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## Larval dispersal, recruitment, and adult distribution of the brooding stony octocoral *Heliopora coerulea* on Ishigaki Island, southwest Japan

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**Abstract** Larval dispersal and recruitment are important factors that determine the distribution of adult corals. The relationships between larval dispersal, recruitment, and the adult distribution of the blue octocoral, *Heliopora coerulea*, were investigated on Shiraho Reef, Ishigaki Island, southwest Japan. *Heliopora coerulea* is a surface brooder that releases planulae in June or July on Shiraho Reef. We observed planulae between 1998 and 2000 and found that they did not swim actively; instead, they crawled into their settlement positions after becoming grounded on the substratum. Planulae occurred throughout the water column and were dispersed by tidal and wind-driven currents around the parent population on the reef flat. Recruitment was observed only within 350 m of the parent populations, including areas between the branches of the adult colony. The planulae of *H. coerulea* had a narrow dispersal range as a result of their mostly benthic, shorter larval duration, and the influence of weaker currents. Thus, the dispersal distance of larvae is determined by their position in the water column, the currents that deliver the larvae, and the competency period of the larvae. The narrow dispersal range of *H. coerulea* was consistent with recruitment of sexually derived larvae onto their natal reef.

**Keywords** *Heliopora coerulea* · Larval dispersal · Currents · Recruitment · Distribution

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### Introduction

Larval dispersal is of fundamental importance in maintaining and extending adult populations of marine organisms (Underwood and Fairweather 1989; Gaines and Bertness 1992; Hughes et al. 2000). Biologically, the dispersal distance of larvae is determined by their position in the water column and the length of time before they settle onto a substrate (competency period), and, physically, this distance is determined by prevailing currents at the time of spawning and larval release, and during the planktonic life stage (Morgan 1995; Shanks 1995; Young 1995). The position of larvae in the water column is determined by their buoyancy and swimming ability. Most larvae are unable to swim horizontally to reach distant settlement sites; however, even weakly swimming ciliated larvae can regulate their vertical positions (Chia et al. 1984; Morgan 1995). Some larvae may control horizontal transport by migrating vertically in response to predictable currents, such as stratified water masses and tidal currents (Shanks 1995; Young 1995). Competency periods, behavior, and current regimes thus directly determine the dispersal distance from the parent populations.

Scleractinian and soft corals in coral reefs have two different modes of sexual reproduction (spawning and brooding) which may correspond to different modes of larval dispersion (Alino and Coll 1989; Harrison and Wallace 1990; Richmond and Hunter 1990; Benayahu 1991). Spawning species release gametes into the water column, followed by external fertilization and development; most eggs are positively buoyant and float to the surface (Babcock and Heyward 1986; Arai et al. 1993). Direct observations of dispersal clearly indicate that eggs and planulae are transported beyond natal reefs by wind-driven surface currents (Wolanski et al. 1989; Willis and Oliver 1990). The larvae require 4 to 7 days to settle (Babcock and Heyward 1986; Harrison and Wallace 1990), and their maximum competency periods are several weeks long (Wilson and Harrison 1998). Thus,

they have the potential for wide dispersal between reefs via ocean currents, as has been observed along the Great Barrier Reef (Williams et al. 1984; Dight et al. 1990), in the Caribbean Sea (Roberts 1997), and in the Gulf of Mexico (Lugo-Fernández et al. 2001). Although three-dimensional hydrodynamic models have predicted that a portion of larvae could be retained in the natal reef long enough to settle (Black et al. 1990, 1991; Black 1993), most spawning species are likely to disperse among reefs (Hughes et al. 2000).

Brooding species, on the other hand, develop their larvae inside polyps and release mature larvae directly into the water column. The planulae are competent after 2 h to several days (e.g., Atoda 1947); hence, their dispersal distance is suggested to be shorter than that of spawning species (Harrison and Wallace 1990). Rapid settlement of planulae has been reported for the surface-brooding gorgonian *Briareum asbestinum* (Brazeau and Lasker 1990). Genetic studies have revealed a narrower dispersal and recruitment range for brooding species (Ayre and Dufty 1994; Benzie et al. 1995). *Seriatopora hystrix* was reported to have high levels of genetic variation in the Great Barrier Reef, which may be caused by relatively short larval pre-competency periods (Ayre and Dufty 1994). However, some planulae of brooding species have longer competency periods, suggesting that they disperse widely by currents (Richmond 1987; Ben-David-Zaslow and Benayahu 1996, 1998). Planulae of the brooding coral *Pocillopora damicornis* can settle as much as 100 days after release (Richmond 1987; Harii et al. 2002) and have been observed to disperse outside of reefs in Hawaii (Hodgson 1985). Thus, larval dispersal among brooding species may be more variable than spawners, depending on larval characteristics and prevailing currents during the planktonic phase.

Differences in spatial distribution patterns of recruits and adults may be related to different reproductive strategies (e.g., Szmant 1986). The larvae of spawning coral disperse widely, and, thus, recruitment patterns are not consistent with adult distribution patterns (Baird and Hughes 1997; Hughes et al. 1999). In contrast, field studies have suggested that brooding corals can recruit inside the natal reef (Babcock 1988; Harriott 1992; Harriott and Banks 1995; Dunstan and Johnson 1998; Hughes et al. 1999). Hughes et al. (1999) explain spatial variation in recruitment and adult distribution at four spatial scales along the Great Barrier Reef in terms of variation between spawners and brooders with wide and narrow dispersal potential, respectively.

