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Larval survivorship, competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*

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Abstract Larval dispersal and recruitment are important in determining adult coral distribution; however, few studies have been made of coral larval dispersal. This study examined the larval behavior, survivorship competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*, in relation to different potential larval dispersal patterns. We also examined the lipid content of *H. coerulea* as a means of flotation and a source of energy. Planulae of *H. coerulea* were on average 3.7 mm in length, lacked

zooxanthellae, and were mostly benthic, probably because of restricted movement and low lipid content (54% by dry weight). Planulae of *P. damicornis* were on average 1.0 mm in length, had zooxanthellae and swam actively. The competency period of *H. coerulea* was shorter (30 days) than that of *P. damicornis* (100 days). Forty percent of *H. coerulea* planulae crawled onto the substrata within 1 h of release, and 47% settled within 6 h. By contrast, fewer than 10% of *P. damicornis* planulae crawled onto the substrata within the first hour and 25% settled within 6 h of release. The planulae of *H. coerulea* may have a narrower dispersal range than those of *P. damicornis*, settling and recruiting near parent colonies. Thus, brooding corals exhibit variations in larval dispersal patterns, which are characterized by their position in the water column and competency periods.

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Introduction

Larval dispersal and recruitment of marine organisms are important for understanding the mechanisms that regulate populations (Underwood and Fairweather 1989). Scleractinian and octocorallian corals have two sexual reproductive modes: spawning and brooding. Spawning corals release sperm and eggs, with larvae requiring several days to develop and settle (Babcock and Heyward 1986; Harrison and Wallace 1990). These larvae may disperse widely outside the natal reef by wind-driven currents (Willis and Oliver 1990). In contrast, brooding corals release larvae directly, which are then ready to settle within much shorter periods (Harrison and Wallace 1990). This increases the chances that brooded larvae may settle on their natal reef (Babcock 1988; Sammarco and Andrews 1988; Harriott 1992; Harriott and Banks 1995; Dunstan and Johnson 1998; Hughes et al. 1999).

Brooding corals can have one or multiple reproductive cycles per year, with varying larval characteristics, such as possession of zooxanthellae, movement

behavior, and competency periods (Atoda 1947a, 1951; Kojis 1986a, b; Richmond 1987; Babcock 1990; Johnson 1992; Harii et al. 2001). Although these variations in brooding corals may account for differences in their dispersal patterns, these have not previously been discussed in relation to larval characteristics.

Competency periods are an important factor in determining larval dispersal range (e.g. Wilson and Harrison 1998). Planulae of the brooding scleractinian, *Pocillopora damicornis*, may disperse widely during their long competency periods (103 days; Richmond 1987), and have been observed to do so outside their natal reef (Hodgson 1985). Long competency periods of brooding soft corals may also be related to biogeographical patterns (Ben-David-Zaslow and Benayahu 1998). By contrast, the ability to settle within a short period (minimum competency period) is important for settling near the adult population (Olson 1985). Settlement rates within 1 day of release and differences between brooding corals have not previously been reported.

Dispersal is determined biologically by larval positions in the water column as well as competency periods (Pechenik 1990; Willis and Oliver 1990; Pawlik 1992; Young 1995). Positively buoyant eggs of spawning corals float to the sea surface and as a result are widely dispersed outside the reef by wind-driven currents during the early stages of fertilization and larval development (Willis and Oliver 1990). Therefore, buoyancy is a factor in determining dispersal range. Arai et al. (1993) considered that 62–70% of the egg dry weight was lipids, which contain buoyant wax esters. However, little is known about the lipid content of the negatively buoyant larvae.

To evaluate larval dispersal strategies and controlling factors, we studied larval behavior, survivorship, competency periods and settlement in two brooding corals with different distributions: *Heliopora coerulea* (Octocorallia) and *P. damicornis* (Scleractinia, Hexacorallia). We also examined the lipid content of *H. coerulea* for constituents associated with flotation and energy availability. *Pocillopora damicornis* planulae are already known to contain 70% lipids by dry weight (Richmond 1987; Arai et al. 1993).

Heliopora coerulea is a hermatypic octocoral, which forms a skeleton. It is a gonochoric brooding species, with planulae that cleave from the surface of female colonies before their yearly release (Babcock 1990). *Pocillopora damicornis*, a well-studied scleractinian coral, releases planulae many times per year (Atoda 1947a; Tanner 1996). In the area of our study, Shiraho Reef, southwestern Japan, the two species have different distributions: *H. coerulea* is densely distributed on the southern end of the reef, whereas *P. damicornis* is distributed over the entire reef flat (Harii and Kayanne, submitted). This difference in distribution is also seen at a larger scale: *H. coerulea* is found only in the tropical Indo-western Pacific, whereas *P. damicornis* is widely distributed throughout the Indo-Pacific (Zann and Bolton 1985; Veron 2000a, b).

