The ecology of coral larvae: settlement patterns, habitat selection and the length of the larval phase.

Thesis submitted by

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Abstract

In order to increase the taxonomic resolution achievable in coral juveniles I compared skeletal morphology of juveniles from known parents from 19 species in 14 genera and 8 families to determine which of these taxa could be reliably distinguished. Three families had features which were both unique and consistent, enabling unequivocal classification throughout their life: the Acroporidae have a porous coenosteum, prominent basal ridges or septa and no columella; the Pocilloporidae have a solid coenosteum, prominent septa and a prominent columella; the Poritidae have septa with prominent teeth. Juveniles in the remaining 5 families examined could not be consistently distinguished. Some genera could be distinguished while the juveniles were young, including the genera of the Pocilloporidae and the Acroporidae The juveniles of broadcast spawned *Porites* could be distinguished from those of brooded *Porites* by the presence of an epitheca. After this time, variation in the growth rates of individuals and thickening of the skeleton obscure differences between the taxa.

I next examined the depth patterns of coral settlement around Lizard Island. Many taxa showed a pronounced and consistent decline in abundance with depth. In particular, *Isopora* and *Pocillopora* recruits were largely restricted to the reef crest. A similar pattern was evident in the adults of these taxa, suggesting that larvae can recognize and respond to cues from the parental habitat. To test this hypothesis the larvae of six common coral species, with contrasting depth distributions, were introduced into aquaria containing tiles conditioned at depths of 2 m and 12 m. Settlement densities on tiles matched those predicted from the depth distribution of adults. I next examined the induction of metamorphosis in larvae of the brooding corals *Stylophora pistillata* (F.

Pocilloporidae) and *Acropora palifera* (F. Acroporidae). *A. palifera* metamorphosed only in assays which included CCA. In contrast, some *S. pistillata* larvae metamorphosed in all assays, including sterilized seawater, which suggests that *S. pistillata* larvae do not require a biologically conditioned surface to settle.

To test the likelihood of localised recruitment and the potential of coral larvae for long distance dispersal, I compared the frequency distribution of settlement and the competence of larvae of five *Acropora* and two faviid corals. Some settlement was recorded within 4 days of gamete release in all species, indicating a shorter pre-competent period than has been generally accepted. Pronounced differences were also apparent among species in the capacity to delay metamorphosis. Settlement competence peaked between 7-10 days, after which the proportion competent to settle dropped rapidly in all species except *A. valida* and *A. millepora.* The maximum competency periods were 110 days for *A. valida*, 60 days for *A. millepora,* 36 days for *G. retiformis*, 34 days for *A. gemmifera* and *P. daedalea* and 14 days for *A. pulchra.* However, larval survivorship in cultures was low in all species. Low survivorship of larvae combined with a rapid drop in the proportion remaining competent to settle suggests that while connections between populations may be sufficient to prevent population divergence the numbers of migrants are unlikely to be high.

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STATEMENT OF SOURCE

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I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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CHAPTER 1 General Introduction

1.1 Introduction

One of the recurrent themes of marine ecology has been the tendency to underestimate the capacity of larvae to influence their fate. For example, the prevailing paradigm for tropical marine organisms with a complex life history is massive export of larvae from the reef of origin followed by dispersal over a wide geographical range (Scheltema 1986). This concept is based primarily on the belief that larvae behave as passive particles with little ability to influence their position in the water column and little ability to sense their environment (Young and Chia 1985). However, this paradigm is now being challenged by recent research which suggests a surprising proportion of larvae may be retained locally, even in species with long larval duration. For example, Jones et al. (1999) marked and recaptured larvae of the coral reef fish, *Pomacentrus amboinensis*, and estimated that 15-60 % of the recruits to Lizard Island were of local origin. Similarly, Ayre and Hughes (2000) measured the population structure in 14 coral species on the Great Barrier Reef and found that, there was "considerable genetic subdivision among sites within reefs suggesting that larval dispersal is surprisingly limited even in species with a relatively long larval duration".

One mechanism by which fish larvae might be retained near their reef of origin has been elucidated. Larval fish can sense nearby reefs (Leis et al. 1996) and swim towards them for sustained periods (Stobutzki and Bellwood 1997). This research had revealed that the larvae of coral reef fishes are not the passive planktonic particles they were traditionally considered to be (e.g. Williams et al. 1984). A mechanism by which coral larvae might be retained on natal reefs has yet to be elaborated. Indeed, the suggestion of limited dispersal between reefs is in conflict with what is known of the mode of

development of the majority of corals which are broadcast spawners, releasing gametes into the water column for external fertilization and development, with a pre-competent period in the larvae of 4.5 to 6 days (see review by Harrison and Wallace 1990). In this thesis, I re-examine pre-competence periods in the larvae of seven broadcast spawning corals and demonstrate that when presented with the necessary cues to induce metamorphosis a high proportion of larvae settle more quickly than has previously been considered likely.

Opinion has long been divided on the potential of corals for long distance dispersal and its biogeographical significance, particularly, with respect to the origin and maintenance of coral assemblages in remote and isolated regions. For example, Heck and McCoy (1978) challenged Dana's (1975) hypothesis of an Indo-Pacific origin for corals in the Eastern Pacific largely on the basis of a lack of evidence for teleplanic dispersal. Surprisingly, Heck and McCoy's (1978) criticism remains valid and the assumption of regular long distance dispersal in corals is based almost entirely on adult distribution patterns and biogeography with empirical support for the assumption being limited (Veron 1995). The potential for long distance dispersal depends on how long coral larvae can survive in the plankton whilst retaining the ability to settle and metamorphose. In this thesis, I present the first empirical estimates of the capacity of the larvae of broadcast spawning corals to delay metamorphosis and demonstrate that the maximum competence periods of many coral larvae are sufficient to allow them to bridge some of the major barriers to dispersal in the Indo-Pacific Oceans.

Another area where reef ecologists have tended to underestimate the ability of larvae to control their fate is in attempts to explain the depth distribution of coral assemblages

where the importance of post-settlement processes, such as competition and predation, has been emphasized (e.g. Connell 1961, Paine 1966). The emphasis on post-settlement processes was based on the belief that few larvae could sense or respond to their environment (Pawlik 1992). Certainly, coral larvae are relatively simple organisms, with few specialized sensory structures (Harrison and Wallace 1990), although recent research has identified neuron like cells in the epidermis of Acropora millepora larvae (Hayward et al. 2001). However, recent research has demonstrated that light intensity and spectral quality affect the settlement density of larvae from zone-specific coral species (Mundy and Babcock 1998). Furthermore, even morphologically simple organisms can respond to a wide range of environmental cues. For examples, 32 chemosensory neurons and 40 protein receptors have been identified in the nematode *Caenorhabitis elegans*, which consequently, can sense numerous diverse chemical signals (White et al. 1986). In this thesis, I demonstrate that habitat selection by larvae at settlement has a strong influence on the depth distribution of the adults of 6 common coral species.

1.1 Thesis outline

In this thesis I examine patterns of settlement, habitat selection by larvae, the induction of metamorphosis, and the length of the larval phase, and demonstrate that these aspects of the ecology of coral larvae have a profound effect on adult distributions. A detailed review of the literature pertinent to each of these subjects in contained in the introduction to the relevant chapters. One of the primary reasons the early life history of coral larvae has been ignored is because of difficulties in identifying coral juveniles. In Chapter 2, I describe the progress I have made in increasing the taxonomic resolution of

coral juveniles after raising the juveniles of 19 species common on the GBR, in 14 genera from 8 families.

In Chapter 3, I use this increase in taxonomic resolution of juveniles to examine the depth distribution of corals at settlement at four locations around Lizard Island. The similarity of the settlement patterns to the depth distributions of the adults suggests that the larvae of some taxa exert some control over where they settle. In the second part of the chapter, I describe an experiment designed to test the hypothesis that larvae prefer to settle on substratum conditioned in the habitat of the adults.

