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Measuring recruitment of minute larvae in a complex field environment: The corallivorous nudibranch *Phestilla sibogae* (Bergh)

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Abstract

The nudibranch *Phestilla sibogae* feeds only on corals of the genus *Porites*. The nudibranch's minute (~200 μm) larvae are specifically induced to settle and metamorphose by a chemical cue released by the coral, causing the larvae to recruit to reefs composed predominantly of *Porites compressa*. In this study, we investigated temporal and spatial patterns of recruitment of *P. sibogae* into coral reefs in Kane'ohe Bay, HI. We collected heads of *P. compressa* at 3-week intervals for 3 years, brought them to the laboratory and maintained them in aquaria fed with filtered seawater for 2 weeks, and then examined them for the presence of juvenile *P. sibogae* that had grown large enough to be seen. We found that *P. sibogae* recruits to the *Porites* reefs of Kane'ohe Bay sporadically and unpredictably throughout the year. Although most coral samples contained no or very few *P. sibogae*, three periods of intense recruitment (90–450 juvenile *P. sibogae* kg^{-1} of coral) were recorded, all in different seasons. Size-frequency analysis of recruits on the coral revealed high rates of post-settlement mortality in the field, most likely due to predation. Given the short pre-competent larval period of *P. sibogae*, the low rate of flushing of Kane'ohe Bay and the patterns of recruitment observed, we conclude that this population of *P. sibogae* is essentially a self-recruiting one. Two of the sampled reefs were characterized by unidirectional flow, allowing us to test a model of transport of larvae of *P. sibogae* responding to dissolved coral cue in turbulent, wavy flow. The model predicts that more larvae will be transported into upstream portions of a reef than into downstream portions, a prediction confirmed by analysis of the field-recruitment data. Furthermore, field releases of larval mimic particles also showed that most mimics landed in the upstream areas of reefs and down among the bases of coral branches, rather than at their tips.

Keywords: Coral reef; Invertebrate larvae; Nudibranch; Recruitment

1. Introduction

Recruitment of animals into benthic marine communities, defined as the addition of new individuals to a population at some point after embryology and larval settlement, has been difficult to assess quantitatively for small, motile invertebrates. The minute size of most settling invertebrate larvae (<0.5 mm) results in equally small early juveniles that are difficult to locate in the field both because of their size and their typically cryptic behavior. Most data on field recruitment of benthic marine invertebrates have been obtained in studies of sessile species such as barnacles (e.g., Connell, 1961;

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Wethey, 1985; Strathmann et al., 1981), bryozoans (Yoshioka, 1982; Brumbaugh et al., 1994) and ascidians (e.g., Stoner, 1990; Hurlbut, 1991) that remain fixed at the site of their attachment and metamorphosis, and edible bivalves that are either sessile (e.g., oysters, Anderson, 1996) or burrowing (e.g., clams, Gunther, 1992). Other studies have focused on crustaceans that are typically large (>1.0 mm) at the time of their initial settlement (e.g., Forward et al., 1996). Motile marine invertebrate species for which some recruitment data are available include herbivorous sea hares (Sarver, 1979; Pennings, 1991), whose recruitment was counted on algal samples taken from the field, and subtidal sea urchins, similarly sampled (Tegner and Dayton, 1977). In this study, we investigated recruitment of the minute (~210 μm) larvae of the coral-feeding nudibranch *Phestilla sibogae* into the complex, three-dimensional structure of a coral reef.

1.1. Life history and larval settlement of P. sibogae

P. sibogae has a distribution across the tropical Pacific Ocean, where it feeds on corals of the genus *Porites* (Harris, 1975; Hadfield, 1977; Rudman, 1981). Its life history is well known (Harris, 1975; Hadfield, 1978; Miller and Hadfield, 1990; Miller, 1993). Hermaphroditic adults mate frequently and produce egg masses that contain 2000–4000 fertilized eggs, the number growing larger with the age and size of the egg-laying adult. Precompetent larvae hatch from the egg masses after 7–8 days at ~25 °C and swim in the sea for 2–3 additional days before achieving metamorphic competence (Hadfield, 1978). Although the larvae are capable of feeding on phytoplankton, they can achieve metamorphic competence and settle without feeding (Kempf and Hadfield, 1985). In laboratory tests, competent larvae settle and metamorphose in response to a small polar molecule secreted by their prey coral, *Porites compressa* (Hadfield and Pennington, 1990). Metamorphosis is rapid, being completed in less than 24 h, when the juveniles immediately begin to eat coral flesh (Hadfield, 1978, 2000). Juveniles require about 3 weeks to reach reproductive maturity, and adults usually survive about 2 months after the onset of egg laying (Miller and Hadfield, 1990; Miller, 1993).

The research reported here is part of a larger project that employs larvae of *P. sibogae* to explore the capacity of small larvae to effectively utilize dissolved settlement cues to recruit into a requisite habitat. Chemically cued larval settlement has been described for many different invertebrate species across a broad range of phyla, with almost all data being reported from laboratory experiments (Hadfield and Paul, 2001). However, "real world" investigations (in the field or in flowing water in a flume) are rare. Our investigation has included measuring the behavioral responses of larvae in the laboratory (Hadfield and Koehl, 2004) and their adhesion strength in a turbulent flow cell, as well as measuring the turbulent wave-driven flow over and through reefs composed predominantly of *P. compressa* in Kane'ohe Bay, HI (Koehl and Hadfield, 2004).

In the present paper, we report on a 3-year study of recruitment timing and location of *P. sibogae* on reefs in Kane'ohe Bay, Hawai'i (Fig. 1). As in the studies on sea hares and echinoids cited above, we determined settlement densities on corals by bringing living colonies into the laboratory and establishing them in tanks supplied with flowing, filtered seawater for approximately 2 weeks, when newly recruited *P. sibogae*, present at the time of collection, had grown large enough to count and measure. In this way, we were able to: (1) determine temporal/seasonal patterns of larval settlement in Kane'ohe Bay, as well as variation from year to year; (2) analyze spatial patterns of recruitment within a reef by comparing among three samples taken across a reef on each collecting date; and (3) gain insights into rates of post-recruitment mortality. In addition, we were able to use our recruitment data for two of the reefs we sampled to test a model of the transport of larvae of *P. sibogae* from the water column onto reefs composed largely of *P. compressa*.

1.2. Model of transport of larvae of P. sibogae into a reef

With data collected in both the laboratory and the field, we developed an individual-based model of the behavior and transport of larvae of *P. sibogae* in the flowing water above a reef of *P. compressa* (Strother et al., 2001, submitted for publication). In the laboratory, we found that larvae of *P. sibogae* quickly retract the ciliated swimming organ (velum), cease swimming and sink when they encounter water containing cue from *P. compressa* in concentrations greater than threshold (Hadfield and Koehl, 2004). Using field measurements of water flow above *P. compressa* reefs (Koehl and Hadfield, 2004; Koehl and Cooper, unpublished data) to design the turbulent, wavy flow above a reef of *P. compressa* in a flume, Reidenbach (2004) measured the fine scale temporally changing distribution in the water column of dissolved substances (e.g., settlement cue) released from the corals. The model developed by Strother et al. (2001, submitted for publication) calculated the trajectories of larvae of *P. sibogae* with the cue-induced sinking

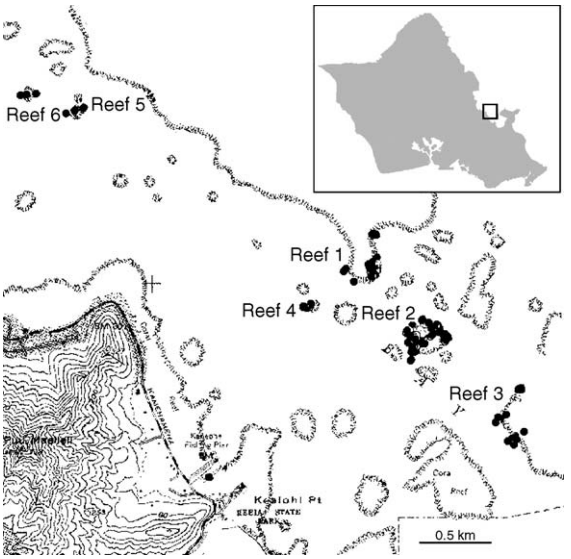

Fig. 1. Map of Kane'ohe Bay, HI illustrating reef numbers assigned in this study and all sites where monthly coral collections were made. Scale bar = 0.5 km. Inset: island of O'ahu with box indicating the portion of Kane'ohe Bay illustrated here.

behavior as they experienced the instantaneous, changing water flow and cue-concentration fields above a reef that were measured by Reidenbach (2004). At each time step, a larva swam or sank depending on the concentration of dissolved chemical cue from *P. compressa* it encountered, and the larva was also transported by the water around it at the instantaneous velocity of the water at that height above the substratum in that phase of the wave. By following thousands of larvae placed randomly in the water column, the rate of transport of larvae into the reef was calculated. This model predicted that, in turbulent, wave-driven flow like that over reefs in Kane'ohe Bay, settlement rates of larvae of *P. sibogae* that sink in response to dissolved cues from *P. compressa* will be about 30% higher than those of larvae that do not sink in cue. This result indicated that behavioral responses to settlement cue in field flow conditions will enhance larval settlement into appropriate habitats.

