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Experimental analysis of recruitment in a scleractinian coral at high latitude

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ABSTRACT: A set of field experiments were conducted to determine the patterns of dispersal and recruitment in the brooding scleractinian coral *Pocillopora damicornis* at high-latitude (32° N), temperate locations in Amakusa, south-western Japan. Planulation occurred only in July (from full moon to last-quarter moon) in 2 consecutive years, confirming a pattern of annual reproduction in this species at the study site. Settlement plates placed beside naturally occurring colonies of *P. damicornis* accumulated more recruits than plates placed away (8 m) from the colonies in both years. Another experiment involving transplantation of *P. damicornis* colonies into an area where the species did not naturally occur but where environmental conditions were considered adequate for its growth also demonstrated that the density of settling planulae was high close to parent colonies but declined steadily with increasing distance. Planulae distribution tended to be more aggregated with increasing distance from their source. The present study demonstrates that the planulae of brooding coral species do not generally disperse over long distances at high latitude.

KEY WORDS: Brooder · Dispersal · Planulae · *Pocillopora damicornis* · Recruitment

INTRODUCTION

Recruitment represents one of the most important aspects in the maintenance of populations. In sessile marine organisms, recruitment generally occurs after dispersal of small mobile larvae. Therefore, recruitment and dispersal need to be considered together in order to grasp the population dynamics of sessile marine organisms such as corals, barnacles and algae.

Studies on coral recruitment have predominantly been carried out in tropical reefs, where recruitment demonstrates considerable spatio-temporal and taxonomic variation (Harrison & Wallace 1990, Richmond & Hunter 1990, Hughes et al. 1999). However, less is known about coral recruitment in temperate or high-latitude reefs. A few reports have shown recruitment of corals at high latitudes to be less intense than in tropical areas and to be dominated by larvae of brooding species belonging to the genera *Pocillopora* and *Acropora* (Harriott 1992, 1995, Harriott & Banks 1995).

Low temperature is the classical explanation for a reduced abundance of scleractinian corals at high latitudes (Dana 1843, Wells 1957). However, as many temperate habitats support some coral species (Jacques et al. 1983, Schuhmacher & Zibrowius 1985), temperature alone is not an insurmountable physiological constraint. Johannes et al. (1983) suggested that latitudinal variation in physical factors (including, but not limited to, temperature) affects corals indirectly by altering biotic interactions, including the shifting of competitive advantage to seaweeds in higher latitudes, and thereby restricts corals to the tropics.

In the majority of marine sessile organisms, dispersal usually takes place during a pelagic larval stage. However, non-pelagic larval development is not uncommon, particularly among species inhabiting high latitudes (Thorson 1950). While the planula larvae of most scleractinian corals spend some time in the water col-

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umn before settling, the extent of dispersal by coral larvae is still unclear (Harrison & Wallace 1990). Some workers have proposed that scleractinian coral larvae have the ability to disperse across reefs and geographic regions (Jackson 1986, Veron 1995), whereas others found that coral larvae have relatively limited dispersal (Gerrodette 1981, Fadlallah & Pearse 1982) and considered rafting (whereby larvae are transported by being attached to some object) as an important dispersal mechanism (Jokiel 1990).

Different modes of coral reproduction, i.e. brooding and spawning, may lead to different patterns in recruitment. For example, planulae of brooding species that are released at an advanced developmental stage may be able to settle quickly near the parent colony compared with the planulae of spawning species (Harrison & Wallace 1990, Richmond & Hunter 1990).

Pocillopora damicornis is well known as a hermaphrodite brooder species (Harriott 1983, Stoddart & Black 1985) that releases well-developed planulae containing zooxanthellae. Planulae usually settle within 2 d of release (Richmond 1985), although some individual larvae may remain planktonic for up to 90 d and still have the ability to settle and metamorphose (Harrigan 1972). Two different views have been expressed concerning the dispersal of planulae in brooding species: (1) dispersal of brooded planulae is limited and they settle quickly near the parent colony (see review by Harrison & Wallace 1990); (2) brooded planulae are capable of dispersing long distances (Richmond 1987). However, to date, these aspects have rarely been examined in detail with experimental approaches. In the present study, a field experiment was carried out to determine the patterns of dispersal and recruitment in *P. damicornis* near the northern limit of its latitudinal range (south-western Japan).