In Chapter 4, I investigate the induction of metamorphosis in larvae of the brooding corals *Stylophora pistillata* (F. Pocilloporidae) and *Acropora palifera* (F. Acroporidae) and demonstrate that unlike most coral larvae investigated to date, *S. pistillata* larvae do not require crustose coralline algae to induce metamorphose. I discuss how this feature of their larval biology may help explain many aspects of the ecology of this species, such as why it is a regular member of early successional coral assemblages.

In Chapter 5, I consider the role of larval biology in the dispersal of corals. I firstly consider the question of self-recruitment in coral populations. Here the relevant feature of larval biology is the pre-competent period. In particular, I establish what proportion of larval cohorts settle through time. This information is essential to estimate the proportion of larvae retained near the reef of origin under various scenarios of water retention. Secondly, I consider long-distance dispersal of corals and how this might influence geographical distribution of species. In this case the relevant feature of larval biology is the capacity of larvae to survive in the plankton whilst retaining the ability to

settle and metamorphose. Finally, I synthesize the results of these two aspects of larvae dispersal and consider how they might affect the patterns of connectivity between populations in a complex system of reefs such as the Great Barrier Reef.

In Chapter 6, I summarise the findings and suggest some areas for future research.

All papers published during the course of my Ph.D. are included in Appendix I

CHAPTER 2 The identification of coral recruits

2.1 Introduction

Measuring the patterns in recruitment of marine organisms is of fundamental importance in understanding the mechanisms which regulate populations and mediate species coexistence (Underwood and Fairweather 1989). An understanding of patterns of recruitment is also a prerequisite for the effective design of marine reserves and an informed response to catastrophic disturbance, such as crown-of-thorns starfish outbreaks and cyclones (Pearson 1981).

Estimating the input of new recruits into coral populations is difficult for a number of reasons. Corals are small at settlement and growth is slow (Babcock 1985) with the result that it can take up to a year before a recruit is visible on the reef substratum (Wallace 1985a). During this year, mortality is high and variable (Rylaarsdam 1983; Sato 1985; Babcock and Mundy 1996). Consequently, it is impossible to determine to what extent patterns measured at recruitment have been altered by post-settlement mortality. For example, aggregative recruitment may reflect either aggregative settlement, which involves larval choice, or result from differential patterns of mortality acting on an essentially random pattern of settlement (Keough and Downes 1982).

To avoid this problem, artificial substrata, which can be removed for microscopic examination, have been used to measure coral settlement patterns (e.g. Birkeland 1977, Wallace and Bull 1982). Coral larvae secrete a skeleton within hours of settlement which remains intact even if the polyp dies and a record of settlement remains unless the skeleton is removed, overgrown or eroded (Richmond 1985). If the time before

collection is short, the counts can provide a reasonable estimate of the supply of new recruits (Wallace 1985b, Hughes et al. 2000). This technique has been used to examine a number of aspects of coral ecology such as seasonal peaks and annual fluctuations of recruitment (Wallace 1985), cross-shelf differences in the relative abundance of recruits (Fisk and Harriott 1990, Sammarco 1991), spatial variation in recruit abundance (Babcock 1989, Baird and Hughes 1997, Harriott and Fisk 1988, Hughes et al. 1999), and stock recruitment relationships in corals (Hughes et al. 2000). However, the taxonomic resolution of new recruits is extremely limited and has restricted the range of questions that can be addressed. Consequently, studies of the population dynamics of corals which include an estimate of settlement are rare (Hughes 1984).

Identifying coral recruits, particularly in regions with a diverse scleractinian fauna such as in the central Indo-Pacific region, has proven to be difficult. Juvenile corals have few reliable taxonomic features and the identification of newly settled corals has been largely subjective. Identification of coral recruits is not as problematic in the Caribbean, where coral assemblages are less diverse and juveniles can be readily classified to genus or species (e.g. Sammarco 1980, Rogers et al. 1984). In an attempt to increase the taxonomic resolution of early recruits, Babcock (1992) raised juveniles from 11 of the 15 scleractinian families common on the Great Barrier Reef (GBR). He concluded that only three of these families have distinct taxonomic characters that are consistent enough within families to allow identification within the first 6 months of life: the families Acroporidae, Pocilloporidae and the Poritidae. Generally, this is the resolution used in recruitment studies on the GBR, with the remaining juveniles recorded as "others" (e.g. Wallace 1985b, Harriott and Fisk 1988, Baird and Hughes 2000). While

some authors have distinguished up to 18 different taxa (e.g. Sammarco 1991), no justification for this level of taxonomic resolution has been provided.

Here I raised the juveniles of 19 coral species common on the GBR in 14 genera from 8 families to identify distinct taxonomic characters that would allow them to be distinguished. I concentrated on the first 6 months of life, because my research aims to estimate larval input into the population i.e. supply. Furthermore, I concentrated on the micro-architecture of the corallum (Wells 1956) i.e. features readily apparent under stereo-dissector microscope. A similar approach has been used before by various authors to examine the process of skeletogenesis (Jell 1974 & 1980, Vandermeulen and Watabe 1973, Le Tissier 1988) and to examine growth and development of juveniles (Stephenson 1931, Atoda 1947 a & b, 1949) but rarely to identify features for use in taxonomy.

2.2 Materials and methods

The larvae of broadcast spawning coral species were raised using a modification of the method described in Babcock and Heyward (1986). Six to 10 colonies of each species were collected from one or two sites on the reefs surrounding Orpheus and Pelorus Island (18°46'S, 146°15'E) in the Townsville Section of the GBR (Table 2.1). Only one cohort was examined per species. Colonies were placed in holding tanks, with one species per tank. Following spawning, the gamete bundles of hermaphroditic species, which contain both eggs and sperm, were collected and broken apart with gentle agitation. The gametes were then placed in plastic buckets with an additional amount of seawater to produce an approximate sperm concentration of 10^5/ mm^3 to optimize fertilization success (Oliver and Babcock 1992, Willis et al. 1998). A sample of

between 9-39 eggs per species was collected and the maximum diameter measured to the nearest unit with a graticule eyepiece under stereo-dissector microscope. When the eggs began to cleave (between 2-4 h) approximately 5000 embryos were collected and gently rinsed in sand filtered sea water (FSW) to remove excess sperm. The embryos were then placed in 15 L fiberglass tanks in sand FSW. The water was changed after 6 h, 18 h and then daily until the majority of the larvae were motile. Once motile the larvae were allowed to settle on conditioned clay tiles. The tiles were maintained on racks in constant flow through aquaria at Orpheus Island Research Station. The gametes of gonochoric species were left in the tanks after the removal of the adults following spawning. In the morning the embryos were collected and placed in the culture tanks and maintained as described above. Brooded larvae were collected by holding adults in flow-through aquaria with containers lined with plankton mesh positioned below the outflow to collect the planulae. Larvae were collected in the morning and settled on conditioned clay tiles. The tiles were then maintained in flow through aquaria.

Samples of the tiles were removed at various times (Table 2.2) and examined under stereo-dissecting microscope. Live specimens were circled with pencil. To reveal the skeleton, recruits were bleached in 10% NaOH solution, then rinsed in fresh water and dried. Specimens were then examined under a stereo-dissecting microscope at 40X and the maximum diameter of the corallum and the maximum diameter of the primary corallite was measured to the nearest unit with a graticule eyepiece. Representative specimens were photographed under a stereo-dissecting microscope. Where scanning electron micrographs are presented, these specimens were removed from the tiles, mounted and vacuum-coated with gold. Photomicrographs were taken with a Phillips XL-20 scanning electron microscope.