The study reported here of recruitment of *P. sibogae* in Kane'ohe Bay provided an opportunity to test in the field a prediction of this model of larval transport. In the wave-driven oscillatory flow across some reefs in Kane'ohe Bay, there is slow (~ 0.02 m s^{-1}) net transport of water across the reef, from the seaward to the shoreward direction (Koehl and Hadfield, 2004). The model assumes that any larvae that are transported down into a coral reef remain there. If this assumption is correct, then larvae should be depleted from the water flowing across the reef and the model can be used to estimate the spatial distribution of larval settlement across the reef. The model predicts that ~90% of the larvae in the water moving across a shallow reef should be transported into the reef in roughly the first (i.e., upstream) 8 m of the reef (Strother et al., submitted for publication). This is probably an underestimate of distance across the reef required to deplete the water of 90% of the larvae for two reasons.

(1) The model uses the cue concentration field at a distance of 1.8–2.0 m from the upstream edge of a reef, and therefore does not include further changes in that concentration field in the water at distances >2.0 m from the upstream end of a reef. The rates of turbulent mixing should be greater in the water immediately above a reef (where the shear in the water is highest, e.g., Tennekes and Lumley, 1972) than higher in the water column. Nonetheless, we expected that some mixing of water from above the portion of the water column that we modeled would have replenished larval supplies right above the reef surface. Water depth over Reefs 1 and 2 varied between about 0.2 and about 1.3 m, depending on time in the tidal cycle. Therefore, in the field, the water (and larvae carried in it) from the portion of the water column above the section we modeled could have been stirred by turbulence down into the layer of water above the reef in which filaments of settlement cue were swirling.

(2) The second reason the model's prediction is probably an underestimate of distance across the reef required to deplete the water of 90% of the larvae is that the model does not incorporate mixing of new larvae from higher in the water column down into the volume of water considered in the model (water 15 cm above a reef, which is the portion of the water column into which settlement cue is mixed by turbulence). Nonetheless, a qualitative prediction of the model was that more larvae should be transported into the upstream portion of a reef than into the downstream section of that reef. We tested this prediction by comparing the recruitment of *P. sibogae* onto upstream versus downstream sections of two reefs in Kane'ohe Bay across which water transport was always in one net direction, regardless of time in the tidal cycle (Bathen, 1968).

The spatial pattern of recruitment of *P. sibogae* on a reef is not only the result of larval transport (i.e., where the larvae landed on the reef), but also of settlement (i.e., at which of their touch-down locations they adhered to the substratum), and of recruitment (i.e., where they

metamorphosed into juveniles and survived). Therefore, although high recruitment on the upstream parts of coral reefs would be consistent with a prediction of our larval transport model, a more direct test of the model would be measurement of positions across a reef where larvae first contact surfaces. Because the larvae of *P. sibogae* are not visible in the field, and because it is not feasible to rear enough larvae for large field-release studies, we tested our larval transport model using larval mimics (particles with sinking velocities like those of larvae of *P. sibogae* sinking in response to settlement cue). We released larval mimics upstream of coral reefs and measured where they first contacted reef surfaces.

1.3. Objectives

The purposes of the study reported here were to: (1) determine the temporal patterns of recruitment of *P. sibogae* into coral reefs in Kane‘ohe Bay, Hawai‘i; (2) assess post-settlement mortality of *P. sibogae* on these reefs; and (3) measure the spatial pattern of recruitment of *P. sibogae* across reefs and of reef contact by larval mimics, to test a prediction of a model of the transport of larvae of *P. sibogae* into reefs of *P. compressa*.

2. Materials and methods

2.1. Recruitment of P. sibogae to the coral reef

Newly settled juveniles of *P. sibogae* are too small and cryptic to be seen in the field in the interstices of a coral reef. Therefore, we collected heads of *P. compressa*, which is both the requisite prey and the source of settlement cue for larvae of the nudibranch, and maintained them in filtered flowing seawater in the laboratory for 2 weeks to allow the *P. sibogae* recruits to grow large enough to be seen and counted.

2.1.1. Coral collections

Under terms of State of Hawai‘i Scientific Collecting Permits Nos. 1999-67, 2001-07, 2002-15 and 2003-34, approximately 10 heads of *P. compressa* were collected from reefs in Kane‘ohe Bay, O‘ahu, Hawai‘i at about 3-week intervals from February 2000 through January 2003. Severe winter weather, boat breakdowns and other mishaps caused some interruptions in this schedule, and a total of 53 collections were made. On each collecting occasion, one-third of the corals were collected from a fore-reef location, one-third from a mid-reef location and the third from a back-reef location. Definition of fore-to back-reef was based on the predominant direction of current flow in Kane‘ohe Bay; thus fore-reef was the reef section facing into the wave-driven current. Sites for all collections are shown in Fig. 1.

It is important to note that the amount of coral that we could collect under the terms of our permit did not allow sampling multiple reefs on any single date. Furthermore, it was important to distribute our collections across different reefs in Kane‘ohe Bay to avoid large scale damage of any local reef sites. Alien algae are growing over and killing the living corals in many parts of Kane‘ohe Bay (Woo et al., 2000; Smith et al., 2002), which rendered it even more important that we not over sample already stressed reef areas. Thus, this coral-sampling program allowed us to evaluate settlement in Kane‘ohe Bay as a whole, but not to determine recruitment patterns at any single site or even a single reef throughout the 3 years of this investigation.

Predominant current directions in Kane‘ohe Bay were determined both from published data for Kane‘ohe Bay (Bathen, 1968) and our personal observations. Collection sites were determined with a Garmin® GPS-75 global positioning instrument mounted in the collection boat and plotted using ArcGIS-9® software. If, due to shallowness, the collecting boat could not be positioned over the site of coral collection, the site location was closely extrapolated by measuring distance and direction from the boat.

The corals were placed in large plastic buckets, covered with seawater and returned to the laboratory within 1–2 h of collection. At the Kewalo Marine Laboratory, the corals from each reef position were placed in separate tanks (46 cm × 122 cm × 34 cm), which were supplied with continuously running seawater passed through a series of three 125 μm filters, and then through a fine-mesh filter with a pore size of 22 μm. Filtering the seawater supply to the corals assured that any *P. sibogae* found on them were recruited before the corals were collected and that none were added after collection. The tanks holding the coral were supplied with intense aeration provided by bubble stones. Potential predators on *P. sibogae* were excluded from the tanks holding the coral, and recruited nudibranchs could not migrate from the tanks.

2.1.2. Assessing field recruitment of P. sibogae

After maintaining the corals as described above for about 14 days, they were closely examined for the presence of the coral-eating nudibranch *P. sibogae*. It was assumed that small nudibranchs on the coral had recruited to the coral prior to collection, because the filters on the seawater line removed particles as large as the 200 μm long larvae of *P. sibogae*. All of the coral from each collection site that was examined for nudibranchs was weighed to the nearest gram after the nudibranchs were

removed, and the density of the nudibranchs was expressed as number per kilogram of coral. On most occasions, all of the coral was examined for the presence of nudibranchs. However, on five occasions, the numbers of *P. sibogae* were so great that a sub-sample of the coral was thoroughly searched and weighed.

