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# Post-Settlement Survival of Reef-Coral Juveniles in Southern Taiwan

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**Kum-Ming Kuo and Keryea Soong (2010)** Post-settlement survival of reef-coral juveniles in southern Taiwan. *Zoological Studies* **49**(6): 724-734. Studies of spatiotemporal settlement patterns of reef corals suggest uneven distributions through space and time. Whether the patterns reflect adaptations of early benthic stages or non-adaptive result from processes preceding settlement are not always clear. They, however, may be distinguished by testing how well newly settled juveniles survive in different places and times of the critical initial post-settlement period. Herein, we compared the survival of young coral that had settled in different seasons and in different habitats. Artificial settling plates were deployed at 2 mo intervals in southern Taiwan, and the fate of each naturally settled coral spat was monitored at 2 mo intervals for at least 1 yr after settlement, in 1998-2000. Spats of Pocilloporidae and *Porites* spp. constituted the majority of coral recruits. Pocilloporids exhibited significant seasonal variations in settlement densities, but poritids showed no such pattern. The probability of pocilloporids surviving an additional 2 mo increased from ~60% at 2 mo old to virtually 100% at 22 mo old. In *Porites*, the 2 mo survival rates were > 90% in all age groups. Survivorship of pocilloporids and poritids was higher for those that settled in the dry season (Nov., Jan., and Mar.) than those that settled in the wet season (May, July, and Sept.), but no corresponding higher settlement rates were found for either taxon in the dry season. Recruits of both taxa showed greater survivorship when settled on younger than on older plates; however, only pocilloporids preferred young plates for settlement. Spat densities and survivorship rates were both higher at the margins than in the center of plates for both taxa. Thus, the settlement season was not related to higher post-recruitment survival, but spatial variation at settlement was, at least for these 2 taxa. http://zoolstud.sinica.edu.tw/Journals/49.6/724.pdf

**Key words:** Survivorship, Settlement, Reproduction, Recruitment.

In sessile marine invertebrates, many biotic and abiotic factors are related to settlement and survival of early benthic stages, which connect the planktonic larval supply to population dynamics and community structures of the benthos (Underwood and Fairweather 1989, Caley et al. 1996). High mortality rates are usually characteristic of this critical period when these small organisms go through metamorphosis and switch from a planktonic to a benthic habitat (Gosselin and Qian 1997, Hunt and Scheibling 1997). Selection and therefore opportunities for adaptation are numerous at this critical stage (Hadfield 2000).

Settlement in reef corals is related to environmental factors such as sedimentation, light, nutrients, depth, substrate orientation, water motion, and temperature (Wallace 1985, Harriott 1992, Maida et al. 1994, Mundy and Babcock 1998, Gilmour 1999, Putnam et al. 2008). Biological factors such as the presence of macroalgae, crustose coralline algae, and soft corals also influence the choice of a permanent site by coral planulae before metamorphosis (Morse and Morse 1991, Maida et al. 1995, Harrington et al. 2004, Birrell et al. 2008). Temporal and spatial patterns of coral settlement densities are often observed at different scales (Fitzhardinge 1985, Harriott 1985, Wallace 1985, Tanner 1996, Dunstan and Johnson 1998, Hughes et al. 2000, Soong et al. 2003). Whether these newly settled spats have different

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fates once permanently fixed to the substratum has been studied in different ways.

Post-settlement mortality rates of corals, like for other sessile invertebrates, may be high; in some cases, few or none survive the 1st yr (Rylassrsdam 1983, Sato 1985, Shlesinger and Loya 1991, Babcock and Mundy 1996, Wilson and Harrison 2005). Many factors such as crustose coralline algae, macroalgae, sedimentation, and soft corals affect the survival of juvenile corals (Wittenberg and Hunte 1992, Maida et al. 2001, Box and Mumby 2007), and factors distinguishable by corals at settlement may increase their survival rates later (Maida et al. 1994, Harrington et al. 2004).

Spatiotemporal patterns of coral settlement often vary (Wallace 1985, Gleason 1996, Tanner 1996). According to the “adaptive for benthic survival” hypothesis proposed here, peak seasons of settlement are ultimately determined by high survival rates in subsequent benthic stages. Similarly, habitats favored by coral spats may also provide a better environment in the benthic stage of corals. Alternatively, selective forces on the seasonality of reproductive activities, mortality patterns in planktonic stages, and even local current patterns may determine differential settlement rates both spatially and temporally. The reproductive season does not cause variation in benthic stage mortalities in this alternative hypothesis. Similar questions about this critical stage of the life history were raised before. For example, Todd and Doyle (1981) suggested that the optimal time to spawn and settle might not match, and reproductive modes with different durations of planktonic stages are adaptive to connect the 2 important events.

In this study, survival of natural coral spats that settled on artificial substrates was monitored for 1 yr to assess the effects of settlement season, substrate age, and settlement position. We attempted to determine if high rates at settlement, either temporal or spatial, corresponded to high survivability in the initial benthic stages.