2.3 Results

2.3.1 Family Acroporidae

Subgenus *Acropora*

The pattern of skeleton formation was similar in all three *Acropora* species in the subgenus *Acropora.* Twenty four hours after settlement, the basal disc had formed with 12 basal ridges in a single cycle (Fig 2.1a & b). Triangular lateral processes were evident on the inner end of basal ridges (Fig 2.1a). These processes develop into rods (or synapticulae) which grow perpendicular to the basal ridges and fuse with adjacent synapticulae to form a continuous ring (Fig 2.1 c, d & f). After 7 days, following further growth and thickening, this becomes the corallite wall (Fig 2.1e & f). The primary septa originate from the corallite wall at a point between the basal ridges after 3 days (Fig 2.1 c & d). A second septal cycle was also evident in rudimentary form (Fig 2.1 c & d). The corallum grows by an extension of the basal disc. The coenosteum forms by the growth of synapticulae between the basal ridges and between spines that form upon them (Fig. 2.1e). After 7 days the spat has all the features which distinguish this family: prominent laminar septa in two cycles, a porous coenosteum and no columella (Fig. 2.1e).

Subgenus *Isopora*

The pattern of skeleton formation in *Acropora palifera* juveniles was very different to that of the subgenus *Acropora acropora.* For example, it was not possible to distinguish a basal disc in any *A. palifera* spat and neither were there any spat in which the basal ridges had formed independent of the coenosteum (Fig. 2.2 a) and it appears that skeletal elements, such as the coenosteum and theca, are deposited synchronously. Within 4 weeks secondary corallites were evident in the juvenile corallum (Fig. 2.2 b).

Genus *Montipora*

The pattern of development in the early juvenile skeleton of *Montipora digitata* was quite different to that in the subgenera *Acropora* and *Isopora*. The skeleton began as an epitheca (Fig. 2.3 a) similar to that of most of the other families (see below) but not seen in the other acroporids. In some spat a second wall formed within the epitheca and rod like septa projected into the calice (Fig. 2.3 b). The pattern of formation of the 2nd wall was not clear.

In addition to differences in the patterns of formation of the juvenile skeleton, the genera of the Family Acroporidae can be distinguished by differences in the size of spat at settlement. The sizes of the spat of the 3 species of the subgenera *Acropora* were very similar with substantial overlap in size range (Table 2.3). The spat of the isoporan *A. palifera* were over twice the size of the *Acropora* spat ranging from 2000 to 2700 micron max diameter at settlement whereas the largest *Acropora* spat was 1375 microns at settlement (Table 2.3). Juveniles in the subgenus *Acropora* took at least one month to reach 2000 microns (e.g. *A. tenuis* Fig. 2.2 c). While the size of the isoporan corallum was significantly larger at settlement, the size of the calice was similar. Consequently, a much larger proportion of the isoporan corallum is coenosteum at settlement. *Montipora digitata* spat were only half the size of the *Acropora acropora* spat at settlement (Table 2.3). The largest *Montipora* spat was 650 microns and this is considerable smaller than 850 microns, the smallest recorded *Acropora acropora* spat (Table 2.3). In summary, there was no overlap in the size range of the spat at settlement (*Montipora* < 650, 650 < *Acropora* < 1375; *Isopora* > 1375), however, differences in the rates of growth of coralla following settlement are likely to eliminate the utility of this feature to distinguish between older juveniles.

2.3.2 Family Agaricidae

The initial stage in the juvenile skeleton of *Pachyseris speciosa* was an epitheca which was evident after 3 days (Fig. 2.4 a). The epitheca is formed by a series of ridges laid down horizontally at the perimeter of the basal plate. Further skeletal development was slow. The epitheca grows vertically and inwards forming an inverted cone after 6 weeks (Fig. 2.4 b). Six primary septa were prominent in some specimens after 6 weeks and a second cycle of septa was evident in some specimens (Fig. 2.4 b). The septa originate from the rim of the epitheca. Neither costae nor columella were visible after 6 weeks. No specimens survived beyond this point. The mean size of the spat at settlement was 650 ± 14.4 microns and ranged from 625 – 675 microns (Table 2.3).

2.3.3 Family Dendrophylliidae

In *Turbinaria mesenterina* a basal disc had formed after 3 days and 3 rudimentary basal ridges were apparent (Fig 2.5 a). After 1 week, 6 basal ridges had formed concurrent with the vertical accretion of skeleton on the edge of the basal disc (Fig 2.5 b). After 1 month the skeleton consisted of a theca and 6 primary septa. Septa appeared to grow as vertical extensions of the basal ridges (Fig 2.5 c & d). Consequently, the basal ridges may be considered septal rudiments, unlike in the Pocilloporidae and the subgenus *Acropora* in which the basal ridges do not develop into septa. A second septal cycle originating from the corallite wall was also evident and some septa extended beyond the wall to form rudimentary costae (Fig 2.5 c). After 2.5 months the primary septa have began to coalesce forming a contorted mass in the center of the corallite (Fig 2.5 d). After 10 months two septa had joined in the center of the corallite to form a laminar

columella (Fig. 2.5 e). The remaining septa had thickened and had prominent teeth (Fig. 2.5 e). The skeleton has yet to extend beyond the corallite wall (Fig. 2.5 e). The mean size of the spat at settlement was 900 ± 35.4 microns and ranged from 800 - 1000 microns (Table 2.3).

2.3.4 Family Faviidae

Skeletal development in all the faviids was very slow. The skeleton begins as a thin basal plate laid down shortly after settlement (e.g. *Leptoria phrygia* Fig 2.7 a). After a week the epitheca has formed (Fig 2.6 a & b, 2.8 a). No *Goniastrea retiformis* survived beyond this stage and further development in *G. aspera* was restricted to the formation of septa which are visible in rudimentary form arising from the rim of the epitheca after 3 months (Fig 2.6 c). In contrast, the septa of *L. phrygia* appeared to originate from the basal disc (Fig 2.7 b). While no transitional stages were discovered between this spat and the well developed spat in Fig 2.7 c, the pattern of development is presumably similar to *Platygyra daedalea*. In *P. daedalea* the primary septa begin to form after 2 months and appear as spines on the inside of the epitheca (Fig. 2.8 b & c). After 3 months the septa have thickened and grown beyond the epitheca concurrent with an extension of the basal plate (Fig 2.8 c). After 4 months the septa have extended to the edge of the new perimeter of the basal plate (Fig 2.8 d & e). A second septal cycle has also formed at the perimeter of the basal disc (Fig 2.8 d & e). The epitheca was still visible in 4 month old spat (Fig 2.8 d and e), however, in *L. phrygia* it was obliterated by thickening of skeletal elements surrounding it after 6 months (e.g. Fig 2.7 c). The size range of spat at settlement was fairly similar in *G. retiformis, G. aspera and P. daedalea* (Table 2.3). In contrast, *L. phrygia* spat were generally larger than those of the other species (Table 2.3). Nonetheless there was considerable overlap in the size range

of spat at settlement and therefore this feature is of little use to distinguish between early juveniles of these faviid taxa (Table 2.2).

2.3.5 Family Fungiidae

In *Fungia horrida* an epitheca had formed after 3 days (Fig. 2.9 a). After two weeks rudimentary septa were evident on the rim of the epitheca and 3 processes had formed in the center of the basal disc (Fig. 2.9 b). After 3 weeks these processes had coalesced to form a columella, the epitheca had thickened and 6 primary septa which originated from the rim of the epitheca were prominent (Fig 2.9 c). After 3 months the corallite had grown by the extension of the basal disc beyond the epitheca (Fig. 2.9 d). The septa had thickened and extended to the outer limit of the basal plate (Fig. 2.9 d). The columella remained prominent in 3 month old spat (Fig 2.9 d). After 4 months a new wall had formed beyond the epitheca from synapticulae growing between the outer edges of the primary and 2nd septa (Fig 2.9 e). The primary septa had also grown into the center of the corallite and obscured the columella (Fig 2.9 e). The epitheca remains visible in this specimen (Fig 2.9 e). A third septal array had began to form from the rim of the new corallite wall. After 4 months, the septa had prominent teeth and sloped towards the center of the corallite and the epitheca was no longer visible (Fig 2.9 f see also Fig. 2.10 which shows a spat on a piece of pumice collected from the beach front in Townsville). The rate of development between individuals of a similar age varied considerably (Fig 2.9 f). The mean size of *F. horrida* spat at settlement was 528 ± 22.7 microns and ranged from 350 - 700 microns (Table 2.3).

