Larval settlement patterns, dispersal potential, and the effect of temperature on settlement of larvae of the reef coral, *Platygyra daedalea*, from the Great Barrier Reef

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**ABSTRACT**

This study examined the initial larval settlement pattern, the settlement-competency period, and the effect of temperature on settlement rates of larvae of the broadcast spawning reef coral, *Platygyra daedalea*, from the Great Barrier Reef. Approximately 19% of larvae attached to settlement substrata 3-4 days after spawning (DAS), prior to complete larval metamorphosis and permanent settlement, which began at 4-6 DAS. This early larval attachment behaviour could enhance the retention of some *P. daedalea* larvae on, or near, their natal reefs, thereby allowing some degree of self-seeding of local populations. In contrast, the maximum larval settlement-competency period was 93-105 DAS, with the peak period of larval settlement occurring at 36-42 DAS and 33-41 DAS in repeated experiments over two years. The delayed period of peak settlement and the extended competency periods of these larvae indicate that there is considerable potential for meso-scale and long-distance dispersal of some *P. daedalea* larvae. Slightly elevated temperatures enhanced the development and settlement rates of *P. daedalea* larvae, which suggests that seawater temperature may be an important factor influencing patterns of coral larval settlement on coral reefs.

**Keywords** Reef coral, Reproduction, Larval settlement, Dispersal, Temperature

**Introduction**

The paucity of data on settlement patterns and competency periods of scleractinian reef coral larvae has resulted in significant scientific debate about the extent to which reef coral populations are maintained by locally derived larvae settling on their natal reef, versus recruitment by larvae dispersed between reefs (reviewed in Harrison and Wallace 1990, Sammarco 1994). Most brooding corals are known to release well developed planulae that are capable of settling soon after release, and these larvae may contribute to recruitment on their natal reefs (e.g. Richmond 1987, Harrison and Wallace 1990, Carlon and Olson 1993, Sakai 1997). In contrast, the majority of reef corals broadcast spawn eggs and sperm into the sea, and subsequent fertilization and larval development processes are completed in the water column (Harrison and Wallace 1990, Richmond and Hunter 1990). Larvae of broadcast spawning corals are reported to have a minimum planktonic development period of ~4 to 10 days before becoming competent to metamorphose and settle permanently (e.g. Shlesinger and Loya 1985, Babcock and Heyward 1986, Heyward and Negri 1999), which increases the likelihood of some larval dispersal away from natal reefs (Harrison et al. 1984, Willis and Oliver 1990, Harrison and Wallace 1990). However, a recent detailed study of larval settlement patterns of *Acropora longicyathus* showed that ~50% of larvae were capable of attaching to settlement tiles at 2-4 days after spawning (DAS), prior to metamorphosis and permanent settlement that began at 3-4 DAS (Harrison 1997). Therefore, some broadcast spawning coral larvae may be retained on their natal reefs, resulting in some degree of self-seeding.

At larger ecological scales, the potential for meso-scale and long-distance dispersal by coral larvae, and the importance of larval dispersal in determining the biogeographic distribution patterns and evolution of scleractinian reef corals are highly controversial issues (Harrison and Wallace 1990, Veron 1995). Many scleractinian corals have a wide geographical distribution range (e.g. Veron 1993, 2000, Wallace 1999), and this is often attributed to long distance larval dispersal by oceanic currents (reviewed in Harrison and Wallace 1990, Veron 1995). The dispersal potential of coral larvae also affects the degree of genetic exchange among coral populations and evolutionary processes.

The potential dispersal distance of coral larvae is mainly determined by larval development rates, the length of the settlement-competency period, larval survivorship and energetics (Richmond 1987), larval settlement behaviour and chemical settlement-inducers (Morse et al. 1996, Heyward and Negri 1999), and the velocity and direction of oceanic currents. However, there is little information available on the competency periods of coral larvae, despite the importance of this information (Harrison and Wallace 1990, Veron 1995). Accordingly, this study used larvae of the broadcast spawning brain coral, *Platygyra daedalea* from the Great Barrier Reef (GBR), to quantify the initial larval attachment and settlement patterns after spawning, the larval settlement-competency period, and the effect of temperature on larval settlement rates.