On a few occasions large nudibranchs and egg masses were found on the corals, indicating that we had actually collected reproductively mature *P. sibogae* with the coral. Furthermore, the 2-week period from collection of the coral to counting of recruits was sufficiently long to allow for generation of free swimming larvae and their recruitment to the coral *after* collection. To eliminate such laboratory-recruited individuals from our assessments of field recruitment, for all occasions except one with many hundreds of recruits (January 22, 2002), all of the nudibranchs were measured, and those with lengths ≤ 6 mm (i.e., smaller than animals newly recruited in the field and grown for 2 weeks; Harris, 1975) were excluded in the determination of recruitment density of *P. sibogae* on that date. (On the occasion when many hundreds of *P. sibogae* were on the coral, we counted as "field recruits" only those slugs >6 mm in body length, but did not record the length of every individual counted.) This approach was conservative, given the range of growth rates exhibited by *P. sibogae*, and resulted in the elimination of as few as one and as many as 1550 individuals in one instance (January 22, 2002).

2.1.3. Temporal and spatial patterns of recruitment

All field-recruitment data for 159 coral samples collected on 53 sampling days were utilized to examine recruitment patterns of *P. sibogae* to six coral reefs in Kane'ohe Bay, O'ahu, Hawai'i (Fig. 1). Some of these reefs were part of, or connected to, the central reef flat in the bay (Reefs 1, 2 and 3), and others were isolated patch reefs in the inner portion of the bay (Reefs 4, 5 and 6). Because corals were collected from this series of reefs over the 3-year period, all data were examined to determine if there were seasonal differences in recruitment in the bay, without reference to particular reefs.

2.2. Testing the model: recruitment relative to flow across the reef

Our model of the transport of *P. sibogae* larvae into a reef composed largely of *P. compressa* releasing settlement cue predicts that recruitment should be heavier on the upstream portions of a reef than on the downstream portions of the reef, as explained in the Introduction (Strother et al., submitted for publication). Net flow across two of the reefs sampled (labeled Reefs 1 and 2 in Figs. 1 and 2) was in the same direction regardless of time in the tidal cycle (Bathen, 1968; Koehl and Hadfield, 2004; personal observations). Therefore, we used those two reefs to assess where larvae recruited relative to upstream positions (i.e., fore- and mid-reef) and downstream positions (i.e., back-reef). This presented a total of 15 collection dates, 7 for Reef 1 and 8 for Reef 2. Because recruitment was highly sporadic, very few or no recruits were found on the majority of collection dates. To avoid biasing the comparison between positions on the reef by including data from times when there were only 1–3 recruits, only data from dates when more than three *P. sibogae* were found on the corals were used in this analysis for the purpose of determining recruitment position on the reef.

To test the prediction that recruitment will be lowest at the downstream end of a reef, we combined the counts for fore-reef and mid-reef (as recruits kg^{-1} coral) and compared them to counts from the back-reef. To do this, we summed the counts in fore-and mid-reef samples and divided that number by the sum of the weights of coral in the two samples. Because a Shapiro–Wilks test (SAS®) revealed that the data were not normally distributed for both reefs, we log-transformed the settlement data before performing one-tailed paired *t*-tests, each pair being from a single collection date. The one-tailed test was selected because we predicted greater settlement in the coral collected nearer the upstream portion of the reef facing the predominant flow. The data were analyzed separately for Reefs 1 and 2.

2.3. Physical transport of larval mimics to surfaces

We also tested the model's prediction that more larvae should be transported into the upstream portions of a reef than into the downstream area by conducting field releases of passive particles that mimicked the sinking behavior of competent larvae of *P. sibogae* that were responding to the coral-produced settlement cue. We counted the numbers of such larval mimics captured on sticky surfaces mounted on coral reefs. These experiments were conducted to determine where larvae would first contact reef surfaces due to physical transport processes alone. The use of passive particles enabled us to separate physical transport from biological factors such as larval choices about whether to attach to surfaces encountered, or post-settlement crawling.

2.3.1. Larval mimics

We released "larval-mimic" particles that could easily be distinguished from natural particulate matter and that had sinking velocities similar to those of the larvae of *P. sibogae* that were responding to settlement

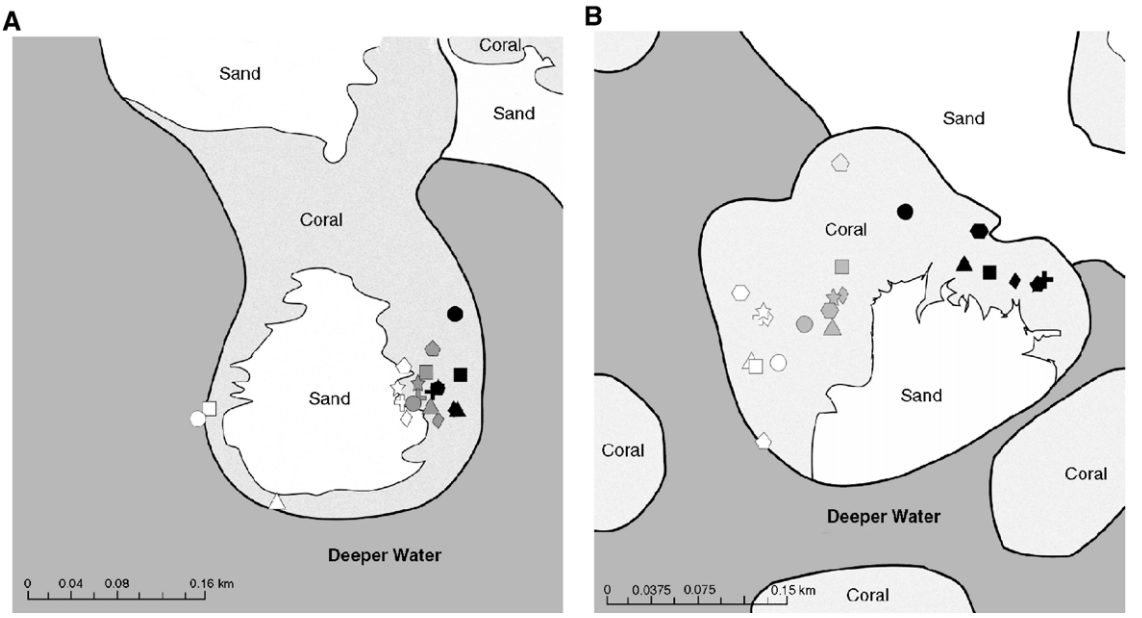

Fig. 2. (A) Map of Reef 1 illustrating where coral samples were collected, all in the year 2001, as follows: circle, 3/29; square, 4/19; triangle, 5/29; pentagon, 7/26; diamond, 9/5; star, 12/3; and cross, 12/12. (B) Map of Reef 2 illustrating where coral samples were collected, all in the year 2000, as follows: circle, 4/6; square, 6/16; triangle, 7/3; pentagon, 7/20; hexagon, 8/2; star, 8/18; diamond, 9/4/6; square, 6/16; triangle, 7/3; pentagon, 7/20; hexagon, 8/2; star, 8/18; diamond, 9/4; and cross, 9/19. Black symbols, fore-reef samples; gray symbols, mid-reef samples; and white symbols, back-reef samples.

cue: plastic Ultrafine Prisma Glitter (#EA 6487, Capri Arts and Crafts). We used the procedures described in Butman et al. (1988) to measure the sinking velocities of each color of Prisma Glitter used (mean mimic-sinking velocity = 0.27 cm s^{-1}, S.D. = 0.019, n = 5 colors; the means of 15 particles per color were used to calculate mean mimic-sinking velocity). Although slightly greater than the downward velocities of competent larvae of *P. sibogae* that cease swimming when exposed to dissolved settlement cue from *P. compressa* (which ranged from 0.05 to 0.34 cm s^{-1}, with a mean of 0.12 cm s^{-1}; Hadfield and Koehl, 2004), and slightly lower than the fall velocities of fully-retracted larvae of *P. sibogae* (which ranged from 0.29 to 0.43 cm s^{-1}, with a mean of 0.33 cm s^{-1}; Hadfield and Koehl, 2004), the sinking velocities of the Ultrafine Prisma Glitter represented the best match to the sinking velocities of *P. sibogae* larvae that we could find among the types of particles available in the bulk quantities necessary for multiple field releases.