Materials and methods

Study site

Shiraho Reef is located along the southeast coast of Ishigaki Island, southwest Japan (Fig. 1). It is a well-developed fringing reef, stretching about 1.5 km along the shore. The reef crest occurs at about 850 m from the shoreline, is exposed during low tides, and separates the water on the reef flat from the outer ocean (Kayanne et al. 1995).

Collection of larvae

Ten to 20 female branches (10 to 20 cm long) of *H. coerulea* and five colonies of *P. damicornis* were collected on Shiraho Reef flat from June to July in 1999 and 2000. Colonies of each species were maintained in two or three 40-l tanks with running seawater flowing at a rate of 2 l min⁻¹, at the Ishigaki Tropical Station, Seikai National Fisheries Research Institute. The planulae were collected from the tank using a plastic collector covered with a 100- μ m mesh. Planulae were collected at least once per day during their release periods and kept in a 5.5-l plastic container filled with filtered (0.2- μ m pore) seawater (FSW).

Larval behavior

The sizes of 20–25 newly released planulae of *H. coerulea* and *P. damicornis* were measured under a dissecting microscope and transferred to six-well tissue-culture plates containing 10 ml FSW. Their behavior was observed under a microscope and recorded using a CCD (charge-coupled device) camera (108DX, Sony) and a

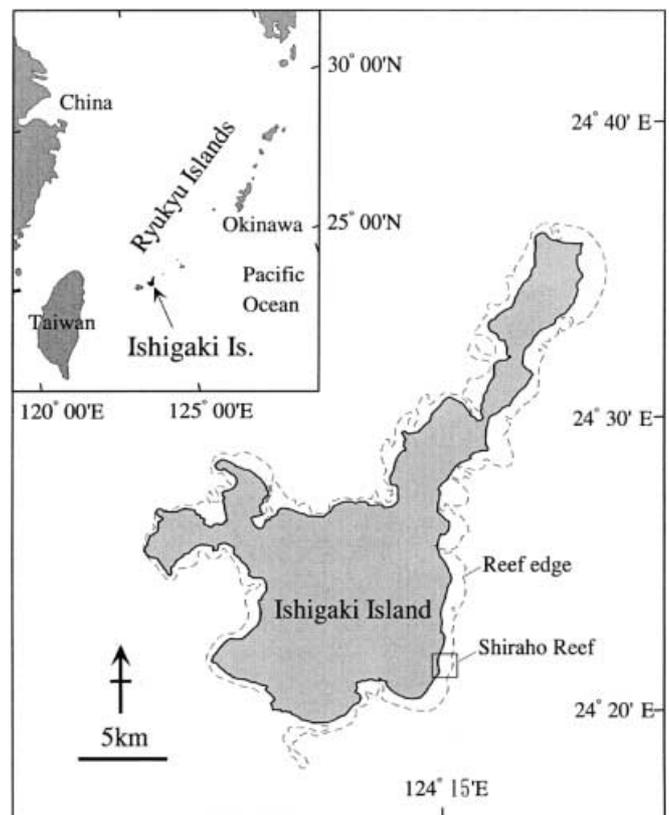


Fig. 1. Map showing location of Shiraho Reef, Ishigaki Island, southwest Japan

digital video (GV-D900, Sony). Swimming speed was calculated by tracking larval movement on a monitor. Five newly released planulae of *H. coerulea* were processed for histological examination using standard techniques, in order to examine their internal structure. Histological sections 6 μm thick were stained with hematoxylin and eosin, and examined using a compound microscope.

Additional newly released planulae were collected to determine their positions in the water column. Fifty planulae were transferred to a 100-cm-tall acrylic cylinder (diameter 4 cm) filled to 90 cm with FSW, in light (about 500 $\mu\text{mol s}^{-1} \text{m}^{-2}$) and dark conditions. After 15 min, the number of planulae were counted in the surface layer (0–1 cm deep), upper layer (1–45 cm deep), lower layer (45–88 cm deep), and bottom layer (0–2 cm above the bottom). Four separate counts were made within 1 h.

Larval survivorship and competency periods

Larval survivorship was studied in 1999. Ten newly released planulae were transferred to each well of a six-well tissue-culture plate containing 10 ml FSW and Ampicillin (50 $\mu\text{g ml}^{-1}$, after Ben-David-Zaslow and Benayahu 1996). Seven hundred and eighty *H. coerulea* planulae and 480 *P. damicornis* planulae were cultured for 72 days and 100 days, respectively. The surviving planulae were counted after 29 days for *H. coerulea* and 39 days for *P. damicornis*.

