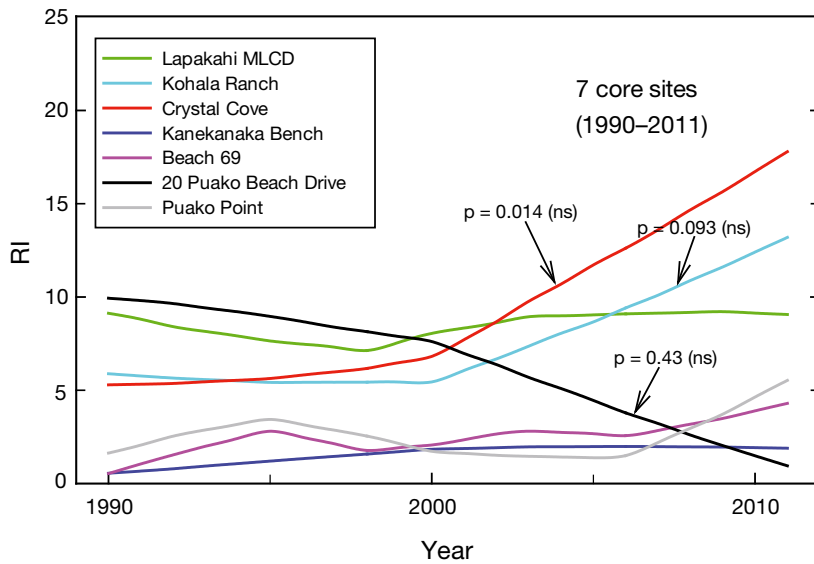
Fig. 4. *Paracirrhites arcatus*. Trend lines of recruit index (RI) during summer (July to September) seasons at each of the 7 Core Sites, North-South Kohala Coast, west Hawaii Island, that were monitored during 1990 through 2011. Sites with significant (Bonferroni-corrected: p < 0.007, as 0.05/7) or apparent but insignificant (ns: 0.007 < p < 0.10) trend are labeled by p-value, where p-values indicate the probability of Type I error

Post-settlement mortality/growth, resident densities, and aggression

Based on length-specific abundances, the M/K estimates for fully recruited (≥6–7 cm) resident arc-eye hawkfish differed among the 7 Core sites and 5 Other sites, based on the 22 and 10 to 12 yr, respectively, of summer censuses (1-way ANCOVA, slope effect, $F_{11,72}$ = 5.60, p < 0.0001; illustrated for each of the 12 sites by Fig. S5 in the Supplement at www.int-res.com/articles/suppl/m485p165_suppl.pdf). The magnitude of M/K also was correlated with the RI (r_S = 0.71, p < 0.01; Table 2), mainly because the pair of sites with the least negative M/K (shallowest slopes) had the lowest RI, and the 2 sites with the most extreme M/K (steepest slopes) had the highest RI (Fig. 6).

Mean densities of resident arc-eyes also differed spatially (10-fold from <3 to 28 fish 100 m^{-2}) among sites (1-way K–W ANOVA, site effect: χ^2 = 118.8, df = 6, p < 0.0001; Table 2), but not among years (1-way K–W ANOVA, year effect: χ^2 = 15.0, df = 21, p = 0.83). Estimates of resident densities varied 5-fold (from 4 to 19 fish 100 m^{-2}) among years and appeared to first increase, then decrease (Fig. 2), but a non-monotonic temporal pattern was not significant (nonparametric regression: p = 0.22). Resident arc-eye densities were uncorrelated with M/K (r_S = −0.45, p = 0.14) and the

RI (r_S = 0.27, p = 0.40), although correlated with recruit density per se. Total cauliflower coral density and RI also were uncorrelated (r_S = 0.24, p = 0.44).