**Methods**

In November 1998, gravid colonies of *P. daedalea* were collected from Heron Island reef flat, southern GBR, a few hours before they spawned on the 7th night after the full moon. Spawned egg-sperm bundles were collected from the water surface of the holding tanks, and gametes were mixed to promote cross-fertilisation.
Gametes were then transferred to six 4 L plastic larval rearing pots with 118 µm plankton mesh lids to allow for seawater exchange (after Babcock and Heyward 1986). One rearing pot was floated in each of three large tanks with running seawater (control tanks) and in three large tanks with heated running seawater (heated tanks). The heated seawater tanks were maintained at 2ºC above ambient seawater temperature by heaters linked to thermistor sensors monitoring the temperatures in the control tanks.

Experiment 1: Initial larval settlement patterns

The initial larval settlement pattern and the effect of elevated temperature during the larval development phase on the subsequent settlement pattern were examined at Heron Island Research Station (HIRS) in November 1998. Fertilized *P. daedalea* eggs developed into motile larvae within ~36-48 hours, and 2.5 day old larvae were used in the experiment. Larvae from the rearing pots in the control tanks, and in the heated tanks, were combined in separate aquaria. Six replicate groups each of ~1000 larvae were counted from the control aquarium, and from the elevated temperature treatment aquarium, and each group of larvae was randomly placed into one of 12 settlement cages in aquaria. Each settlement cage consisted of a 5 L plastic container with two side panels of 118 µm plankton mesh for water exchange, and each cage was placed in a 20 L aquarium to maintain the larvae with running seawater under indirect natural light (ambient seawater temperature was 25.5-27.5 ºC). A pair of biologically conditioned terracotta settlement tiles was placed horizontally in each cage, and two plastic frames were placed at opposite corners of the tile pair to provide 1 cm gaps between the tiles and between the lower tile and the bottom of the cage. The tiles (11 x 11 x 1 cm) had been biologically conditioned by being submerged on Heron Island reef flat for three to four months beforehand, and had assemblages of crustose coralline algae, filamentous algae and other benthos present. The tiles were examined under a microscope to ensure that there were no naturally settled juvenile coral spat present, prior to their placement in settlement cages.

The tile pairs were examined at 4 DAS, one day after the experiment began, and then every second day (at 6, 8, 10, 12, and 14 DAS). The numbers of attached larvae, newly settled spat, and recently detached or dead settled spat on the top and the bottom surfaces of each tile were recorded by viewing the tiles under a dissecting microscope at x15 magnification, while the tiles were submerged in seawater in a shallow tray. Attached larvae were defined as planulae that had attached to substrata or algae but had not undergone contraction and metamorphosis into a juvenile polyp and were therefore capable of detaching and moving, whereas settled spat were distinguished by having undergone oral-aboral contraction and metamorphosis into settled juvenile polyps (*sensu* Harrison and Wallace 1990). At each examination, newly settled spat were marked with a fine line near the polyp using a pencil, to distinguish them from other newly settled spat at subsequent examinations. When a line without an adjacent living settled polyp was observed in a subsequent census, this was recorded as a recently detached or dead settled spat, and the line was crossed through.


For the first larval settlement-competency period experiment with *P. daedalea* larvae, 5 experimental settlement runs were completed during 1998-1999. The first 2 settlement runs were completed at HIRS during November 1998, while the last 3 settlement runs were done at Southern Cross University (SCU), as the larvae and experiments had to be transferred to SCU at 16 DAS for logistical reasons. At SCU, the *P. daedalea* larvae from the control tanks and the heated tanks at HIRS were transferred into separate 20 L glass aquaria exposed to indirect natural light, which were maintained at 27ºC (control aquarium) or 29ºC (elevated temperature aquarium), respectively, by placing each aquarium in water baths heated by thermostatically controlled heaters. Biologically conditioned terracotta tiles were also transferred from HIRS to SCU at 16 DAS, and were maintained in aerated aquaria at 27ºC. At SCU, seawater in each of the rearing and experimental settlement aquaria was changed every 3-4 days, using seawater collected from the subtropical northern NSW coast.