Competency periods were also determined from the settlement rate observed from June to September 1999. Planulae were maintained in 5.5-l containers containing FSW and ampicillin (50 $\mu\text{g ml}^{-1}$) until used for the settlement experiment. After washing three times with FSW, 20 planulae were transferred to each of five plastic containers (diameter 15 cm, height 9 cm) filled with 1 l aerated FSW. Settlement plates (5 cm \times 5 cm unglazed bathroom tile), which had been submerged at Shiraho Reef for 2 months before the experiment, so as to establish natural biological conditions (Wilson and Harrison 1998), were set 5 mm above the bottom of the containers. Five replicates were established. During the prior submerged period at Shiraho Reef, brown seaweeds, sponges, molluscs, polychaetes, and ascidiaceans also settled on the tiles, which were primarily covered with coralline algae (> 60% coverage). Coralline algae are known to induce settlement of planulae (Morse et al. 1988); therefore most of the other benthos was removed to make uniform conditions for settlement and facilitate observation of settled planulae. The experiments were assembled in 1 day and at 1, 2, 5, 7, 10, 15, 20, 30, 40, and 72 days after the release of *H. coerulea* planulae, and in 1 day and at 5, 10, 20, 30, 40, 72, and 100 days after the release of *P. damicornis* planulae. The planulae settled on the tiles were counted using a dissecting microscope 48 h after starting the experiments.

In 2000, to observe the settlement rate within 30 h of release, 50 and 20 newly released planulae of *H. coerulea* and *P. damicornis*, respectively, were placed in containers (diameter 15 cm, height 9 cm) filled with 1-l FSW. Experimental conditions were identical to those described above for the competency experiment. The planulae either crawling or settled on the tiles were counted, using the dissecting microscope, every hour during the first 6 h, every 3 h during the following 6 h, and every 6 hours thereafter, until 30 h had elapsed. The tiles were kept submerged during examination. The experiments were conducted four times for *H. coerulea* and once for *P. damicornis*.

In all experiments, the seawater temperature in the container was kept between 28°C and 29°C using an air conditioner or water jet bath.

Lipid analysis

Fifty to 100 planulae of *H. coerulea* were collected on pre-combusted GF/F (400°C for 4 h) filters in the first day and at 7, 14 and 21 days after the release. The number of filters used each day was 4, 3, 2 and 1, respectively. They were subsequently rinsed with distilled water to remove salt and stored frozen at –20°C to –80°C until subsequent lipid analysis.

Lipids were analyzed using the method of Yamamoto et al. (2000): first extracted by five, 5-min rounds of ultrasonication with 5 ml dichloromethane–methanol (6:4), then concentrated and passed through a short bed of Na_2SO_4 to remove water. An aliquot of the extracted lipid was analyzed using a thin-layer chromatography-frame ionization detector (TLC–FID), using an Iatroscan MK–5 TLC–FID analyzer (Iatron Laboratories Inc., Tokyo). The frame ionization detector was operated at a hydrogen flow-rate of 160 ml min^{-1} , an air flow-rate of 2,000 ml min^{-1} , and a scan speed of 0.4 cm s^{-1} . Silica gel SIII chromatodots were developed with polar solvents, and passed through the detector twice at a scan speed of 0.17 cm s^{-1} before use. Approximately 0.3 mg of lipid sample was dissolved in 100 μl of dichloromethane, and a 5- μl aliquot was applied using a 5- μl microsyringe. After spotting, the rods were conditioned for 10 min at a constant humidity of 65% and subsequently suspended for 10 min in a developing tank (developed for 20 min in hexane:diethylether (96:4)). After development, the rods were dried at 60°C for 5 min. Lipid classes were quantified using FID calibration curves, obtained by analyzing standard compounds in the same manner as above. The standards included palmitic acid palmityl ester (Sigma., St Louis, Mo., USA) for wax esters, 1,2-dipalmitoyl-3-oleoyl-rac-glycerol (Sigma) for triacylglycerols, cholesterol (GL Science Co., Tokyo, Japan) for sterols and 1- α -phosphatidylcholine (Sigma) for phospholipids.

