

Larval dispersal of *Pocillopora damicornis* at high latitude coral communities

Penyebaran larva karang *Pocillopora damicornis* di daerah lintang tinggi

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Abstract: In order to elucidate the patterns of dispersal in scleractinian coral *Pocillopora damicornis* near the northern limit of its latitudinal range, a total of 50 colonies (15-25 cm in diameter) of this coral were collected from Ooshima Island, Japan, and transplanted within one hour to the area of Satsuki, where they were not present before. Three concentric areas were established such as; the parental area (PA), intermediate area (IA) and outer area (OA). A total of 831 new corals were found in 1997 while 54.3% of these occurred in PA, 30.5% in IA and 15.1% in OA. In 1998, 52.3% of recruits settled in PA, 30.5% in IA and 17.2% in OA. A significant difference in the density of recruits was found among three areas, but recruit density was not significantly different between years and there was no interaction between area and year. There was no significant difference in the number of recruits among different directions, indicating no tendency for larvae to be concentrated in one particular direction. The present study suggests that the planulae of *P. damicornis* have limited dispersal distances at high-latitudes©

Keywords: *Pocillopora damicornis*; larval dispersal; high latitude; coral.

Abstrak: Untuk menjelaskan pola penyebaran karang scleractinia *Pocillopora damicornis* yang berada di batas Utara penyebarannya, total 50 koloni (15-25 cm) dari karang ini dikumpulkan dari Pulau Ooshima, Jepang, dan di transplantasikan dalam waktu satu jam ke daerah Satsuki yang tidak ditemukan jenis ini. Tiga daerah ditetapkan yaitu, Daerah Induk (PA), Daerah Tengah (IA), dan Daerah Luar (OA). Sebanyak 831 karang baru ditemukan pada tahun 1997, sementara 54,3% ditemukan di PA, 30,5% di IA dan 15,1% di OA. Pada tahun 1998, 52,3% ditemukan di PA, 30,5% di IA, dan 17,2% di OA. Ditemukan perbedaan yang signifikan untuk kepadatan antara ketiga daerah tersebut, tetapi tidak ada perbedaan yang signifikan antar tahun dan tidak ada interaksi antara daerah dan tahun. Tidak ada perbedaan yang signifikan dalam jumlah pada arah yang berbeda sehingga hal ini menunjukkan tidak ada kecenderungan bagi larva untuk terkonsentrasi pada satu arah tertentu. Penelitian ini menunjukkan bahwa planula *P. damicornis* memiliki jarak penyebaran terbatas pada komunitas karang di daerah lintang tinggi©

Kata-kata kunci: *Pocillopora damicornis*; penyebaran larva; lintang tinggi; karang.

INTRODUCTION

Low temperature is the classical explanation for a reduced abundance of scleractinian coral at high latitudes (Wells, 1957). However, as many temperate habitats support some coral species (Jacques *et al.*, 1983; Schuhmacher and 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) affect corals indirectly by altering biotic interactions, including the shifting of competitive advantage to seaweeds in higher latitudes, and thereby restricting 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 coral spend some time in the water column before settling, the extent of dispersal by coral larvae is still unclear (Harrison and Wallace, 1990). Some workers have proposed that scleractinian coral larvae have the ability to disperse across reef and geographic regions (Jackson 1986; Veron 1995), whereas others found that coral larvae have relatively low dispersal ranges or may disperse by being attached to some object as an important dispersal mechanism (Jokiel,

1990). This is consistent with the large geographic ranges of many marine taxa (Hughes *et al.*, 2002; Paulay and Meyer, 2002), and with comparative estimates of dispersal distance from genetic data (Kinlan and Gaines, 2003). However, recent work also suggests that a large proportion of marine larvae may be retained locally, even in species with extended larval durations (Sponaugle *et al.*, 2002; Kinlan and Gaines, 2003; Hellberg, 2007).