The variation in dispersal ranges of coral larvae has generally been discussed in relation to the two modes of reproduction. However, variation in dispersal also exists among species that have the same reproductive strategy but live under different environmental conditions. The actual dispersal distance is likely determined by the competency period of a species, larval position in the water column, and currents that deliver the larvae. However, how these factors determine larval dispersal has never been investigated. Moreover, variations in

larval dispersal within the same reproductive mode have only been explained by differences in competency periods (e.g., Ben-David-Zaslow and Benayahu 1998). One reason for the scarcity of such research is the difficulty in tracking all processes from spawning (or release of planulae) to settlement.

In this study, we investigated the process from planulae release through dispersal to settlement of the brooding stony octocoral *Heliopora coerulea*, and the factors that determined its dispersal range. *Heliopora coerulea* is a narrow disperser, which allows for the tracking of all processes from release to settlement. In contrast to most octocorallians, which are soft corals (i.e., they form no skeleton), this species is a hermatypic octocoral that forms a skeleton. Its planulae develop in female polyps and subsequently attach themselves onto the female colony before release (Babcock 1990). This may allow larvae to develop further, so that released planulae are able to settle quickly, thus giving a narrow dispersal range and the advantage of settling in a habitat proven to be suitable for adult growth and reproduction.

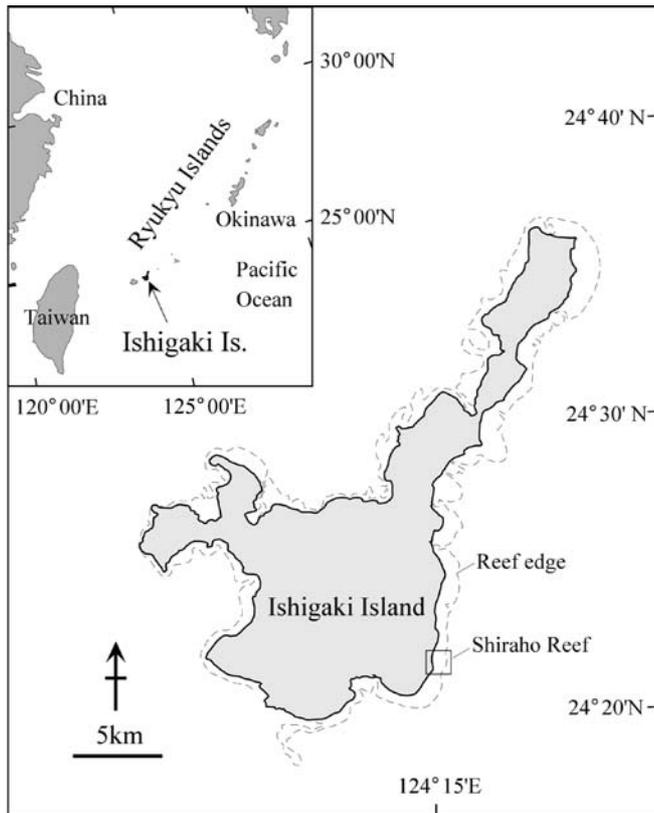
The study area, Shiraho Reef, Ishigaki Island, southwest Japan, is known for the abundance of this species (Takahashi et al. 1985; Nakamori et al. 1992; Iryu et al. 1995; Kayanne et al. 2002). In general, *H. coerulea* is found only in the tropical Indo-western Pacific (Zann and Bolton 1985; Veron 2000). Until now, however, no studies have been conducted on the sexual reproduction or the detailed distribution of *H. coerulea* in Japan. Adult *H. coerulea* colonies are unevenly distributed on the Shiraho Reef, and are distributed only in specific localities around Ishigaki Island (Nakamori et al. 1992). *Heliopora coerulea* has also been reported to have an uneven distribution in several other regions, including the Onotoa and Tarawa Atolls in the Gilbert Islands (Banner 1952; Zann and Bolton 1985), the Marshall Islands (Wells 1954, 1957), Indonesia (Tomascik et al. 1997), and the Indian Sea (Sheppard 2000). This species is relatively uncommon throughout most of its range. Banner (1952) showed that *H. coerulea* was distributed over a 1-km-wide area on the leeward reef flat of the Onotoa Atoll, in the Gilbert Islands, and Zann and Bolton (1985) reported that *H. coerulea* was most abundant in the moderate wave energy zone of the Tarawa Atoll, in the Gilbert Islands.