2.3.2. Collection tabs

The surfaces on which larval mimics were captured on the reef were flexible plastic tabs (Post-it® Flags #680), that had a colored region (2.5 × 1.6 cm) and a clear, adhesive region (2.5 × 2.7 cm). Each capture surface was made by wrapping the adhesive region of the plastic tab around a twist-tie and securing it with laboratory label tape on which its identification number was written. The colored area of each tab was then coated with Vaseline® petroleum jelly. The jelly-coated surfaces of two tabs were stuck together and the pair of tabs was put in a plastic name-tag badge for transport to the field. In the field, these pairs of tabs were slid apart to evenly spread the Vaseline on their surfaces and then each tab was attached to a coral branch, as shown in Fig. 3.

2.3.3. Field experiments

We conducted field releases of larval mimics at nine different reef sites in Kane'ohe Bay. Each reef was composed predominantly of *P. compressa* and was exposed to oscillatory wave-driven water flow with a net shoreward direction of water transport (Koehl and Hadfield, 2004) regardless of time in the tidal cycle (Bathen, 1968). The mean width of the reefs parallel to the direction of net water transport was 9.9 m (S.D. = 1.7, n = 9 reef sites). For each site, we selected a release point above a bare sand or rock substratum that was seaward of the reef and released 60 ml of fluorescein dye (5% solution by weight in sea water) to determine the path of net water flow from the release point across the reef. The mean distance between the release point and the seaward edge of the reef first encountered by the dye was 2.0 m (S.D. = 0.5 m, n = 9 sites), measured to the nearest 10 cm using a tape measure.

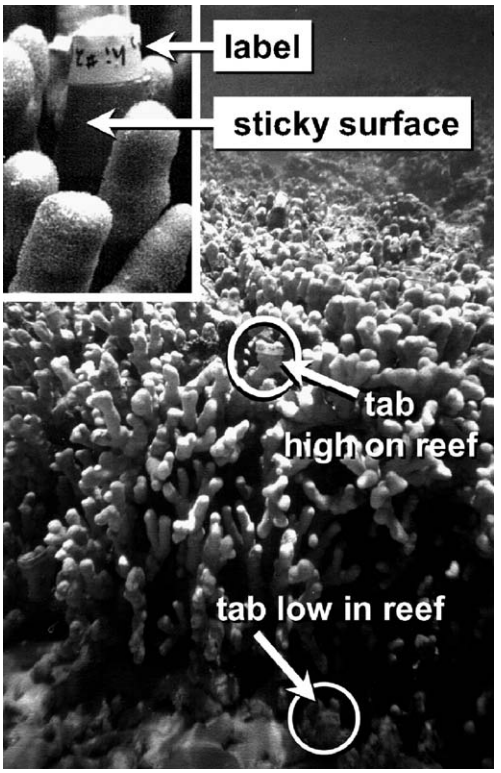

Fig. 3. Photograph of the seaward edge of a reef in Kane'ohe Bay showing positions of the collecting tabs attached to branches of *Porites compressa* at the top of the reef and down within the reef. The inset shows a close-up view of a tab attached to a branch of *Porites compressa*. The Vaseline-coated tab ("sticky surface") and the tape label are indicated.

Sixty collection tabs were attached to the reef in positions across which the dye from the release point had moved: 20 tabs on the fore-reef (within one meter of the seaward edge of the reef), 20 tabs on the back-reef (within one meter of the shoreward edge of the reef) and 20 tabs in the mid-reef (a position mid-way between the fore- and back-reef positions). Water depth at each of these positions was measured to the nearest 0.01 m; the depth was the distance between the top of the tallest coral at a position and the surface of the water. Because the sites were subjected to wave-driven flow, the mean of the heights of the water surface for six successive wave crests and wave troughs passing over the measurement position was used for the water depth. The mean of the mean water depths above the fore-reef sites was 0.53 m (S.D. = 0.18, $n = 9$ sites), above the mid-reef sites was 0.51 m (S.D. = 2.3, $n = 9$ sites) and above the back-reef sites was 0.50 m (S.D. = 0.13, $n = 9$ sites). At each of these reef positions, 10 tabs were placed around the tips of branches of living *P. compressa* at the top surface of the reef (Fig. 3) and 10 were placed around branches of dead coral down within the reef, approximately 0.5 m below the top of the reef (Fig. 3).

A suspension of 60.4 g of larval mimics (glitter) in 1 L of a 5% solution of fluorescein in sea water was introduced into the water at the release point seaward of the reef. The suspension was thoroughly shaken in a wide-mouth jar and then rapidly poured out just below the water surface while the water was being vigorously stirred up and down with a diving fin to mix the suspension evenly across the depth of the water (the water upstream of the reefs was deeper than the water above the reefs; the mean of mean water depth, measured as described above, of the release points was 1.1 m, S.D. = 0.2, $n = 9$ sites). The dye permitted us to assess how evenly the released suspension was mixed vertically into the water column and to track the progress of the water across the reef. After dye was no longer visible on the reef (usually after 15 to 20 min), we removed the collection tabs from the reef, starting at the seaward end of the reef. The Vaseline®-coated surface of each tab was covered by a protective piece of transparent plastic (2.0 × 3.0 cm) cut from overhead transparencies, and the tab was then placed in a clear plastic name-tag badge which was stored in a Ziplock® bag for transport to the laboratory.

All larval mimic particles were counted using a dissecting microscope (Wild M7). The Ultrafine Prisma Glitter was easy to distinguish from other particulate matter captured on the tabs. All the glitter in the name-tag badge containing a collecting tab was counted. A transparent plastic grid was placed over each name-tag badge to assure that all particles in each box of the grid were counted, and the badge was turned over and all larval mimics not visible from the front side were also counted.

2.3.4. Measurement of adhesion of larval mimics to collection surfaces

Microscope slides were coated with Vaseline® in the same way as the collection tabs were coated. Two slides were stuck together by their coated surfaces and then slid apart, using the same technique as had been used for the collection tabs, to assure a smooth, even coat of Vaseline® on each slide. Larval mimics were stirred into a bucket of sea water at 25 °C, and each coated slide was swished back and forth in the bucket at peak velocities of 30 cm s^{-1} to mimic the instantaneous velocities of the oscillatory wave-driven flow to which *P. compressa* reefs are exposed in Kane'ohe Bay (Koehl and Hadfield, 2004). We did this so that larval mimics would be brought into contact with the Vaseline®-coated surface in a similar manner to their encounters with Vaseline®-coated collection tabs in the field. The slide was then mounted flush with the floor of a

flow channel designed to produce known wall shear stresses (Schultz et al., 2000), and the "nominal wall shear stresses" required to remove the mimics from the Vaseline®-coated surface were measured as described in detail in Koehl and Hadfield (2004). Because the Vaseline® and the attached larval mimics might have had some fine surface texture that was greater in height than the viscous length scale in the test section of the channel, 6 to 35 μm for the range of flow rates available (Schultz et al., 2000), the actual wall shear stresses encountered by larval mimics