## MATERIALS AND METHODS

The study site, Hobihu, is located on fringing reefs at Nanwan Bay, southern Taiwan (21°55'N, 120°45'E, Fig. 1). Both soft and hard corals are abundant there (Dai 1991); recent surveys recorded 258 species of hard coral and 52 species of soft corals in the area (C.-F. Dai, pers. comm.). In 3 of 4 yr, coral settlement rates were highest in Hobihu among 8 sites in the area (Soong et al. 2003).

Five to 8 racks of vertical plates (Fig. 2) were fixed on the bottom, at about 4-5 m in depth, every 2 mo from Sept. 1998 to July 1999 for a total of 6 deployments. Each rack held 11 parallel, surface roughened, square PVC plates (15 × 15 × 0.3 cm), separated by 1 cm spacers. Racks were 10 m from each other, and about 25-35 cm above the reef substratum. In total, 37 racks (407 plates) were monitored for 1-2 yr.

The position, size, and condition (alive or dead) of each coral spat were recorded in situ every 2 mo. To assist in relocating individual coral spats in subsequent surveys, a transparent acetate

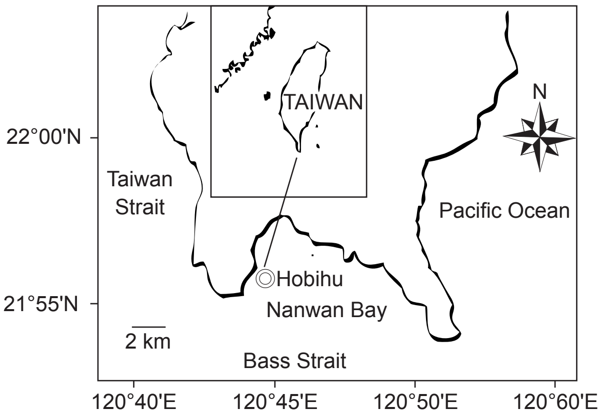

**Fig. 1.** Site of the coral-settlement study in southern Taiwan.

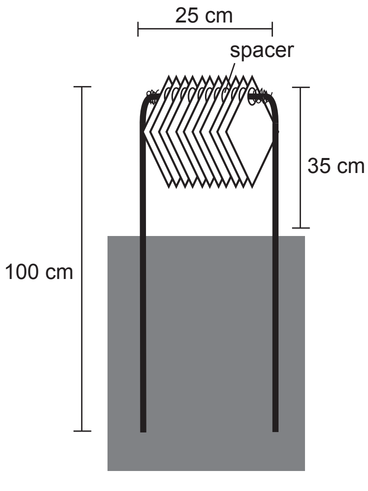

**Fig. 2.** Settlement racks used in the coral-recruitment study in southern Taiwan. Racks were set into the sediment (darker area).

sheet with grid lines was used to mark the position of each juvenile. X and Y coordinates on the plate were recorded for each spat, and coordinates of new recruits were added each time the spat was checked. Data for each rack were recorded at least 6 times (over 12 mo) and up to 12 times (over 24 mo) during the investigation. For each coral spat, the month of settlement, position on the plate (in terms of the zones described below), size and condition at each time point, and month of mortality if it occurred, were recorded. Identification of the recruits to genus level became more certain as they grew larger.

Settlement was defined as the 1st appearance between the previous and current examination. Because the exact date of settlement was unknown, we assumed that each new recruit was 2 mo old when first recorded. A spat was considered dead when (1) only the bare skeleton remained, (2) it was totally covered by other encrusting organisms or algae, or (3) the entire individual had disappeared from the plate. Plate age was defined as the number of months the plates had been submerged in the sea upon examination. For example, a plate was 2 mo old at its 1st check.

To compare survivorship among juveniles which had settled on plates of different ages, plates were grouped into 2 age categories (young and old) to ensure adequate sample sizes within each group. Because the 2 coral taxa had different frequency distributions on plates of different ages, we used different criteria to achieve similar numbers of recruits of each taxon for young and old plates. For the Pocilloporidae, corals settled on plates that were < 6 mo old were combined in the "young" category; conversely, those on plates ≥ 6 mo old were combined in the "old" category. For *Porites*, 12 mo was used to separate plates into "young" and "old".

To study settlement preferences, we divided the available plates into 2 groups, relatively young and relatively old plates, based on the time the plates had been immersed in seawater at each survey. Half of the plates in the water were designated relatively young and the other half relatively old; however, in July 1999, 40% were designated as relatively young plates and the others as relatively old because there were only 5 age groups. Plates examined before Mar. 1999 were not used for this analysis because there was an insufficient range of plate ages. In our study, the settlement preference was based on the position of recruits upon 1st appearance; therefore, any mortality between the actual settlement and the 1st check could not be determined.

To investigate if the settlement season affected mortality rates, recruits that had settled in different months were grouped in either the dry (Nov. to Mar.) or wet season (May to Sept.) due to small sample sizes. This categorization was based on 30 yr of climate records in the study area derived from a weather station located 5 km north of the sampling site (Central Weather Bureau, Taiwan). Monthly precipitation averages in the area are known to exceed 100 mm in the wet season (May-Oct.). The wet season is also the hot season when monthly average air temperatures exceed 25°C (Fig. 3).