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## Materials and methods

### Study site and distribution of adults

Shiraho Reef is located off the southeast coast of Ishigaki Island, southwest Japan (Fig. 1). It is a well-developed fringing reef that stretches about 1.5 km along the shore, being about 850 m from the shoreline to the reef crest. The latter is exposed during low tides and separates the water on the reef flat from the outer ocean. *Heliopora coerulea* is densely distributed on the reef flat along the southern part of Shiraho Reef (Kayanne et al. 1995). Most of the colony tops reach sea level to form micro-atolls and are fused into a reef pavement from several to hundreds of square meters wide (Fig. 2). The tops of the colonies are exposed during low tides and

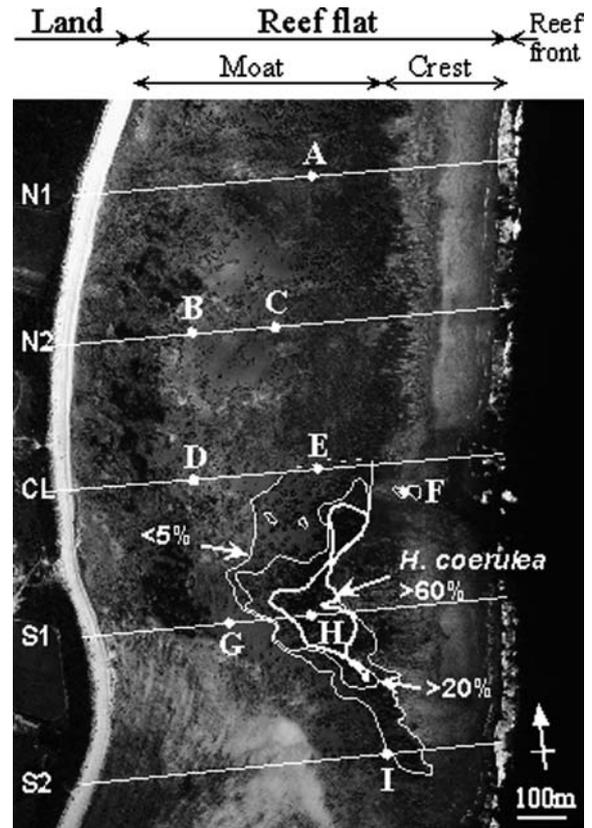


**Fig. 1** Map of Ishigaki Island, showing the location of Shiraho Reef

have no living coral tissue. All sides of the patches and micro-atolls were examined between two transect lines: CL and S2 (see Fig. 2), and were plotted on an aerial photograph to record the present coverage of *H. coerulea*. In addition, a visual survey of the Shiraho Reef slope was conducted by scuba diving seaward of lines CL, S1, and S2. *Heliopora coerulea* is unevenly distributed on the reef, forming a massive reef pavement behind the crest. Its abundance is > 60% at the center of its distribution. However, around this zone, coverage by *H. coerulea* decreases sharply, forming small patches several meters to several decimeters in diameter. In these areas, *Porites cylindrica* and *Montipora digitata* coexist with *H. coerulea*. The latter is much less common on the reef slope than on the reef flat. Throughout the paper, we refer to the dense localized population of *H. coerulea* in the reef-flat area in Fig. 2 as ‘the patch of *H. coerulea*.’

#### Brooding, planulae release, and settlement

To determine reproductive periods, colonies of *H. coerulea* were observed by snorkeling or scuba diving every few days in June and July between 1998 and 2000. In 1998, 33 colonies were tagged randomly to determine their sex ratios. The colonies were then dissected and observed under a dissecting microscope in the laboratory. Reproducing female colonies were classified as being in one of two stages: ‘surface brooding’ (Fig. 3A) or ‘planula release’ (Fig. 3B). A colony was classified as ‘surface-brooding’ stage when at least one planula had emerged to the surface and as ‘planula release’ stage when at least one planula had drifted free. Male branches (5 cm long) were broken off and examined by eye for the appearance and disappearance of mature spermaries. The numbers of male and female colonies so examined were as follows: 1999, 10 male and 40 female; 2000, 10 male and 30 female. Also, in 2000,



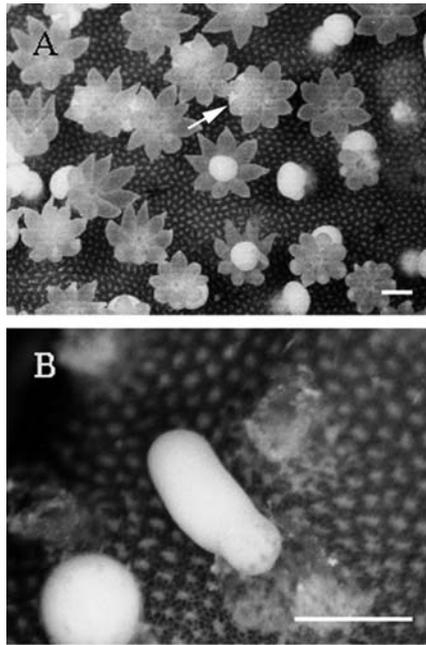
**Fig. 2** Aerial photograph of Shiraho Reef taken in 1995 with five transects from the shoreline (N1, N2, CL, S1, S2). Stations A to I indicate the main observation points at which planulae were sampled and recruitment racks were positioned. The current meter was set at Stn. H. *Heliopora coerulea* was distributed densely along the S1 transect line

four branches from different female colonies were tagged in order to investigate the timing of planula release. Photographs of these branches were taken on 18 occasions from 21 to 24 July. The number of released planulae per unit area of branch was counted to obtain an estimate of fecundity.

Fecundity and settlement rates were also investigated in laboratory studies. About 20 female branches (<20 cm long) of *H. coerulea* were collected during reproductive periods in 1998. Colonies were maintained in four 40-L tanks with running seawater (flow rate 2 L min<sup>-1</sup>). Surface brooding and planula release were observed under a dissecting microscope and with a video recorder. After the release of planulae was complete, five branches were bleached and sun-dried, and the number of polyps in six to ten quadrats (1×1 cm<sup>2</sup>) on each branch was counted to estimate fecundity per square centimeter. Planulae were collected from the tank using a plastic collector covered with 100-μm mesh and cultured in a plastic container filled with filtered (0.2 μm) seawater and with dead coral for settlement after collection from the colony.