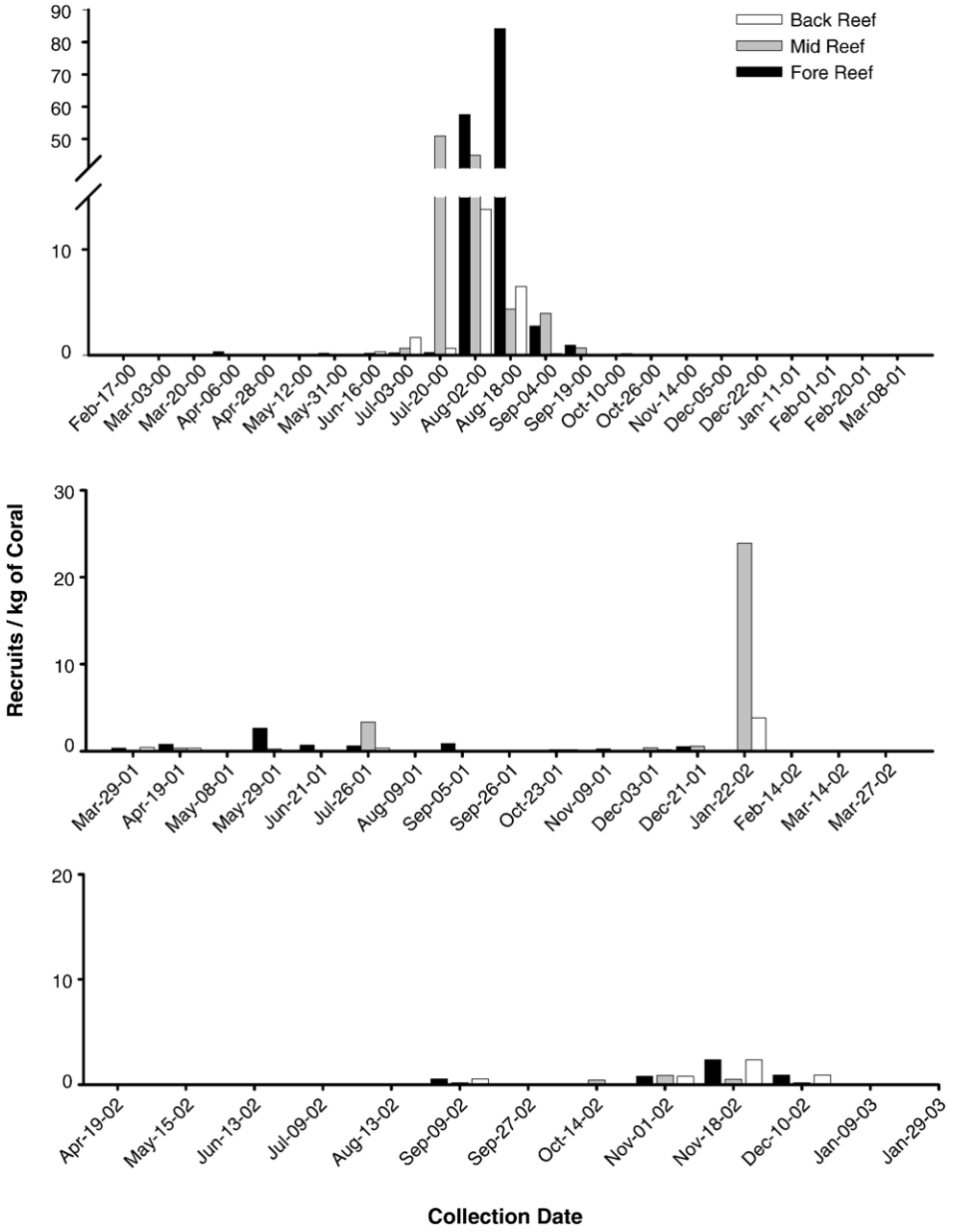

Fig. 4. Numbers of recruits per collecting date over the three-year study. (Top) Samples from February 17, 2000 through March 8, 2001: all samples from Reef 2; (middle) samples from March 29, 2001 through March 27, 2002: samples were collected from Reef 1 on 3/292001, 4/19/2001, 5/29/2001, 7/26/2001, 8/9/2001, 9/5/2001, 9/26/2001, 10/23/2001, 12/3/2001, 12/21/2001 and 1/22/2002; samples were collected from Reef 5 on 5/8/2001; samples were collected from Reef 6 on 6/21/2001; samples were collected from Reef 2 on 11/9/2001; and samples were collected from Reef 3 on 2/14/2002, 3/14/2002 and 3/27/2002. (Bottom) Samples from April 19, 2002 through January 29, 2003: samples were collected from Reef 1 on 4/19/2002; samples were collected from Reef 3 on 5/15, 2002 and 9/27/2002; samples were collected from Reef 4 on 10/14/2002; all other samples were collected from Reef 2.

during our experiments may have been slightly higher than those determined for the smooth test section during calibration. Thus, we use the term "nominal wall shear stress" when reporting the results of our larval-mimic adhesion experiments, since it represents the stress determined during calibration of a smooth test section rather than the actual stresses encountered by individual larva mimics.

3. Results

3.1. Spatial and temporal patterns of recruitment of P. sibogae in Kane'ohe Bay, O'ahu, Hawai'i

Six spatially separated reef sites were included in this sampling program (Fig. 1). Data on dates, reef locations and numbers of newly recruited *P. sibogae* in each of the three samples collected on each date are provided in Fig. 4. Coral collected from Reefs 1 and 2 yielded the most recruits over the 3-year collecting program. Recruit numbers were very low on Reefs 4, 5 and 6, and no recruits were found in samples collected from Reef 3 on three of four dates when collections were made (a total of 12 samples).

There was considerable variation in numbers of recruits between sampling dates (Fig. 4). When the coral samples were thoroughly searched 2 weeks after being collected from the field and maintained in laboratory tanks, specimens of *P. sibogae* were found on at least one of the samples collected on 31 (58.5%) of the 53 separate sampling dates over 3 years. Sixty-seven (42%) of the 159 samples taken included one or more recently recruited *P. sibogae*. However, when counts of recruits measuring less than 6 mm were removed and the data were standardized as number of recruits kg^{-1} coral, 45 (67%) of the 67 samples with any recruits contained less than 1.0 recruit kg^{-1} of coral, and two or more recruits kg^{-1} of coral were found on only 14 (21%) of the samples with recruits. Large numbers of recruits (10–84 kg^{-1} of coral) characterized six (9%) of the samples that contained any recruits and only 4% of all samples.

Analysis of the frequency distribution of abundance of recruits is presented in Fig. 5. The mean number of recruits larger than 6 mm for all 159 samples in all months was 2.02 kg^{-1} of coral. The large standard deviation of this mean, 9.82, reflects the wide variation among samples collected. These data indicate that mass recruitment is rare on most reefs, but does occur.

There was no seasonal pattern to recruitment of *P. sibogae* onto the coral reefs we monitored in Kane'ohe Bay. Recruits were found in every month of the year during at least one of the years when samples were taken (Fig. 4). However, the recruitment data reveal great fluctuations, characterized by long periods with no recruitment interspersed with a few periods of intense recruitment (Fig. 4). Very large recruitment events occurred in both summer and winter months, e.g., on Reef 2 in July–September 2000, and on Reef 1 in July 2001 and January 2002. The sampling procedure employed in this study did not include collections from more than one reef per collecting date, so we cannot say whether or not these large recruitment events were localized or were more broadly distributed in Kane'ohe Bay. All of the samples in the first year (February 17, 2000–March 8, 2001) were taken from Reef 2, indicating that, at this location, recruitment numbers increased greatly during July through September and declined again in the fall and winter (Fig. 4). From March 29, 2001 through January 22, 2002, nearly all samples were collected on Reef 1, where recruit numbers were found to increase in May through June, remain very low throughout the fall months, and then peak in January. In September and October 2002, small numbers of recruits were found in samples collected from the south-bay patch reef, Reef 3, mid-bay patch Reef 4 and from portions of Reef 2. Overall, the recruitment data present a picture of high variability and relatively low predictability on any given reef and date.

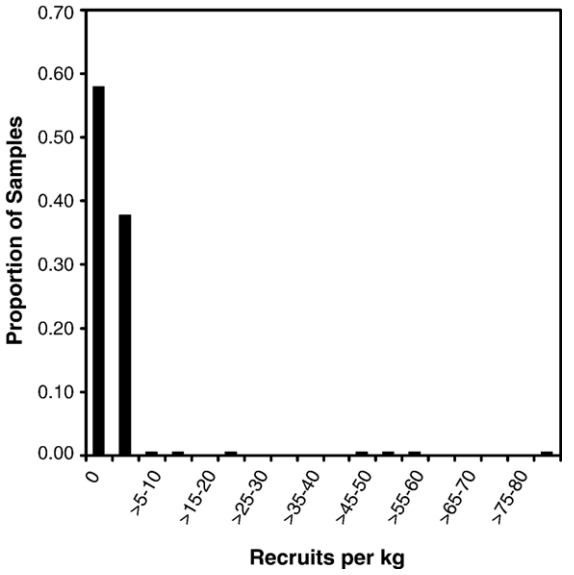

Fig. 5. Frequency distribution of recruitment density (number of recruits kg^{-1} coral) for all coral samples collected ($n=159$). Categories of recruitment density are plotted on the horizontal axis in 5 recruits kg^{-1} size classes, and the proportion of coral samples in each category is shown on the vertical axis.

3.2. Size-frequency distribution of recruits

Specimens of *P. sibogae* found on the corals after a 2-week maintenance period in laboratory tanks supplied with filtered seawater ranged in length from 1 to 35 mm. After eliminating counts of animals less than 6 mm (to assure that all animals counted had recruited in the field), all samples with 10 recruits or more showed a broad range of recruit sizes, typically 7 mm to about 25 mm in length. When small numbers of animals were found, they frequently included animals in larger size classes, indicating that they had recruited to the reef well before the corals were collected. Fig. 6 illustrates examples of size-frequency distributions in samples that contained few (13–18), intermediate numbers (46–54) and many recruits (90–179).