To compare coral spat preferences towards settlement in certain positions, plates were divided into 3 zones: center (9 × 9 cm = 81.0 $cm^2$, in the center of the plate), margin (66.2 $cm^2$, within 2.5 cm of the edge), and middle (77.8 $cm^2$) in between the center and margins. To assess survivorship, spats in the center and middle positions were pooled into non-marginal areas to compare to those settled in marginal positions on the plates. The few corals that settled on the 2 outer plate surfaces of the racks were ignored. Only those on the 20 surfaces facing the other plates were included in our analyses.

Survivorship comparisons were made using non-parametric statistics. Each variable, i.e., season of settlement (season), position on the plate (position), and plate age when the spat settled (plate age), was analyzed with the other 2 variables serving as stratifications. For example, when we analyzed the effect of plate age, the original dataset was divided into 4 subsets by the

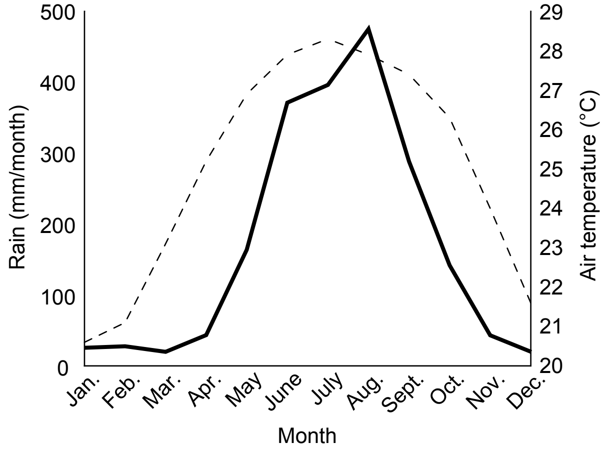

**Fig. 3.** Average monthly total rainfall (solid line) and average air temperatures (clashed line) in 1970-2000 recorded 5 km north of the study area at Hengchun, southern Taiwan.

other 2 variables, i.e., position (marginal and non-marginal) and season (dry and wet). Age ranks of recruits on old and young plates were then scored within respective subsets of data. Then ranks from all subsets were pooled to estimate the *p* value of the statistical test. A log-rank test was used to compare survivorships under different variables. Of the possible combinations, we used only the one with the largest sample size to present survivorship results in the figures. For example, only results on the margin of plates in the wet season of Pocilloporidae were used to compare survival of spats settled on young vs. old plates. For *Porites*, spats on the margins of all plates were used to compare the effects of plate age because there was no significant seasonal pattern. All statistics were calculated with Statview 5 (SAS Institute).

## RESULTS

### Settlement

In total, 546 spats of hard corals and a low number of soft corals belonging to 12 families were recorded in the study. Spat densities averaged 14.8 per rack (equivalent to 32.5 spats/m$^2$) over the duration of the investigation. Genera belonging to the Pocilloporidae (*Pocillopora*, *Seriatopora*, and *Stylopora*) constituted 51%; members of the Poritidae (*Porites* spp. and a few *Alveopora* sp.) 31%, Astrocoeniidae (*Stylocoeniella guentheri*) 6%, Xeniidae (*Anthelia flava*, a soft coral) 5%, Acroporidae (*Acropora* spp., 2%), and others (< 5%) constituted the rest of the families. The starting sizes of these spats were about 3 mm in maximal diameter. Most (93%) were hermatypic corals, and many could not be identified to species. Because most taxa contributed relatively few recruits, detailed quantitative comparisons were limited to the Pocilloporidae and *Porites* spp.

Overall, most of the Pocilloporidae settled on young (< 6 mo old) plates, although such plates were available only in the 1st year of the experiment. Most *Porites* settled on plates 10-14 mo old. In the Pocilloporidae, relatively younger plates had significantly higher recruit densities than relatively older plates ($p = 0.01$, Wilcoxon signed-ranks tests), whereas no pattern comparing < 12 - with ≥ 12 mo old plates was found for Porites ($p = 0.91$, Wilcoxon signed-ranks tests, Fig. 4). Most spats were < 1 cm during the investigation.

Because of the above pattern, assessment of seasonal patterns of settlement was based on different sets of racks in these 2 taxa. For the Pocilloporidae, comparisons were made among 2 mo old racks; the highest density of settlement was found in May 1999, and all other months had < 20% of the maximum (Fig. 5). Differences in settlement among months were significant ($p = 0.01$, Kruskall-Wallis test). For *Porites*, comparisons included new spats on all racks available, and no obvious seasonal pattern was found, e.g., between Sept. 1999 and Sept. 2000 (Fig. 5, $p = 0.42$, Kruskall-Wallis test). More coral spats were found at the margin than in the center of plates ($p < 0.01$, Friedman tests). This spatial pattern is consistent when data were analyzed within individual months (Fig. 6).