Pocillopora damicornis is well known as a hermaphrodite brooding species (Stoddart and Black, 1985) which releases well-developed planulae containing zooxanthellae. Planulae usually settle within two days after release (Richmond, 1985), though some individual larvae may remain planktonic for up to 90 days 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 and (2) the 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 elucidate the patterns of dispersal in *P. damicornis* near the northern limit of its latitudinal range (south-western Japan).

was dominated by *A. solitaryensis*, *A. hyacinthus*, and *Porites* sp., and no *P. Damicornis* occurred (Tioho *et al.*, 2001). 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 onto the rock substrate using under-water epoxy within an area about 10 m in diameter (designated as the “parent colony area” or PA). In order to facilitate analysis of the dispersal of coral larvae from the parent colonies, three concentric areas (10 m wide rings) were established outside the PA: (i) intermediate area (IA), located outside the PA, and (ii) outer area (OA) located outside the IA (Fig. 2a). A total of 100 quadrats (each measuring 25 x 25 cm) were placed randomly in the PA, while in the IA and OA 20 quadrats (25 x 25 cm) were placed at 1 m intervals along 10 different directions (0°, 36°, 72°, 108°, 144°, 180°, 216°, 252°, 288° and 324°) (Fig. 2b). The number of recruits was recorded two weeks after annual planulation (Tioho, 2000); because of the difficulties of identifying very small juvenile recruits *in situ*, only the ‘visible’ recruits of *P. damicornis* were counted. In 1998 newly-recruited colonies were clearly distinguished from those recruited in the previous year as the latter

MATERIALS AND METHODS

Study site

The present work was conducted at Satsuki (32° 10'N, 130° 02'E) of Amakusa, south-western Japan (Fig. 1). In common with many high-latitude coral assemblages, scleractinian corals are relatively abundant with a tabular coral *Acropora solitaryensis* being the most dominant species in shallow (2-15 m deep) waters. Over 15m of depth the sea floor predominantly consists of sand and loose cobbles and are scars.

Dispersal experiment

In order to investigate larval dispersal, a total of 50 colonies (15-25 cm in diameter) of *P. damicornis* were collected from Ooshima Island in July 19, 1997, and transplanted within one hour to the area of Satsuki (it is about 10 Km from Ooshima Island), where they were not present before. As with most non-reef communities, corals in Satsuki grew on rocks but did not form their own substrates. In the experimental area the natural coral assemblage

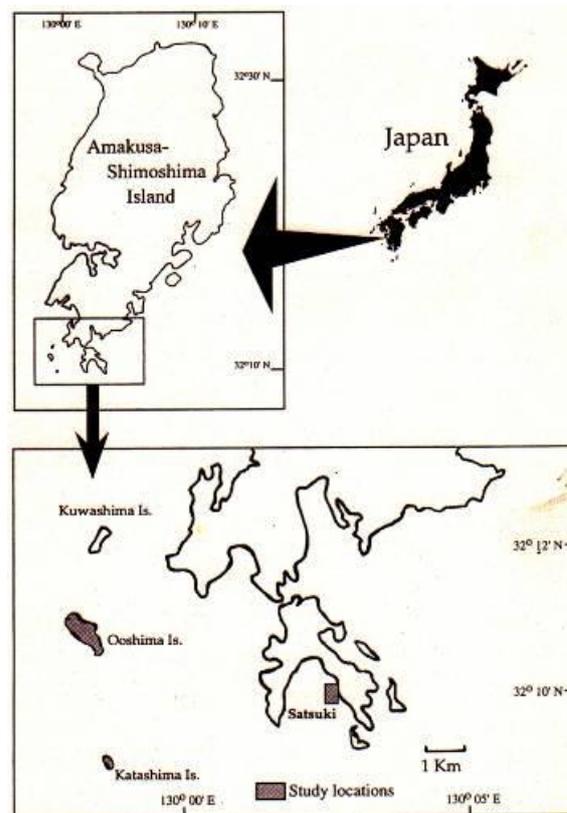


Figure 1. Location of the Study Site

were all >5 cm in size, while the former were <2 cm.