3.3. Field test of a prediction of a larval transport model: spatial patterns of recruitment on a reef

Because the net water flow across Reefs 1 and 2 was in the same direction during all phases of the tidal cycle

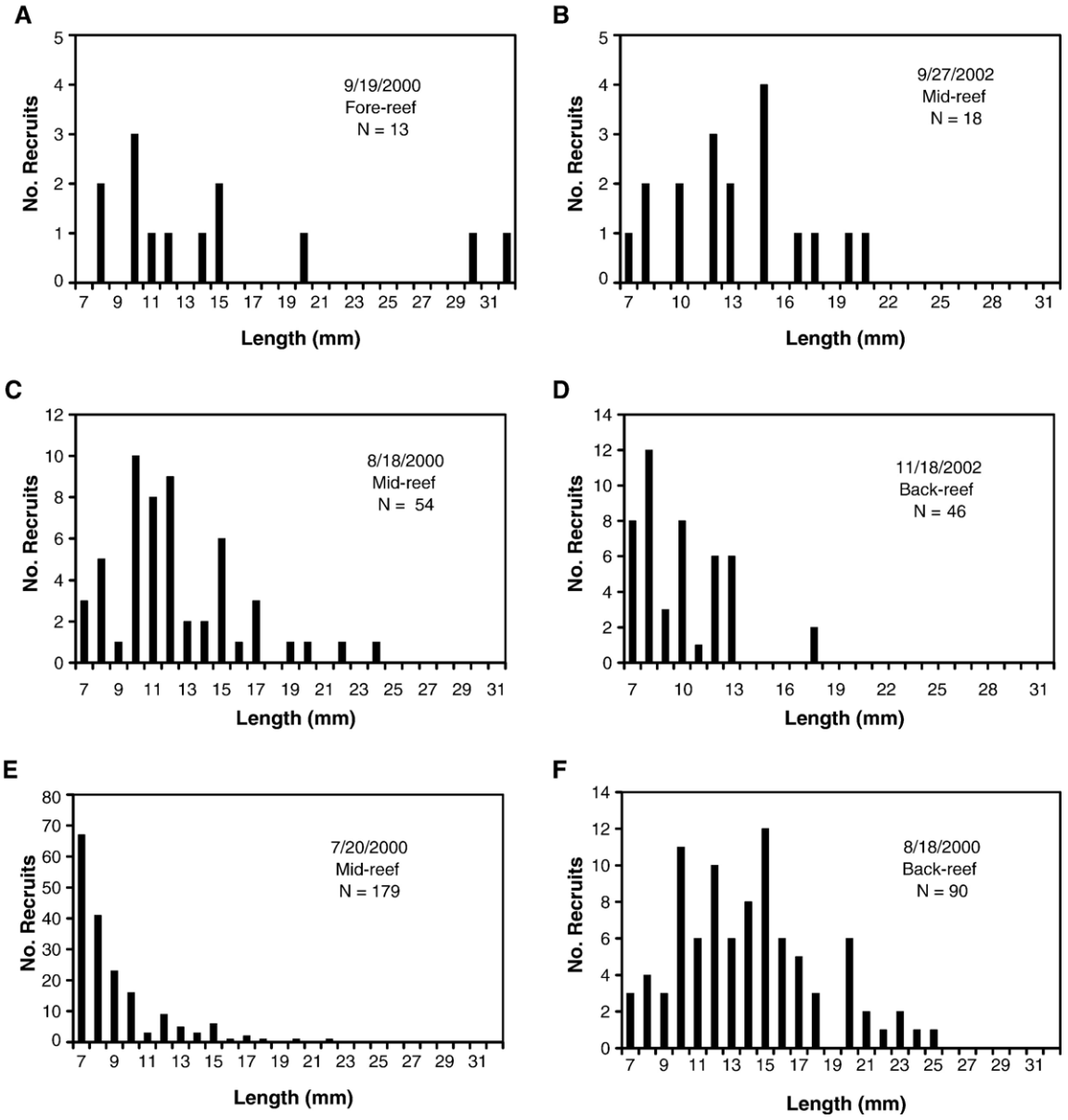

Fig. 6. Recruit size-frequency distributions for six collections, including samples with small (A, B), moderate (C, D) and large (E, F) numbers of recruits. Note that vertical scales differ between graphs.

(Bathen, 1968), we could use the recruitment data from those two reefs to test a prediction of our model of larval transport (Strother et al., submitted for publication), described above. The model predicted that most of the larvae of *P. sibogae* carried in the water column ≤15 cm above the coral should be transported into the upstream part of the reef. Finding greater numbers of recruits of *P. sibogae* on the fore- and mid-reef samples than in the back-reef samples would support this prediction. We thus compared abundance of recruits in fore-plus mid-reef samples versus back-reef samples for seven sampling dates on Reef 1 and eight sampling dates on Reef 2 (positions of these collections are illustrated in Fig. 2), using a one-tailed paired *t*-test to examine the prediction that settlement (*P. sibogae* kg^{-1} coral) would be greater in the fore-and mid-reef samples than in the back-reef sample. Significantly more larvae settled in the fore-plus-mid-reef samples on both Reef 1 ($p=0.009$) and Reef 2 ($p=0.038$), as predicted.

3.4. Field test of a prediction of a larval transport model: spatial patterns of reef contact by larval mimics

The higher numbers of *P. sibogae* recruits on the seaward parts of Reefs 1 and 2 could have been due to differential attachment or survival of *P. sibogae* rather than simply to larval transport into the reef. Therefore, another more direct field test of the prediction of our larval transport model was our measurement of the positions on the reef at which larval mimics first contacted reef surfaces. We found that most larval mimics landed on the fore-reef, as predicted by the model (Fig. 7). We also found that more mimics landed down within the reef than on branch tips at the top of the reef (Fig. 7).

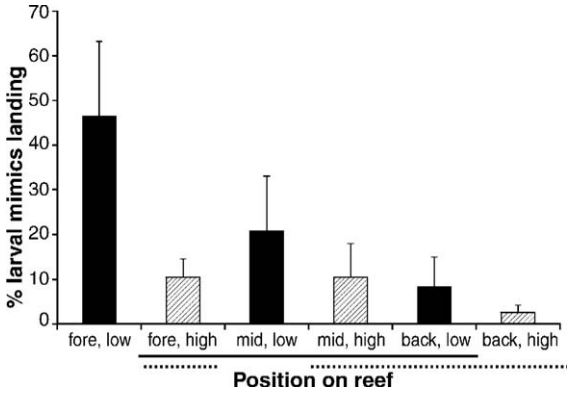

Fig. 7. Plot of the percent of the larval mimics caught on all collecting tabs during an experiment at each position on the reef (ten collecting tabs per experiment per position). The mean number of particles caught on all 60 collecting tabs used in an experiment was 300 (S.D.=204, $n=9$ experiments). The height of each bar is the mean for that site ($n=9$ experiments), and the error bars represent one standard deviation. Black bars indicate positions at the top of the reef, and grey bars indicate positions low within the reef. Lines under the graph indicate those reef positions that were not significantly different from each other (ANOVA, Bonferroni/Dunn tests done on arcsine-transformed data, significance level 5%).

Flow-tank measurements of the adhesive strength of larval mimics to Vaseline®-coated slides showed that the mean nominal wall-shear stress required to dislodge the mimics was 84 Pa (S.D.=7, $n=3$ experiments, with 64 to 114 mimic particles per experiment).

4. Discussion

The coral reefs of Kane'ohe Bay, Hawai'i provide an ideal location for a study of recruitment of a motile invertebrate predator whose minute larvae are known to settle in response to a soluble cue from their prey coral. That coral, *P. compressa*, is both the spatially and numerically dominant coral on these reefs, and thus, in many places, provides a nearly continuous recruitment substratum for larvae of *P. sibogae*. Because *P. compressa* is a rapidly growing coral (Hunter, 1988), it can be sampled on a modestly sustained level without lasting damage to the reefs. Therefore, the substratum–the prey coral–was sampled according to a planned program and examined for recruits at a later time when they had grown large enough to be seen. The results demonstrate the validity of this approach for measuring recruitment of cryptic motile animals that are too small to be seen in the field when they first recruit into complex substrata.