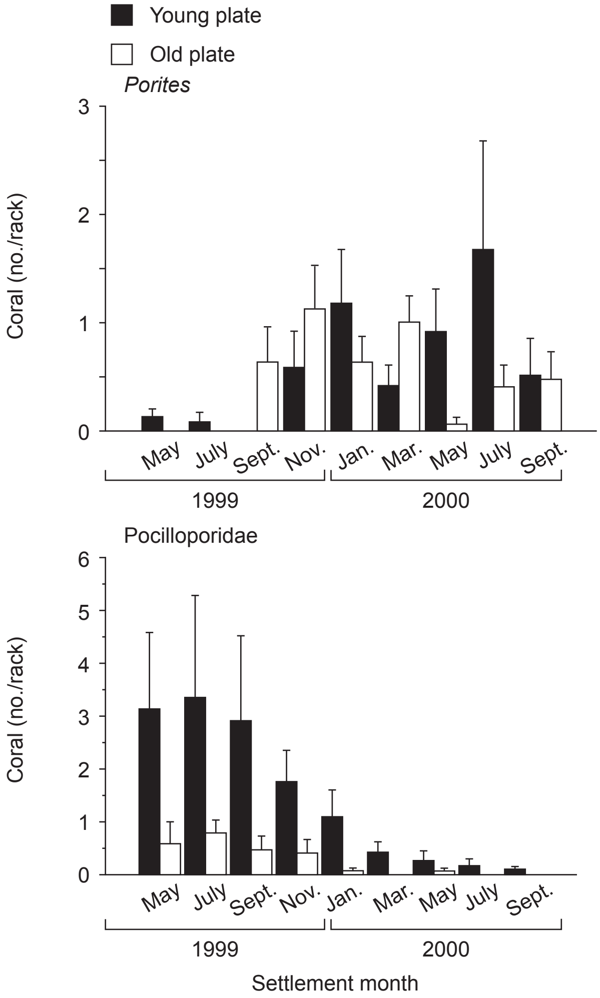

**Fig. 4.** Comparisons of mean numbers (± standard error) of newly settled corals on plates of different ages by sampling month (May 1999 to Sept. 2000) in southern Taiwan.

## Survivorship

Survival rates by 2-mo periods increased with age of pocilloporid spats ($R^2 = 0.70$, $p < 0.01$, linear regression, Fig. 7). This analysis showed that most juvenile pocilloporids survived when they reached ~22 mo of age. Recruits of *Porites* had higher overall survival rates (92%-97%), and no significant correlation was found with age (Fig. 7). Survivorship significantly differed among taxa ($p < 0.01$, log-rank tests). Pocilloporids and *Anthelia* had the lowest survival rates throughout the survey. For example, only ~10% of these 2 taxa survived for 20 mo after settlement, whereas ~70% of poritids and *Stylocoeniella* survived for the same period. Acropora had intermediate survivorship (Fig. 8).

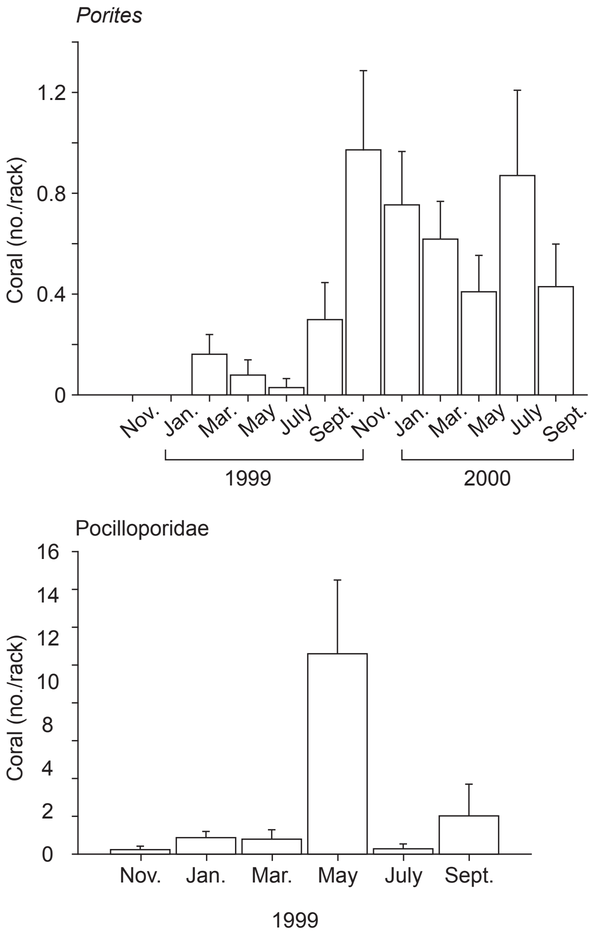

**Fig. 5.** Seasonal changes in coral-recruit densities in southern Taiwan. For the Pocilloporidae, results were based on recruits on 2 mo old plates. For *Porites*, results were based on all available plates. Error bars indicate 1 standard error. See figure 4 for justification of using plates of different ages for the 2 taxa.