Intraspecific aggression occurred in arc-eye and redbarred hawkfishes and leopard and scarface blennies. Nearly all arc-eye aggression involved resident conspecifics only (106 of 109 agonistic bouts); 81.1% of these 106 bouts were directed at smaller individuals (goodness-of-fit χ^2 = 41.1, df = 1, p < 0.001). On only 2 occasions was a recruit arc-eye seen being attacked by a resident conspecific, and only once was a recruit seen attacking another (equal-sized) recruit. Interspecific aggression was observed for 3 of the 6 shelter guild members (arc-eye, redbarred, and blackside hawkfishes); in 66 of 69 total cases (all sites and years pooled), arc-eyes were the aggressor, and, in 60 of the 66 cases, the aggressee was a species of wrasse, damselfish, or goatfish that shared the arc-eye diet of benthic and planktonic crustacean prey, rather than just another coral shelter-guild member, an herbivore, or a coral-
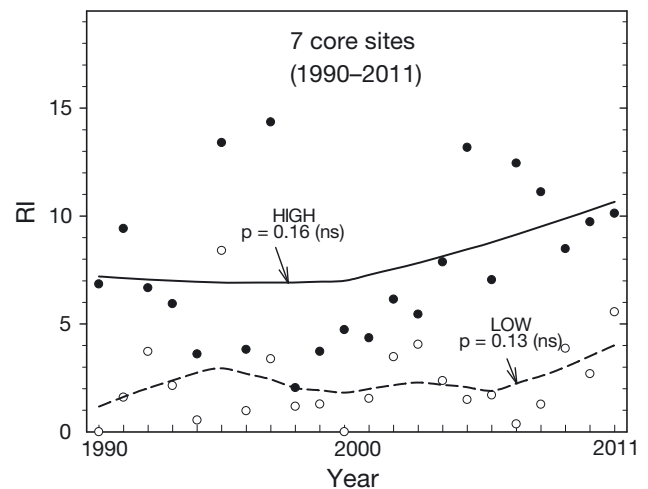

Fig. 5. *Paracirrhites arcatus*. Scatterplot and trend lines of recruit index (RI) during summer (July to September) seasons at the 4 'HIGH' (pooled) and the 3 'LOW' (pooled) of the 7 Core Sites, North-South Kohala Coast, west Hawaii Island, that were monitored during 1990 through 2011. p-values indicate the probability of Type I error. Filled and hollow circles: 'HIGH' and 'LOW' sites, respectively
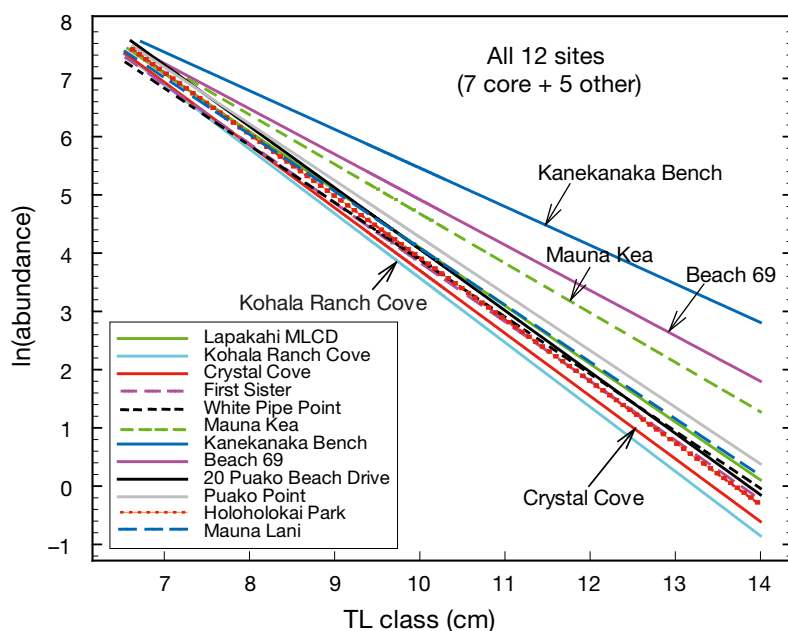
Fig. 6. *Paracirrhites arcatus*. Plots of ln(abundance) (numbers of resident fish tallied on timed fixed-area censuses) regressed on total length (TL, cm) class, truncated at the first, fully recruited (6–7 cm TL) length class to produce slopes representing the resident mortality/growth (*M/K*) rate. Regressions used all available summer census data at each of the 7 Core and 5 Other sites

livore (p < 0.001). Agonistic observations were too infrequent to evaluate possible site and year effects. For additional information on species interactants, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m485p165_supp.pdf.

Simulated currents and larval dispersal

Flow vectors of currents varied appreciably nearshore along the 26 km coast in which recruitment was empirically monitored. Currents had generally higher velocities along the Kohala Peninsula, to the north-northwest (upcoast) of the Kawaihae region (Fig. 7). Even though nearshore surface currents are low (relative to offshore surface currents) everywhere along Hawaii's west coast, the dearth of current vectors adjacent to the coast near Kawaihae (Fig. 7) illustrates the relatively poor nearshore water circulation in this region. Average current velocities also varied among May to September periods of the 3 years, with patterns in 2009 and 2010 more similar to one another than to the pattern in 2011 (Fig. 7).

