## Spawning, Settlement and Post-Settlement Mortality of *Pocillopora damicornis* (L.) from the Central Phillippines

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### ABSTRACT

*Pocillopora damicornis*, a ubiquitous, opportunistic coral, was selected for laboratory seeding experiments because of its adaptability to laboratory conditions. Adults, collected from a nearby reef and maintained in laboratory aquaria, were monitored daily for one-month periods, to determine the timing of planula release. Planulae were then allowed to settle in aquaria, to quantify settlement patterns and success, as well as post-settlement mortality. Results showed that this species spawns nightly for one week immediately after new moon through out the year. Planulae showed high settlement success onto conditioned substrates (61.65$\pm$11.3%; n=2354 total planulae and n=4 spawning periods), and early growth in lab aquaria averaged 1.54$\pm$0.151 mm per month for the first six months. These results indicated that his species can be successfully spawned and settled under laboratory conditions. Further work is currently underway to transplant lab-reared juvenile colonies onto a degraded reef site for reef rehabilitation.

### Introduction

*Pocillopora damicornis* is a ubiquitous, opportunistic species often found in degraded reef areas throughout the tropical Pacific. Colonies may reach a maximum of 3 m in diameter (Stoddart 1984, in Kinzie and Sarmiento 1986), although most studies report much smaller sizes (Richmond and Jokiel 1984; Chou and Quek 1978). Brooded planulae are shed on a monthly basis (Richmond and Jokiel 1984; Stimson 1978). This species is one of the most well-studied among the scleractinia, not only because of its ubiquity, but because it has proved to be easily maintained in laboratory aquaria. Over the years, studies of this species by numerous authors have provided valuable insight into various aspects of coral biology, such as lunar periodicity in spawning (Richmond and Jokiel 1984; Tanner 1996; Harriott 1983; Stimson 1978; Chou and Quek 1992), larval settlement preferences (Harrigan 1972; Harriot 1983); gametogenesis and sexual reproduction (Chavez 1986; Holloran 1986), larval dispersal (Richmond 1987); effects of colony size on branch extension (Kinzie and Sarmiento 1986) and larva production (Holloran 1986), and planula metamorphosis (Richmond 1985). Recent interest in the use of *P. damicornis* as an environmental indicator has also led to studies involving responses of both adult colonies and planulae to various environmental hazards (Te 1991; Hodgson 1990; Stambler et al. 1991).

Despite the intense attention *P. damicornis* has received elsewhere, its use in research in the Philippines has been limited. Laboratory and field experimentation has largely focused on species within the genus *Acropora* (Yap and Gomez 1981, 1984, 1985; Auberson 1982a and b; Yap *et al.* 1992), primarily examining responses to transplantation. Yap *et al.* (1992) looked at the feasibility of using ecological dominants to reestablish coral populations in Pangasinan. *Pocillopora damicornis* was one of the three species chosen, although the authors concluded it was not suitable for the method of transplantation used, as it exhibited high mortality. This species has very short, fine branches, which may have been more affected by contact with the epoxy used for reattachment than the other two species used (Raymundo, pers. obs.). The initial results we report in this paper indicate that *P. damicornis* may be very suited to a specific method of transplantation involving initial rearing under laboratory conditions.

One objective of this study was to document the time of spawning for this species in the Philippines, which has not yet been established, although this event has been well-documented elsewhere (see Table 1). Further objectives were to study settlement, post-settlement mortality, and early growth under laboratory conditions. Results of this work are currently being used in reef rehabilitation experiments, to determine the applicability of transplanting lab-reared *P. damicornis* to degraded reef habitats.

## Methods

### *Timing of Spawning*

To determine the timing of planula release, five adult colonies, between 10 and 20 cm diameter (Richmond and Jokiel 1984; Harriot 1983), were collected from Bantayan reef, Dumaguete City, at the beginning of the month in February, April, June, July and October 1997. New colonies were collected for each of these periods and the previously collected colonies were returned to the reef. Colonies were tagged and maintained in rearing tanks with aeration and flowing unfiltered seawater. Each night in February, adults were placed in separate buckets supplied with flowing (0.5 li min$^{-1}$) unfiltered seawater and an outlet draining into plankton mesh cups (125 μ mesh size; Richmond and Jokiel 1984). Planulae were collected from the cups and counted the following morning and the adults returned to the rearing tank until the next night. During subsequent months, this routine was following nightly only during the established spawning time, and on randomly selected nights throughout the rest of the month. Regression analysis was used to determine correlation between colony size and number of planulae released.