#### Larval dispersal, currents, and recruitment

The spatial and vertical distribution of planulae was investigated using a plankton net and a hand pump. In 1999, the plankton net (45-cm diameter, 100-μm mesh nylon) was towed vertically three to seven times at each site, at depths ranging from 0.65 to 3.5 m during five intermittent periods from 16 to 24 July at 2 to 14 sites. In 2000, net tows were conducted every day from 19 to 27 July during low



**Fig. 3** Surface brooding (A) and release (B) of *H. coerulea*. Arrow indicates a surface-brooding polyp. Scale bars 1 mm

and high daytime tides, and at both tides at night from 22 to 23 July. The hand pump was used to collect water samples at the surface and at depths of 1 m and 20 cm above the bottom in the middle of the *H. coerulea* patch (Stn. H), concurrent with the net sampling tows from 20 to 27 July 2000 (see Fig. 2). Planulae were then collected from the pump samples with a plankton net (20-cm diameter, 100- $\mu$ m mesh nylon) and counted.

From 8 June to 30 July 1999 and from 5 June to 27 July 2000, we investigated the strength of currents that would tend to disperse planula larvae from the patch of adult *H. coerulea*. Current directions and velocities were measured at Stn. H using an electromagnetic current meter (ACM-8M, Alec Electronics Co., LTD). The sensor was set 50 cm above the bottom, and data were collected every 10 min. Wind directions and velocities were measured at hourly intervals using a wind meter (Kadec-kaze, Cona System). Tide levels at Shiraho Reef were calculated using tide tables for Ishigaki Port (Japan Meteorological Agency 1997–1999).

We investigated the retention in, and dispersion from, the site by examining the spatial pattern of *H. coerulea* settlement using settlement plates (10 $\times$ 10-cm<sup>2</sup> ceramic tiles) with the following three scales.

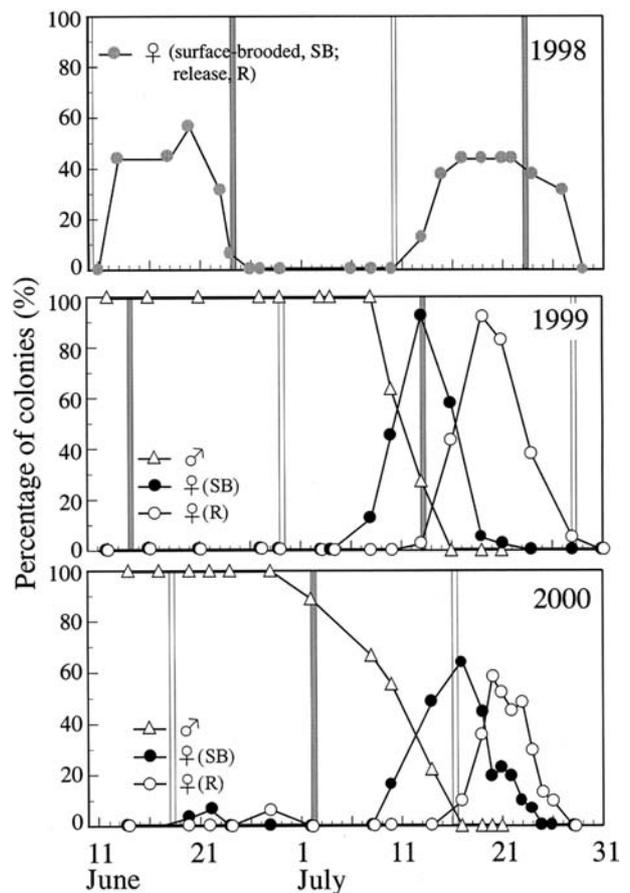
1. *Adjacent areas*: in 1999, we deployed plates at seven sites (Stn. A, and Stns. C to I; Fig. 2) and, in 2000, at nine sites (Stns. A to I). At each site, nine pairs of plates (upper and lower surfaces) were positioned in sandwich pairs on each side of a stainless-steel mesh rack. In both years, the racks were set horizontally 20 cm above the reef substrate in March and were collected in September.
2. *Around and within the patch of adult colonies*: in 2000, four additional plates (lower surfaces) were placed horizontally at 33 sites from June to September 2000 to observe local recruitment within the patch of adult colonies.
3. *Within colonies*: from June to September 1999 and 2000, 100 and 35 plates, respectively, were placed between the branches of selected *H. coerulea* colonies.

After collection, the plates were bleached in chlorine solution to remove organic matter, and the number of *H. coerulea* spat, identifiable by their blue skeletal color, was counted under a dissecting microscope.