Simulation results generally agreed with the spatial pattern of observed recruitment. The magnitude of simulated settlement by larvae varied among sectors of the west Hawaii coast that included the empirically monitored sites (3-way *G*-test on release series, sector, and year-by-sector effect: ML χ^2 = 313 [5-sector model], df = 4; ML χ^2 = 551 [8-sector model], df = 7; both p < 0.0001). The sectors centered on the North Kohala sites (Lapakahi, Kohala Ranch-Crystal Cove) had the overall highest simulated settlement, followed by the South Kohala sectors in the Puako region and at Mauna Lani (Table 3). The sector including the census sites in and near the Waialea Bay Marine Life Conservation District (MLCD; Kanekanaka Bench, Beach 69, Mauna Kea) near Kawaihae consistently received the lowest numbers of simulated larvae (Table 3).

Simulated settlement varied more greatly over time than observed recruitment did, but the potential effects of space-time interaction and release series did not compromise evaluation of our simulations. Simulated settlement varied among years (3-way *G*-test, yr effect: ML χ^2 > 8000, df = 2, p < 0.0001). Interestingly, the overall magnitude of simulated larval settlement in sectors including the 12 sites that were monitored during the last decade varied >5-fold among July to September periods of the last 3 years (Table 3). Despite a significant (p < 0.0001) sector–by–year interaction, the strength of the sector effect appeared sufficient to justify pooling years to represent spatial patterns (Figs. 7 & 8). The effect of release series was insignificant whether based on just the 5 sectors having monitored sites or on all 8 sectors spanning the North-South Kohala Coast (5-sector model: p = 0.39; 8-sector model: p = 0.29). Patterns based on sample sizes of 500 were robust; a sensitivity analysis was performed and releases of 100 to 2500 propagules site[-1] d^{-1} yielded identical probability matrices (data not shown).

Simulated settlement varied appreciably along the Hawaii Island coastline, including the west coast (Fig. 8). Predicted settlement was generally greater at and near headlands, including the Kohala Peninsula, and most notably at and near several points farther downcoast to the south (Keahole and Kauna Points) versus away from these geological features (Fig. 8).
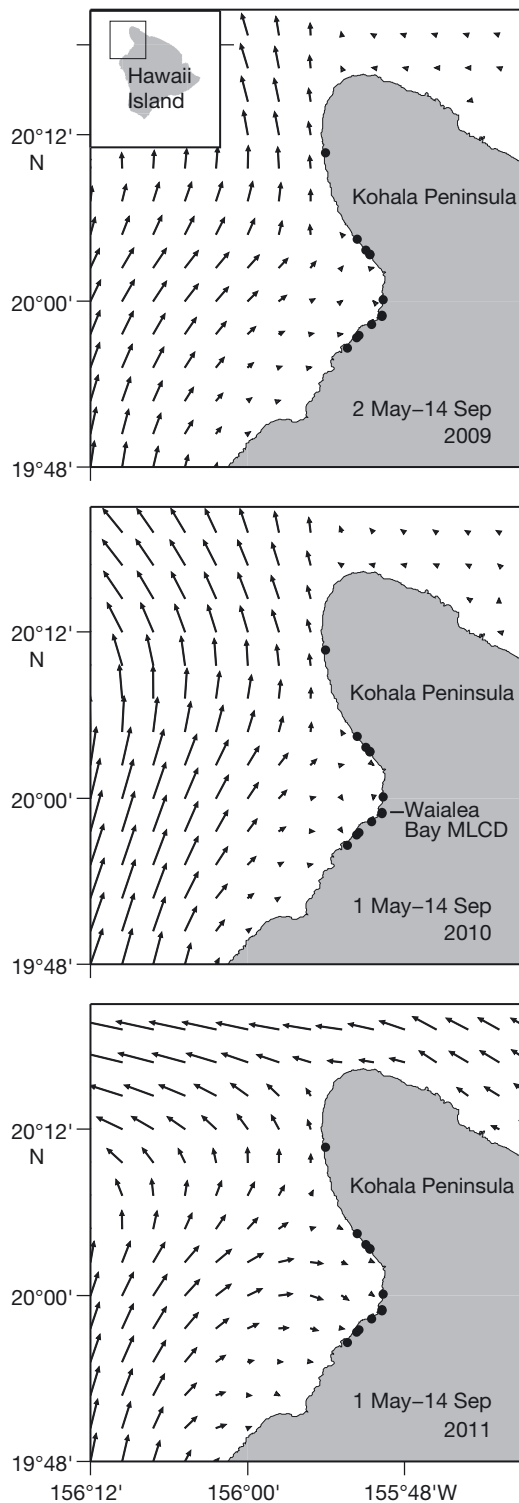
Fig. 7. Flow vectors of currents generated along the North-South Kohala Coast, west Hawaii Island, during the spring-summer (May to mid-September) spawning-settlement seasons of 2009, 2010, and 2011. Vectors generated by running the Hybrid Coordinate Ocean Model (HYCOM; Bleck 2002). Solid circles: the 12 sites at which recruitment was empirically monitored (2 sites obscured by compressed scale)