Results

Larval behavior

Planulae of *H. coerulea* were white, 3.7 mm long ($\text{SD} \pm 0.4 \text{ mm}$, $n = 25$), and lacked zooxanthellae, a mouth, and mesenteries. They had short cilia, and their speed of movement ranged from 0.2 to 0.9 mm min^{-1} . In the experimental water column, 73.3% ($\text{SD} \pm 13.2\%$) and 72.7% ($\text{SD} \pm 7.5\%$) positioned themselves in the bottom layer under light and dark conditions, respectively (Table 1). Planulae of *P. damicornis* were 1.0 mm long ($\text{SD} \pm 0.2 \text{ mm}$, $n = 20$), had zooxanthellae, a mouth and mesenteries. They were motile, their speed of movement varied between 10.0 cm min^{-1} and 11.3 cm min^{-1} . They floated mostly in the surface layer, but also

Table 1. *Heliopora coerulea* and *Pocillopora damicornis*. Larval positions in the water column. Surface layer 0–1 cm deep; upper 1–45 cm deep; lower 45–88 cm above bottom; bottom layer 0–2 cm above bottom

		Light				Dark			
		Surface	Upper	Lower	Bottom	Surface	Upper	Lower	Bottom
<i>H. coerulea</i>	Average (%)	4.7	3.3	18.7	73.3	13.3	4.0	10.0	72.7
	SD (%)	1.0	1.9	11.0	13.2	3.8	2.8	5.7	7.5
<i>P. damicornis</i>	Average (%)	81.0	12.0	2.0	5.0	93.0	7.0	0.0	0.0
	SD (%)	8.4	7.5	1.6	2.0	7.1	7.1	0.0	0.0

occurred in the upper layer in the experimental water column (Table 1). Under light conditions, 81.0% (SD \pm 8.4%) were found in the surface layer and 12.0% (SD \pm 7.5%) in the upper layer. Under dark conditions, 93.0% (SD \pm 7.1%) floated near the surface.

Larval survivorship and competency periods

Figure 2 shows the average survivorship of planulae for *Heliopora coerulea* and *P. damicornis*. For both species, > 98% of planulae survived until the 20th day after release. Fifty-percent-mortality periods were 70 days for *H. coerulea* and 100 days for *P. damicornis*.

The competency periods of the planulae were assessed from the percentages of planulae settled on the plates (Fig. 3). For *H. coerulea*, 74.0% (SD \pm 14.7%) had settled within 1 day of release. The percentage decreased to 44.0% (SD \pm 17.1%) 1 day after release and 3.0% (SD \pm 4.5%) 20 days after release. The maximum competency period was 30 days after release (2.0%, SD \pm 2.7%). For *P. damicornis*, 62.0% (SD \pm 24.1%) had settled within 1 day of release, 55.5% (SD \pm 21.8%) being settled 30 days after release. These two settlement rates showed no significant difference (*t*-test, $P > 0.05$).

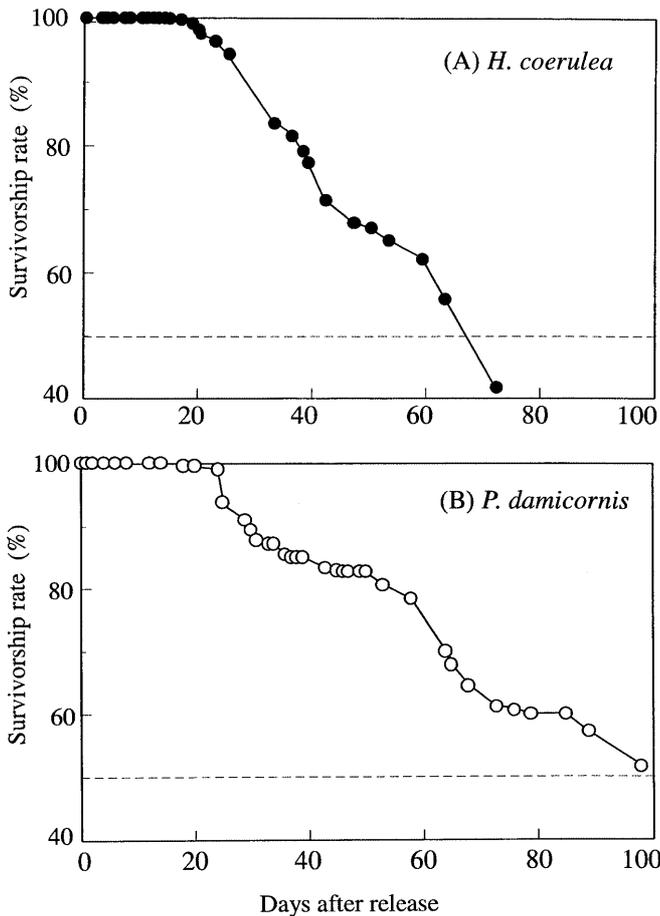


Fig. 2A, B. *Heliopora coerulea* and *Pocillopora damicornis*. Survivorship of *H. coerulea* (A) and *P. damicornis* (B). Broken lines in each graph correspond to 50% survivorship