MATERIALS AND METHODS

Study site. The present study was conducted at 3 locations in Amakusa, south-western Japan (Fig. 1): (1) Ooshima Island, 32° 11′ N, 129° 58′ E; (2) Katashima Island, 32° 09′ N, 129° 59′ E; and (3) Satsuki, 32° 10′ N, 130° 02′ E. More than 100 scleractinian species have been recorded from Amakusa (Veron 1992). At the study site, scleractinian corals were abundant, with the tabular coral *Acropora solitaryensis* being the most dominant species in shallow (2 to 15 m deep) waters. At depths of >15 m, the sea floor predominantly consists of sand and loose cobbles and corals are scarce.

Planulation. The seasonal pattern of reproduction in *Pocillopora damicornis* was observed from April 1997 to November 1998. At monthly intervals, 30 samples (each sample consisting of 3 apical branches of ca 5 cm from 1 colony) of *P. damicornis* were collected, and the polyps were examined for the presence of planulae under a dissecting microscope.

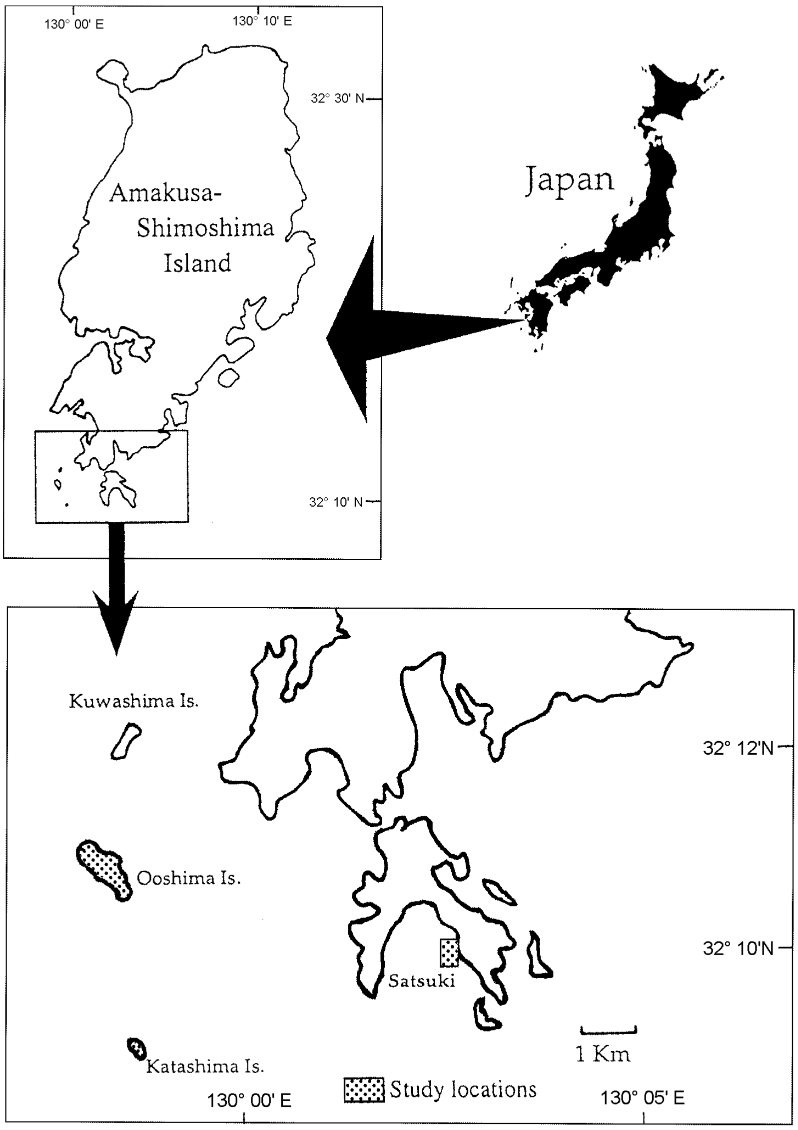

Fig. 1. Map of study site showing 3 sampling locations (Ooshima, Katashima and Satsuki) in Amakusa, south-western Japan