Table 3. Numbers of simulated virtual larvae that successfully settled, for each summer (July to September) period during 2009, 2010, and 2011, within each of the eight 5 km sectors of the North-South Kohala Coast, west Hawaii Island. **Bold**: sectors (n = 5) within which the 12 empirically monitored sites occurred

Sector	2009	2010	2011	Sum of 3 yr
300[a]	**4186**	**2326**	**454**	**6966**
299	4715	2380	518	7613
298	5123	2589	591	8303
297[b]	**4168**	**2005**	**613**	**6786**
296	2987	1528	593	5108
295[c]	**2447**	**1561**	**692**	**4700**
294[d]	**3532**	**2356**	**822**	**6710**
293[e]	**3586**	**2550**	**839**	**6975**
Sum of 5 sectors	17919	10798	3420	32137
Sum of 8 sectors	30744	17295	5122	53161

[a]Sector including the Lapakahi Marine Life Conservation District (MLCD) site
[b]Sector including the Kohala Ranch, Crystal Cove, First Sister, and White Pipe Point sites
[c]Sector including the 2 sites (Kanekanaka Bench, Beach 69) within the Waialea Bay MLCD and the adjacent Mauna Kea site
[d]Sector including the 20 Puako Beach Drive and Puako Point sites in the Puako FRA and the adjacent Holo-holokai Beach Park site
[e]Sector including the Mauna Lani site

DISCUSSION

Empirical recruitment patterns

Although several species in this coral-sheltering guild did not prefer cauliflower coral over other benthic substrata, all species associated with cauliflower coral to some extent and provided a meaningful common basis of comparison. That recruitment differed inter-annually was expected; such variations are typical in tropical marine reef and other fishes (reviewed by Doherty 2002). The seasonality in recruitment that we observed for arc-eye hawkfish and the other guild members is consistent with the predominantly late winter through spring spawning and summer settlement periods recognized for many Hawaiian reef fishes (Walsh 1987, DeMartini 1996, DeMartini & Anderson 2007). Although our observations indicate that some spawning occurs throughout the year, the average one-third greater recruitment that we observed during July to September periods justify our focus on the summer season of most larval production by these species.