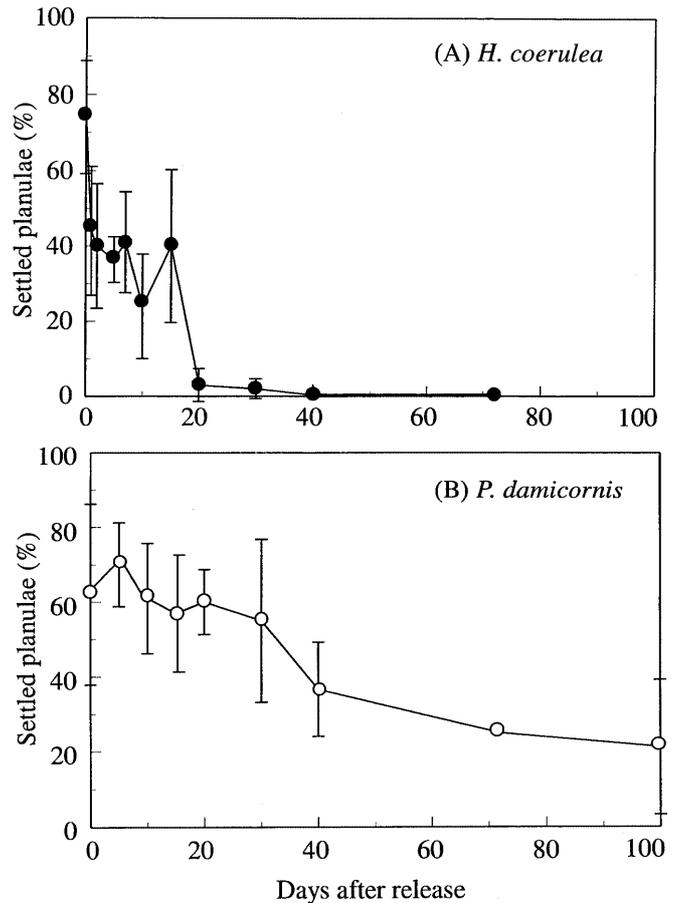


Fig. 3A, B. *Heliopora coerulea* and *Pocillopora damicornis*. Changes in mean percentage of settled planulae (\pm SD) up to 100 days after release. A *H. coerulea*; B *P. damicornis*

The maximum competency period during the experiment was 100 days after release (21.3%, SD \pm 18.0%).

Figure 4 shows the average percentage of crawling and settled planulae on the plate 30 h after release. For *H. coerulea*, 40.1% (SD \pm 8.1%) of planulae had crawled to settle on the plate within 1 h of release. The number of settled planulae increased as the number of crawling planulae decreased. The relative abundance of settled planulae was 18.4% (SD \pm 11.8%) at 3 hours after release, 46.9% (SD \pm 11.8%) at 6 h and 82.4% (SD \pm 6.2%) at the end of the experiment (30 h after release). For *P. damicornis*, the relative abundance of crawling planulae was less than 10% during the entire experiment. The relative abundance of settled planulae was lower than for *H. coerulea*, 13.0% (SD \pm 5.7%) having settled by 3 h after release and 25.5% (SD \pm 7.9) at 6 h. However, 75.0% (SD \pm 7.9%) of *P. damicornis* had settled by 30 h after release.

Lipid analysis

Newly released planulae of *H. coerulea* contained 54.2% (SD \pm 4.1%, $n=4$) lipid by dry weight (Fig. 5). The percentage of lipid decreased to 51.2% (SD \pm 11.3%,

