

Substratum preferences in planula larvae of two species of scleractinian corals, *Goniastrea retiformis* and *Stylaraea punctata*

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Abstract To test whether coral planulae recruit randomly to different coral reef habitats or have specific substratum preferences, the settling behavior of planulae from two shallow water coral species from Pago Bay, Guam (13°25.02N, 144°47.30E) were examined in the laboratory in June and July of 1995. *Goniastrea retiformis* is generally restricted to the shallow reef front (<10 m depth) in areas dominated by crustose coralline algae (CCA), while *Stylaraea punctata* is abundant on inner reef flats where CCA coverage is low and sand and carbonate rubble covered by biofilms is common. When presented with four substrata (1) carbonate rock scrubbed free of biofilm and dried as a control, (2) the CCA *Hydrolithon reinboldii*, (3) the CCA *Peyssonelia* sp., and (4) naturally conditioned carbonate rubble covered by a biofilm, *G. retiformis* larvae showed a significant preference for *H. reinboldii*, and *S. punctata* larvae for the carbonate biofilm treatment. The preference shown by *S. punctata* larvae for biofilmed surfaces did not diminish with increasing larval age up to 11 days. These results suggest that the larvae of both species are capable of habitat selection, and

that the preferred substrata among those tested bears a relationship to the habitats in which adult colonies were found.

Introduction

Many sessile, benthic marine invertebrates have planktonic larvae that differ morphologically and physiologically from the juvenile and adult forms, and constitute the dispersal stage in the organisms' life history. The period during which these larvae can successfully settle and metamorphose into the juvenile form is called the competency period, and is affected by both intrinsic and extrinsic factors including nutritional mode, resource availability, temperature and the presence of specific chemical cues (Richmond 1987). Successful reproduction is only the first step in the process of population replenishment, maintenance and growth. Larvae must recruit, that is, settle and metamorphose, in order to become part of the population. Settlement is a physical process, during which larvae leave the water column and come into contact with the substratum, and is often reversible, with larvae contacting unsuitable substrata returning to the water column. Metamorphosis is a physiological process, during which morphological, physiological and metabolic changes occur, and with few exceptions, is non-reversible (Richmond 1985). Once larvae settle and come into contact with the substratum, chemicals associated with the substratum, conspecifics or preferred prey may be responsible for metamorphic induction (Morse 1990; Pawlik and Hadfield 1990; Hadfield and Paul 2001). Studies of larval recruitment in corals can help determine the extent to which distribution patterns are shaped by post-metamorphic events, with settlement and metamorphosis occurring randomly in available space, rather than pre-metamorphic events, such as the organisms' responses to

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specific environmental factors (i.e., specific sites and chemical cues), in shaping the final observed distribution patterns (Babcock and Mundy 1996; Morse et al. 1988; Mundy and Babcock 2000; Carlon 2002; Baird et al. 2003).

Several studies have examined settlement preferences of coral planula larvae. Planulae of some corals do not exhibit any apparent specificity. For example, *Pocillopora damicornis* larvae can settle and metamorphose on almost any hard surface as long as it is covered with biological films (Harrigan 1972) and these larvae are relatively unaffected by reductions in light underneath *Acropora hyacinthus* colonies (Baird and Hughes 2000). Similarly, *Stylophora pistillata* larvae metamorphosed in all treatment assays examined, including unfiltered seawater (Baird and Morse 2004). Larvae of the corals *Porites porites* (Goreau et al. 1981) and *Favia fragum* (Lewis 1974) also seem to have little substratum specificity.

In contrast, some corals are very specific in terms of where they settle and metamorphose. Morse et al. (1988) found that *Agaricia agaricites humilis* larvae are very specific, differentiating among crustose coralline algae, and only settling and metamorphosing on certain CCA species. *Agaricia tenuifolia* and *A. agaricites danai* larvae also show settlement preferences for coralline algae, but the requirement for specific coralline algae is not as stringent as in *A. agaricites humilis*. *Acropora tenuis* and *A. millepora* larvae have also been found to preferentially settle on the CCA *Titanoderma prototypum*, over other CCA species (Harrington et al. 2004). *Acropora nasuta*, *A. tenuis* and *A. digitifera* also require specific CCA to settle and metamorphose (Morse et al. 1996).