2.3.6 Family Merulinidae

In *Hydnophora exesa* and *Merulina ampliata* the skeleton began as a thin basal plate (Fig. 2.11 a) followed by the formation of a epitheca in spat 2 weeks old (Fig 2.11 b and c). No *H. exesa* spat survived beyond this stage and further development in *M. ampliata* was restricted to the formation of the rudimentary septa which appear to originate from the basal disc after 1 month (Fig 2.11 d). The mean size of *H. exesa* spat at settlement was 585 ± 23.2 microns and ranged from 500 - 625 microns which was very similar to *M. ampliata* with a mean size at settlement of 572 ± 14.2 microns and ranged from 400 - 650 microns (Table 2.3).

2.3.7 Family Pocilloporidae

The pattern of skeleton formation, including the origin and structure of the septa, columella and corallite wall was similar in *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata*. Twelve hours after settlement the basal plate had formed complete with 24 basal ridges in 3 cycles of different lengths; 6 primary, 6 secondary and 12 tertiary ridges (Fig 2.12 a, b & c). As the primary basal ridges grow in to the center of the corallite, they grow up and away from the basal plate (Fig. 2.12 g, h & i) and fuse to form the columella 4 days after settlement (Fig 2.12 j, k & l). Secondary septa did not appear before day 4, and appeared to originate from the corallite wall (Fig 2.12 j, k & l). A third septal cycle was rarely apparent, even after 7 weeks (Fig 2.13 a, b & c). The corallite wall formed as follows: after 12 hours, triangular lateral processes were evident on the inner end of the primary and secondary basal ridges (Fig 2.12 a, b & c). These processes then developed into laminar triangular outgrowths, or

synapticulae (Fig 2.12 d, e & f), similar to those seen in the *Acropora* (Fig. 2.1 a & f). After 2 days these synapticulae fuse with those adjacent to form the corallite wall (Fig. 2.12 g, h & i). At this age the corallum has all the features that distinguish the pocilloporids from the juveniles of other families: a prominent columella; well developed septa and a solid coenosteum.

No obvious differences were apparent in the structure of the septa or columella in the three species. Septa were typically laminar, although occasionally consisted of a vertical row of spines. The septal margins were occasionally forked and septa were often exert (Fig. 2.13 a, b & c). The columella was typically pistillate although some specimens had club-shaped columella or the columella was a pyramid with a broad base. This variation in the shape of the columella was evident in all three species.

Despite the similarities in the patterns of skeleton formation, significant differences in the morphology of the juvenile corallum allow *Seriatopora hystrix*, *Stylophora pistillata* and *Pocillopora damicornis*, to be distinguished. The diameter of the primary corallite initially decreased in all species until the corallite wall was completed after 4 days (Fig. 2.14). On completion of the corallite wall the corallite diameter remained constant in all species (Fig 2.14 *Seriatopora hystrix* $F = 0.297$, $p = 0.87$; *Stylophora pistillata* $F = 2.358$, $p = 0.064$; *Pocillopora damicornis* $F = 1.33$, $p = 0.275$), and the difference in the diameter of the primary corallite was significant among species ($F = 3.41$, $p < 0.000$).

Another prominent difference between the species at settlement is the diameter of the corallum (Fig. 2.15). *Pocillopora damicornis* had the largest corallum of 1758 ± 42.1

μm, followed by *Seriatopora hystrix*, 1255 ± 13.8 μm, then *Stylophora pistillata,* 1025 ± 50 μm. The differences in the diameters of the coralla between these species after settlement corresponds to differences in the sizes of the larvae on release (Table 2.1). However, differences in the rates of growth of the coralla quickly eliminate the utility of this feature to distinguish between juveniles of *S. hystrix* and *S. pistillata* (Fig. 2.15).

The effectiveness of the primary corallite diameter as a character for distinguishing between *Seriatopora hystrix*, *Stylophora pistillata* and *Pocillopora damicornis* is demonstrated by the limited overlap in the range of this feature between species. If the species boundaries are defined as follows: *Seriatopora hystrix* ≤ 450 microns, 450 microns < *Stylophora pistillata* < 550 microns, *Pocillopora damicornis* ≥ 550 microns, only 7 of the 272 samples, or 3.0 %, would have been incorrectly identified when censused between 4 and 60 days after settlement (Fig. 2.14).

2.3.8 Family Poritidae

The pattern and rate of skeletal development were very similar in *Porites australiensis* and *P. cylindrica*. The juvenile skeleton begins as a basal plate with the epitheca apparent after 3 days (Fig. 2.16 a and 2.17 a). Within 2 weeks six primary septa have formed within the epitheca originating from the basal plate (Fig. 2.16 b). Within a month the six primary septa have thickened and each had a single prominent vertical tooth (Fig. 2.16 c). Within 3 months the corallite had grown by the extension of the basal plate beyond the epitheca (Fig. 2.16 d). The primary septa had grown beyond the epitheca extending to the perimeter of the new boundary of the basal plate (Fig. 2.16 d and 2.17 b). A second cycle of septa, which originated at the perimeter of the basal plate, was also apparent (Fig. 2.16 d and 2.17 b). After 3 months the secondary septa

have fused with the primary septa to form 4 pairs of laterals and a triplet leaving the directive independent (Fig 2.16 e and 2.17 c). The epitheca was still visible within the juvenile corallite (Fig 2.16 e). After 5 months two corallites were present in some spat and the epitheca was no longer visible (Fig 2.16 f). After 8 months the juvenile corallum had 10 –12 corallites (Fig. 2.17 d). The mean size of *P. australiensis* spat at settlement was 576 ± 23.2 microns and ranged from 400 - 675 microns which was very similar to *P. cylindrica* with spat of 562 ± 17.62 microns which ranged from 500 - 650 microns (Table 2.3).

Figure 2.16 c & d are representative of the majority of poritid recruits on settlement tiles placed on the GBR for a period of 8 weeks to coincide with the mass spawning (e.g. Hughes et al. 1999). However, a second type of poritid spat also occurs on these tiles. These spat are considerably larger, they do not have a epitheca and the typical adult pattern of corallite structure is evident. In contrast, the adult pattern does not appear in *Porites australiensis* and *P. cylindrica* before 3 months (Fig 2.18 a & b).

The size of the eggs or larvae when released from the adult corals (Table 2.4) was an excellent indication of the size of the spat at settlement (Fig. 2.19; $r^2 = 0.9702$). In general, spat were approximately two times larger than the average diameter of the larvae.

2.4 Discussion

The juveniles of some scleractinian taxa have a unique combination of characters which allow them to be distinguished from other taxa. Nonetheless, the number of taxa successfully identified remains a small fraction of the total species pool.

Juveniles of the family Acroporidae have a porous coenosteum, prominent septa in two cycles and they lack a columella. The three species examined within the subgenera *Acropora*, *A. cytherea*, *A. pulchra* and *A. valida* were indistinguishable from each other and are identical to the *A. millepora* and *A. tenuis* spat in Babcock (1992) and those in Wallace (1999). The similarity between the spat of different species persists for up to a year (Wallace 1999). It may take up to two years for *Acropora* colonies to develop sufficient features such as color and radial corallite structure to enable species to be identified by an observer familiar with the appearance of adults in the field (Wallace et al. 1986).

The early development of the skeleton in *Montipora digitata* juveniles was different to other acroporids. Young spat had an epitheca and no basal ridges were observed. A similar pattern of development is evident in *M. verrucosa* spat from Hawaii (Fitzhardinge 1988) and *M. digitata* from Magnetic Island (Babcock 1992) which suggests that this may be a general feature of the genus. However, five month old *M. digitata* spat are indistinguishable from other acroporids (Babcock 1992) and consequently this feature will only be useful for identification of young *Montipora* recruits. Similarly, while recruits of brooders in the subgenus *Isopora* could be distinguished from other young acroporids by the morphology of the coenosteum, the differences disappear in older juveniles. For example, it is not be possible to distinguish a 5 month old *Acropora millepora*, *A. tenuis* or *M. digitata* juvenile from a 1 month isoporan recruit (Babcock 1992).