Our 22 yr time series was sufficient to establish that recruitment varies spatially among census sites and
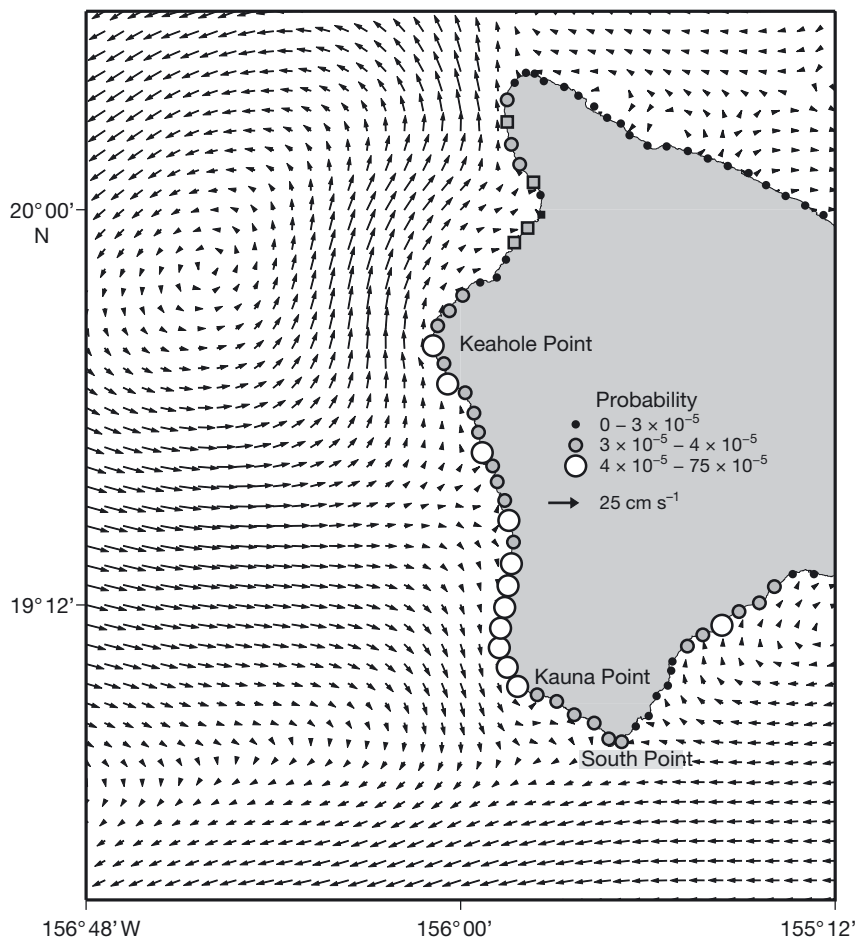
Fig. 8. Simulated successful settlement for virtual larvae along the west coast of Hawaii Island; larvae were released at approximately 5 km intervals (in 'sectors') along shorelines of all of the main Hawaiian Islands (MHI), including the entire west coast of Hawaii Island, during May through July of 2009, 2010, and 2011. Projected settlement generated by running a particle dispersal model combined with currents from the Hybrid Coordinate Ocean Model (HYCOM; Bleck 2002). Squares: simulation sectors having empirically monitored sites; circles: sectors lacking monitored sites. Larvae were released from all sectors equally in the simulations

Post-settlement factors

Length-specific abundances that vary alongshore among sites are consistent with rates of predation, growth (competition), or both that also vary among sites for arc-eye hawkfish. Our observation that M/K rates and recruitment of this species were related among sites further suggests that post-settlement processes also partly contributed to the persistent, site-specific differences in recruitment that we documented. It is important to note that, for these populations of arc-eye hawkfish, the lagged numerical responses in resident densities that we observed represent year-class effects (positive), rather than density-dependent suppression of recruitment by residents (negative). Obviously, the latter can be important for other species (Hixon & Webster 2002, Hixon et al. 2012) and might be important for arc-eye populations elsewhere.

The observation that recruit arc-eye hawkfish disproportionately cohabit cauliflower coral colonies with resident conspecifics suggests that the latter either tolerate the presence of settlers or, more likely, facilitate settlement (Anderson et al. 2007). Habitat quality (density of coral colonies) differed among sites but was uncorrelated with the RI even though both recruit and resident arc-eye densities were strongly correlated with coral density and with one another. Also, there is at most

that these spatial differences are persistent and predictable despite large overall variation in recruitment magnitude among years. Persistent spatial differences in recruitment suggest that either presettlement factors (such as the transport of larvae by currents) differ alongshore in consistent manner or that one or more post-settlement factors (such as predation or competition) persistently differ among sites and importantly modify settlement (Hixon & Jones 2005). Our observation that arc-eye recruitment actually varied only 15% (based on the RI) to 46% (based on recruit densities) among the last 3 years, while simulated settlement varied more than 5-fold, is consistent with a dampening of settlement variation by post-settlement factors.

a weak positive relation between the presence of multiple arc-eyes in a coral head and the size of coral head (E. DeMartini pers. obs.). Altogether, this suggests that, if intraspecific competition exists in these arc-eye populations, competition for shelter is weak. Intraspecific aggression is not uncommon among adult arc-eye hawkfish and often involves reproductive territoriality (DeMartini 1996). Given the likely interference competition between arc-eyes and other species for food resources (see below, this section), it is possible though that a presently unknown proportion of arc-eye intraspecific aggression is unrelated to reproduction.