Crustose coralline red algae (CCA) induce settlement and metamorphosis in many corals (Morse et al. 1988; Heyward and Negri 1999; Raimondi and Morse 2000; Baird and Morse 2004; Harrington et al. 2004). Crustose coralline algae dominate reef front areas, so coral larvae might be using them as indicators of suitable habitats and conditions. The actual chemical that triggers metamorphosis in corals can be found in the cell walls of the CCA (Morse and Morse 1991) or it can be from bacteria associated with the alga's surface (Negri et al. 2001). Larvae of the coral *Acropora willisiae* and *A. millepora* were induced to metamorphose by *Pseudoalteromonas* bacteria isolated from the coralline algae *Hydrolithon onkodes* (Negri et al. 2001). In addition, Baird and Morse (2004) suggested that both large and small water borne molecules induce metamorphosis in *Stylophora pistillata* planulae, many of which may be of bacterial origin.

To determine the role of larval selectivity in affecting coral recruitment patterns, two species were selected for study in Guam, Micronesia that exhibit different reproductive and distribution characteristics. The coral *Goniastrea retiformis* was selected for its habitat distribution pattern

and reproductive mode. On Guam, it is mainly restricted to the shallow forereef (<10 m), an area dominated by crustose coralline algae. *G. retiformis* is a simultaneous hermaphroditic spawning species (Richmond and Hunter 1990). During spawning, eggs and sperm are packaged together within individual polyps, and released in bundles. The eggs are buoyant and rise to the surface of the water, carrying the sperm with them. After the egg and sperm bundles reach the surface of the water, the gametes separate, and fertilization takes place. Eggs from *G. retiformis* did not contain zooxanthellae from their maternal line, but rather, acquired them from the environment. The mean oocyte diameter for *G. retiformis* is about 300 μm with a range of 270–340 μm .

In contrast, *Stylaraea punctata* is only found on the shallow water areas of inner reef flats on Guam, and reproduces by brooding larvae. It is the smallest of all zooxanthellate scleractinian corals, usually growing to no more than 20 mm in diameter. The larvae of *S. punctata* show plasticity in form and change from an elongated form to a pear-shaped form while swimming and crawling. The elongated form measured ca. 600 \times 400 μm –900 \times 300 μm . The pear-shaped larvae were ca. 500 \times 400 μm in size.

S. punctata was of particular interest because crustose coralline algae were observed to overgrow colonies in the field (Fig. 1). While many corals studied so far appear to prefer substrata covered with coralline algae, *S. punctata* did not follow that pattern. In the field, colonies of *S. punctata* are found in areas where crustose coralline algae cover is low, while sand and bare substrata covered with microbial/diatomaceous films are common.

In this paper, we present the results of experiments performed to address larval substratum preferences in these two species of corals, and how this may contribute to the observed distribution patterns of these species. We hypothesize that larval selectivity is related to habitat distribution.



Fig. 1 Crustose red coralline alga *Hydrolithon reinboldii* overgrowing a colony of *Stylaraea punctata*. Scale bar 1 mm

To test this hypothesis, we compared the larval selectivity of *G. retiformis* and *S. punctata* larvae.

Materials and methods

Collection of coral colonies

Colonies of *G. retiformis* and *S. punctata* were collected from Pago Bay, Guam, (13°25.02N, 144°47.30E) in 1995 for this study. *G. retiformis* were sampled in the field 1–2 weeks before the expected spawning time to determine whether they were reproductively mature (Richmond and Hunter 1990). The presence of colored eggs indicated that the colonies were ripe. Ripe colonies were collected a few days before the June full moon and maintained in flow through seawater tanks. Commencing the night of the June full moon, colonies were observed each night for spawning activity and to collect gametes for controlled crosses.

Colonies of *S. punctata* were collected from the reef flat at Pago Bay, Guam. Only colonies larger than 10 mm in diameter were collected since smaller colonies may not have been reproductively mature. Coral colonies were placed in 3-l plastic containers under running seawater.

Collection of larvae

For *G. retiformis*, the procedures used for fertilization of eggs and rearing of larvae were as described by Richmond (1988). During spawning, coral gamete bundles were collected and the eggs and sperm separated using 45- μm nylon screens. The sperm were small enough to pass through the 45- μm nylon screens while the eggs were retained. Sperm were washed from the eggs using UV sterilized and Millipore filtered seawater and were collected in a beaker. Fertilizations were performed by adding 1 ml of a diluted sperm suspension obtained from one coral colony, to a glass beaker containing about 300 eggs from a different colony, resulting in a sperm concentration of about 10^5 sperm ml^{-1} . This concentration ensures sufficient sperm to fertilize the eggs but was found to be low enough to prevent polyspermy. Several coral colonies were used to make several crosses to yield enough larvae to conduct the experiments. Outcrossing was found to yield fertilization rates exceeding 90%, and high quality larvae. After fertilization, developing embryos were kept in UV sterilized seawater at a density of ca. 1 larva ml^{-1} . The embryos and larvae were cultured outside under natural light and at ambient temperatures of 27–28°C. We observed *Goniastrea* larvae to be fully ciliated and mobile within 18 h with the first substratum exploration and settlement behavior observed within 72 h.