*Settlement Success and Post-settlement Mortality*

Commercially available coral tiles (Mactan Stone) were selected as settlement surfaces. The tiles were broken into pieces of approximately 200 $cm^3$ and conditioned in sea water for at least one week prior to use, to allow bacterial and algal communities to develop. To encourage settlement, planulae were placed in 500ml bowls of fresh seawater, containing four to five tile pieces, at a density of 20 planulae $500ml^{-1}$ (Richmond, pers. com.). Bowls were then placed in a water bath for 24 hr to keep the water temperature between 25 to 27°C. If several larvae were observed still swimming on the surface at this point, the water was changed and the larvae left to settle for an additional 24 hrs. After this, any remaining unsettled larvae were released into a separate tank, so the substrate pieces in the bowl could be censused. Successful settlement was determined by visual inspection using a magnifying glass. Substrate pieces containing coral spat were then transferred to lightly shaded, aerated rearing tanks supplied with flowing unfiltered sea water. Temperature in these tanks ranged daily from 24.5°C to 28.5°C. Mortality on each of these pieces was censused daily for one week using a magnifying glass, by noting how many spat were absent from the previous day's count.

To determine differences in settlement success and survivorship in planulae of different parents, nine settlement bowls (n=180 planulae/colony) were set up for each of five parents in July. Sixty planulae were stocked in three bowls per day for three consecutive days per colony, starting on the first day the colony spawned more than 70 planulae. The bowls were then placed in replicate tanks; one bowl per parent per tank per day. Planulae and spat were censused for settlement and mortality as was stated previously. Data were analyzed for between-parent differences using Analysis of Variance and regression (Snedecor and Cochran 1989).

*Settlement Preferences*

Although settlement preferences of *P. damicornis* planulae are well-documented (Harrigan 1972; Harriot 1983; Hodgson 1990), we tested specific preferences for two types of substrate locally available. Substrate tested were volcanic beach rocks, common on the intertidal and subtidal areas on Bantayan Beach, and the tile pieces mentioned above. In addition, because algal growth in laboratory rearing tanks was a potential problem, we tested preferences for rock surfaces containing a thick algal covering vs. those on which visible algae had been removed. Rocks were first allowed to develop an algal "coat" for two weeks in aquaria, after which we scraped/brushed the surfaces of half of them prior to settlement. Two clean rocks and two algae-covered rocks were then placed in each settlement bowl. Seven replicate bowls were prepared in this fashion and stocked with planulae at a density of 20 planulae $500ml^{-1}$. Data were analyzed for differential settlement using Chi-square analysis for pooled variation (Snedecor and Cochran 1989).

### *Growth Rate of Juvenile Colonies*

Growth rate in lab aquaria was determined using individuals from the February cohort (n=220 individuals). To avoid excessive handling and injury of very young colonies, measurements of maximum colony diameter were taken each week from 20 randomly selected spat, using a mechanical hand-held caliper. At one month of age, 30 colonies from this cohort were randomly selected and labelled with an identification number for regular growth measurements. Maximum diameter and diameter perpendicular to maximum were obtained weekly for six months.

## Results

### *Spawning in Pocillopora damicornis*

Release of planulae in *P. damicornis* in the Philippines was found to occur for seven to nine nights starting one night after new moon for each month tested. No planulae were found at any other time during the months tested. This schedule is most similar to that found in Enewetak (Richmond and Jokiel 1984) and southern Taiwan (Dai *et al.* 1992). Large variations in total planulae released were observed both between adults within a single spawning period and between different spawning periods (n=25 spawners; and five spawning periods; see Fig.1), but peak values of 1,000-3,000 per day per colony were consistent with those observed by Richmond and Jokiel (1984). A regression of colony size on total planulae released did not suggest any correlation between the two ($r^2$=0.5%; F=0.084; p=0.775), within the size range available from the natural population. Results did suggest, however, a seasonality in numbers released, with a peak release in April, corresponding to the summer dry season (Fig.1). This contradicts findings by Harriot (1983), who noted reproductive activity predominantly during winter on the Great Barrier Reef (GBR), Australia, but is consistent with findings of Tanner (1996), who observed most reproductive activity during the summer months on the southern GBR. Dai *et al.* (1992) found planula release most concentrated from August to April, the cooler months in the northern hemisphere, though they stressed that planulation most likely occured throughout the year.