Our observations of interspecific aggression suggest that other post-settlement factors such as

interference competition among feeding guild members might be important. The low levels of occupancy of cauliflower corals by the fishes of this coral-sheltering guild further suggests weak interspecific competition for shelter. Our observations of interspecific aggression among members of the benthivore-planktivore feeding guild suggest, rather, that arc-eye hawkfish are competing with other species for food. Regardless of the mechanism, it is nonetheless clear that post-settlement processes on the reef, as well as transport prior to settlement, importantly influence recruitment of the arc-eye populations we studied. Even if site differences in recruitment were entirely a result of transport phenomena, however, our empirical data by themselves cannot be used to distinguish between differences that represent the result of accumulation due to retention of locally produced larvae, the result of persistently higher rates of transport of larvae produced elsewhere to certain sites, or some measures of both. Further research is needed that links larval sources and settlement sites.

Simulation findings

Surface currents along the west Hawaii coastline primarily represent eddy flows generated by prevailing E-NE trade winds that wax and wane seasonally; both cyclonic (counter-clockwise) and anti-cyclonic (clockwise) eddies make contact to some extent along the entire west Hawaii coast, with cyclonic eddies predominating north of Keahole Point (about mid-island) and anti-cyclonic eddies occurring mostly south of Keahole Point (Jia et al. 2011). The duration of these eddies can be as long as several months (Patzert 1969). Simulated dispersion results using pooled input data for the summers of 2009, 2010, and 2011 indicate that settlement 'hot spots' exist and that these occur at and near geomorphological features. Perhaps because these features are exposed to faster currents of trade wind-generated mesoscale eddies, they intercept greater numbers of larvae overall per unit time. These same coastline features might also promote larval retention through the formation of smaller-scale localized eddies (e.g. Morgan et al. 2009b, Harrison et al. 2013). Thus, the correspondence that we found between velocities of surface currents contacting on the coastline and the position of settlement 'hot-spots' is consistent with accumulation as a result of transport from elsewhere, with localized retention

of larvae in eddies caused by habitat features, or with both factors.

Simulated transport and settlement results at our monitored sites differed among the 3 consecutive summers for which input data exist, but spatial patterns were very similar during 2009 and 2010; the latter is consistent with our empirical observations of persistent spatial patterns in recruitment among years. Our findings for the summers of 2009–2011 are further consistent with those of Christie et al. (2010), who used HYCOM simulations of surface currents along the west Hawaii coast during June to August 2006 to evaluate connectivity of yellow tang surgeonfish *Zebrasoma flavescens*, the major ornamental species in Hawaii.

Comparisons of empirical observations and simulations with prior studies

Our observations of generally faster surface current flows along the Kohala Peninsula imply that the delivery rates of planktonic larvae are higher along this segment of coastline, assuming that larval supply is homogeneous across segments, compared to delivery rates within the geographically sheltered region near Kawaihae. Given higher delivery rates, it is reasonable that recruitment at these Kohala sites should be higher as observed. Results of our dispersal simulations further indicate that settlement of larvae during the summer season should be higher along the Kohala Peninsula versus the Kawaihae region; and our empirical recruitment data for 2009–2011 generally concur. Simulation results indicate that settlement should be higher still at and near additional headlands, farther downcoast of our census sites along west Hawaii Island.

Other empirical studies have shown that settlement of planktonic larvae is higher at or near headlands, but most of these studies have been in the temperate zone and many are for invertebrate, not fish larvae (Wing et al. 1995a,b, 2003, Graham & Largier 1997, Roughan et al. 2005, Morgan et al. 2009a,b). The preponderance of these are case studies within regions of intense periodic upwelling such as near headlands north of Point Conception in California; examples include cases that implicate accumulation resulting either from the reseeding of locally produced larvae in the lees of headlands (e.g. Mace & Morgan 2006a) or greater delivery rates of planktonic larvae produced elsewhere to headland shores (e.g. Mace & Morgan 2006b). Eddy formation off of west Hawaii Island generates cells

of upwelled water (Jia et al. 2011) that either may or may not augment nutrient availability and increase local productivity. Interestingly, Allen et al. (2007) documented persistently higher abundances of larger YOY white seabass (F. Sciaenidae) along the Palos Verdes Peninsula, a major headland within the Southern California Bight; their findings document generally higher recruitment near a headland within a region that does not experience persistent upwelling.