The collection of *S. punctata* larvae from the parent colonies followed the procedures described by Richmond and

Jokiel (1984) for *Pocillopora damicornis*, another brooding species. Corals were placed into 3 l containers that overflowed into larval collectors with sides made from 45- μm nylon screens. Larvae were collected every day. Collected larvae were maintained in UV sterilized and Millipore filtered seawater until they were ready to be used in the experiments. The adult colonies and larvae of *S. punctata* were maintained outside under natural light and ambient water temperatures of 27–28°C.

Substratum preferences

Goniastrea retiformis larvae

Experiments were carried out in 250-ml glass jars containing 150-ml of UV sterilized and Millipore filtered seawater and one piece of test substratum. The following substrata were tested: pieces of the crustose coralline alga, *Hydroliothon reinboldii*, the crustose red alga, *Peyssonelia* sp. and pieces of naturally conditioned carbonate rubble on which no coralline algae were growing. The naturally conditioned carbonate rubble pieces were collected from the field and placed in the water tables until they were used in the experiments. Reef rocks that were scrubbed and dried to get rid of coralline algae or microbial films were used as controls. Six replicate jars for each treatment were set up simultaneously with a single piece of test substratum in each, and 15, 3-day-old larvae were placed into each. Experimental jars were arranged in a randomized block design. We did not aerate the experimental jars; preliminary work showed that we got better recruitment rates if we did not bubble air into the vessels.

Stylaraea punctata larvae

The experiments on the *S. punctata* larvae were set up in a different way, with the same four substrata treatments being placed together, but not touching one another, on the floor of each of the six replicate containers. Due to the limited number of competent *S. punctata* larvae, only ten larvae were added to each container and the larvae were <1 day old.

Effect of time on substratum preference of Stylaraea punctata larvae

To study the effect of time following fertilization on substratum preference and selectivity, the experiment described above was repeated with 3-, 7-, 9- and 11-day-old larvae.

Statistical analysis

The experiment was scored after 24 h by counting the number of metamorphosed individuals and the total number of

individuals recovered. Data were expressed as the proportion of larvae that had metamorphosed. The total number of individuals for calculations included free-swimming, settled and metamorphosed larvae. A Kruskal–Wallis ANOVA was used to test for differences among the different substrata for the preference experiments, while one-way ANOVA was used to assess the difference in preference of *S. punctata* larvae over time.

Results and discussion

Preference of *Goniastrea retiformis* larvae

There were significant differences in the number of larvae that metamorphosed on different substrata ($P = 0.006$; Fig. 2). More larvae settled on the crustose coralline alga, *H. reinboldii* than on the other substrata (Fig. 2). There was no settlement or metamorphosis on the controls (Fig. 2). At the end of the experiment, most of the larvae had attached to the substratum, but had not fully metamorphosed. The larvae that had attached and formed a basal plate were counted as metamorphosed.

Preference of *Stylaraea punctata* larvae

There were significant differences in the number of larvae that settled and metamorphosed on the different substrata ($P = 0.001$; Fig. 3). Significantly more larvae settled and metamorphosed on the microbial film than on the other substrata ($P < 0.05$, $n = 6$; Fig. 3). No larvae settled and metamorphosed on the control substrata (Fig. 3).