Data analysis

The data were transformed using logarithms before applying ANOVA. A two-way ANOVA was used to analyze the effect of distance and year on the dispersal of natural populations.

Morisita's Index of Dispersion (Morisita, 1959) was used to assess the dispersion patterns of coral recruits at different distances from the center of dispersal. The index is calculated as:

$$I_{\delta} = \frac{q \sum_{i=1}^q x_i (x_i - 1)}{N (N - 1)}$$

Where x is the number of recruits in a quadrat and N is the number of sampling units. This index

equals one for a random distribution, is greater than one for an aggregated distribution, and is less than one for a uniform distribution. The significance of the departure from randomness was assessed by calculating :

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

RESULTS AND DISCUSSION

On the natural substrate in Satsuki, a total of 831 new corals were found on the 300 quadrats (25 x 25 cm) placed in the three concentric areas in 1997. About 54.3% of these occurred in the parent colony area (PA), 30.5% in the intermediate area (IA), and 15.1% in the outer area (OA). In 1998, the same pattern of recruitment was observed, with 52.3% of recruits setting in the PA, 30.5% in the IA and 17.2% in the OA (Table 1). All the new colonies were found settled in small crevices of 5-8 cm. A significant difference in the density of recruits was found among three areas ($n=100$, $df=2$, $p= 0.0001$), but recruit density was not significantly different between years ($n=100$, $df= 2$, $p= 0.8221$) and there was no interaction between area and year ($n=100$, $df=2$, $p= 0.6126$) (Fig. 3).

The planula larvae of *P. damicornis* released from the PA appeared to disperse in all directions (Fig. 4A, B). There was no significant difference in the number of recruits among different directions (One-Way ANOVA, $F= 0.925$, $p = 0.505$ (1997); ($F = 1.070$, $p = 0.386$ (1998), indicating no tendency for larvae to be concentrated in one particular direction.

In the PA, the newly settled corals tended to disperse uniformly ($I_{\delta} = 0.91$), while they showed an aggregated patterns in both the IA and OA ($I_{\delta} = 1.48$ and 2.65 respectively). The patterns of dispersion were similar in the two years (Table 1). Figure 5 shows Morisita's Index of Dispersion I_{δ} plotted against distance from PA, indicating that the planulae of *P. damicornis* tended to aggregate with increasing distance from their source.

Corals that settled in the vicinity of their parent colony (PA) showed a uniform dispersion pattern, but with increasing the distance from the PA, recruited corals showed aggregated patterns in both the IA and OA. Many studies have reported that coral planulae have strong tendency to settle close to one another under laboratory conditions and subsequently fuse to form an aggregated colony (see review in Harrison and Wallace, 1990). Smith