4.1. Temporal patterns of recruitment

Recruits of *P. sibogae* were found on coral during every month of the year in Kane'ohe Bay, and especially large cohorts were recorded during different seasons in each year of our study: July–September, January and October–November. Finding recruitment of *P. sibogae* throughout the year provides confirmation of laboratory observations that the species breeds throughout the year (Hadfield, unpublished personal observations). In a study of the herbivorous Hawaiian sea hare, *Aplysia Juliana*, Sarver (1979) employed a similar methodology to the present study. Sarver collected the algal food of the sea hares, weighed it and maintained it in the laboratory until the newly recruited sea hares were large enough to be seen and measured. That study also found highly variable year-around larval settlement on the algae, although recruitment was higher in summer months. Athough recorded as recruits kg^{-1} of algae, overall recruitment was greater

during months when the preferred alga was more abundant. Two locations, about 2.5 km apart, were sampled in the study of *A. Juliana* with similar recruitment patterns recorded. Because planktonic larval development of *A. juliana* lasts at least 30 days (Switzer-Dunlap and Hadfield, 1977), it is likely that larvae recruiting to the two sites were drawn from a large and highly mixed pool transported in local currents. Pennings (1991), who also collected algal samples to locate newly settled *Aplysia californica*, found recruitment to be highly seasonal and relatively predictable at sites on Catalina Island, California.

Recruitment intensity of *P. sibogae* was highly variable. On only five dates over the 3-year sampling period (5% of samples) were there 10 or more recruits kg^{-1} of coral (Fig. 4). In four coral collections from Reef 2 in July and August 2000 and one collection from Reef 1 in January 2002, between 50 and 300 recruits kg^{-1} of *P. compressa* were counted. Furthermore, on these dates, elevated numbers of recruits were found in two or more of the three samples taken across a reef. No particular or unusual phenomena were noted (i.e., extreme tides or weather conditions) that correlate with these periods of increased recruitment intensity. Judging from the wide range of recruit sizes found in these samples (Fig. 6), it is highly unlikely that they represent single "clouds" of competent larvae that settled onto the reef at the same time.

Patterns of dispersion have been evaluated for a variety of benthic invertebrate species. The distribution of recruitment numbers that we recorded (i.e., many coral samples with no or very small numbers of individuals and few coral samples with many, Fig. 5) closely fits a pattern considered "over-dispersed" by Grayson and Chapman (2004), who found a similar distribution for adult chitons on the bottoms of intertidal boulders. Because our study recorded recruitment before predation or out-migration could reduce it, we can be relatively certain that post-settlement mortality (as it would occur in the field) and behavior of adults, the two alternate explanations for non-random spatial patterns noted by Underwood and Denley (1984), were not the cause(s) for the observed distribution. Similarly, given the extensive distribution of *P. compressa*, the nudibranch's prey coral and typical substratum, it is highly unlikely that variation in habitat selection by the larvae caused the wide variation of recruitment events. It appears much more likely that this distribution arises from the reproductive and larval biology of this species, combined with the water-flow patterns in this somewhat confined bay. Larvae of *P. sibogae* that hatch from egg masses laid onto the bases of coral branches move upward into the water column as a result of strong positive phototropism during the daylight hours (Miller and Hadfield, 1986). This positions the larvae in the layers of the bay waters that are moving most rapidly, with their direction of movement due mostly to tides (Bathen, 1968). Where ever the larvae happen to be positioned in the bay, horizontally and vertically, when they become metamorphically competent 2–3 days after hatching, they will settle when they come into high enough concentrations of the coral cue. Because both the magnitude and direction of tidal flow in the bay change from hour to hour and day to day, the locations of larvae at the time of competence must be highly variable, producing the over-dispersion of recruits across coral samples recorded in this study.

Recruitment intensity must reflect events that occur while larvae are in the plankton. Predation by planktivorous fish will take a toll on the abundance of larvae, and mixing over the 2–3-day pre-competent period and after would be expected to disperse a hatching cohort of larvae (a large egg mass of *P. sibogae* contains 3000–4000 larvae) rather than allowing them to remain in a "cloud". If, when measured 2–3 weeks after settlement, recruits are all very close to the same size, it may be concluded that they recruited simultaneously, possibly the progeny from a single egg mass. However, this was not observed (Fig. 6). Instead, on dates when large numbers of recruits were found, they typically ranged in size from seven up to 35 mm in length. Extrapolating from published growth-rate data (Harris, 1975; Todd et al., 1997), specimens of *P. sibogae* over this size range would have been from a few days to more than a month post-settlement at the time of collection (14 days before they were measured). It thus appears that the large numbers of recruits we occasionally found on Reefs 1 and 2 were indicative of sporadic but prolonged periods of recruitment to those reefs. Those prolonged periods of high recruitment were noted for a 4–5-month period on Reef 2 in summer 2000, a 2-month period on Reef 1 in winter 2001, and a 4-month period on Reef 2 between September and December 2002. Because samples were not taken at multiple sites in Kane'ohe Bay on any one date, we cannot state whether or not these high recruitment bouts were occurring only locally or broadly throughout the bay. We did note, however, that these periods of high recruitment were always followed by periods of near zero recruitment and that no seasonal trend occurred.

In the context of a complete ecological study of recruitment in *P. sibogae*, we were severely limited by the amount of the substratum (the stony coral *P. compressa*) that we could collect due to practical, legal and ethical considerations. *P. compressa* is a protected species in Hawai'i and can be collected only under terms of a permit issued by the State of Hawai'i Division of Aquatic

Resources. The corals collected for this study met the monthly limit allowed by our permit, and thus we could not collect multiple samples from multiple reefs across Kane'ohe Bay each month, which would have composed a more complete sampling regime. Furthermore, overgrowth by alien algal species is rapidly reducing the amount of *P. compressa* in Kane'ohe Bay, making extensive sampling even more unwarranted. Thus, this 3-year study of recruitment in Kane'ohe Bay will not likely be repeated. With that understanding and within the restrictions we note against multiple-site sampling, we have nonetheless gained important information about the temporal patterns of recruitment of *P. sibogae*.

4.2. Self-recruitment in Kane'ohe Bay

In a recent review, Sponaugle et al. (2002) defined a series of eight biological and three physical variables that correlate closely with self-recruitment. The population of *P. sibogae* as well as its physical setting in Kane'ohe Bay, Hawai'i fit many of these criteria, including: (1) a parental investment in eggs that allows prehatching development of advanced larvae that may swim for only a brief time before being competent to settle; (2) a plastic pelagic larval period that allows settlement early in the pelagic stage or to persist in the plankton until requisite sites are encountered, plus behavioral patterns that enhance site-specific recruitment; and (3) larval sensory capability to recognize and respond to an environmental cue associated with a requisite post-settlement environment. Sponaugle et al. note (p. 351), "Although much work remains to be done in this area, the prediction is that the stronger the cues and the better able a larva is to detect and respond to such cues, the greater the likelihood is of self-recruitment."

Physical characteristics of Kane'ohe Bay that favor self-recruitment in a species like *P. sibogae* include relative isolation of the embayment, relatively small basin size and flow characteristics that can aid larval retention. Although the planktonic larval period for *P. sibogae* can extend for at least several weeks (Miller and Hadfield, 1990), the mandatory (i.e., pre-metamorphically competent) larval period lasts only 2–3 days (Hadfield, 1978, 1984). This mandatory larval period is short relative to the flushing time for water in Kane'ohe Bay, another criterion for self-recruitment. Because Kane'ohe Bay is semi-enclosed, flushing time for bay waters varies between 8 and 13 days, varying in different parts of the bay (Smith et al., 1981), despite significant water flow into the bay due to tides, waves across the outer reefs and fresh-water input (Bathen, 1968). Furthermore, flow patterns within Kane'ohe Bay due to tidal currents (Bathen, 1968) should carry suspended larvae back and forth in mainly north–south directions (see Fig. 1). Larvae carried in those tidal currents that pass back and forth across the outer shallow reef regions or the mid-bay patch reefs may have repeated opportunities to recruit to these areas of the bay where living *P. compressa* dominates the substratum. The data presented here support this, with newly settled juveniles of *P. sibogae* recorded at least once on all of the reefs that were sampled. Another physical feature of habitats of self-recruiting populations is recirculation of water from the site back towards the shore; such recirculating flow can carry planktonic larvae back to the home of their parents. Some of the currents that might carry larvae through a southern channel and out of Kane'ohe Bay are re-directed shoreward in patterns that would carry larvae back into Kane'ohe Bay across the coral reefs in its central portion (Bathen, 1968). Assuredly, *P. sibogae* does occur at other sites in the Hawaiian Islands, and larvae from outside Kane'ohe Bay might be expected to occasionally, though rarely, enter the bay. In summary, although many larvae of *P. sibogae* that hatch in the bay may be transported out of the bay, their short pre-competent periods relative to the lengthy flushing period for all bay waters, and their chances of being carried back into the bay in recirculating water, should provide an ample supply of larvae for self-recruitment onto the corals in Kane'ohe Bay.