For each of the settlement runs, four to six groups of larvae (larval numbers counted) were collected from the rearing pots in control tanks at HIRS, or from the control aquarium at SCU, and were placed into settlement cages. Settlement aquaria in runs 1 and 2 at HIRS were maintained with running seawater at 25.5-27.5ºC under indirect natural light. At SCU, settlement aquaria in runs 3 to 5 were maintained under indirect natural light with aerated static seawater at 27ºC, by immersion in thermostatically controlled water baths. As the number of larvae remaining alive in the control aquaria decreased over time, six groups of ~1000 larvae were used in settlement runs 1 and 2, four groups of ~500 larvae were used in settlement runs 3 and 4, and four groups of ~150 larvae were used in settlement run 5. Settlement runs 1 to 5 were started on 3, 9, 21, 36 and 69 DAS, respectively. The first examination of the tiles in each run was done after a 6 day settlement period, then the tiles were examined approximately every 6 days (Fig. 2). The tiles were examined for attached larvae, newly settled spat, and recently detached or dead settled spat on the four tile surfaces of tile pairs, as for Experiment 1. Settlement runs 1 and 2 were continued for 6 days, run 3 continued for 13 days, and runs 4 and 5 were continued for approximately 2 months, until no motile planulae remained in the settlement aquaria.


The settlement-competency period experiment was repeated during 1999-2000 to compare settlement
patterns between years. Gravid colonies of *P. daedalea* were collected from Heron Island reef flat just prior to spawning on the 7th night after the full moon in November 1999, and larvae were reared in pots in the control tanks with ambient seawater temperature at HIRS, as for Experiment 1. Larvae, and biologically conditioned settlement tiles that had been submerged on Heron Island reef for several months, were transported to SCU at 4 DAS, and were maintained in 20 L glass aquaria under indirect natural light at 27°C. Two long-term experimental settlement runs were completed; settlement run 1 began 5 DAS, while settlement run 2 began 33 DAS. Fewer larvae were available than for the 1998-1999 experiment. Therefore, for both settlement runs, three groups of ~350 larvae were counted, and each group of larvae was placed into one of three replicate 2 L plastic settlement aquaria, each containing a biologically conditioned terracotta tile. Each tile was held 1 cm above the bottom of the settlement aquarium using plastic frames at two opposite tile corners. Tiles were examined approximately every week until no larvae remained in the settlement aquaria, and the numbers of attached larvae, newly settled spat, and recently detached or dead settled spat on the upper and lower tile surfaces were recorded, as for Experiment 2a.

Experiments 3a and 3b: Temperature and larval settlement

The effects of temperature on larval settlement patterns were examined in two experiments that coincided with settlement runs 3 and 4 of the 1998-1999 larval competency experiment (Experiment 2a). These temperature experiments were done in the same manner as the larval competency experiment, which served as the ambient temperature controls, except that temperature was varied in the additional temperature treatments. For each temperature treatment code in the temperature experiments, the first letter denotes the conditions in which the larvae were reared, while the second letter denotes the temperature treatment during the larval settlement period [L: low temperature (25°C), C: control temperature (27°C), H: elevated temperature (29°C)].

For Experiment 3a, run 3 of the larval competency experiment (Experiment 2a) served as the control treatment (27°C). Two groups of ~500 larvae from the elevated temperature aquarium were counted and placed into 2 settlement aquaria containing settlement tiles, and these aquaria were maintained at 29°C (HH treatment). The experiment began 21 DAS and the tubes were examined 6 days later at 27 DAS, and then at 34 DAS, coinciding with the census periods for the settlement competency run 3 tiles. Two additional temperature treatments were included in Experiment 3b, which coincided with run 4 of the settlement-competency experiment (Experiment 2a). The four temperature treatments consisted of the Control (run 4), CL, CH and HH temperature treatments. For each temperature treatment, 3 groups of ~500 larvae were collected from the control or the elevated temperature larval rearing aquaria and counted, then placed into 3 replicate settlement aquaria containing biologically conditioned tiles, with the aquaria maintained at the appropriate temperature. This experiment began 56 DAS, and tiles were examined at 42, 54, 71, and 102 DAS, coinciding with the census dates for the settlement competency run 4 tiles.