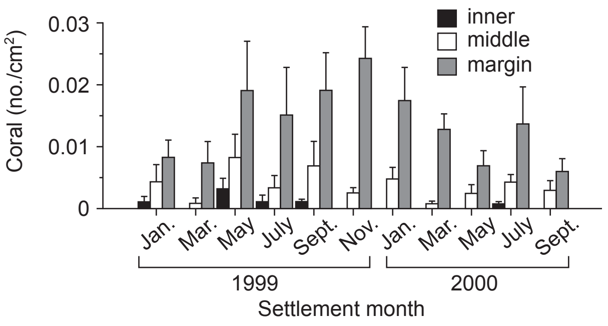

**Fig. 6.** Juvenile-coral densities (± standard error) on different parts of the settlement plates by month in southern Taiwan.

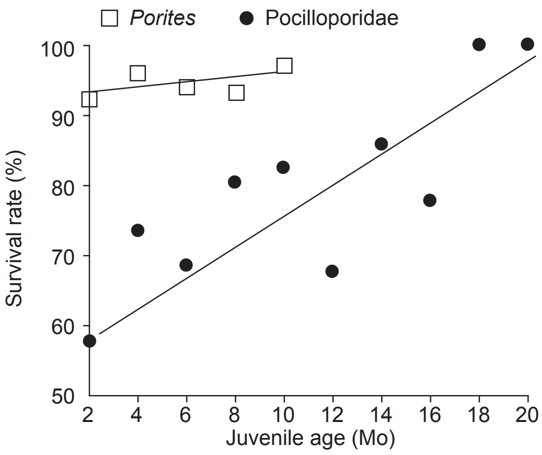

**Fig. 7.** Relationships between 2-mo survival rates and age of juvenile *Porites* (Y = 92% + 0.35X, $R^2 = 0.31$, $p = 0.33$) and Pocilloporidae (Y = 59% + 1.87X, $R^2 = 0.70$, $p < 0.01$) on settlement plates in southern Taiwan.

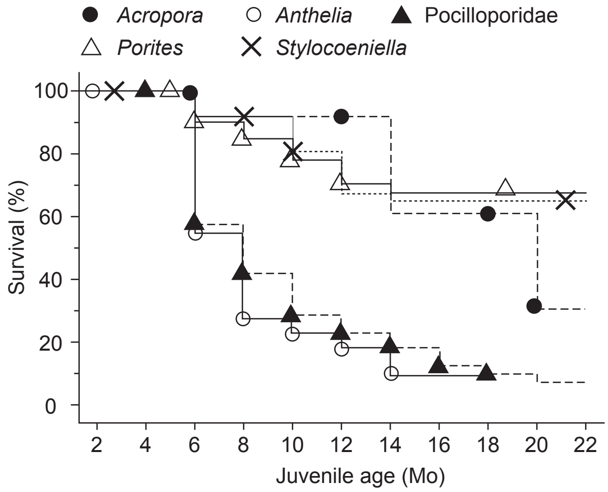

**Fig. 8.** Survivorship of juvenile corals by individual taxa according to the numbers of months since settlement on plates in southern Taiwan.

In addition to differences among coral taxa, spatial and temporal factors also contributed to survivorship (Table 1). Plate age and settlement season both significantly affected juvenile survival of the Pocilloporidae (Table 2). Recruits on young plates (< 6 mo) survived better than those on old ones (≥ 6 mo, Fig. 9). Settling in the dry season also positively affected their survival (Fig. 10). The possible effect of position on the plates on survival, however, was not significant (Fig. 11, Table 2).

Plate age significantly affected the survivorship of *Porites* (Table 2); recruits on young plates (< 12 mo) survived better than those on old plates (≥ 12 mo, Fig. 9). Settlement in the dry season (Nov.-Mar.) seemed to improve survivorship (Fig. 10), but the difference was not significant ($p$ = 0.07, log-rank test). The effect of position on the plates on survivorship of *Porites* was significant (Table 2); spats that settled at the margin of plates survived longer (Fig. 11).

**Table 1.** Summary of statistically significant factors affecting recruitment and survival of the initial benthic stages of the 2 coral taxa

| Characteristic | Pocilloporidae | *Porites* |
|---|---|---|
| Source of recruitment variation | | |
| Season (Fig. 5) | Yes | No |
| Position on the plate (Fig. 6) | Yes | Yes |
| Plate age (Fig. 4) | Yes | No |
| Source of survival variation (Table 2) | | |
| Season of settlement (Fig. 10) | Yes | No |
| Position on the plate (Fig. 11) | No | Yes |
| Plate age (Fig. 9) | Yes | Yes |

Yes, a significant difference was found; No, no significant difference was found ($p$ > 0.05, tests dependent on the characteristic).