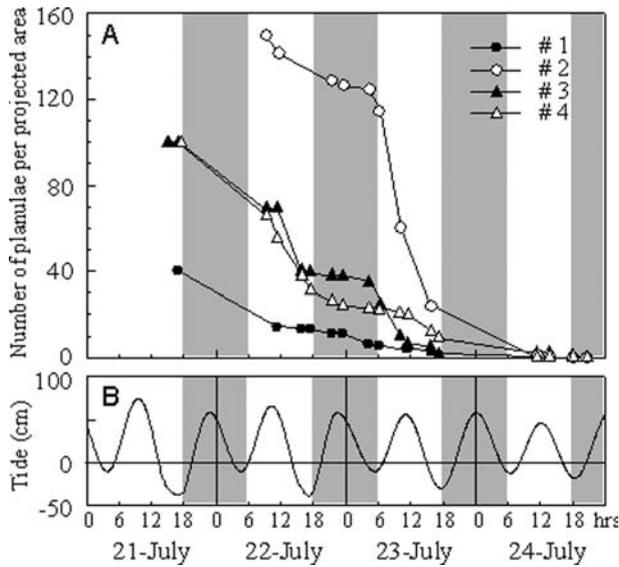
## Results

### Planulae release and settlement

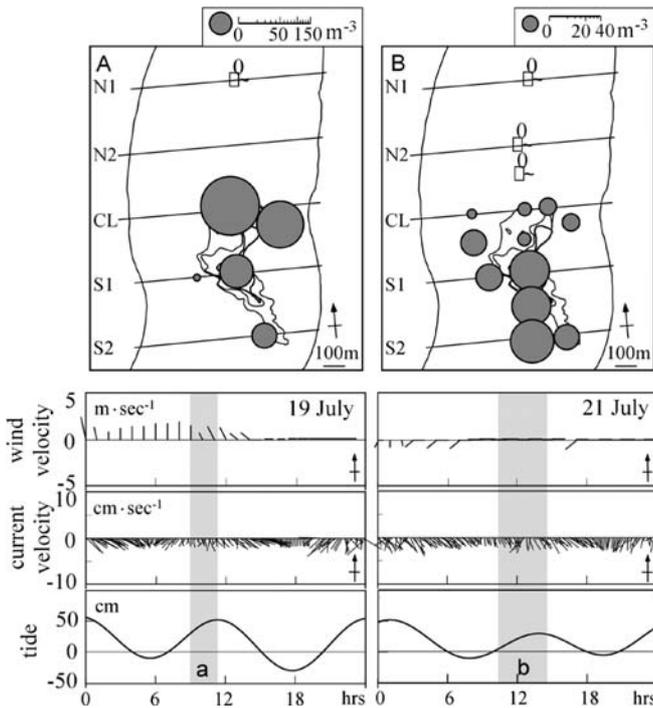
The larva's transition from brooding inside the polyp to surface brooding was documented with the time-series video. It showed the emergence and release from swollen female polyps over a period of 1 h. The polyps then contracted, and the planulae attached themselves beside the polyps (Fig. 3A); at this stage, planulae were covered with a mucus sac. After an average of 4 days after being surface brooded, each planula emerged from its sac and began drifting (Fig. 3B). Sixteen of 33 colonies dissected in 1998 were female, a ratio not statistically different from 1:1 (chi-square test). Mostly one and rarely two oocytes occurred within each female polyp. Fecundity, based on one oocyte per polyp and the number of polyps per square centimeter, was approximately 22 planulae cm<sup>-2</sup> year<sup>-1</sup>.



**Fig. 4** Percent male and female colonies at Shiraho Reef with spermaries and planulae, respectively, from 1998 to 2000. Total number of observed colonies was 16 female colonies in 1998 (see results), 10 male and 40 female colonies in 1999, and 10 male and 30 female colonies in 2000. White bars indicate full moon and shaded bars represent new moon.  $\triangle$  Male colony with spermaries;  $\bullet$  female colony; SB surface-brooding colony; R planulae-releasing colony

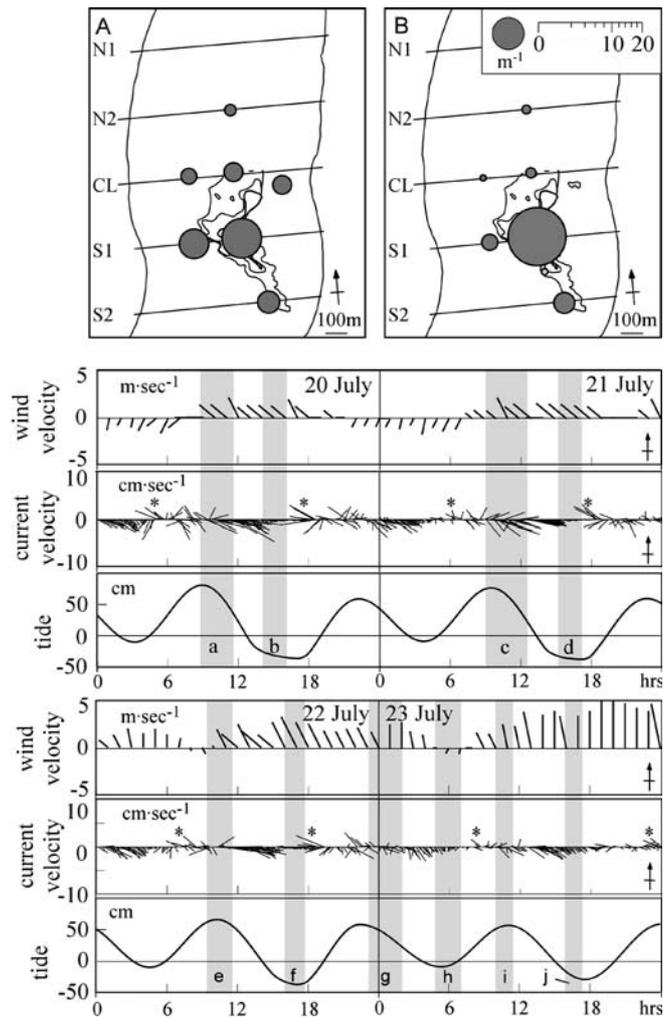


**Fig. 5** **A** Changes in number of planulae observed on each of four coral branches from 21 to 24 July 2000. **B** Tidal water level changes from mean sea level. *Shaded area* indicates night time (18:00 to 6:00)