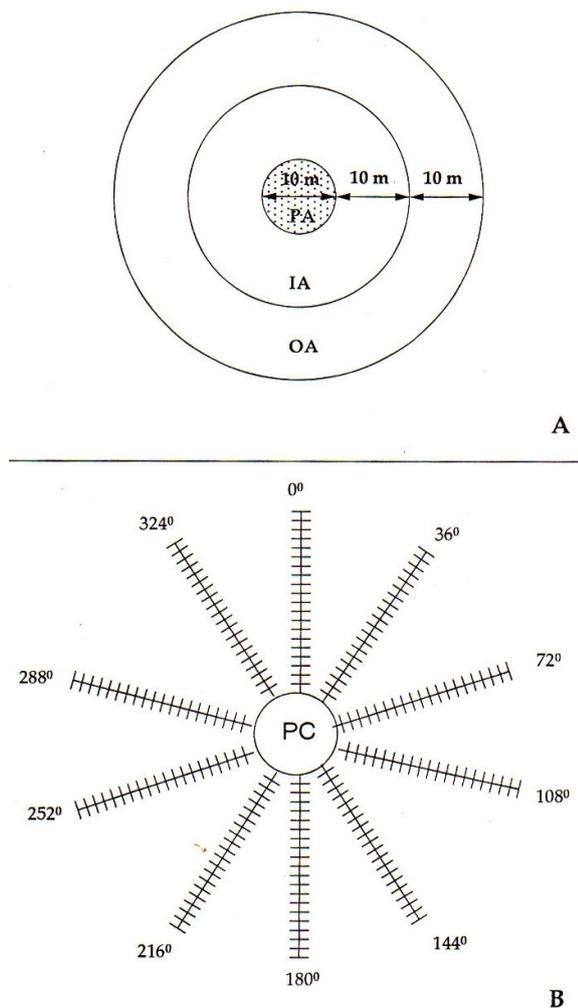


Figure. 2. Design of the larval dispersal experiment in Satsuki. (A) Positioning of transplanted colonies (PA) and two areas outside the (PA); (B) Position of the quadrats (25 x 25 cm) along ten different directions.

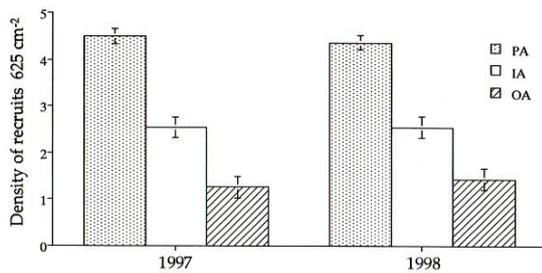


Figure 3. *Pocillopora damicornis*. Mean (± 1 SE, $n=100$) number of recruits per 625 cm² settled on natural substrates in three different areas (PA, IA, OA) in 1997 and 1998. (Two-Way ANOVA, significantly different between area, $p=0.0002$, but not between years $p=0.8221$, and interaction area versus year $p=0.6126$).

(1996) found that aggregation of coral recruits resulted from the low dispersal ability of brooders. The aggregated spatial distribution of corals may also be related to asexual processes, for example, Highsmith (1992) found that some corals with branching or plating morphologies are capable of asexual reproduction through fission of adult colonies. Fission of a large colony may lead to an aggregation of small colonies. In the case of *P. damicornis*, planulae produced through asexual reproduction are also well known in some places (Stoddart, 1983).

Larval dispersal

Some previous studies on tropical and subtropical reefs have found that the abundance of recruits of brooding species was positively correlated with adult abundance, indicating rapid settlement and short dispersal distance from their parent colonies (Harriott, 1992; Smith, 1996). The present study has demonstrated that the planulae of a brooding species *P. damicornis* tended to disperse short distances and settle relatively close to their parent colonies on natural substrates. Szamant-Froelich *et al.* (1985) and Ward (1992) also reported that planulae of brooding *Favia fragum* in

the Caribbean and *P. damicornis* in Western Australia settle and metamorphose rapidly. Localized dispersal in the field has also been observed in brooded planulae of *A. palifera* which settle quickly after release. Planulae were observed attaching to the reef within 5 m of their parent colony (Harrison and Wallace, 1990). Rapid settlement of *A. palifera* planulae has also been observed in the laboratory (Potts, 1984). Restricted larval dispersal (less than 0.5 to 1 m from the parent colony) has also been noted for non-pelagic (benthic) planula of a solitary coral *Balanophyllia elegans* (Gerrodette, 1981; Fadlallah and Pearse, 1982). Harii *et al.* (2002) found that *Helioporacoerulea* larvae settled close to the parent colony due to the larval competency period and the amount of energy (zooxanthellae) in the larval planulae.

On the other hand, Richmond (1987) found that planulae of *P. 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 up to 103 day after release, which represents a sufficiently long time for them to disperse from central to the eastern Pacific (Richmond, 1987). Consequently, Richmond (1987) surmised that the planulae of this species disperse over long distances.