**Table 2.** Survivorship comparisons of recruits of the Pocilloporidae and *Porites*. Within each variable, the other 2 variables were used for stratification (see text for details). For each test, traits with better survivorship were placed above those with poorer ones

| Variable | Traits | $p$ in log-rank test |
|---|---|---|
| Pocilloporidae ($n$ = 277) | | |
| Settlement season | Dry (Nov., Jan., Mar.)<br>Wet (May, July, Sept.) | 0.04 |
| Position on plate | MarginNon-margin | 0.07 |
| Plate age | Young (< 6 mo)<br>Old (≥ 6 mo) | < 0.01 |
| *Porites* ($n$ = 168) | | |
| Settlement season | Dry (Nov., Jan., Mar.)<br>Wet (May, July, Sept.) | 0.07 |
| Position on plate | MarginNon-margin | 0.03 |
| Plate age | Young (< 12 mo)<br>Old (≥ 12 mo) | < 0.01 |

## DISCUSSION

Ideally, coral spat survivorship studies should utilize totally natural habitats (Edmunds 2004, Norström et al. 2007); however, this is often not feasible due to the small size of coral larvae and the often cryptic sites of settlement on the reef

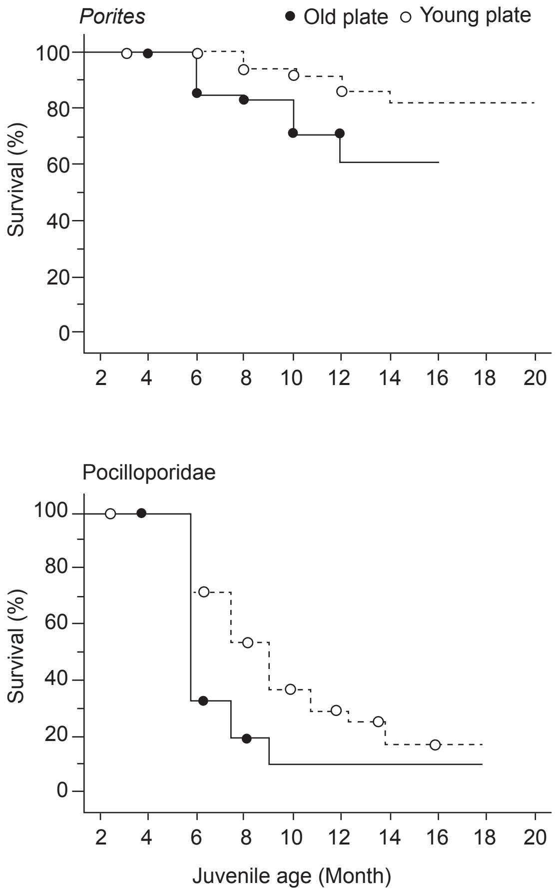

**Fig. 9.** Survivorship of *Porites* and Pocilloporidae juveniles settling on plates immersed in seawater for different periods. To achieve similar sample sizes, 12 mo was used to separate young (<) from old (≥) plates in *Porites* ($n$ = 82), whereas 6 mo was used as a criterion for the Pocilloporidae ($n$ = 116). Only recruits on the margin of plates in the warm season for Pocilloporidae and in all seasons for *Porites* are shown (see Table 1 for justification).

(Vermeij and Sandin 2008). Therefore, most studies examined settlement on artificial substrates (Harriott and Fisk 1987). Seasonal or spatial patterns of survivorship in nature are assumed to be revealed from that on artificial substrates. But, if encroaching neighbors are the principal source of mortality of coral spats, then mortality rates should differ between artificial and natural substrata, since the latter is often inhabited by established organisms.

In fact, our results do suggest the importance of neighbors since survivorship was significantly higher for spats settled on younger than on older plates (Table 2, Fig. 9). Unfortunately, we did not record the neighboring organisms of individual coral spats due to the complex nature of the former. Given the potential effect of other established organisms, our deductions here are based on the assumption that there was no interactions among factors explored, e.g., season and age of the plates on mortality patterns.

The strong temporal pattern of pocilloporid settlement on new plates (Fig. 5) was unexpected because planulation of several common genera in the Pocilloporidae occurs throughout the year in Taiwan (Fan and Dai 1996 2002 2003). If such a temporal pattern is adaptive for benthic juvenile survival, we would expect 2 phenomena. First, high survivorship for those settled in May is predicted; and second, high reproductive output around May than in other seasons should be the case. The 1st prediction was not supported by our survivorship analysis. Survival was higher