**Fig. 6** Number of planulae per  $m^3$ , currents, wind velocities, and tides at Shiraho Reef in July 1999. *Bars* for current and wind velocity indicate direction. *Circles* indicate number of planulae per  $m^3$ . *Shaded areas* (a and b) indicate periods of plankton netting

Figure 4 shows the percentage of male colonies with spermaries, and females in surface-brooding or releasing stages. Surface-brooding colonies appeared within one to several days after the spermaries had disappeared, in



**Fig. 7** Number of planulae per  $m^3$ , currents, wind velocities and tides at Shiraho Reef in July 2000. *Bars* for current and wind velocity indicate direction. *Circles* indicate number of planulae per  $m^3$ . *Shaded areas* (a to j) indicate periods of plankton netting. *Asterisks* show flood tides

both 1999 and 2000. Each female polyp released planulae only once a year. The timing of appearance of surface brooding bore no consistent relationship to the lunar cycle. Surface brooding was observed at least 2 or 3 days after the full moon in June and July 1998, 7 days after the full moon in June 1999, and 8 days before the full moon in July 2000. Release periods were similarly variable within the months of June and July: 23 to 24 June and 17 to 27 July in 1998; 13 to 28 July in 1999; 17 to 26 July in 2000. Peak planulae releases were 19 July 1999 and 20 to 23 July 2000.

The timing of planula release bore no simple relationship to tidal cycle or time of day (Fig. 5). Planula release was observed both during the day (6:00 to 18:00) and at night (18:00 to 6:00). More planulae were released during the day than at night in colonies #3 and #4 on 22 July and #2 to #4 on 23 July 2000. Planulae averaged 3.7 mm long ( $n=25$ ,  $SD=0.4$  mm) and 0.4 mm wide

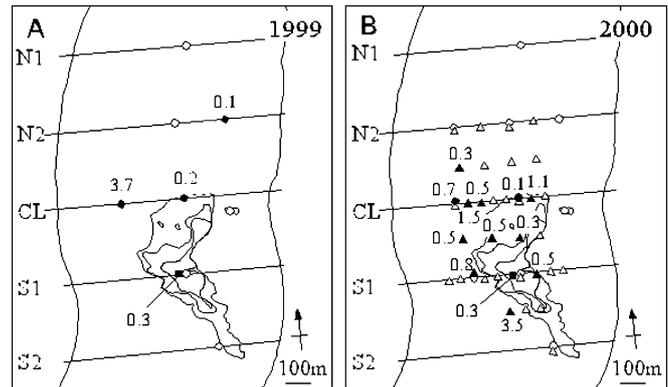
( $n=25$ ,  $SD=0.1$  mm) in July 1998 (Harii et al. 2002). Individuals that did not actively swim were white, indicating a lack of zooxanthellae. When the planulae became grounded on the substratum, they crawled across it and performed settlement behavior. About 2 weeks after settlement, each polyp divided into two, and the skeleton turned blue.

#### Larval dispersal, currents, and recruitment

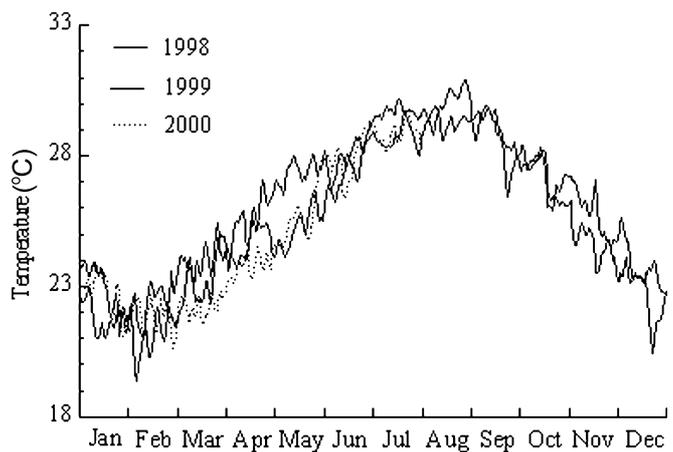
There was very limited evidence of dispersal beyond the limits of the reef flat patch of *H. coerulea* (Figs. 6 and 7). Planulae were observed from 16 to 21 July 1999 and from 19 to 26 July 2000. At Stn. H, planulae were most abundant on 19 July 1999 (34 planulae  $m^{-3}$ ) and from 20 to 23 July 2000 (ca. 15 planulae  $m^{-3}$ ). Planulae were usually found between the CL and S2 transect lines, and none was observed at the northernmost site on the reef, approximately 600 m to the north of the patch of adults. The number of planulae changed with the tides at each site in 2000 (Fig. 7), large numbers being found during low tides and smaller numbers during high tides at Stn. H. In contrast, the opposite pattern was observed at Stns. D and G, closer to the shoreline. Planulae appeared at different depths, near the surface, at mid-depth (0.5 to 1 m), and 20 cm above the bottom during the release periods at Stn. H; percentages at those depths were 23, 27, and 50%, respectively.