Planula release in *Pocillopora damicornis* was examined in the laboratory in July 1997 (when the field-collected samples contained planulae) from full moon to new moon to check for lunar periodicity in planulation. Twenty healthy colonies (elliptically shaped, ca 20 to 25 cm largest dimension) were collected on 18 July 1997 from Ooshima and Katashima Islands, Amakusa, and transported within 1 h to the laboratory, without exposure to the air, to minimise stress on corals. Each colony was maintained in a 25 l bucket supplied with running sea water. Planulation was closely observed from full moon to last-quarter moon, particularly after sunset until late morning, in order to ascertain the timing of planula release. Released planulae were collected through a small hose running into a plastic bottle (10 cm in diameter and 10 cm tall) with 2 windows (4 cm^2) covered by a plankton net (mesh size 100 µm). Planulae were counted every morning.

Recruitment experiment. Recruitment and dispersal in *Pocillopora damicornis* were investigated in Ooshima Island and Satsuki, Amakusa. Fifteen concrete blocks (40 × 20 × 10 cm) were positioned near (5 to 10 cm) a colony, while a further 15 blocks were placed approximately 8 to 10 m away from the nearest colony. To each concrete block, 6 settlement plates (ceramic tiles measuring 10 × 10 × 2 cm) were fixed by bolts and nuts. All plates were submerged on 19 July 1997, 1 d before the start of planulation in this species, and retrieved after 3 mo. In order to investigate inter-annual variation in recruitment, new plates were also deployed in the same manner on 9 July 1998 and retrieved after 3 mo. The possibility of recruitment during the periods from November 1997 to June 1998 and from November 1998 to June 1999 was also examined by deploying new plates during these periods. Immediately after collection, the settlement plates were labelled and all soft tissues were removed by immersing them in hypochlorite solution. The plates were dried, all surfaces were examined, and the coral spat of *P. damicornis* were identified under a dissecting microscope. Blocks were treated as replicates in the subsequent data analysis.

In order to investigate dispersal, a total of 50 colonies (15 to 25 cm largest dimension) of *Pocillopora damicornis* were collected from Ooshima Island in February 1997 and transplanted within 1 h to an area of Satsuki where they had previously not been present. As with most non-reef communities, corals in Satsuki grow on rocks but do not form their own substrates. In the experimental area, the natural coral assemblage was dominated by *Acropora solitaryensis*, *A. hyacinthus* and *Porites* sp., and no *P. damicornis* occurred. Therefore, small colonies of *P. damicornis* (<2 cm) found in this area should be considered as recruits from the transplanted colonies.

The coral colonies were attached to the rock substrate using underwater epoxy over an area of about 10 m in diameter (designated the central colony area). To facilitate the measurement of larval dispersal, a total of 100 quadrats (each measuring 25 × 25 cm) were placed randomly in the central colony area, while outside this area 20 quadrats (25 × 25 cm) were placed at 1 m intervals in each of 10 different directions (0°, 36°, 72°, 108°, 144°, 180°, 216°, 252°, 288° and 324°). The number of recruits in each of these 300 quadrats was recorded 2 wk after annual planulation: because of the difficulties in identifying very small juvenile recruits *in situ*, only the 'visible' recruits of *Pocillopora damicornis* were counted (Wallace 1983). In 1998, newly recruited colonies were clearly distinguished from those recruited in the previous year as the latter were all larger than 5 cm, while the former were <2 cm.

Data analysis. The data were transformed using logarithms before applying ANOVA. A 2-way ANOVA was used to analyse the effect of distance and year on the dispersal of natural and transplanted populations.