The genera of Acroporidae examined in this study could be distinguished by the size of the spat at settlement. The utility of this feature to distinguish wild acroporid spat depends on how similar the size of the spat is within the genera. Comparable data on the size of spat at settlement is lacking except for *M. verrucosa* which has spat of a similar size at settlement to *M. digitata* (Fitzhardinge 1988). However, the high correlation between egg size and size of spat at settlement (Fig 2.19, $r^2 = 0.97$) enables the size of the egg to serve as a proxy for the size of spat at settlement. I found egg size to be very similar between species within the respective genera and subgenera, *Montipora*, *Acropora* and *Isopora*. In addition, the size reported for eggs of other species within these taxa is within the range presented here (see review by Harrison and Wallace 1990). The exception may be some high latitude *Montipora* which release eggs > 500 μm diameter (A. Heyward pers. comm.). This suggests that wild spat of these taxa, at least in the tropics, can be distinguished by size at settlement. However, size differences at settlement are likely to be quickly obscured by differences in the growth rate of individuals, which is typically highly variable. Furthermore, the morphology of the juveniles in the other genera of the Family, *Astreopora* and *Anacropora,* remains unknown.

Juveniles of the family Pocilloporidae can be distinguished from all other families examined in this study by a prominent columella, prominent septa in two cycles, and a solid coenosteum. Furthermore, the genera *Pocillopora*, *Seriatopora* and *Stylophora* can be distinguished by differences in the diameter of the primary corallite (DPC) and this represents a considerable advance on the generally accepted taxonomic resolution within this Family. However, it remains necessary to establish whether or not the diameter of the primary corallite is a conservative character at the generic or the species

level by comparison with other species of the genera *Seriatopora, Stylophora* and *Pocillopora.* The pattern of skeleton formation observed in *Pocillopora damicornis* is similar to that described by Stephenson (1931) from the GBR; Le Tissier (1988) from Thailand; Vandermeulen and Watabe (1973) from Hawaii and Atoda (1947 a) from Palau. Likewise, the pattern of skeleton formation in *Stylophora pistillata* and *Seriatopora hystrix* was similar to that described by Atoda (1947 b and 1951). The similarity in the patterns of skeleton formation in specimens from widely separated locations within the Indo-Pacific suggest that there is little geographical variation in these patterns. However, there are some inaccuracies in these earlier descriptions. Atoda (47 a & b, 51) and Vandermeulen and Watabe (1973) describe the basal ridges as septal rudiments when it is clear from the developmental series outlined above that only the primary septa maintain a connection with the basal ridges, whereas septa in higher cycles originate from the corallite wall (as was correctly noted by Le Tissier 1988). Le Tissier (1988) noted correctly the formation of the corallite wall from the "anastomosis between lateral outgrowths from skeletal spines". However, the term "spines" is not an accurate description of these broad laminar structures, which are only visible in rudimentary form (le Tissier 1988).

A species-specific difference in the diameter of the corallites is not apparent in adult pocilloporids in which the corallite diameter varies widely within and between colonies (Veron and Pichon 1976). The calices of *P. damicornis* range from 0.7 to 1.5 mm in diameter; those of *Stylophora pistillata* from 1 to 1.5 mm; and those of *Seriatopora hystrix* are described as "variable" (Veron and Pichon 1976). The fact that the adult corallites are larger than the primary corallites of the juveniles indicates that at some stage the diameter of new corallites must increase. The use of the DPC to separate the

species is thus limited to the short period when the primary corallite is still obvious in the juvenile corallum. This period is likely to be between 4-8 months, after which the primary corallite is no longer discernible.

The spat of the two poritid species, *Porites australiensis* and *P. cylindrica*, raised in this study could not be distinguished from each other. This is perhaps surprising because the adults are distinguished by differences in the micro-architecture of individual corallites. However, while the typical poritid pattern of four laterals, a triplet and a dorsal directive was apparent after 4 months in these species, finer features of the micro-architecture of the poritid corallite, such as the pali etc, which are necessary to distinguish the species had not clearly differentiated. Furthermore, there is often considerable variation between the micro-architecture of corallites within a single adult corallum. However, two distinct types of poritid spat are found on tiles placed in the wild which I believe represent the juveniles that arise from brooded poritid larvae and those that arise from externally developed larvae respectively. The few studies which have raised the juveniles of brooding *Porites* support this hypothesis. For example, the juveniles of the brooding species *P. stephensoni* (*P. haddoni*) are initially much larger (typically over 1mm) than those of the broadcast spawners, *P. australiensis* and *P. cylindrica*, the spat lack an epitheca, and the adult pattern of micro-architecture is evident in specimens as young as 3 weeks old (Stephenson 1931). Furthermore in the brooders *P. porites* and *P. mayeri*, all primary skeletal elements develop simultaneously (i.e. the intermediate stages of development seen in *P. australiensis* and *P. cylindrica* are not evident), and there is no epitheca (Jell 1980, Goreau and Hayes 1977). An epitheca is, however, evident in the spat of the broadcast spawning *Porites compressa* in Hawaii (Fitzhardinge 1988). Perhaps the most distinctive feature of the spat of poritid spawners

is the epitheca, which is absent in the spat of brooded poritids. Interestingly, the presence of the epitheca in juveniles would appear to be related to the size of the propagules rather than phylogeny or reproductive mode. In all species with eggs smaller than 500 microns a distinct epitheca was the first skeletal element to appear and the juveniles of broadcast spawning species with large eggs, such as the *Acropora* and *Turbinaria mesenterina* did not produce an epitheca. Consequently, I predict the presence of an epitheca may enable the distinction between the recruits of brooders and spawners in other genera with mixed modes of development where the size of the eggs released is much less than the size of the larvae on release e.g. *Pocillopora* (Harrison and Wallace 1990).

Fungia horrida had a number of features which distinguished it from other taxa including a distinct columella within an epitheca. A similar pattern is evident in *F. fungites* juveniles (Babcock 1992) suggesting this feature may be characteristic of the family Fungiidae. However, after 4 months the fungiid juveniles appeared very similar to those of *Culicia* sp. (Babcock 1992) indicating that the family may only be distinguished for a limited period.

Juveniles of the families Agaricidae, Faviidae, and Merulinidae were all characterized by very slow rates of development. In these families, the epitheca was the only element of the skeleton to develop in the first 2 months. In contrast, other elements of the skeleton, such as septa, are well developed within one month of settlement in spat of the Acroporidae, Pocilloporidae and Poritidae. The structure of the corallite and septa are remarkably similar in the Agaricidae, Faviidae and Merulinidae, which are indistinguishable from spat of the families Faviidae, Mussidae, Oculinidae, Pectiniidae,

and Caryophylliidae raised by Babcock (1992). These results suggests it will take about a year for the primary corallite to complete development in these genera and species specific structure may take 2 to 3 years to develop.

The greatest taxonomic resolution is achievable when juveniles are young. For example, the genera of the Acroporidae and the Pocilloporidae can be separated between 2 weeks and one month following settlement (Table 2.5). If greater taxonomic resolution is the aim of the study a short soak length is therefore recommended. Furthermore, the shorter the soak length the more accurate the estimate of supply as the loss of recruits through overgrowth by fouling organisms will be minimized. In addition, the longer the soak the greater the bias towards species with an extended breeding season, such as the pocilloporids (Baird and Hughes 2000, Hughes et al. 2001).

Finally, a word of caution. This study examined spat originating from a limited number of parents, from a single geographic location and only one cohort was examined for each species. Consequently, it remains to be determined whether the results will hold over the geographic range of these species, whether the morphology will vary between years and what role genes will play in determining morphology. Furthermore, the morphology of many coral species varies under different environmental conditions and spat raised in the lab may differ from field raised recruits. Future studies are required to address these issues and establish the generality of the results.