Data on mean larval settlement rates, and mean rates of larval detachment or mortality among treatments were analysed using one way Anova or t-tests and LSD post hoc tests of significance, using SPSS statistics programs.

Results

In Experiment 1, *Platygyra daedalea* planulae reared in the heated tanks were more active at 2.5 DAS compared with those from the control tanks. The initial larval settlement (five settled spat) also occurred slightly earlier, at 3-4 DAS, for larvae reared in the heated tanks compared with larvae reared in the control tanks, which began to settle at 4-6 DAS (Fig. 1). Settlement rates of larvae from both treatments increased slightly at 6-8 DAS (~4%/2 days), then gradually decreased over time (Fig. 1). There was no significant difference in mean total settlement between the control (12.1%) and the heated larval rearing treatments (12.3%) (t-test, p = 0.985). Approximately 19% of the larvae reared in both treatments were attached onto the settlement substrata or algae at the first census 3-4 DAS, and the number of attached larvae present gradually decreased during the experiment (Fig. 1). The mean loss of settled spat was 13.9% for larvae reared in the control treatment and 11.9% for larvae from the elevated temperature treatment, and there was no significant difference between these treatments (t-test, p = 0.731).

![Fig. 1 Mean percentage of newly settled (S) and attached (A) *P. daedalea* larvae reared in control (ambient) and heated temperature treatments (+2°C). Error bars are standard errors.](image-url)

In the 1998-1999 larval competency experiment (Experiment 2a), moderate rates of larval settlement were recorded during the first two 6-day settlement runs at HIRS (mean total settlement of 8.5% and 7.1%, respectively), higher rates of settlement were recorded in runs 3 and 4 at SCU (mean total settlement of 24.4% and 41.1%, respectively), and moderate settlement rates were recorded in run 5 from 75 to 105 DAS (mean total settlement of 14.8%) (Fig. 2). The last four larvae...
observed to settle were recorded settling during the period 93-105 DAS in run 5 (Fig. 2). The last living *P. daedalea* larva was observed at 124 DAS, and this larva was rotating slowly, and had a dark colouration.

The peak larval settlement period during the settlement-competency experiment was determined by comparing the mean settlement rates at the first census (i.e. settlement during the first 6 days) among the 5 runs (Fig. 2a). As the location of the experiments changed from HIRS to SCU after run 2, statistical analyses were performed separately among the runs at each location. There was no significant difference between the mean larval settlement rates during the first 6 day settlement periods in run 1 and run 2 at HIRS (t-test, p = 0.672). For settlement runs at SCU, the highest mean larval settlement rate during the first 6 day settlement period was recorded in run 4 at 36-42 DAS (23%/6 days), which was significantly higher than for the first 6 day settlement period of run 5 (t-test, p = 0.042).

In settlement runs at HIRS, about 50% of the total larval settlement occurred on the upper surface of the top tiles. In settlement runs 3 and 4 at SCU, the majority of larvae settled on the bottom surfaces of the tile pairs, whereas in run 5, the majority of the settled larvae were recorded on the upper surface of the lower tiles.

In the second settlement-competency experiment in 1999-2000 (Experiment 2b), the highest mean settlement rates were again recorded during the first week of the two settlement runs, then settlement rates declined over time (Fig. 3). The mean total percentage larval settlement in the first week of settlement run 2 (65.6%) was significantly higher than that in settlement run 1 (22.7%) (t-test, p = 0.001). The mean total percentage larval settlement in the HH treatment (51.8%) was also significantly higher than that in the control treatment (24.6%) (t-test, p = 0.022). More than 80% of the settled spat were recorded on the bottom surfaces of the tile pairs in both treatments. Fewer attached larvae were recorded in the HH temperature treatment than in the control treatment. The mean percentage of detached or dead settled spat was 1.2% in the control, and 0% in the HH temperature treatment.