Morisita's index of dispersion (Morisita 1959, Elliott 1977) was used to assess the dispersion patterns of coral recruits at different distances from the centre of dispersal. The index (I_δ) was calculated as:

$$I_\delta = n\frac{\sum(x^2)-\sum x}{(\sum x)^2-\sum x}$$

where x is the number of recruits in a quadrat and n is the number of sampling units. This index equals 1 for a random distribution, is >1 for an aggregated distribution, and <1 for a uniform distribution. The significance of departure from randomness was assessed by calculating the χ^2 value (Elliott 1977):

$$\chi^2 = I_\delta\left(\sum x - 1\right) + n - \sum x$$

RESULTS

Planulation

Observation of field-collected samples of *Pocillopora damicornis* showed that planulation occurred only in July of the 2 consecutive years, clearly pointing to an annual pattern of reproduction with a single short period of planulation. Corals from 2 different locations (Ooshima and Katashima Islands) showed a similar pattern of planula release at the time of full moon (20 July), continuing until 1 d after the last-quarter moon (27 July) (Fig. 2A). There was no significant difference (Mann-Whitney U-test, p = 0.650) in the number of planulae released between the 2 locations. Although the number of planulae released each day varied among colonies,

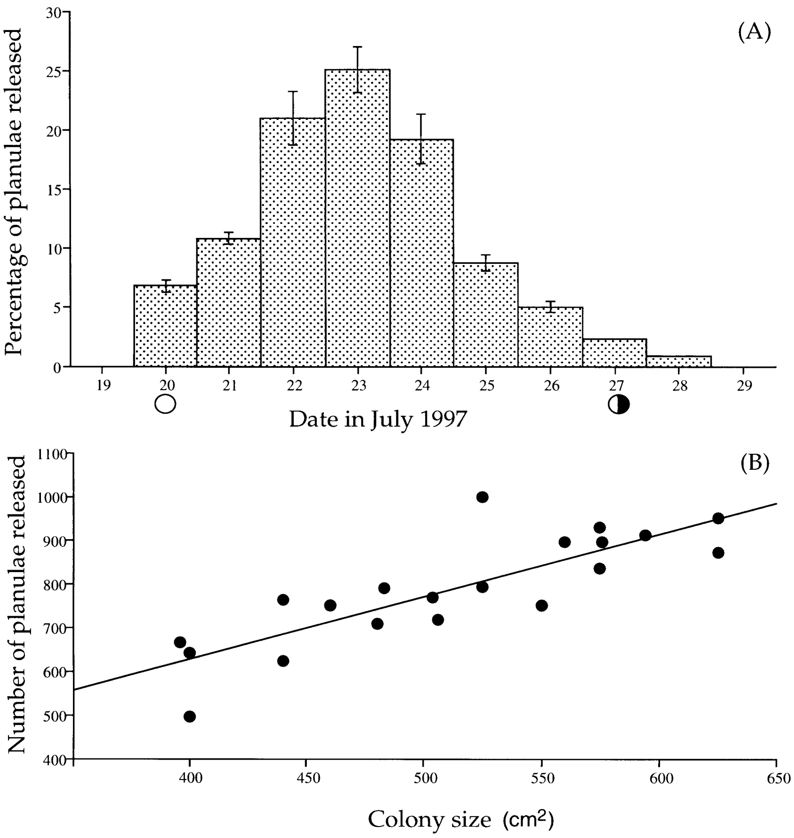

Fig. 2. *Pocillopora damicornis.* (A) Percentage (mean ± 1 SE, n = 20) of planulae released on each date, taking the cumulative total number released by each colony as 100%; full moon (20 July) and half moon (27 July) are indicated. (B) Relationship between number of planulae released and colony size (top surface area, cm^2); regression is: $y = 59.6 + 1.43x$, $r^2 = 0.68$, $p < 0.0001$

the peak number (proportion) of planulae released always occurred 3 or 4 d after full moon. Thereafter, the number of planula released declined, until no planula was seen in the collecting bottle on 29 July. Planulation always took place from early to late morning, and was usually correlated with low tide.

The total number of planulae released was significantly related to colony size (defined here as projected top surface area approximated as an ellipse, 0.25π × length × width), indicating that planulae production is affected by colony size in this species (Fig. 2B). It is notable that a 50% increase in colony size (from 400 to 600 cm^2) was accompanied by an approximately 50% increase in planulae output.