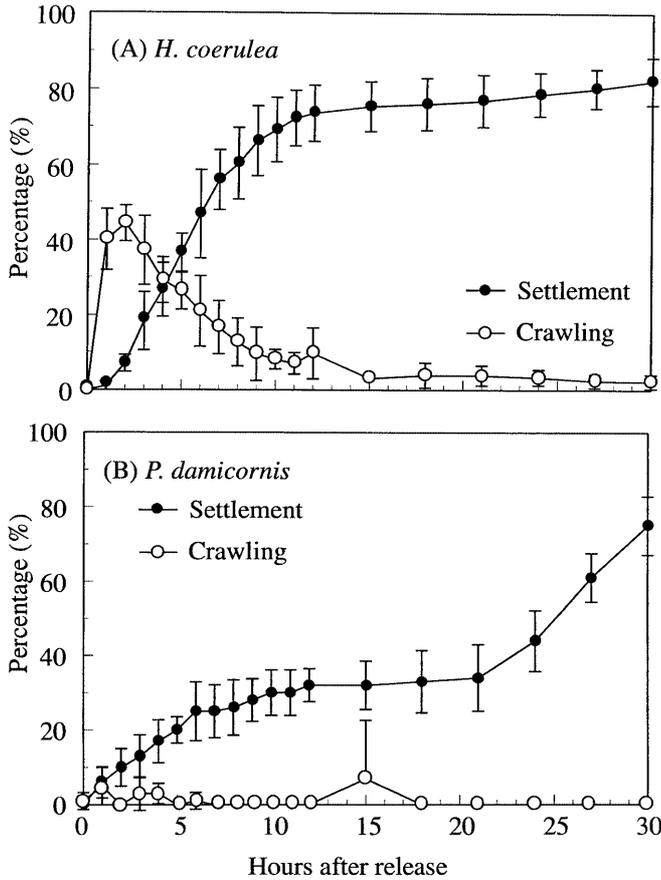


Fig. 4A, B. *Heliopora coerulea* and *Pocillopora damicornis*. Mean percentage of crawling (settlement behavior) and settled planulae (\pm SD) on plates. A *H. coerulea*; B *P. damicornis*

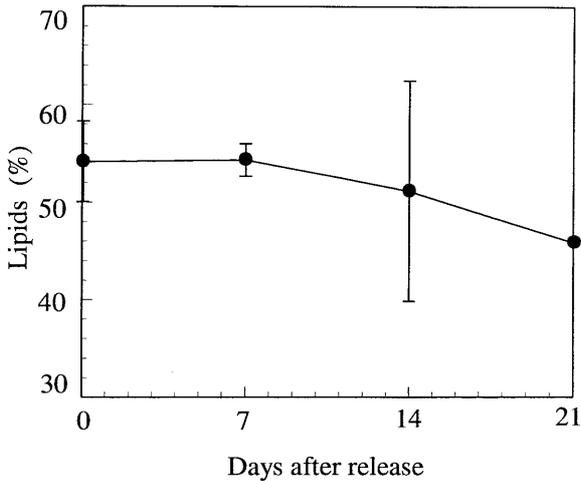


Fig. 5. *Heliopora coerulea*. Relative abundance of lipids by dry weight in *H. coerulea* planulae

$n=2$) during the first 14 days and to 45.9% ($n=1$) during the next 7 days. The lipids in newly released planulae included mainly wax ester (av. 23%) and phospholipid (av. 32%) (Fig. 6).

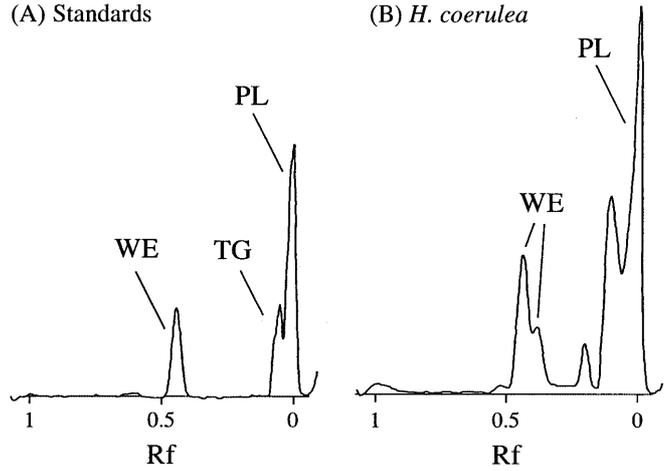


Fig. 6A, B. *Heliopora coerulea*. TLC-FID chromatograms of lipid classes in planulae of *H. coerulea*. A Standard; B planulae. WE Wax esters; TG triacylglycerols; PL phospholipids

Discussion and conclusions

Larval dispersal patterns of *H. coerulea* and *P. damicornis*

Planulae of *H. coerulea* and *P. damicornis* have different settlement behavior. The crawling rate of *H. coerulea* was high for the 1st h after release, after which the settlement rate increased. This apparently reflected the fact that *H. coerulea* planulae search for a settlement place primarily by crawling on the substratum. In contrast, the crawling rate of *P. damicornis* was lower, suggesting that most planulae of this species swim vertically in the water column and search in different sites for a suitable place to settle. Planulae of the temperate scleractinian coral *Balanophyllia elegans* are benthic, crawling on the substratum and settling soon after release (Gerroddette 1981; Fadlallah and Pearse 1982). *Parerythropodium fulvum fulvum* (Octocorallia) and the scleractinian *Acropora palifera* are also benthic and can settle soon after release (Benayahu and Loya 1983; Best and Rising 1987). Clearly, benthic planulae tend to settle nearer the parent colonies than swimming planulae.