The total number of days a single colony released planulae varied slightly between seven to nine days. All colonies followed a similar pattern; few were shed for the first day or two, with gradually increasing numbers, reaching a peak on the fourth or fifth day, followed by a sharp decline for the last two days. In July and October, at least two of the five spawning colonies failed to release more than a few planulae during the entire spawning period.

We speculated that *P. damicornis* began shedding planulae soon after dark, probably before midnight, as we found that many larvae were competent to settle (and some already had) by 8:00 a.m. the next morning. Most planulae began the close inspection and searching behavior of the substrate, documented by Harrigan (1972) soon after they were introduced into the settlement bowls the morning after spawning. Rarely, planulae would fail to settle for two to three days after spawning and would continue swimming on the surface, showing no signs of searching behavior, but appearing active and healthy.

*Settlement Success and Post-Settlement Mortality*

Table 2 summarizes settlement success and mortality data for the four months spawning was documented (as stated earlier, October data are still being processed). These numbers show total planulae stocked, successfuly settled and mortality per spawning period, rather than numbers per settlement bowl per spawning period, as there was no significant difference in settlement success between bowls ($r^2$=0.1%; F=0.106; p=0.9019). Settlement was generally high, averaging 61.65% for four months, and seven-day mortality was consistently low, averaging 28.12% for four months.

Results of the study on between-parent differences in larval settlement success and mortality are presented in Table 3. A significant difference was found in settlement success among larvae of different parents (F=19.693; $p \leq 0.0001$; n=3 parents and n=180 planulae per parent), but differences in post-settlement mortality among larvae of different parents were not significant. A regression of total planulae released per colony (for June and July; n=10 colonies) on settlement success of larvae from each colony yielded no significant relationship ($r^2$=0.7%; F=0.052, p=0.8246).

*Settlement Preferences*

Post-settlement censuses of coral spat did not indicate any preference for either the beach rock substrate or the limestone tile substrate. This is consistent with findings from other authors (Harrigan 1972; Harriot 1983), who found that *P. damicornis* larvae show little substrate specificity and may settle on a diverse array of substrate types.

The microscopic communites of algae that condition the surface of settlement rocks consisted of diatoms and filamentous green algae. However, in the early stage of these experiments, thick communities of the green algae*Polysiphonia upolensis* and *Chaetomorpha linum*, and the blue-green algae *Lyngbya* sp. and *Oscillatoria* sp. aggressively colonized the upper surfaces of all substrate pieces conditioned for longer than one week. As flora in the rearing tanks progressed through what appeared to be successional stages, these species disappeared and large clumps of the red algae *Laurencia columellaris* and *Champia* sp. and the brown alga *Dictyota dichotoma* grew on the rocks, heavily shading older growing colonies and resulting occasionally in their death. Chi-square analysis revealed that larvae preferentially settled on surfaces containing thick algal growth ($X^2_{calc}$=32.187; $X^2_{1,.05}$=3.84). Work is ongoing to determine longer-term effects of shading by algae on coral growth and survival in lab conditions.

*Growth Rate of Juvenile Colonies*

The 30 juvenile colonies selected from the February cohort for weekly growth measurements showed an average increase in maximum diameter of 1.54 +/- 0.151mm for six months after settlement (Fig. 2). However, growth did not follow a constant neasurements indicated an acceleration in growth rate starting at 15 weeks (see Fig. ɔ mortality was observed among the 30 older colonies being assessed for growth ʒ the six-month study period.

In addition, coral spat showed a strong tendency to fuse when growth in diameter ed in physical contact between two clonal colonies. In March, 158 colonies from ebruary cohort were censused for fusion; 43 colonies were found fusing (27.2%). an average of 2.69 colonies per fusing group. This tendency continued as colonies and grew closer to one another. The first signs of competition and overgrowth were ved with older colonies coming into contact with younger ones from different ts, which had settled on the same rock at a later date. The younger, smaller colonies oped a necrotic, bleached band of tissue on the side facing the larger colony. This widened and became covered with epibionts as contact increased. Within two to weeks, the smaller colony had died and was completely overgrown by the older Other observations indicated that, although fusion appears to be a common omenon, competition can also occur among colonies of similar size. In non-eting colonies, basal growth spreads out laterally in contact with the substrate. ins of colonies in competition with each other exhibited upward growth at the area ntact, rather than lateral along the substrate.