Pattern of recruitment

The number of recruits found on the 90 settlement plates submerged from July to October was similar in both years (1997, 70 recruits; 1998, 65 recruits). No coral spat was found from November 1997 to June 1998 or from November 1998 to June 1999, indicating that *Pocillopora damicornis* in Amakusa releases planulae only in summer. All juvenile corals were on the lower surface of the plates and none recruited on the upper surface, which was completely covered by barnacles and bryozoans. There was a significant difference in recruit density between the plates placed near *P. damicornis* colonies and those placed 8 to 10 m away (2-way ANOVA, $F = 13.095$, df = 1, p = 0.001), while no significant difference was found between the 2 years ($F = 0.093$, df = 1, p = 0.762); there was no interaction between year and distance ($F = 0.980$, df = 1, p = 0.326).

Dispersal pattern

The planulae of *Pocillopora damicornis* released from the central colony area appeared to disperse in all directions. There was no significant difference in the number of recruits among different directions (1-way ANOVA, $F = 0.925$, p = 0.505 (1997); $F = 1.070$, p = 0.386 (1998)). However, when directions were categorised into either east or west (with north and south numbers being equally divided), a significantly higher number of recruits occurred in the west than in the east in 1998 (binomial test, p < 0.01) but not in 1997 (p > 0.05). Thus, there was no consistent trend in terms of dispersal directions from year to year. All the recruits (a total of 831 in 1997 and 836 in 1998) were found in small crevices of 5 to 8 cm deep.

Recruit density was significantly negatively correlated with distance, and the regressions were nearly the same in the 2 years (Fig. 3). Considering the 95% CL of the regressions, these indicate that recruit density would drop to zero at 30 to 40 m distance from the parent colonies. The coefficients of determinant (r^2) in these regressions were relatively high, explaining about 70 to 80% of the variation in recruit density. Although the regression of the form $y = ax^b$ (linear regression on a log-log scale) was also fitted to the data, this achieved a poorer fit, with $r^2 = 0.48$ to 0.67.

Fig. 4 shows Morisita's index of dispersion, I_δ, plotted against distance. There was a significant positive correlation (Spearman's rank correlation, n = 20, $r_s = 0.59$, p = 0.01) between I_δ and distance, indicating that the planulae of *Pocillopora damicornis* tended to be more aggregated with increasing distance from their source.

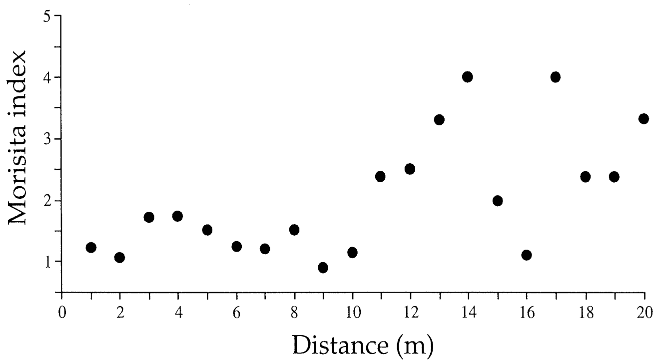

Fig. 4. *Pocillopora damicornis.* Morisita's index of dispersion (I_δ) plotted against distance (m) from edge of central colony area

DISCUSSION

Planulation

The present study showed that *Pocillopora damicornis* in Amakusa releases planulae once a year between full moon and last-quarter moon in July when the water temperature is 25 to 27°C. Seasonal and lunar periodicity in planula release has also been reported for this species from the Great Barrier Reef (Harriott 1983, Tanner 1996). In high-latitude reefs of Western Australia (32° S), *P. damicornis* released planulae at sea-water temperatures in the range of 25 to 26°C (Stoddart 1984, Stoddart & Black 1985). Some studies, however, have reported this species to planulate monthly or year-round in tropical sites with monthly water temperatures above 27°C (Atoda 1947, Harrigan 1972, Stimson 1978, Richmond & Jokiel 1984).