Table 2.1 Date and time of spawning, reproductive mode and sexuality for the 19 corals species examined. Spawning corals release gametes and fertilization and larval development occurs in the plankton. Brooders release well-developed larvae following fertilization in the polyp. H = hermaphroditic, G = gonochoric.

Family	Species	date	time	mode	sex
Acroporidae	*Acropora cytherea*	28/11/96	22:20	spawn	H
Acroporidae	*Acropora pulchra*	18/11/97	22:00	spawn	H
Acroporidae	*Acropora valida*	23/11/96	23:00	spawn	H
Acroporidae	*Acropora palifera*	25/11/96	6:00	brood	H
Acroporidae	*Montipora digitata*	26/11/99	19:30	spawn	H
Agaricidae	*Pachyseris speciosa*	9/12/98	21:30	spawn	G
Dendrophylliidae	*Turbinaria mesenterina*	20/11/97	20:30	spawn	H
Faviidae	*Goniastrea aspera*	28/11/96	21:20	spawn	H
Faviidae	*Goniastrea retiformis*	19/11/97	21:30	spawn	H
Faviidae	*Leptoria phrygia*	19/11/97	20:30	spawn	H
Faviidae	*Platygyra daedalea*	30/11/96	19:00	spawn	H
Fungiidae	*Fungia horrida*	30/11/96	19:30	spawn	G
Merulinidae	*Hydnophora exesa*	20/11/97	20:15	spawn	H
Merulinidae	*Merulina ampliata*	20/11/97	20:00	spawn	H
Pocilloporidae	*Pocillopora damicornis*	12/10/89	6:00	brood	H
Pocilloporidae	*Seriatopora hystrix*	1/12/96	6:00	brood	H
Pocilloporidae	*Stylophora pistillata*	4/12/96	6:00	brood	H
Poritidae	*Porites australiensis*	1/12/96	20:30	spawn	G
Poritidae	*Porites cylindrica*	11/11/95	20:00	spawn	G

Table 2.2 The approximate number of spat examined at each age.

		age								
Family	Species	1-3 d	7-10 d	2 w	1 m	2 m	3 m	4m	6 m	10 m
Acroporidae	*Acropora cytherea*	18	12							
Acroporidae	*Acropora pulchra*	14	5							
Acroporidae	*Acropora valida*	12	15							
Acroporidae	*Acropora tenuis*				65					
Acroporidae	*Acropora palifera*	8	8		18					
Acroporidae	*Montipora digitata*					8				
Agaricidae	*Pachyseris speciosa*	8				3				
Dendrophylliidae	*Turbinaria mesenterina*	5	15		9	18				2
Faviidae	*Goniastrea aspera*	23		60						
Faviidae	*Goniastrea retiformis*	2	22				5			
Faviidae	*Leptoria phrygia*	36	14						2	
Faviidae	*Platygyra daedalea*	26	30			8	5	3		
Fungiidae	*Fungia horrida*	30	5	19	13		14	4	19	
Merulinidae	*Hydnophora exesa*	5					3			
Merulinidae	*Merulina ampliata*	17		8	9					
Poritidae	*Porites australiensis*	34		11	6		14	32		
Poritidae	*Porites cylindrica*	13					10			1
		12h	1 d	2 d	4 d	2 m				
Pocilloporidae	*Pocillopora damicornis*	30	10	12	30	23				
Pocilloporidae	*Seriatopora hystrix*	35	37	30	11	45				
Pocilloporidae	*Stylophora pistillata*	28	12	26	18	28				

Table 2.3 The maximum diameter of the corallum at settlement in the 19 coral species examined.

		corallum diameter				
Family	Species	mean	se	min	max	n
Acroporidae	*Acropora cytherea*	1108	29.6	850	1375	18
Acroporidae	*Acropora pulchra*	1097	12.9	1025	1150	14
Acroporidae	*Acropora valida*	1186	27.8	1000	1375	12
Acroporidae	*Acropora palifera*	2323	61.6	2000	2700	8
Acroporidae	*Montipora digitata*	609	8.1	575	650	8
Agaricidae	*Pachyseris speciosa*	650	14.4	625	675	8
Dendrophylliidae	*Turbinaria mesenterina*	900	35.4	800	1000	5
Fiidae	*Goniastrea aspera*	565	8.6	500	650	23
Faviidae	*Goniastrea retiformis*	595	10.6	500	700	2
Faviidae	*Leptoria phrygia*	778	13.1	525	950	36
Faviidae	*Platygyra daedalea*	607	7.9	525	700	26
Fungiidae	*Fungia horrida*	528	22.7	350	750	30
Merulinidae	*Hydnophora exesa*	585	23.2	500	625	5
Merulinidae	*Merulina ampliata*	572	14.2	400	650	17
Pocilloporidae	*Pocillopora damicornis*	1755	42.2	1375	2275	30
Pocilloporidae	*Seriatopora hystrix*	1255	13.8	1300	1375	35
Pocilloporidae	*Stylophora pistillata*	1025	50.0	975	1075	28
Poritidae	*Porites australiensis*	576	11.3	400	675	34
Poritidae	*Porites cylindrica*	562	17.6	500	600	13

Table 2.4 The maximum diameter of propagules at release in the 19 coral species examined.

		egg diameter				
Family	Species	mean	se	min	max	n
Acroporidae	*Acropora cytherea*	600	9.0	525	675	18
Acroporidae	*Acropora palifera*	1195	11.7	1125	1250	10
Acroporidae	*Acropora pulchra*	575	9.5	500	650	18
Acroporidae	*Acropora valida*	596	11.2	550	675	17
Acroporidae	*Montipora digitata*	337	6.6	175	400	39
Agaricidae	*Pachyseris speciosa*	368	3.6	325	400	30
Dendrophylliidae	*Turbinaria mesenterina*	531	13.7	400	650	20
Faviidae	*Goniastrea aspera*	349	6.1	300	400	29
Faviidae	*Goniastrea retiformis*	371	3.6	325	425	38
Faviidae	*Leptoria phrygia*	450	6.1	325	500	19
Faviidae	*Platygyra daedalea*	396	3.6	350	450	38
Fungiidae	*Fungia horrida*	215	10.0	150	250	10
Merulinidae	*Hydnophora exesa*	348	6.6	275	425	29
Merulinidae	*Merulina ampliata*	339	6.3	300	425	7
Pocilloporidae	*Pocillopora damicornis*	864	15.1	800	950	9
Pocilloporidae	*Seriatopora hystrix*	625	7.9	550	700	25
Pocilloporidae	*Stylophora pistillata*	549	7.1	475	625	26
Poritidae	*Porites australiensis*	245	6.8	150	325	20
Poritidae	*Porites cylindrica*	250	8.3	200	300	17

Table 2.5 The age range during which the Scleractinian taxa examined are distinguishable

Family	Genera	1 week	2 weeks	1 month	2 month	4 months	6 months
Acroporidae					Acroporidae	Acroporidae	Acroporidae
Acroporidae	*Acropora*	*Acropora*	*Acropora*	*Acropora*			
Acroporidae	*Isopora*	*Isopora*	*Isopora*	*Isopora*			
Acroporidae	*Montipora*		*Montipora*	*Montipora*			
Agaricidae	*Pachyseris*						
Dendrophylliidae							
Dendrophylliidae	*Turbinaria*						
Faviidae							
Faviidae	*Goniastrea*						
Faviidae	*Leptoria*						
Faviidae	*Platygyra*						
Fungiidae							
Fungiidae	*Fungia*		*Fungia*	*Fungia*	*Fungia*	*Fungia*	
Merulinidae							
Merulinidae	*Hydnophora*						
Merulinidae	*Merulina*						
Pocilloporidae							Pocilloporidae
Pocilloporidae	*Pocillopora*	*Pocillopora*	*Pocillopora*	*Pocillopora*	*Pocillopora*	*Pocillopora*	
Pocilloporidae	*Seriatopora*	*Seriatopora*	*Seriatopora*	*Seriatopora*	*Seriatopora*	*Seriatopora*	
Pocilloporidae	*Stylophora*	*Stylophora*	*Stylophora*	*Stylophora*	*Stylophora*	*Stylophora*	
Poritidae						Poritidae	Poritidae
Poritidae	*Porites*						
	brooders	*brooders*	*brooders*	*brooders*	*brooders*		
	spawners		*spawners*	*spawners*	*spawners*		
others		others	others	others	others	others	others
number		7	10	10	8	7	4