Results of the present study clearly showed that the planulae of *P. damicornis* tend to settle close to their parent colony if suitable vacant substrates are available. Scleractinian planulae have an ability to discriminate among settlement sites, and generally prefer cryptic microhabitats, often on the under-surface of conditioned natural substrata (Harrison and Wallace, 1990). On the other hand, planulae of *P. damicornis* may disperse long distance by water current if they cannot find suitable substrates for settling soon after release. However, planula longevity is not necessarily a reliable indicator of larval dispersal potential, because dispersal will only be effective during the

Table 1. Total number of recruits (% in brackets) and Morishita's Index of Dispersion (I_{δ}) of *Pocillopora damicornis* on three different areas in 1997 and 1998. PA: parent area, IA: intermediate area, OA: outer area.

Area	No. of recruits		Morishita Index (I_{δ})	
	1997	1998	1997	1998
PA	451 (54.3)	437 (52.3)	Random (0.91)	Random (0.91)
IA	254 (30.5)	255 (30.5)	Aggregated (1.42)	Aggregated (1.48)
OA	126 (15.1)	144 (17.2)	Aggregated (3.25)	Aggregated (2.65)

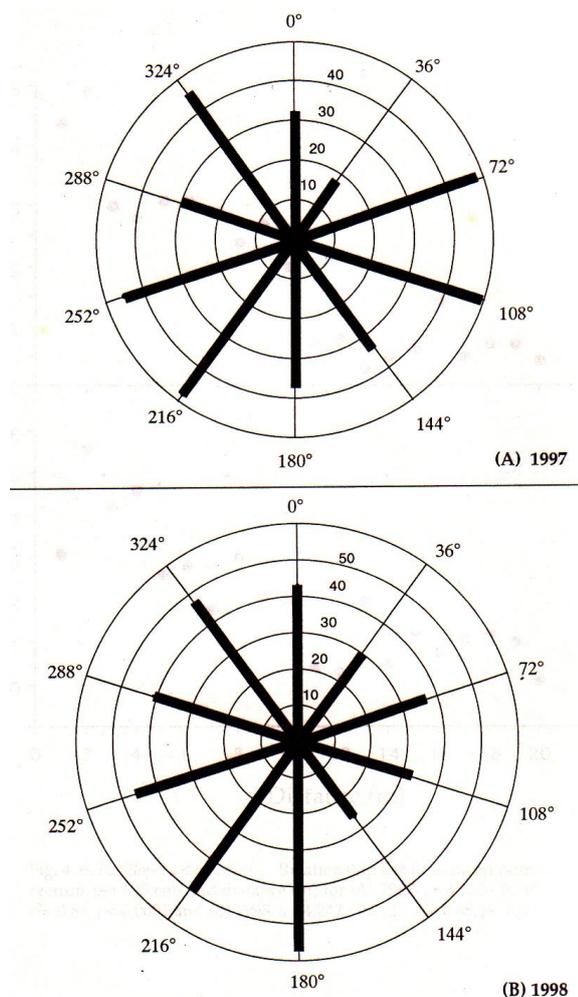


Figure 4. *Pocillopora damicornis*. Total numbers of newly-recruited colonies found along 10 different axes (each with twenty 25 x 25 cm quadrats) around the PA in (A) 1997 and (B) 1998.

period in which planulae remain competent to successfully settle and metamorphose (Harrigan, 1972; Richmond, 1987).

Several studies have found evidence that larval planulae settling in a reef may come from other reefs, while other studies have suggested that some reefs may be self-seeded (see review in Richmond and Hunter, 1990). Harriott and Fisk (1988) reported that high coral recruitment did not correspond with the abundance of adult populations because they found the highest level of recruitment on the reefs damaged by *Acanthaster planci* predation. They suggested that coral larvae may have been transported from adjacent reefs by the local current. In contrast, Black *et al.* (1991) found that the parent reefs may constitute a highly important source of recruiting larvae using a numerical modeling approach.

CONCLUSIONS

The present study clearly showed that the planulae of *P. damicornis* at high-latitude coral community have limited dispersal distances from their parent colonies.

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Tioho: larval dispersal of Pocillopora damicornis at high latitude coral communities

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