In the second temperature experiment (Experiment 3b) coinciding with run 4 of Experiment 2a, the highest rates of larval settlement also occurred in the elevated temperature treatments (HH and CH) (Fig. 4). The mean percentage larval settlement at the first examination in the CH (42.6%) and the HH (41.5%) temperature treatments were significantly higher than those in the control (23.0%) and the CL (17.0%) treatments (anova, df = 3, 9, F = 5.190, p = 0.024; LSD Post Hoc tests). The CH and HH treatments also had higher mean total percentage larval settlement (64.3% and 54.3%, respectively) than the control (41.0%) and the CL (37.4%) treatments, although only the CH treatment was significantly higher than the control and CL treatments (anova, df = 3, 9, F = 4.716, p = 0.030, LSD Post Hoc tests). The mean percentage larval attachment at the first examination was significantly higher in the CL temperature treatment compared with the other three temperature treatments (anova, df = 3, 9, F = 4.850, p = 0.028, LSD Post Hoc tests). The mean percentage detachment or mortality of settled spat was similar among the four temperature treatments (less than 8%), and there were no significant differences among these treatments (anova, df = 3, 9, F = 1.794, p = 0.218).

![Fig. 2](image1.png)  
**Fig. 2** Mean percentage of newly settled *P. daedalea* larvae in 5 settlement runs at HIRS and SCU in 1998-1999. Error bars are standard errors.

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longicyathus of localised retention and self-seeding versus dispersal (A).

In addition to determining the larval pre-competency period of broadcast spawning coral larvae, it is also important to examine the initial larval development and extend the pre-competency period for subtropical P. daedalea. Whereas lower seawater temperatures may slow the rate of planulae development and shorten their pre-competency period, seawater temperatures may increase the rate of planulae development earlier, compared with larvae reared in the control tanks. Wilson and Harrison in prep. The delayed period of peak settlement and the extended settlement-competency period of P. daedalea larvae are likely to contribute to the broad biogeographical distribution range of this species, which extends throughout much of the Indo-Pacific region from the Red Sea and East Africa to French Polynesia (Veron 1993, 2000).

Nozawa and Harrison (Heyward and Negri 1999), and 1-4 days for four species in Okinawa, southern Japan (Heyward et al. 1987, Nozawa and Harrison in prep). In contrast to these relatively rapid development rates, longer pre-competency periods have been reported for some broadcast spawning corals in high latitude regions. Wilson and Harrison (1998) recorded a 12 day pre-competency period for subtropical Acanthastrea lordhovensis planulae from the Solitary Islands, eastern Australia (30°S) where summer seawater temperatures are 22-26°C, and 6-10 day pre-competency periods were recorded for larvae of five broadcast spawning coral species from the northern Gulf of Eilat, Red Sea (29°30’N) (Shlesinger and Loya 1985, 1991). In Experiment 1, P. daedalea larvae reared in the heated tanks were more active and settlement began 1-2 days earlier, compared with larvae reared in the control tanks. Together, these results suggest that slightly elevated seawater temperatures may increase the rate of planulae development and shorten their pre-competency period, whereas lower seawater temperatures may slow the rate of planulae development and extend the pre-competency period of broadcast spawning coral larvae.

In addition to determining the larval pre-competency period, it is also important to examine the initial larval attachment behaviour for understanding the likelihood of localised retention and self-seeding versus dispersal of coral larvae. Harrison (1997) observed ~50% of A. longicyathus larvae attached to settlement tiles in experiments at One Tree Island reef, southern GBR, between 2-4 DAS, prior to larval metamorphosis and settlement which began at 3-4 DAS. In the present study, about 19% of P. daedalea larvae were attached to the settlement tiles and algae at 3-4 DAS, prior to the onset of metamorphosis and settlement, which began at 4-6 DAS. This precocious attachment behaviour could provide a mechanism for some larvae of broadcast spawning corals remaining on, or near, their natal reef, prior to developing full settlement competency. If these planulae remain attached during their subsequent development until they become competent to settle, this would increase the potential for some degree of self-seeding of these coral populations, through increased rates of larval retention and settlement on natal reefs. Therefore, more larvae of broadcast spawning corals may remain on, or near, their natal reefs through this early attachment behaviour, than was indicated by previous data based solely on the initial settlement periods of planulae.