In this study, the maximum competency period was 30 days for *H. coerulea*, whereas *P. damicornis* planulae were competent to settle 100 days after their release. This agrees with the result of Richmond (1987), who found the competency period of *P. damicornis* to be up to 103 days. The competency period of *H. coerulea* in this study was shorter than that of planulae of other coral species, for example, *Parerythropodium f. fulvum*, *Xenia umbellata* and *Heteroxenia fuscescens* (Octocorallia) (planulae competent from 49 to 76 days), the scleractinians *Acanthastrea lordhowensis* and *Goniastrea australiensis* (competent for 56 and 78 days, respectively) (Ben-David-Zaslow and Benayahu 1996, 1998; Wilson and Harrison 1998).

The difference in the larval dispersal characteristics of the two species may explain the differing adult distributions of *H. coerulea* and *P. damicornis*. At the reef scale, minimum competency periods and larval positions in the water column are important for dispersal for both species. At Shiraho Reef, most of the water mass flows with tidal cycles at a speed of less than 4 cm s^{-1} . However, the thin uppermost layer flows with a speed of several to $> 10 \text{ cm s}^{-1}$, driven by wind (Harii and Kayanne, submitted). Most planulae of *H. coerulea* aggregated in the bottom layer in the experimental water column, thereby remaining near a parent population and recruiting to it. In contrast, the planulae of *P. damicornis* aggregated near the surface in the experimental water column, and if they behave the same way in the field, wind-driven currents would disperse them. *Heliopora coerulea* is densely distributed only in the southwestern part of Shiraho Reef (Harii and Kayanne, submitted), whereas *P. damicornis* generally has a ubiquitous reef distribution pattern (Veron 1995). This may reflect the different settlement ranges of the planulae.

This tendency is also true on the larger scale. *H. coerulea* and *P. damicornis* are known to have different biogeographic distributions, the former being more restricted to the Indo-Western Pacific region (Zann and Bolton 1985; Veron 2000a, b). It has been suggested that a limited potential for dispersal in *H. coerulea* has resulted in that species' restricted distribution, although the larval dispersal of that species has not previously been reported (Zann and Bolton 1985; Babcock 1990). The present study supports this suggestion, because the competency periods of *H. coerulea* planulae are shorter than those of other corals. Also, the former planulae may sink in the water column in deep water and may not be able to disperse outside the reef. In fact, 50% of the total planulae collected in the water column were observed near the bottom at Shiraho Reef (Harii and Kayanne, submitted). In contrast, *P. damicornis* planulae can disperse widely outside their natal reef because of their long competency periods and position in the upper part of the water column.

Distribution of the adult coral population is determined not only by larval dispersal pattern but also by death of post-recruitment and/or adult colonies (e.g. Hughes and Jackson 1985; Smith 1992; Babcock and Mundy 1996). For example, Smith (1992) suggested that the lower mortality rate of *Diploria* spp. compared to that of the high-mortality *Porites asterooides* corals might explain their abundance on the Bermuda Reef, in the North Atlantic. Babcock and Mundy (1996) suggested that pre-settlement factors, such as orientation of settlement for sedimentation and light levels, may play an important role in determining reef-scale distribution patterns. This study, on the other hand, may also provide a good correlation between larval dispersal potential and the adult distributions of two species.

Roles of lipids and zooxanthellae in larval dispersal patterns

This study demonstrated that the larvae of *H. coerulea* and *P. damicornis* differed both in the vertical positions in the water column and competency periods. The lipid concentration in planulae of *H. coerulea* was lower than that in *P. damicornis* (Richmond 1987). Since planulae of *H. coerulea* are benthic, compared with those of *P. damicornis*, which are positively buoyant, and because the former planulae do not swim actively, it is likely that the lipid has a function as a buoyancy agent, with the amount of lipid influencing the vertical position of planulae in the water column.

The eggs of spawning scleractinian corals, *Acropora millepora*, *A. tenuis*, and *Montipora digitata* are rich in lipid (62% to 70% lipid by dry weight), the primary component of it being wax ester (about 70% to 80% of total lipid) (Arai et al. 1993). Therefore, the eggs of many spawning corals are positively buoyant and can disperse widely by wind-driven currents (Willis and Oliver 1990; Arai et al. 1993). In contrast, the benthic planulae of the soft coral, *Heteroxenia fuscescens*, contain 51.5% lipid (Ben-David-Zaslow and Benayahu 1996, 2000). In this study, the lipid-lean *H. coerulea* and lipid-rich *P. damicornis* planulae had different vertical distributions.