The larvae failed to disperse to the north in significant numbers, despite the occurrence of wind-driven surface currents in that direction (Fig. 7). Currents observed at the surface differed from those in the middle and bottom layers of the water column. Current velocity and direction at the surface were driven by wind; currents flowed at  $8\text{ cm s}^{-1}$  in a northerly direction when a southerly wind blew at  $5\text{ m s}^{-1}$ . At the same time, current velocity in the middle layer of the water column was  $1.5\text{ cm s}^{-1}$  toward the southeast. Current velocity in the middle was below  $1\text{ cm s}^{-1}$  during the low tide and averaged  $3\text{ cm s}^{-1}$  during the high tide. Water flowed toward the shoreline at flood tide with a maximum velocity of  $6.4\text{ cm s}^{-1}$ , marked by asterisks in Fig. 7. Water flowed mainly southeastward during neap and ebb tides (19 and 21 June 1999 and 23 June 2000), and flowed out through the reef channel some 800 m from the shore on the S2 transect. The patterns of planula dispersal are thus more related to mid-water than surface currents.

On the settlement plates, *H. coerulea* recruited only on the lower plates, while algae and sediment accumulated on the upper plates. In both 1999 and 2000 (Fig. 8), strongest recruitment was observed near the parent populations between the CL and S2 transects, and fewer recruits were observed at the northern sites. Larger numbers of recruits were observed at Stn. G (3.7 spats per  $100\text{ cm}^{-2}$ ) in 1999 and 450 m from the shoreline between transects S1 and S2 (3.5 spats per  $100\text{ cm}^{-2}$ ) in 2000. In both years, 0.3 spats per  $100\text{ cm}^{-2}$  were observed between the branches of *H. coerulea*.



**Fig. 8** Number of recruits of *H. coerulea* per  $100\text{ cm}^2$  in **A** 1999 and **B** 2000. Closed symbols indicate the sites with recruits and empty symbols indicate no recruits. In **B**, circles show the settling period from March to September; triangles show the settling period from June to September; and squares show the settling between branches of *H. coerulea* from June to September



**Fig. 9** Seasonal fluctuations in mean daily water temperature at Ishigaki Port, Ishigaki Island, from 1998 to 2000

## Discussion

### Reproductive biology of *H. coerulea*

At Shiraho Reef, *H. coerulea* is a gonochoric, surface-brooding species that produces one or two planulae per polyp, as has also been observed by Babcock (1990) on Orpheus Island on the Great Barrier Reef. However, at Shiraho Reef, reproductive periods differed over the 3 years of the study. These differences may be explained by the different ocean temperatures during that time (Fig. 9). In 1998, water temperature was higher in May than in the other two years, and may have allowed some colonies to mature earlier than others. For many marine invertebrates, the maturation of gametes is controlled by water temperature (Giese and Pearse 1974; Harrison and Wallace 1990; Harii et al. 2001).

Many corals were bleached by high temperatures in 1998, but no *H. coerulea* were damaged (Kayanne et al. 2002). In 1999, *H. coerulea* reproduced normally, suggesting that this species can tolerate high water temperatures without detriment to its reproduction in the following year.

The release periods lasted from 10 to 15 days, and, in contrast to the Great Barrier Reef (Babcock 1990), synchronicity with lunar cycles was not obvious (Fig. 4). At Shiraho Reef, *H. coerulea* tended to release more planulae during the day than at night (Fig. 5), in contrast to many scleractinian corals that spawn or release planulae mainly at night (Harrison et al. 1984; Richmond and Jokiel 1984; Tanner 1996). The release of *H. coerulea* planulae was not synchronized with high or low tides.

#### Factors controlling the dispersal of *H. coerulea* larvae on Shiraho Reef

Planulae of *H. coerulea* were most dense in the water column at times of planulae release (Fig. 4, 6 and 7). The areas of planulae dispersal and recruitment coincided closely, mostly within 350 m of the dense population of *H. coerulea*. The spatial overlap among adults, larvae, and areas of recruitment suggests that planulae dispersed and settled within 350 m of the adult population that had released them.

We suggest that the dispersal area of *H. coerulea* planulae is determined by water movement, since planulae were not observed to actively swim. Planulae were distributed throughout the water column at Shiraho Reef, with 70% of the larvae in the mid- to lower water column. During low tides, they were observed around Stn. H, whereas, during high tide, they were also observed in other areas, including nearer the shoreline (Stns. D and G), and south and north of the population. Thus, planulae were dispersed toward the shoreline by flood tides, and south- and northward during high tides. Our laboratory experiment showed that planulae can settle within 1 h after release (Harii et al. 2002), a period during which water could move 36 to 108 m (corresponding to  $1 \text{ cm s}^{-1}$  at low tides to  $3 \text{ cm s}^{-1}$  at high tides, respectively). The distance of water movement within the time of potential planulae settlement matched the actual dispersal/recruitment of planulae, and thus supports the conjecture that planulae settle around the parent population. On the other hand, the planulae at the surface (30%) had potential to be transported by more rapid wind-driven surface currents, but we observed no planulae or recruits to the north. This might be explained by an experimental result that *H. coerulea* planulae can settle in slower flow speed (Harii and Kayanne 2002). Our observations clearly suggest that dispersal takes place mainly in mid-water, and that the localized distribution of *H. coerulea* is determined by position of its larvae in the water column and by their short competency period.