In contrast to these data on the initial settlement patterns of P. daedalea larvae, the peak period of larval settlement was delayed for more than one month after spawning, 36-42 DAS in Experiment 2a, and 33-41 DAS in Experiment 2b. Furthermore, some of these P. daedalea larvae survived for up to 4 months, and the maximum settlement-competency period recorded was 93-105 days. These delayed settlement patterns greatly increase the likelihood of some P. daedalea being dispersed away from their natal reef and increase their potential for settlement on distant reefs. Moreover, these data also indicate that there is considerable potential for long distance dispersal of some P. daedalea larvae during their extended settlement-competency period, although the effective dispersal range would depend upon the number of competent planulae surviving over time. The 93-105 day larval competency period of P. daedalea larvae is the longest maximum competency period reported so far for larvae of broadcast spawning scleractinian corals (Caryophyllia smithii, 8-10 weeks, Tranter et al. 1982; Goniatrea australensis, 46-56 days, A. lordhovensis, 73-78 days, Wilson and Harrison 1998; Acropora millepora, 60 days, Acropora valida, 90 days, Baird 1998; Acropora solitarius, 65-72 days, Cyphastrea serailia, 57-64 days, Nozawa and Harrison in prep). The delayed period of peak settlement and the extended settlement-competency period of P. daedalea larvae are likely to contribute to the broad biogeographical distribution range of this species, which extends throughout much of the Indo-Pacific region from the Red Sea and East Africa to French Polynesia (Veron 1993, 2000).

The results from this study differ from previous settlement-competency studies of other coral planulae, which reported peak larval settlement periods occurring within a week of the initial settlement period. For example, the peak settlement period in A. longicyathus larvae occurred between 4-12 DAS (Harrison 1997) and from 7-13 DAS for larvae of A. valida and A. millepora (Baird 1998, Heyward and Negri 1999). These
differences in the timing of peak larval settlement among different coral species may cause very significant differences in the number of larvae recruiting locally or being dispersed away from their natal reefs.

The experiments on the effects of temperature on larval development and settlement, show that seawater temperature can significantly influence the rate of larval attachment and settlement of P. daedalea larvae. In Experiment 1, although larvae reared in the heated tanks started to settle earlier than those from control tanks, there were no significant differences in mean total larval settlement between the two temperature treatments after 14 days. In contrast to this, Experiments 3a and 3b demonstrated that slightly elevated seawater temperatures (29°C) significantly increased the initial rate of settlement, and increased the total mean percentage settlement compared with the control treatments (Fig. 4).

Some previous studies have also reported that seawater temperature affects larval settlement patterns of other coral species. Coles (1985) found that short exposure to high temperature enhanced the settlement rate of larvae from the brooding coral Pocillopora damicornis. Wilson and Harrison (1997) reported that the highest larval settlement occurred at 26°C for larvae of the subtropical broadcast spawning corals, G. australensis and A. lordhowensis, which corresponds to the maximum seawater temperature during the main spawning season at the subtropical Solitary Islands. Zaslow and Benayahu (1996) reported that higher metamorphosis rates of larvae of the planulating soft coral, Heteroxenia fuscescens, occurred during the warmer months (spring-summer) than during the cooler months (winter-early spring) in the Red Sea. These results indicate that seawater temperature can significantly influence the rate of settlement of coral larvae, which has important implications for larval settlement patterns on coral reefs.

The orientation of larval settlement varied among the settlement runs in Experiment 2. This change in settlement orientation may be partly related to the change in environmental conditions, such as light intensity (Mundy and Babcock 1998), due to relocation of the experiments from HIRS to SCU. However, this does not explain the changes in larval settlement orientation from the bottom to the top tile surfaces, which occurred from settlement run 3 to run 5 at SCU. These changes may have been associated with the observed reduction in larval buoyancy and motility over this period, as fewer larvae may have been sufficiently buoyant or motile to successfully settle on the undersides of the tiles towards the end of their competency period.

Clearly, further experimental studies of larval development, settlement behaviour and settlement-competency periods in a wide range of reef coral species are needed in order to better understand the processes controlling coral settlement and recruitment patterns on reefs, and the potential for inter-reef dispersal versus self-seeding of coral populations. These data are also required to assess the importance of larval dispersal for the biogeography and evolution of scleractinian corals.

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