Some lipids, such as wax esters, also function as energy stores (Arai et al. 1993). The percentage of wax ester in total lipid for *H. coerulea* (23%) was lower than that of acroporid planulae (about 70–80% of total lipid; Arai et al. 1993). This study demonstrated that the lipid-lean planulae, having a lower proportion of wax ester, have a shorter competency period than the lipid-rich *P. damicornis* planulae (Richmond 1987), supporting the hypothesis that lipid is an important factor controlling the competency period of planulae (Richmond 1987).

In addition, it has been reported that photosynthetically fixed carbon can pass into host tissue from zooxanthellae (Tytler and Spencer-David 1986). Planulae of *H. coerulea* lack zooxanthellae and therefore cannot gain photosynthetic energy. In contrast planulae of *Pocillopora damicornis* may gain photosynthetic energy from their zooxanthellae, further boosting their competency period (Richmond 1987). Ben-David-Zaslow and Benayahu (1998) suggested that the photosynthates available to zooxanthellate planulae of soft corals enable them to survive beyond their settlement competency periods.

This study clearly suggests that lipid content and composition, and zooxanthellae, are important factors controlling larval dispersal.

Variations in reproductive strategies of brooding corals

This study demonstrated that *H. coerulea* and *P. damicornis* have different larval dispersal patterns, related to

their different larval characteristics. *Heliopora coerulea* releases large azooxanthellate planulae (> 3.0 mm) only once per year (Babcock 1990; Harii and Kayanne, submitted). These have a short competency period and low fecundity, but may have a higher chance to settle on a suitable place where adult colonies can grow (Harii and Kayanne, submitted). This pattern is similar to that of planulae of *Parerythropodium fulvum fulvum*, *Heteroxenia fuscescens* and *Acropora (Isopora) palifera* (Benayahu and Loya 1983; Best and Rising 1987; Ben-David-Zaslow and Benayahu 1996). For example, the benthic planulae of *Acropora palifera* have been reported as settling near the parent colonies in the field (Best and Rising 1987).

In contrast, *P. damicornis* releases small zooxanthellate planulae (~1.0 mm) throughout the year (Atoda 1947a; Tanner 1996), and these planulae have a long competency period. This pattern is the case for many brooding scleractinian corals, including *Stylophora pistillata*, *Seriatopora hystrix*, *Favia fragum*, *Porites asterooides* and *Manicina areolata* (Atoda 1947b, 1951; Szmant 1986; Johnson 1992). *Stylophora pistillata* has a high mortality, due to the small colony size, but recruits ubiquitously by larval settlement (Loya 1976; Shlesinger et al. 1998). Such planulae can disperse widely outside the natal reef and broaden their biogeographic distributions (Richmond 1987; this study).

The planulae of brooding species have been reported as recruiting on the natal reef (Babcock 1988; Sammarco and Andrews 1988; Harriott 1992; Harriott and Banks 1995; Dunstan and Johnson 1998; Hughes et al. 1999). In the present study, contrasting larval dispersal patterns were identified for two brooding corals. A further dispersal pattern, which includes both narrow and wide-ranging dispersal, is also known. *Alveopora japonica* releases both positively buoyant and benthic planulae, related to different stages of development, once per year (Harii et al. 2001). Such planulae are considered to have the characteristics of *H. coerulea* and of *P. damicornis* planulae. Furthermore, recent studies have demonstrated that both *Goniastrea aspera* and *Oulastrea crispata* release eggs as well as benthic planulae, with the suggestion that the planulae settle near the parent colonies (Sakai 1997; Lam 2000). Larval dispersal distance is thus likely to be highly variable among brooding corals.

Szmant (1986) compiled the reproductive strategy of corals and suggested that brooding corals have one strategy: they have small colonies, multiple reproductive cycles per year, and can occupy less favorable habitats because of their higher recruitment levels. This type of reproductive strategy is the one represented by *P. damicornis*. Although they are subject to a relatively high mortality (Yap et al. 1992), they produce a large number of small larvae (e.g. Atoda 1947a), and can maintain a widespread adult distribution with small colonies. On the other hand, *H. coerulea* colonies can grow large (> 1 m), and have a single reproductive event per year. They maintain dense populations in some specific reefs (Zann and Bolton 1985; Harii and

Kayanne, submitted). This suggests that their mortality might be low, and that they maintain dense populations close to their parent colonies.

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