The population of *P. sibogae* in Kane'ohe Bay appears to be a rare exception to the generalization that most marine populations that rely on recruitment of larvae from the plankton are demographically open (Caley et al., 1996). Todd (1998) reviewed genetic data that he and colleagues gathered during a multi-year study of a nudibranch species that produces lecithotrophic larvae with a 1–2-day precompetent period and concluded, "…local populations can be demographically closed on very small scales (10^2–10^3 m)." Todd attributed much of larval retention in such species to larval behavior, which may also account for retention of larvae of *P. sibogae* in Kane'ohe Bay. Their switch from positively phototropic swimming during the precompetent period to photo-indifference once competent (Miller and Hadfield, 1990) may dispose them to spend periods out of rapidly moving surface waters beginning 2–3 days after hatching, thereby enhancing their retention in the bay.

4.3. Fates of recruited juveniles

On occasions when there were large numbers of recruits of *P. sibogae* present in a coral sample, their size/age distributions were typically very broad, with large

numbers of small individuals, and smaller numbers of larger ones (e.g., Fig. 6E). The most likely explanation for this is post-recruitment predation on the nudibranchs. Gochfeld and Aeby (1997) experimentally determined that there are many fish and crustacean predators of *P. sibogae* in Kane'ohe Bay. Because the fish consume *P. sibogae* found on the accessible outer surfaces of coral colonies and the crustaceans move and feed among deeper regions of the corals, most of the depredations we recorded were probably due to crustaceans. Taken together, these observations suggest that recruitment over time spans of 2–4 weeks may have been much higher than what we recorded. For example, in each of a consecutive series of samples taken from various locations on Reef 2 during the summer of 2000, 50–60 recruits in the 7–8 mm size classes were observed, but only 6 individuals larger than 15 mm. Thus, daily recruitment rates during periods of intense recruitment are best estimated by numbers of *P. sibogae* in the 7–8 mm size class. If predation in the field had not reduced the numbers of recruits that settled during the 20–25 days that preceded the collection of each coral sample, then we should have found roughly 50–60 individuals in the larger size classes in our counts. Therefore, overall arrival of new *P. sibogae* recruits during the month preceding the collection of each sample may have been roughly five times greater than our data indicate. It is quite clear that survival of *P. compressa* in many regions of Kane'ohe Bay, where recruitment of the coral predator *P. sibogae* can be intense, must depend on the limitation of *P. sibogae* numbers by predation upon them, as noted by Gochfeld and Aeby (1997).

4.4. Field tests of larval transport model

Competent larvae of *P. sibogae* sink in response to a dissolved chemical cue released by their prey coral, *P. compressa* (Hadfield and Koehl, 2004). The consequences of such cue-induced sinking on the transport of larvae from the water column into a shallow reef exposed to turbulent, wave-driven water flow was explored using a mathematical model that showed that such sinking could enhance the rate of larval transport into a reef (Strother et al., 2001, submitted for publication). The spatial patterns of recruitment that we documented in the study reported here are consistent with a prediction of this model that more larvae should be transported into the upstream portion of a reef than into the downstream section of that reef. Two of the reefs we monitored were subjected to net water flow in one direction regardless of the time in the tidal cycle (Bathen, 1968), and on those reefs we found greater numbers of recruits per kg of coral on the portion of the reef facing the predominant flow than in the back-reef samples. In contrast, on other reefs we sampled that were subjected to net water flow in different directions at different times of the tidal cycle (i.e., different regions of the reef were upstream at different times of the day) (Bathen, 1968), we found no spatial pattern of recruitment, as expected.

Although the spatial pattern of recruitment that we observed on reefs exposed to only one net direction of water flow was consistent with the predictions of our larval transport model, that spatial pattern might have been due to greater attachment or post-settlement survival of *P. sibogae* on the upstream regions of the reefs rather than to the transport of larvae into the reef. Therefore, we also conducted field releases of larval mimics to measure where on the reef particles with sinking velocities like those of larvae of *P. sibogae* were transported and first contacted coral surfaces. The results of these experiments were also consistent with the predictions of our transport model: more particles contacted reef surfaces in the upstream region of a reef than in downstream locations.

In the larval mimic experiments described above, we assumed that all larval mimics that contacted the collecting tabs mounted on the reef remained attached to those tabs. Since the boundary shear stresses on surfaces on the tips of *P. compressa* branches exposed to wave-driven flow like the water movement we measured in the field (Koehl and Hadfield, 2004) are much lower than the boundary shear stresses (84 Pa) required to wash larval mimics off Vaseline-coated surfaces, it is unlikely that larval mimics washed off our collecting tabs after they became stuck to them. Reidenbach (2004) exposed a reef constructed of skeletons of *P. compressa* in a laboratory flume to wave-driven flow similar to that measured in the field and used laser-Doppler anemometry to measure water velocities 200 μm from surfaces of the corals. He then used these velocities to calculate instantaneous boundary-shear stresses along the surfaces of the corals, and found that the "maximum bed stress" (i.e., 99% of the time the instantaneous stress ≤ maximum bed stress) was 1.16 Pa at the tips of coral branches on the top of the reef and was lower along coral branches within the reef (Reidenbach, pers. com.). Thus, the wall shear stresses required to dislodge larval mimics from Vaseline®-coated surfaces were almost eight times greater than the peak forces they were likely to have experienced in the field.

4.5. Vertical distribution of settling larvae within a coral reef

We found that more larval mimics were collected on the tabs deployed on surfaces down within reefs than on

the tabs on coral branches at the tops of reefs. Since mimics were not likely to have washed off our collecting tabs, this spatial pattern reflected where the larval mimics first contacted reef surfaces. Measurements of the attachment strength of newly settled *P. sibogae* indicated that they should be able to adhere to surfaces within a reef where water movement is slow, but would be swept off surfaces at the top of a reef that are exposed to rapidly flowing water (Koehl and Hadfield, 2004). Furthermore, the concentration of settlement cue from *P. compressa* in the water within the interstices of reefs in Kane'ohe Bay was high enough to induce metamorphosis by larvae of *P. sibogae* (Hadfield and Scheuer, 1985; Hadfield and Koehl, 2004). Therefore, not only do more larvae of *P. sibogae* contact surfaces within reefs than on top of reefs, but those larvae that land within reefs are more likely to settle and recruit there than those landing on reef tops.

4.6. Conclusions

Measurement of recruitment at or soon after settlement in benthic invertebrate species with very small larvae is impossible by direct observation in the field. Thus, we employed an approach wherein we sampled a tightly requisite recruitment substratum (a specific species of coral) and maintained it in laboratory aquaria, free of additional recruitment and predation, until the juveniles grew large enough to be seen and counted. Using this technique, we found that recruitment occurred sporadically, with no seasonal pattern. When recruitment did occur, it typically involved multiple individuals, thereby assuring mates for those present. Analysis of the size-frequency distribution of recruits indicated that some sites occasionally gained recruits approximately daily for periods of a month or longer. These data also revealed that decimation of recruits occurred quite rapidly in the field as the juvenile nudibranchs grew, probably due to predation. Such mortality of juvenile *P. sibogae* no doubt protects the *Porites*-dominated reefs from major damage due to grazing by the nudibranch. We found that the heaviest recruitment of *P. sibogae* was on the upstream portions of those reefs across which net water flow was unidirectional. This spatial pattern was also shown by the deposition of larval mimics across reefs and was consistent with a prediction of a model of the transport of larvae that sink in response to chemical cues from a reef.

Acknowledgements

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