**ussion**

That the timing and seasonality of spawning of *P. damicornis* resembles most ly that found in Enewetak and southern Taiwan should not be surprising,considering ocation of both of these islands relative to the Philippines. Seasonal variations in ate and water temperature would be similar. Although the triggering effect of a cular lunar phase is not as easily understood, many workers have noted that the ig of gamete or lavae release may be dictated by conditions under which their val will be maximized (Crisp 1976; Todd and Doyle 1981). The timing of release settlement behavior of the planulae we observed would reduce the probability of ality by diurnal plantivores, as most larvae were competent to begin settlement by ning.

The larval settlement behavior we observed in *P. damicornis* is consistent with Stimson (1978) considered an adaptation for species colonizing shallow reef flat s with fast moving water. Propagules of these species must settle quickly, or be ot out to sea or to deeper areas in the reef. Our unpublished observations on reefs in the Central Visayas, Philippines, indicate that *P. damicornis* is found only in ow reef flat areas, usually above 30', and is most common on disturbed reef areas, aining few of the large, slow-growing"climax" species. The ability of the larvae we rved to settle within 12 hr of release would ensure that most of them would stay in the environment where adult colonies appear to thrive (Birkeland *et al.* 1981). It teresting to note, however, the few planulae who failed to settled within the 48 hour ement period we provided, but continued to swim vigorously. Harrigan (1972) noted ie of *P. damicornis* which were still competent to settle at 212 days after release.

Richmond (1987). in a detailed study of this phenomenon. noted that, while most larvae were observed to settle within 2hr of release from the parent, five out of 100 planulae being observed continued to remain viable after 103 days. He suggested these larvae may provide the mechanism for the long-distance dispersal which has allowed *P. damicornis* to establish populations as far away as Hawaii. Our observations support his findings and are consistent with the current hypotheses of the Indo-Pacific as the center of coral diversity (Veron 1995) and modern eastern Pacific reefs as the result of long-range dispersal from the western Pacific (Dana 1975). The mechanism by which a larva either "chooses" to settle at a later date or is genetically programmed to do so is not understood. but it raises an interesting question: do adults of this species regularly produce a small number of larvae designed for long-distance travel. or are all larvae potentially capable of this and. if so. what triggers specific larvae to exhibit this behavior?

Harrigan (1972) reported that Hawaiian colonies 5 to 6 cm in diameter were capable of producing planulae and these were estimated by Stimson (1978) to be approximately 2 years old. Our early growth measurements suggest that Philippine *P. damicornis* colonies may grow faster. reaching this diameter by 1 1/2 years, and may be able to reproduce sooner. The observed frequency of fusion among young colonies is especially relevant when considering the consequences of colony size in relation to reproductive potential and size-related mortality. We observed that increase in colony diameter started out slowly, acclerating at approximately four months of age. It was not clear why this was so, but it is reasonable to hypothesize that the colony's limited energy resources could not be entirely channelled into growth at this stage. Fusion instantly resulted in a larger colony, and was so complete that the boundaries between the individual colonies was invisible, having been filled in by new tissue. Fusing with adjacent colonies, therefore, would allow each to attain reproductive size at a younger age and provide a quicker size refuge against early size-related mortality.

The results of this preliminary work indicate that *Pocillopora damicornis* is well-adapted to laboratory conditions. Due. no doubt, to the lack of large predators and benthic grazers which may disrupt newly-settled coral spat, mortality in lab aquaria is low. Water quality is high, although warmer aquarium temperatures may be a potential problem (Yap *et al.* 1992). However, our results indicate that normal tank conditions are sufficient for young colonies to survive and grow. Work in progress suggests that *P. damicornis* colonies can be easily spawned and reared in lab aquaria for future transplantation to degraded reef sites. and that growing colonies to a minimum size in lab aquaria prior to transplantation can maximize survival of the transplants. We conclude that this species is particularly well-suited for this type of transplantation and reef rehabilitation work.