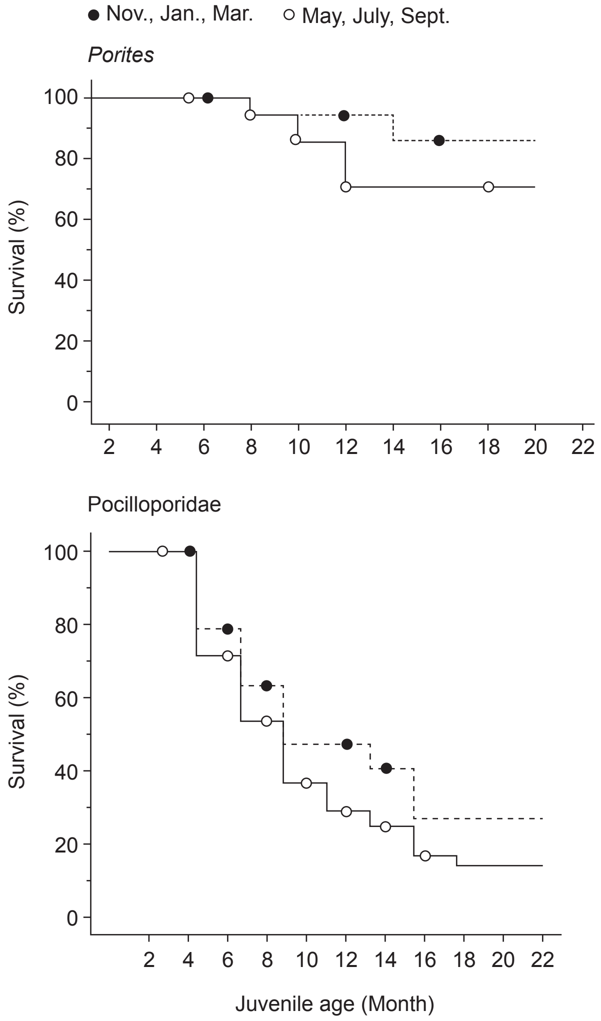

**Fig. 10.** Survivorship of *Porites* and Pocilloporidae juveniles settling on plates in different seasons in southern Taiwan. Only those on the margins of young plates are shown.

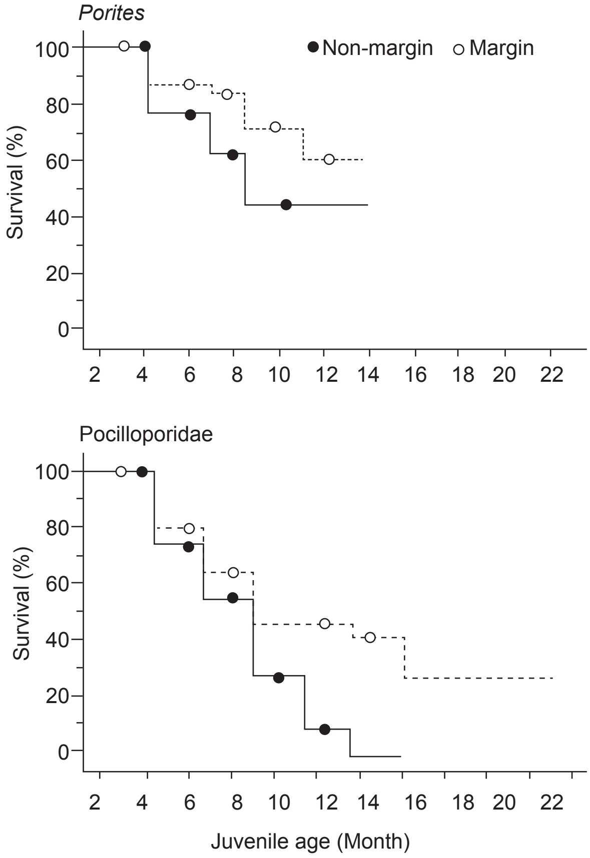

**Fig. 11.** Survivorship of *Porites* and Pocilloporidae juveniles settled at different positions on plates in southern Taiwan. Recruits on young plates were included in the analysis for both taxa, and only those settled in the dry season were used for the Pocilloporidae ($n$ = 30), whereas recruits in all seasons were used for *Porites* ($n$ = 64); see table 1 for justification.

for those that settled in the dry season (Table 2, Fig. 10), but May is actually in the beginning of the wet season in southern Taiwan. Those that settled in May were not expected to gain any temporal advantages in survival rates. For the 2nd prediction, year-round planulation in 3 genera of the Pocilloporidae (Fan and Dai 1996 2002 2003) suggests that any seasonal difference in investment would be of limited magnitude.

One explanation seems plausible and does not rule out that the recruitment season is adaptive for post-settlement stages. Seasonal patterns of mortality rates found here may be local, i.e., applicable only to southern Taiwan. High mortality of coral spats settled in the wet season may have been due to the associated high sedimentation rates that have occurred in fringing reefs of Taiwan in recent years (Dai 1992). Similar mortality patterns may be less likely near small islands or on reefs far from coasts where sedimentation is less likely to cause spat mortality. The season of reproduction, on the other hand, might not be responsive to local environmental factors at such small scales. If a significant portion of settlement was not contributed by "self-seeding" of local reproductive colonies, but from distant dispersal (Graham et al. 2008), it is even less likely that the corals can adapt to the local environment.

The high rate of pocilloporid settlement in May also suggests that success rates of coral planktonic larvae may be highly variable and depend on many factors (Harrison and Wallace 1990). For example, local currents may have the potential to retain larvae in certain seasons but to transport them outside at other times (Roughgarden et al. 1991). Whether this is the case at our study sites remains to be investigated. On the other hand, it is possible that mortality in the early benthic period is so high and variable (Gosselin and Qian 1997, Hunt and Scheibling 1997) that when we first checked the plates at 2 mo, the recorded pattern already differed from that of initial settlement. This argument, of course, invokes an interaction between season and mortality at the earliest stages. The seasonal pattern of coral settlement is often variable both between years and between sites (Wallace 1985, Adjeroud et al. 2007, Mangubhai et al. 2007). If this is the case in southern Taiwan, then the temporal pattern of pocillioporid settlement observed in this investigation may differ in other years. In other words, the high temporal variation in settlement rates found here might not occur in other years.