#### Variation in larval dispersal and its controlling factors

Limited dispersal has been reported for benthic planulae of the solitary coral *Balanophyllia elegans* in California (Gerrodette 1981) and the soft coral *Parerythropodium fulvum fulvum* in the Red Sea (Benayahu and Loya 1983). Planulae of the surface-brooding gorgonian *Briareum asbestinum* in the Caribbean are negatively buoyant and settle rapidly after displacement from the colony (Brazeau and Lasker 1990). Other corals, including *Goniastrea aspera* and *Oulastrea crispata*, release eggs as well as benthic planulae, and planulae settle near the parent colonies (Sakai 1997; Lam 2000). Local recruitment in the reef has also been reported for ascidians, whose larvae can settle 10 to 15 min after release (Olson 1985). These examples show that brooding corals generally have limited dispersal ranges because of their benthic position and short competency periods.

In contrast, planulae of the brooding coral *Pocillopora damicornis* swim vertically within the water column (Atoda 1947) and have been observed to disperse outside the reef in Hawaii (Hodgson 1985). They can disperse over a wider range because of their longer competency period [2 h to 103 days; Richmond (1987)]. Some soft corals also have longer competency periods, and studies conducted in the Red Sea suggest that planulae can disperse widely (Ben-David-Zaslow and Benayahu 1998). A recent study demonstrated that *Alveopora japonica* released both swimming and benthic planulae at different stages (Harii et al. 2001). The larval dispersal range of brooding species may be more variable, corresponding to the variation in larval position in the water as well as their competency period.

Unlike *H. coerulea*, the eggs of spawning scleractinian species are positively buoyant (Babcock and Heyward 1986; Arai et al. 1993) and are dispersed by wind-driven currents (Oliver and Willis 1987; Willis and Oliver 1988, 1990). Their planulae settle from 4 to 7 days after fertilization (Babcock and Heyward 1986), their maximum competency periods range from 26 to 78 days (Wilson and Harrison 1998), and they disperse by oceanic currents (Dight et al. 1990; Roberts 1997; Lugo-Fernández et al. 2001). Thus, the wide dispersal range of spawning species is determined fundamentally by their longer competency period and their buoyant characteristics. However, hydrodynamic conditions may prohibit the wide dispersal of spawning species. Numerical simulations showed that the planulae of spawning species could also recruit onto the natal reef by local circulatory currents (Black et al. 1990, 1991; Black 1993).

Larval dispersal of corals has been mainly explained by their two reproductive strategies (e.g. Szmant 1986; Harrison and Wallace 1990). We believe it should also be discussed in relation to their competency period, position in the water column, and currents that actually deliver the larvae. Szmant (1986) found higher local recruitment in brooders than in spawners in the Caribbean Sea. Recently, Ayre and Hughes (2000) found

different levels of gene flow among four spawning and five brooding corals along the Great Barrier Reef, indicating that gene flow is not solely determined by reproductive mode. Among brooding corals, three species (*Acropora cuneata*, *A. palifera*, *P. damicornis*) showed no genetic variation, while two other species (*Seriatopora hystrix* and *Stylophora pistillata*) displayed low levels of gene flow, suggesting different larval dispersal ranges and complex current patterns (Ayre et al. 1997; Ayre and Hughes 2000). The variation in larval density thus does not simply correspond to the reproductive mode, even when brooding and spawning species do have a tendencies for narrow and wide dispersal, respectively.

#### Relationship between adult distribution and recruitment of *H. coerulea*

Our observations directly demonstrated the narrow dispersal potential of *H. coerulea* larvae, which corresponded to the distribution of adults. We believe that the local topographic and oceanographic conditions are very important in all cases. At Shiraho Reef, the current is weak during low tide because the reef crest is well developed (Kayanne et al. 1995). Even the average current around this reef is weaker than at other fringing reefs, such as the Kabira Reef on Ishigaki Island (Yamano et al. 1998). Such a low current velocity may contribute to recruitment within the reef. Thus, spatial heterogeneity in *H. coerulea* distribution is likely to be the result of limited planulae dispersal and recruitment potentials.

It has already been suggested that planulae of brooding corals can recruit onto their natal reefs (Babcock 1988; Harrison and Wallace 1990; Harriott 1992; Harriott and Banks 1995; Dunstan and Johnson 1998; Hughes et al. 1999). Babcock (1988) found that both recruitment and adult distribution of brooding scleractinian corals were more spatially variable than that of spawning species at the reef scale. Hughes et al. (1999) found that recruitment varied greatly among reefs and for brooding species, which may cause their shorter larval duration and lower levels of gene flow; adult distribution also varied at the same scale as well as at a larger scale (> 250 km). Our observations supported these variations in brooding recruits and adult abundance reported by Hughes et al. (1999). Post-settlement mortality is also important in the distribution of adults (e.g., Dunstan and Johnson 1998). Even if the rate of post-settlement mortality is high for *H. coerulea*, the fact that larvae recruit so densely around the adult colonies tends to reinforce the existing local distribution pattern.

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