Our planulation data show a positive relationship between colony size and number of larvae released, indicating that large colonies produce more larvae than smaller ones. Similarly, planulae production by *Pocillopora damicornis* in the central Pacific is related to colony size (Richmond 1987). In contrast, Harrigan (1972) found no relationship between the number of planulae released and the surface area of a coral head in *P. damicornis*. Moreover, Holloran (1986) found that the planulation rate increased with increasing colony size up to 8 cm in radius, but thereafter decreased with increasing size. He suggested that the 'canopy-understory relationship' affects larvae production, whereby the canopy of a large colony severely shades the understory (inner regions) of the same colony. This might lead to a relatively small number of reproductive polyps even though the colony is large. In the present study, however, no such phenomenon was observed, and planulae production increased by about 50% concurrent with a 50% increase in colony size (= area), suggesting that reproductive output is roughly a function of surface area in this species.

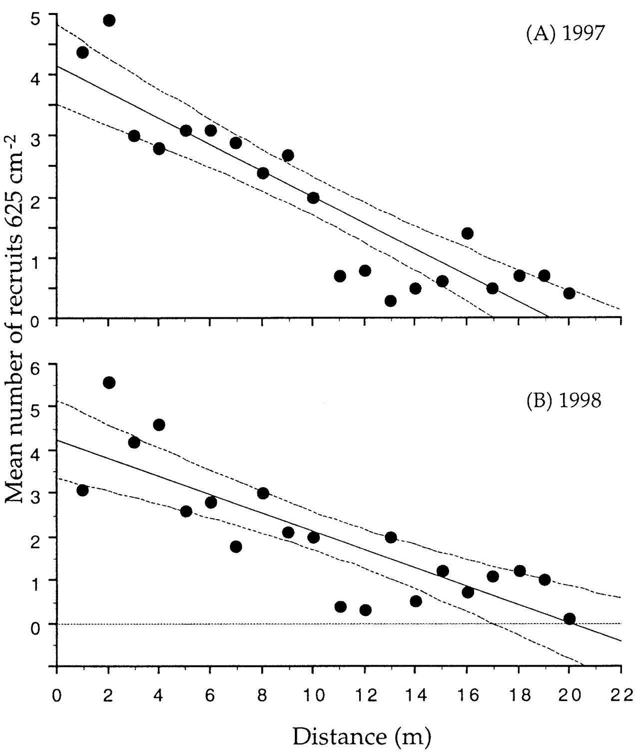

Fig. 3. *Pocillopora damicornis.* Relationship between mean number of recruits per 625 cm^2 area and distance from edge of central colony area in 1997 ($y = 4.163 - 0.216x$, $r^2 = 0.81$, $p < 0.0001$) and 1998 ($y = 4.242 - 0.212x$, $r^2 = 0.68$, $p < 0.0001$)

Pattern of recruitment

It has been reported that the recruitment of spawning corals declines while that of brooding corals (pocilloporids and the isoporan *Acropora* spp.) increases with increasing latitude, resulting in the dominance of brooders at high latitudes (Harriott 1992, 1995, Preece & Johnson 1993, Harriott & Banks 1995, Dunstan & Johnson 1998).

The recruitment rates (number of recruits per unit area) of *Pocillopora damicornis* observed in the present study (3.8 recruits m^{-2} in Ooshima Island and 11.2 recruits m^{-2} in Satsuki) were higher than that reported for a more tropical reef in Okinawa (0.2 m^{-2}: Yeemin 1991), but similar to that (11.6 recruits m^{-2}) reported from Coconut Island, Hawaii (Fitzhardinge 1989). Recruitment of pocilloporid corals is also high at high latitudes in the southern hemisphere. For example, studies at the Solitary (30° S) Islands and Lord Howe Island (31° S), southern Australia, revealed the dominance of pocilloporid taxa (17.3 and 61.2 m^{-2}, respectively) among coral recruits in these reefs (Harriott 1992, Harriott & Banks 1995). In contrast, Banks & Harriott (1996) reported that the most abundant recruited taxa in the Gneering Shoals (26° S) belonged to the Acroporidae (65%). Similarly, Wallace (1985) found the dominance of acroporids among recruits in Big Broadhurst Reef (18° S), Great Barrier Reef.