The issue of reseeding versus distance-dispersal, of course, has more general biophysical implications than proximity to benthic habitat features (Warner & Cowen 2002). Paris & Cowen (2004), for example, described local retention of reef fish larvae resulting from the interaction between vertically stratified oceanic currents and vertical migration of larvae (ontogenetic changes in behavior). These and other theoretical and empirical studies present strong evidence that much of the variance in recruitment of benthic marine populations can be explained by dynamic transport processes rather than solely biological processes in the plankton. In a recent study of recruitment patterns in another guild of deeper-dwelling (10 to 12 m) ornamental fishes on west Hawaii reefs, Fox et al. (2012) detected few significant relationships between recruitment magnitude and various potential oceanographic and meteorological variables (chlorophyll-a; presence of cold-cyclonic eddies and upwelling indicated by sea surface temperature or the generic presence of eddies indicated by sea surface height). Fox et al. (2012) observed significant negative correlations (between the presence of cold-core eddies and 2 mo lagged abundances of YOY of the 5 most abundant species) that explained little of the observed total variance in recruitment. Perhaps Gaines & Bertness' (1992) now-decades-old assertion that transport processes can trump other pre-settlement mechanisms such as predation on or food limitation of larvae is correct after all. Our data for arc-eye hawkfish and those of Fox et al. (2012) are consistent with this assertion, and our data further illustrate that the post-settlement processes of predation or interspecific competition can indeed modify settlement patterns that are driven by transport processes. The importance of post-settlement processes as well as transport processes as determinants of recruitment that are illustrated by our study indicates the need to design and conduct more comprehensive 'recruitment' surveys in the future that also include study of the comparative demographics of post-settlement versus post-recruitment life-history stages.

Implications for marine protected areas site-selection

Demonstration of predictable, persistently high recruitment near geomorphological features like headlands is valuable information when siting protected areas. Additional no-take marine protected areas (MPAs) have been recommended for the MHI (Friedlander et al. 2007). For MPAs to be effective, they need to produce (outsource) as well as receive dispersive propagules (whether self-seeded or produced elsewhere), produce ('spillover') exploitable stages that emigrate beyond their boundaries (DeMartini 1993), or they need to do both, to replenish the spawning stocks within them (Carr & Reed 1993). Stamoulis & Friedlander (2013) recently demonstrated spillover from a no-take MPA on Oahu while suggesting that propagule export was likely the more important function.

Our recruitment time series has documented persistent, site-specific patterns of recruit and resident arc-eye hawkfish abundance over 2 decades across 7 Core Sites in regions of the North-South Kohala coast, representing a range of management types. Our data also suggest a recent (year 2000+) change in dynamics at some but not other sites, both in open-access areas and within State of Hawaii MLCD and Fish Replenishment Areas (FRAs) in which the extraction of ornamental fishes has been prohibited since before or after 1999 (Tissot et al. 2004, Williams et al. 2009). The abundance of resident-stage arc-eyes either has not increased or has trended lower in recent years at sites within the Lapakahi MLCD, Waialea Bay MLCD, and Puako FRA no-take areas and has appeared to decline at some sites in other (open-access) areas as well. The latter sites are distant from traditional collection areas near Kailua-Kona and the Keahole (Kona) Airport that have supported most effort in the west Hawaii ornamental fishery (Walsh et al. 2003) and are relatively little fished. A major sedimentation event (runoff from heavy rainfall that broached land construction barriers) in October 2006 (S. Cotton pers. comm.) has contributed to recently greater cauliflower coral mortality at some of the northern sites (Kohala Ranch Cove, Crystal Cove), and crown-of-thorns starfish predation on cauliflower corals increased at Holoholokai Park to the south after 2002 (E. DeMartini unpubl. data). Thus, the recent apparent declines in resident-stage arc-eyes at sites in open-access areas as well as MPAs are more likely to have been caused by loss of coral habitat than from extraction by the ornamental fishery. Habitat loss has been shown capable of over-

riding the protection afforded by MPAs (Jones et al. 2004).

With the caveat that no-take MPA protection might not be important for secondary species like arc-eye hawkfish and other species that contribute even less to the ornamental fishery, we suggest that proximity to prominent geomorphological features be considered as a criterion used to select the location of no-take MPAs for the conservation of intensively extracted ornamentals and other (consumptive extraction) species on the reefs of west Hawaii Island. The relevance of our observations and simulations for the placement of MPAs at other MHIs and on reefs outside of the Hawaiian Archipelago is presently unknown and is a topic in need of further research.

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