Figure 2.1 a. *Acropora cytherea* 1 day b. *A. valida* 1 day c. *A. cytherea* 3 days d. *A. valida* 3 days e. *A. cytherea* 7 days f. *A. pulchra* 1-3 days. Scale bar = 500 microns

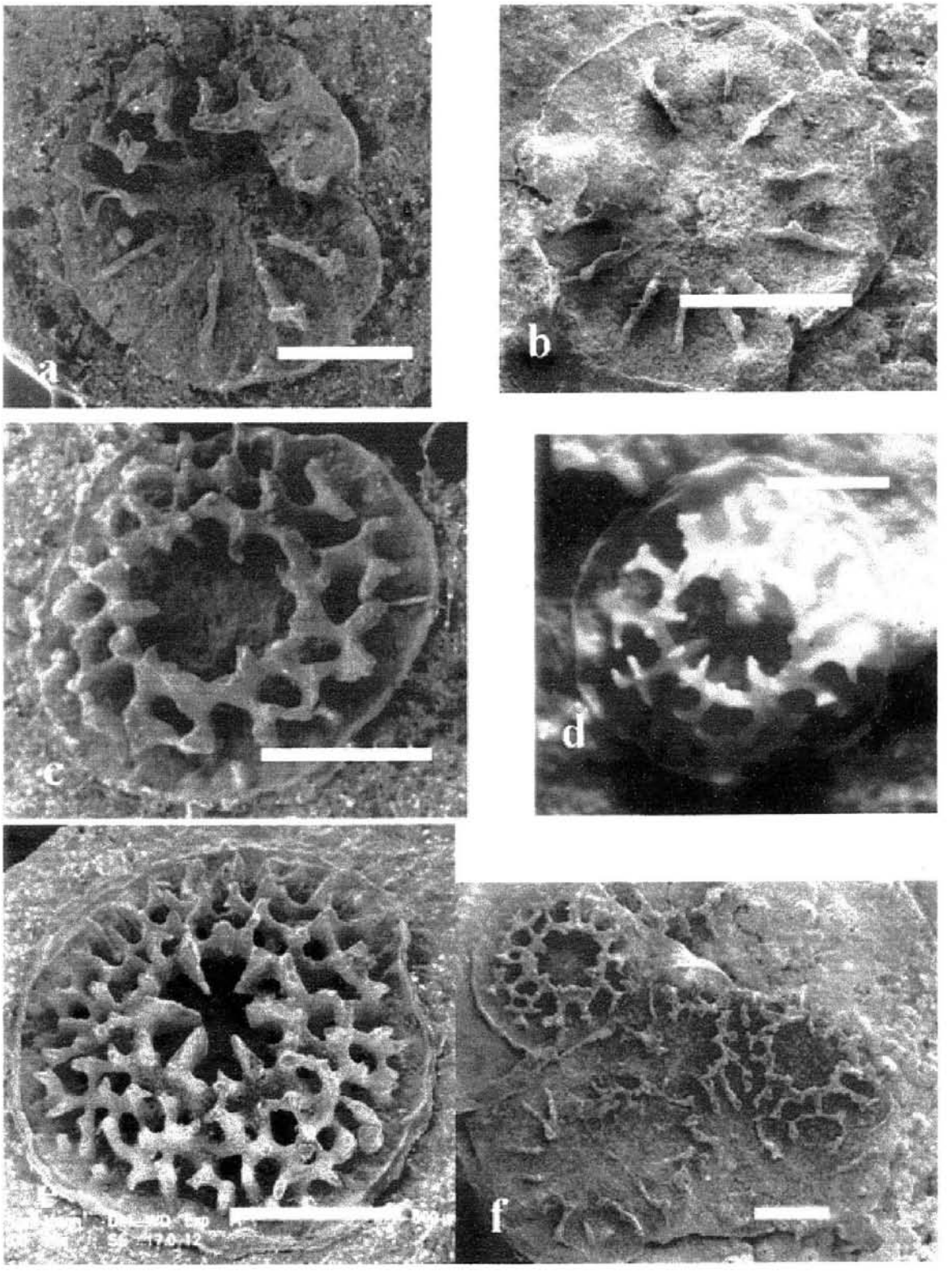


Figure 2.2 a. *Acropora palifera* 3 days b. *A. palifera* 1 month c. *A. tenuis* 1 month.

Scale bar = 500 microns

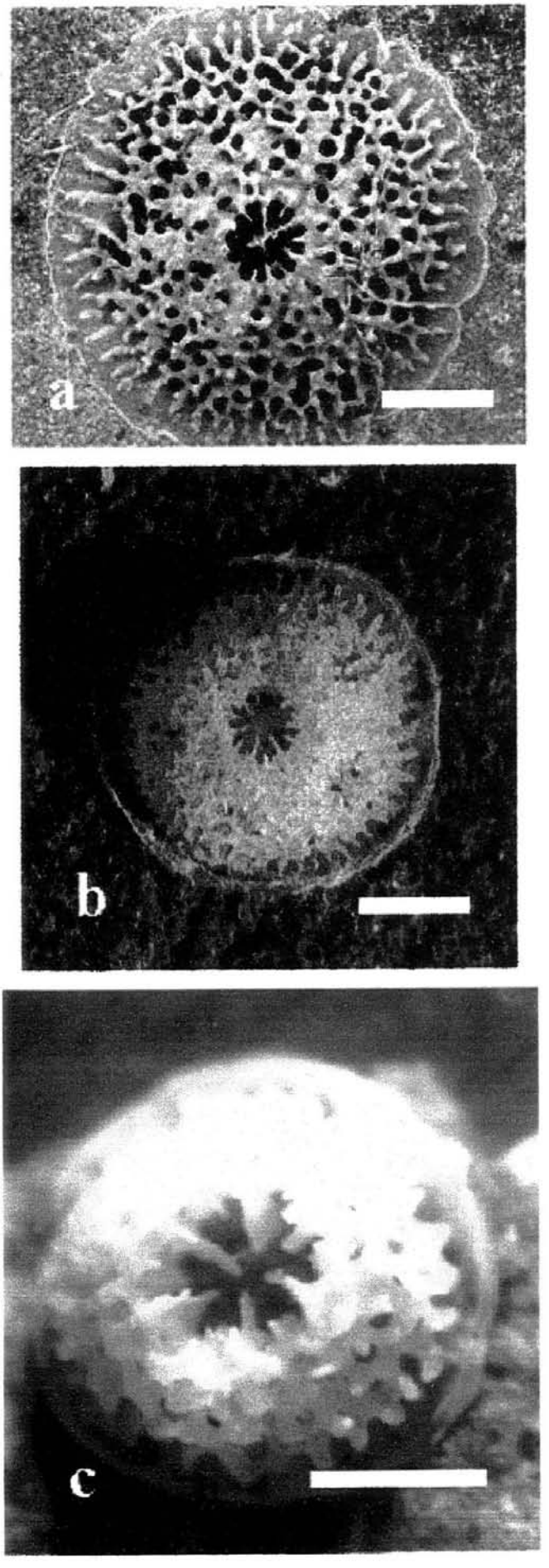


Figure 2.3 a. *Montipora digitata* stage i b. *M. digitata* stage ii Scale bar = 500 microns