It has been reported that factors such as larval supply, substratum availability and competition for space with other sessile organisms affect coral recruitment (Sammarco 1991, Harriott 1992, 1995, Harriott & Banks 1995, Miller 1995, Miller & Hay 1996). In the Solitary Islands, corals settled predominantly on the upper surfaces of settlement plates; this was attributed to a reduction in light and competition with bryozoans and barnacles on the lower surface (Harriott & Banks 1995). Somewhat different results were obtained in the present study: all the settled planulae were observed on the lower surface of the settlement plates, while on the natural substrate they always settled in relatively protected places such as small crevices. This may reflect the influence of predation or grazing. Scleractinian planulae are able to discriminate potential settlement places, and generally prefer cryptic microhabitats, often on the under-surface of conditioned natural substrata (Harrison & Wallace 1990). As corals occurring in high latitudes do not build their own substrates, suitable substrates for settlement and metamorphosis of larvae are important.

Corals that settled in the vicinity of their parents (i.e. in the central colony area) showed a random dispersion pattern, but with increasing distance from the centre recruits showed more aggregated patterns. It has been reported that coral planulae have a strong tendency to settle close to one another under laboratory conditions, and subsequently fuse to form an aggregated colony (see review by Harrison & Wallace 1990). Mutual attraction of planulae as well as the availability of suitable substrates (i.e. small crevices) may have affected the aggregation pattern of *Pocillopora damicornis* in the present study.

Larval dispersal

Some studies on tropical and sub-tropical reefs have found the abundance of the recruits of brooding species to be positively correlated with adult abundance, pointing to rapid settlement and limited dispersal from their parent colonies (Harriott 1992, Smith 1992, 1997). The present study has experimentally demonstrated that the planulae of the brooding species *Pocillopora damicornis* tend to disperse over only short distances and to settle relatively close to their parent colonies. This gives weight to previous studies suggesting rapid settlement and limited dispersal of coral planulae (e.g. *Favia fragum* in the Caribbean [Szmant-Froelich et al. 1985] and *P. damicornis* in western Australia [Ward 1992]). *Acropora palifera* also showed rapid settlement in the laboratory (Potts 1984) and localised dispersal in the field (Harrison & Wallace 1990): planulae were found within 5 m of their parent colony. Similarly, restricted larval dispersal (less than 0.5 to 1 m from the parent colony) was observed for the non-pelagic (benthic) planulae of the solitary coral *Balanophyllia elegans* (Gerrodette 1981, Fadlallah & Pearse 1982).

On the other hand, Richmond (1987) found that planulae of *Pocillopora damicornis* contained a high proportion of lipid, which may be indicative of good dispersal ability. High lipid reserve is associated with large larval size. It has been demonstrated that *P. damicornis* planulae are capable of successfully settling and metamorphosing for up to 103 d after release, which represents a sufficiently long time for them to disperse from the central to the eastern Pacific (Richmond 1987). Consequently, Richmond surmised that the planulae of this species can disperse over long distances. However, it is unknown whether and how frequently such long-distance dispersal occurs under natural conditions in this species. The present study suggests that the possibility is very low.

Several studies have proposed that larval planulae settling in a reef may have come from other reefs, while other studies have suggested that reefs may be self-seeded (Richmond & Hunter 1990). Harriott & Fisk (1988) and Fisk & Harriott (1990) reported that in their studies high coral recruitment did not correspond with the abundance of adult populations, as the highest level of recruitment was seen on reefs damaged by *Acanthaster planci* predation. Consequently, they suggested that coral larvae may have been transported from adjacent reefs by the local current. In contrast, Black et al. (1991), using a numerical modeling approach, found that the parent reefs could constitute an important source of recruiting larvae. The present study provides clear evidence that the planulae of *Pocillopora damicornis* have rather limited dispersal distances. However, it should be noted that this does not absolutely prove the absence of long-distance dispersal in this species. This may still happen on very rare occasions under certain circumstances.

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