The extended settlement season of poritids (Fig. 5) was also unexpected, since poritids known in Taiwan are annual broadcast spawners that presumably spawn once a year (Richmond and Hunter 1990, Dai et al. 1992). It also suggests that either they have a long and flexible planktonic stage, or their spats that settled in different seasons originated from remote reefs. Thus, the "late settlers" might have travelled from distant reefs before settling on southern Taiwanese reefs (Babcock 1989, Lugo-Fernandez et al. 2001). None of the above scenarios would predict a seasonal pattern of benthic-stage survivorship.

Coral settlement in many other regions is reported to be seasonal, mostly occurring in spring and summer after mass spawning events (Wallace 1985, Glassom et al. 2004, Adjeroud et al. 2007). Settlement seasons in those cases were a result of the season of reproduction. The risk of staying in the water column may outweigh the risk of settling at a less-appropriate time. As such, the time of settlement and post-settlement mortality are just side effects of pre-settlement adaptations (e.g., larval development and fertilization rates) that determine the reproductive seasons.

Unlike pocilloporids, poritids did not demonstrate any preference towards relatively young plates (Fig. 4). This, in itself, suggests that poritid larvae may preferentially settle on old plates, because old plates should have less primary space available than young plates (Birkeland 1977, Gunkel 1997). About 87% of poritid spats were found either on or near coralline algae in this study (unpubl. data). Their larvae may require biological cues before settlement and metamorphosis like those reported for some other corals (Morse and Morse 1991, Baird and Hughes 1997). The contrast in substrate preference of these 2 taxa partly explains why pocilloporid spats predominated in many coral recruitment studies that employed artificial substrates for relatively short immersion durations (Wallace 1985, Harriott 1992, Harriott and Banks 1995, Dunstan and Johnson 1998). Settlement rates of corals requiring biological cues may thus be underestimated when using young plates.

Higher survival rates of both taxa on young plates than on old ones were likely due to biological factors. Biotic factors on young plates should be less complicated than on old ones, since young communities should be simpler and their constituents less well-established. Competitive pressure is generally thought to be higher in long-established communities (Connell 1978) where space preemption and overgrowth by others may be extensive (Vermeij 2006). Other corals, sponges, and macroalgae are all known to adversely affect the survival of juvenile corals (Koh and Sweatman 2000, Maida et al. 2001, McCook et al. 2001). These modular organisms; however, need time to reach large sizes and achieve competitive superiority. The sensitivity of juvenile corals was remarkable in this study because the plate ages were all relatively young, i.e., < 6 mo vs. ≥ 6 mo for Pocilloporidae and < 12 mo vs. ≥ 12 mo for *Porites*. The clean plates we used simulated a substrate recently disturbed and had extensive primary space. Settled juvenile corals may enjoy high survival rates when plates are young. But very soon, e.g., 6 mo for Pocilloporidae, they may begin to encounter challenges that can kill new coral spat. Spats that settled earlier may have passed a critical stage, e.g., a threshold size, and thus only newcomers suffered high mortality rates when settling on old plates. For most reef substrates in nature, the benthic communities are likely more complicated and variable than 6-mo-old communities on plastic plates, thus the challenges must be even greater. The choice of substrate at settlement must, therefore, be critical in nature. In considering differences in survivorship, the settlement preference for young plates by pocilloporids is thus reasonable, whereas the lack of a preference in poritids requires further explanation.

On average, poritids had much higher survival rates than pocilloporids in our investigation (Figs. 7, 8), so any selective pressure at this stage must be less stringent than that on pocilloporids. It is possible that biological cues used by poritids contribute to their overall high survival rates, enabling them to tolerate harsher environments on old plates. The propensity to discriminate at the time of settlement may differ among species (Mundy and Babcock 1998). Less-selective species may have a higher probability of finding a space to settle, but may suffer higher post-settlement mortality. Whereas species with particular preferences may have difficulty finding a suitable settlement site, but once settled, the chosen habitats may provide suitable environments for rapid initial growth and thus improve survival rates.

A preference for marginal areas of the plates (Fig. 6) coupled with greater survivorship of coral juveniles in these zones (Fig. 11) suggests that this bias of settling larvae may be adaptive. Maida et al. (1994) reported a similar phenomenon at one of their 2 studied islands. Planulae of corals have the ability to choose substrata for settlement and metamorphosis (Lewis 1974, Chia and Bickell 1978, Morse and Morse 1991, Baird et al. 2003). This ability may be very specific and directly contributes to juvenile survivorship (Harrington et al. 2004). Marginal zones in our setup may have been the only habitat on the plates with adequate light for photosynthesis by zooxanthellate corals (Maida et al. 1994, Babcock and Mundy 1996).

In conclusion, the temporal variance in coral settlement found here probably resulted from pre-settlement processes unrelated to survivability of the settled spat. Spatial variations in coral settlement, on the other hand, are likely to be preferences that contribute to post-settlement survival.

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