**Table 1. Timing of spawning of *Pocillopora damicornis* at sites throughout the tropical Pacific.**

| Location | Timing of Spawning | Source |
|---|---|---|
| Palau | All lunar phases exc. full moon | Atoda 1947 (in Stimson 1978) |
| Hawaii | planulae released throughout the year on full moon | Stimson 1978 |
| Hawaii | Type B: between 1st quarter and full moon<br>Type Y: 3rd quarter moon | Richmond and Jokiel 1984 |
| Enewetak | between new moon and 1st quarter | Richmond and Jokiel 1984 |
| Southern Taiwan | October through April, either new moon or 1st quarter | Dai et al. 1992 |
| Singapore | 2-3 days prior to new moon | Chou and Quek 1992 |
| Heron Island, Austr. S. Great Barrier Reef | October through April, 3rd quarter moon | Tanner 1996 |
| Lizard Island, Austr. Great Barrier Reef | during winter: at full moon; during summer: at new moon | Harriot 1983 |

**Table 2. Summary of settlement success and post-settlement mortality in *P. damicornis* for four spawning periods (n=5 spawners per period).**

| Month | Total No. Planulae Stocked | Settlement Success (#settled/#stocked x 100) | One-week Mortality (#dead/#settled x 100) |
|---|---|---|---|
| February | 682 | 320/682 =46.9% | 100/320 =31.25% |
| April | 500 | 327/500 =65.4% | 71/327 =21.7% |
| June | 510 | 377/510 =73.9% | 182/377 =48.27% |
| July | 662 | 400/662 =60.4% | 56/400 =11.2% |
| Mean +/- SD for all months | --- | 61.65 +/- 11.30% | 28.12 +/- 15.74% |

**Table 3. Analysis of Variance for between-parent differences in larval settlement success and post-settlement mortality for July cohort (n=3 adult colonies and n=180 planulae per adult).**

| Source | df | Sums of Squares | Mean Square | *F* | *P* |
|---|---|---|---|---|---|
| *A. Settlement Success* | | | | | |
| Parent effect | 2 | 1.19019 | 0.59093 | 19.693 | ≤0.0001 |
| Tank effect | 2 | 0.003519 | 0.001759 | 0.05822 | 0.9436 |
| Error | 22 | 0.664815 | 0.030219 | | |
| ***B. Post-Settlement Mortality*** | | | | | |
| Parent effect | 2 | 0.011025 | 0.005512 | 0.56290 | 0.5775 |
| Tank effect | 2 | 0.043317 | 0.021659 | 2.2117 | 0.1333 |
| Error | 22 | 0.215441 | 0.009793 | | |

**Figure 1. Mean total planulae shed per spawning period by *Pocillopora damicornis* (n=5 source colonies/mo.; Mean +/-SE)**

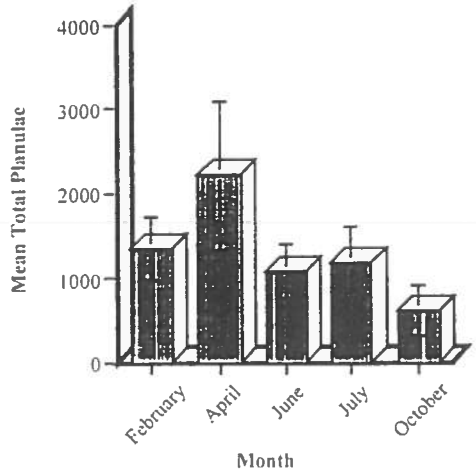
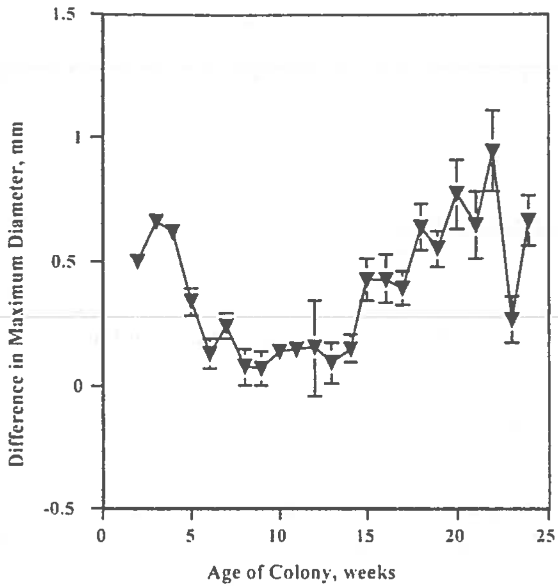



**Figure 2. Mean growth rate of juvenile colonies of *P. damicornis* (n=30 juveniles)**

**Figure 3. Mean weekly difference in maximum diameter of juvenile *P. damicornis* colonies (Mean +/- SE; n=30)**

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