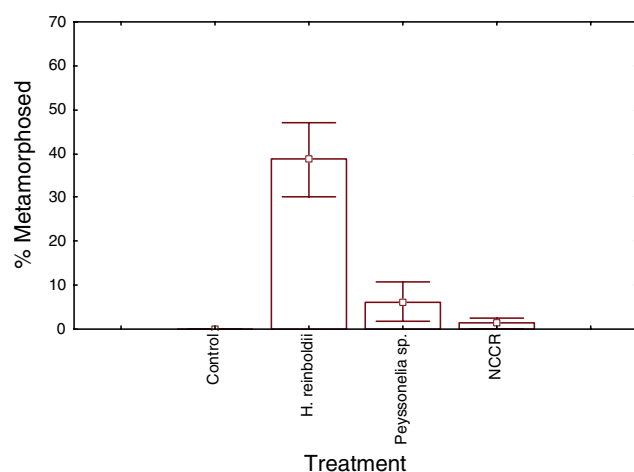


Fig. 2 Substratum preference of 3-day-old *Goniastrea retiformis* larvae. There were six replicates of each treatment with 15 larvae per replicate. NCCR naturally conditioned carbonate rubble. Kruskal–Wallis ANOVA revealed significant differences among the treatments ($P = 0.006$). Values shown are mean \pm SE

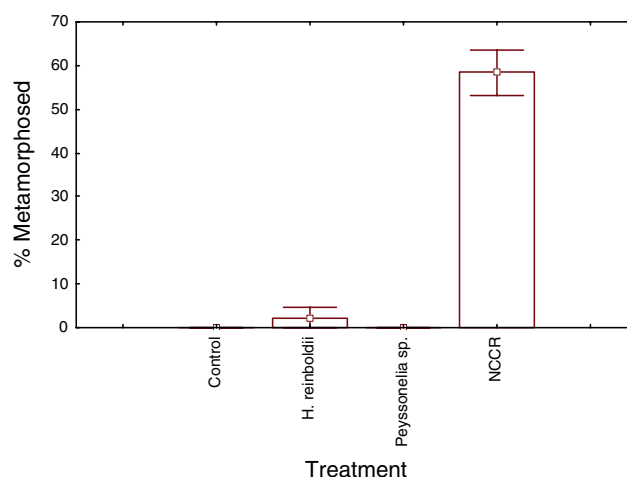


Fig. 3 Substratum preference of 1-day-old *Stylaraea punctata* larvae. There were six replicates of each treatment with ten larvae per replicate. NCCR naturally conditioned carbonate rubble. Kruskal–Wallis analysis revealed significant differences among treatments ($P = 0.001$). Values shown are mean \pm SE

Effect of time on preference of *Stylaraea punctata* larvae

The preference of *S. punctata* larvae for the microbial film treatment, *H. reinboldii*, *Peyssonella* sp., and the control did not significantly change over a period of eleven days (Table 1).

The average recovery (free-swimming, settled and metamorphosed) for the *G. retiformis* preference experiment was 79% while the recovery for the <1 day old *S. punctata* preference experiment was 73% (Supplementary table). The recovery rate was not related to the age of the larvae used. The *S. punctata* preference experiment using 9-day-old larvae had the highest recovery at 83% while 7-day-old larvae had the lowest at 65% (Supplementary table). Larval losses were probably the result of mortality and decomposition since we did not see any recruitment on the walls of the experimental containers.

The results of this research demonstrated two distinctly different recruitment responses in coral larvae from two different species of stony corals: a preference for the crustose coralline alga *H. reinboldii* in *Gonistrea retiformis*, and an avoidance of this substratum, with a preference for biofilms in *S. punctata*. Previous studies have demonstrated that some corals do not have strict preferences for a particular substratum during settlement and metamorphosis (Baird and Morse 2004; Goreau et al. 1981; Harrigan 1972; Lewis 1974), while other corals only settle and metamorphose on specific substrata (Morse et al. 1988, 1996; Morse and Morse 1991; Negri et al. 2001; Raimondi and Morse 2000; Baird and Morse 2004; Harrington et al. 2004). Because *S. punctata* reproduce by brooding, we expected it to be non-selective like other brooders that have been studied before

Table 1 Settlement preference of *S. punctata* larvae over time

Time (days)	Control	<i>H. reinboldii</i>	<i>Peyssonellia</i> sp.	Naturally conditioned carbonate rubble
1	0	2.3	0	58.5
3	0	1.7	1.7	53.0
7	0	2.8	0	65.1
9	0	0	0	64.5
11	0	5.5	0	44.2

Values shown are percent of larvae that metamorphosed on each substrata. No significant difference in preference for microbial films over the 5 days tested (one-way ANOVA, $P = 0.34$)

(Harrigan 1972; Lewis 1974; Goreau et al. 1981; Baird and Morse 2004). The results of this work show that larvae of *S. punctata* are highly specific in where they settle and metamorphose, in both preference and apparently avoidance (Fig. 3, Table 1). The results indicate that reproductive mode is not a good predictor of whether coral larvae will be specific in where they settle and metamorphose, rather, adult distribution is a better indicator of whether larvae will be specific or general with respect to recruitment patterns. *S. punctata* colonies have a limited distribution pattern that is similar to that of spawners and unlike many brooders that have widely distributed adult colonies.

Adult colonies of *S. punctata* were frequently found overgrown by coralline algae in the field (Fig. 1) as a result of their small size and slow growth rate. *G. retiformis* recruits are only susceptible to being overgrown by coralline algae when they are juveniles. Once they reach a certain size, coralline algae are not able to overgrow them. Since *S. punctata* have small colonies, they never attain a refuge in size where they cannot be overgrown by coralline algae. Thus, the survivorship of larvae avoiding crustose coralline algae is expected to be higher than for those larvae that recruit on faster growing species of crustose coralline algae.

While the specific substratum-associated metamorphic inducers addressed in this study may have differed, both types of larval responses support habitat selection and enhanced levels of post-metamorphic survivorship. The preference of *G. retiformis* larvae for crustose coralline algae (Figs. 2, 3) is similar to that observed in several other coral species studied (Morse et al. 1988, 1996; Morse and Morse 1991; Heyward and Negri 1999; Raimondi and Morse 2000; Negri et al. 2001; Baird and Morse 2004; Harrington et al. 2004). Crustose coralline algae may act as an environmental indicator of adequate light, water motion and water quality. Additionally, juvenile corals can be smothered by turf and fleshy alga and avoidance of these types of substrata is adaptive in corals.

Substrata covered with crustose coralline algae do not have high coverage of turf and fleshy algae. One character-

istic of some crustose coralline algal species is the regular shedding of their surface layers of cells, which may reduce epiphytic and epizootic competitors for space. Most corals readily overgrow coralline algae, thus this substratum is also appropriate from a space and competition perspective.

The preference of *S. punctata* larvae for microbial film did not decrease over time. Studies of several different invertebrate species have shown that larvae may lose selectivity when the larval phase is prolonged (Coon et al. 1990; Rittschof et al. 1984; Highsmith 1982). The maintenance of stringency and specificity in *S. punctata* demonstrated in this study is similar to what Morse et al. (1996) demonstrated for larvae of several *Acropora* species. The reason why preference in *S. punctata* larvae did not decrease over time might be attributed to the length of the experiments. The experiment was designed so that all of the choices were available to the larvae. If only one substratum was presented to the larvae, then the larvae might have lost selectivity and settled and metamorphosed on that substratum.

It is also possible that since all the choices were available to *S. punctata* larvae, they could have received the metamorphic inducer from one substratum and metamorphosed on another. But if this were the case, we would expect the number of metamorphosed larvae on all of the test substrata to be similar. The results did not show this outcome, rather it showed that most larvae metamorphosed on naturally conditioned surfaces (Fig. 3, Table 1).

The more likely reason why preference does not decrease through time in *S. punctata* larvae in contrast with some other invertebrate larvae may be because the maintenance of larval substrata preference is critical for survival. Individuals that recruit to carbonate rubble within the shallow water reef flat habitat in which they are found have a better chance of survival than those that lose their selectivity over time and settle on coralline algae, or disperse to other habitats more favorable to other species, since recruits will have a greater likelihood of being overgrown.

Two models have been used to describe recruitment patterns of marine invertebrates (Morse et al. 1988). In the “lottery” model, recruitment occurs randomly when space becomes available while in the “deterministic” model, the larval selectivity for appropriate substrata is important in determining spatial patterns in recruitment (Morse et al. 1988). The results of this study support the “deterministic” model.

An interesting question that still needs to be resolved is the nature and source of the metamorphic inducers for *G. retiformis* and *S. punctata*. Previous studies have raised questions as to whether inducers associated with crustose coralline algae and other biofilms are of algal or bacterial origin. Alternatively, there may be chemicals produced by coralline algae and other organisms that serve to inhibit recruitment of *S. punctata* and other types of larvae.

Additional research on recruitment specificity is needed on the growing number of corals from which planulae larvae can be collected or raised. The role of competition, predation, and disturbance in shaping distribution patterns have been well documented, but there are relatively few studies on the role of larval habitat selection in setting distribution patterns (reviewed by Pawlik and Hadfield 1990). Additional research testing particular substrata that induce settlement and metamorphosis in corals will contribute to the knowledge of important factors that shape distribution patterns and are responsible for the persistence of coral reefs. Likewise, studies of recruitment inhibition are needed to better understand coral reef ecosystem dynamics.

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References

- Babcock R, Mundy C (1996) Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. *J Exp Mar Biol Ecol* 206:179–201
- Baird AH, Hughes TP (2000) Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understory assemblages. *J Exp Mar Biol Ecol* 251:117–132
- Baird AH, Morse ANC (2004) Induction of metamorphosis in larvae of the brooding corals *Acropora palifera* and *Stylophora pistillata*. *Mar Freshw Res* 55:469–472
- Baird AH, Babcock RC, Mundy CP (2003) Habitat selection by larvae influences the depth distribution of six common coral species. *Mar Ecol Prog Ser* 252:289–293
- Carlson DB (2002) Production and supply of larvae as determinants of zonation in a brooding tropical coral. *J Exp Mar Biol Ecol* 268:33–46
- Coon SL, Fitt WK, Bonar DB (1990) Competence and delay of metamorphosis in the Pacific oyster *Crassostrea gigas*. *Mar Biol* 106:379–387
- Goreau NI, Goreau TJ, Hayes AL (1981) Settling, survivorship and spatial aggregation in planulae and juveniles of the coral *Porites porites* (Pallas). *Bull Mar Sci* 31:424–435
- Hadfield MG, Paul VJ (2001) Natural chemical cues for settlement and metamorphosis of marine invertebrate larvae. In: McClintock JB, Baker BJ (eds) *Marine chemical ecology*. CRC Press, Boca Raton, pp 431–462
- Harrigan JS (1972) The planulae larvae of *Pocillopora damicornis*, lunar periodicity of swarming and substratum selection behavior. Ph.D. thesis, University of Hawaii, Hawaii, p 319
- Harrington L, Fabricius K, De'ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:3428–3437
- Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. *Coral Reefs* 18:273–279
- Highsmith RC (1982) Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites: adult sand dollar beds. *Ecology* 63:329–337
- Lewis JB (1974) The settlement behavior of planulae larvae of the hermatypic coral *Favia fragum* (Esper). *J Exp Mar Biol Ecol* 15:165–172
- Morse DE (1990) Recent progress in larval settlement and metamorphosis: closing the gaps between molecular biology and ecology. *Bull Mar Sci* 46:465–483
- Morse DE, Morse ANC (1991) Enzymatic characterization of the morphogen recognized by *Agaricia humilis* (scleractinian coral) larvae. *Biol Bull* 181:104–122
- Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric agariciid corals. *J Exp Mar Biol Ecol* 116:193–217
- Morse ANC, Iwao K, Baba M, Shimoike K, Hayashibara T, Omori M (1996) An ancient chemosensory mechanism brings new life to coral reefs. *Biol Bull* 191:149–154
- Mundy C, Babcock R (2000) Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? A case study of three contrasting species. *Mar Ecol Prog Ser* 198:109–119
- Negri AP, Webster NS, Hill RT, Heyward AJ (2001) Metamorphosis of broadcast spawning corals in response to bacteria isolated from crustose algae. *Mar Ecol Prog Ser* 223:121–131
- Pawlik JR, Hadfield MG (1990) A symposium on chemical factors that influence the settlement and metamorphosis of marine invertebrate larvae: introduction and perspective. *Bull Mar Sci* 46:450–454
- Raimondi PT, Morse ANC (2000) The consequences of complex larval behavior in a coral. *Ecology* 81:3193–3211
- Richmond RH (1985) Reversible metamorphosis in coral planulae larvae. *Mar Ecol Prog Ser* 22:181–185
- Richmond RH (1987) Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. *Mar Biol* 93:527–533
- Richmond RH (1988) Competency and dispersal potential of planula larvae of a spawning versus a brooding coral. *Proc 6th Int Coral Reef Symp* 2:827–831
- Richmond RH, Hunter CC (1990) Reproduction and recruitment of corals: comparisons among Caribbean, the Tropical Pacific, and the Red Sea. *Mar Ecol Prog Ser* 60:185–203
- Richmond RH, Jokiel PL (1984) Lunar periodicity in larva release in the reef coral *Pocillopora damicornis*. *Mar Biol* 93:527–533
- Rittschof D, Branscomb ES, Costlow JD (1984) Settlement and behavior in relation to flow and surface in larval barnacles, *Balanus amphitrite* Darwin. *J Exp Mar Biol Ecol* 82:31–146