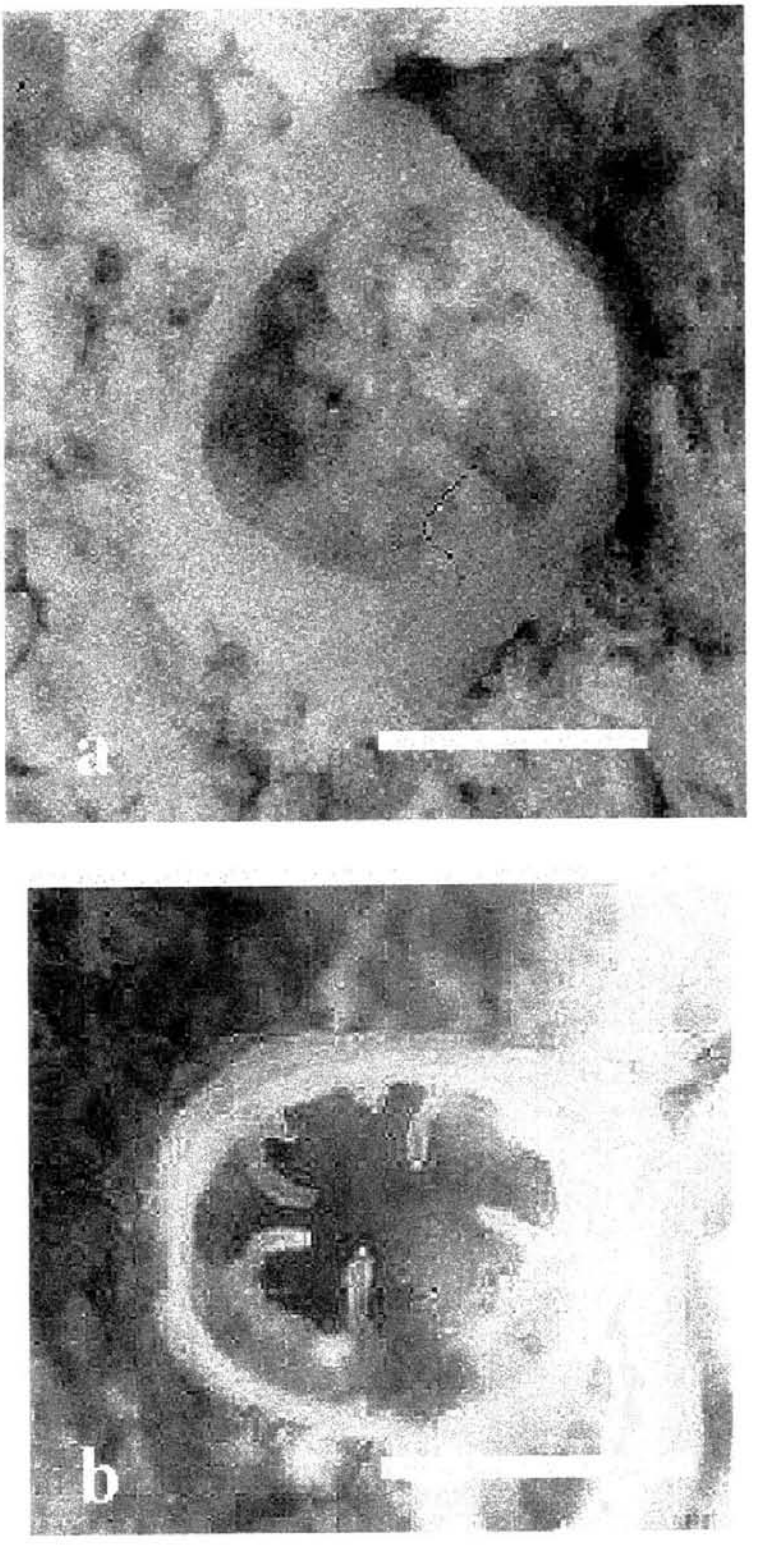


Figure 2.4 a. *Pachyseris speciosa* 3 days b. *P. speciosa* 6 weeks. Scale bar = 500 microns

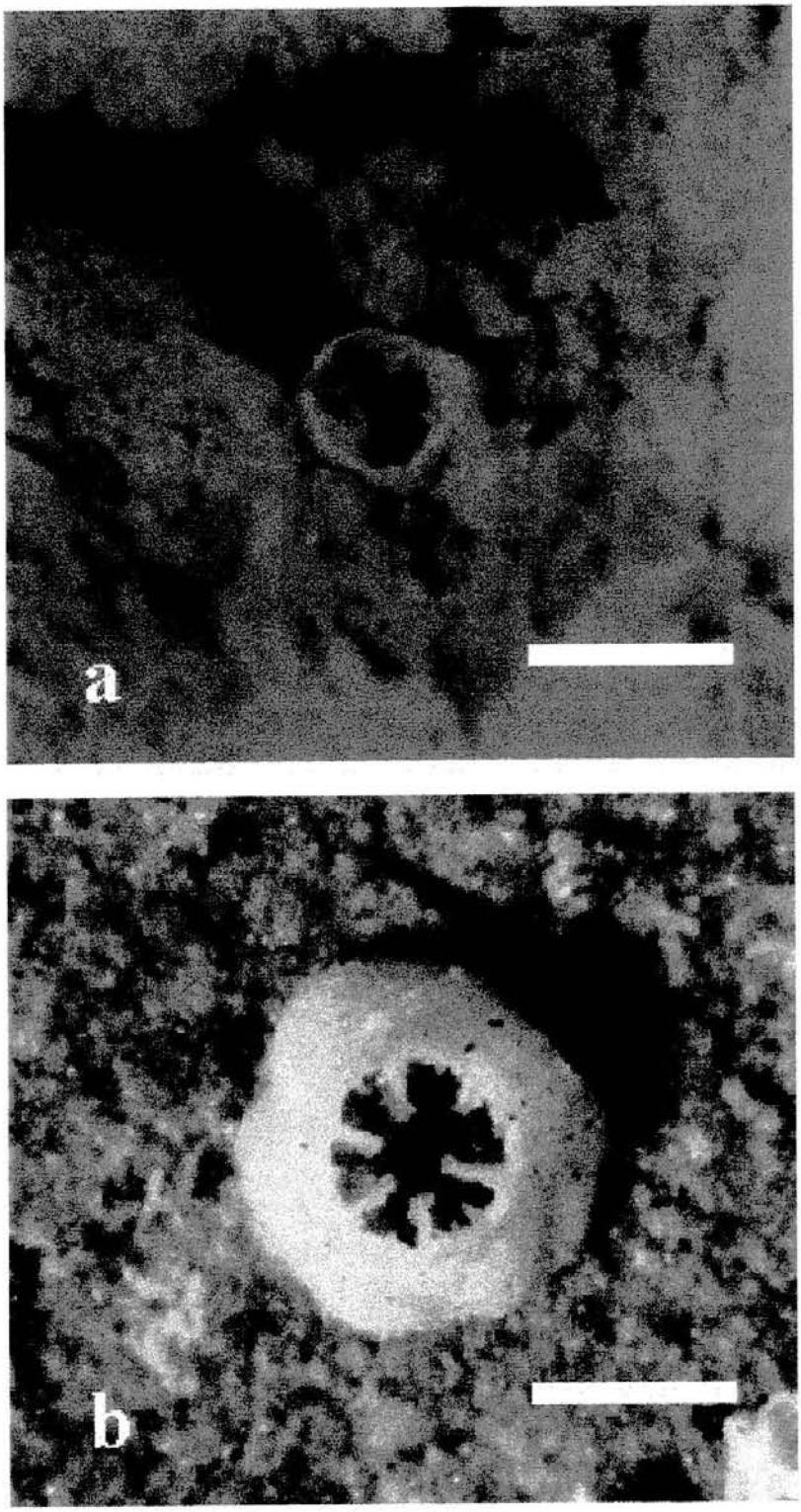


Figure 2.5 a. *Turbinaria mesenterina* 3 days b. *T. mesenterina* 7 days c. *T. mesenterina* 1 month d. *T. mesenterina* 2 months e. *T. mesenterina* 10 months. Scale bar = 500 microns

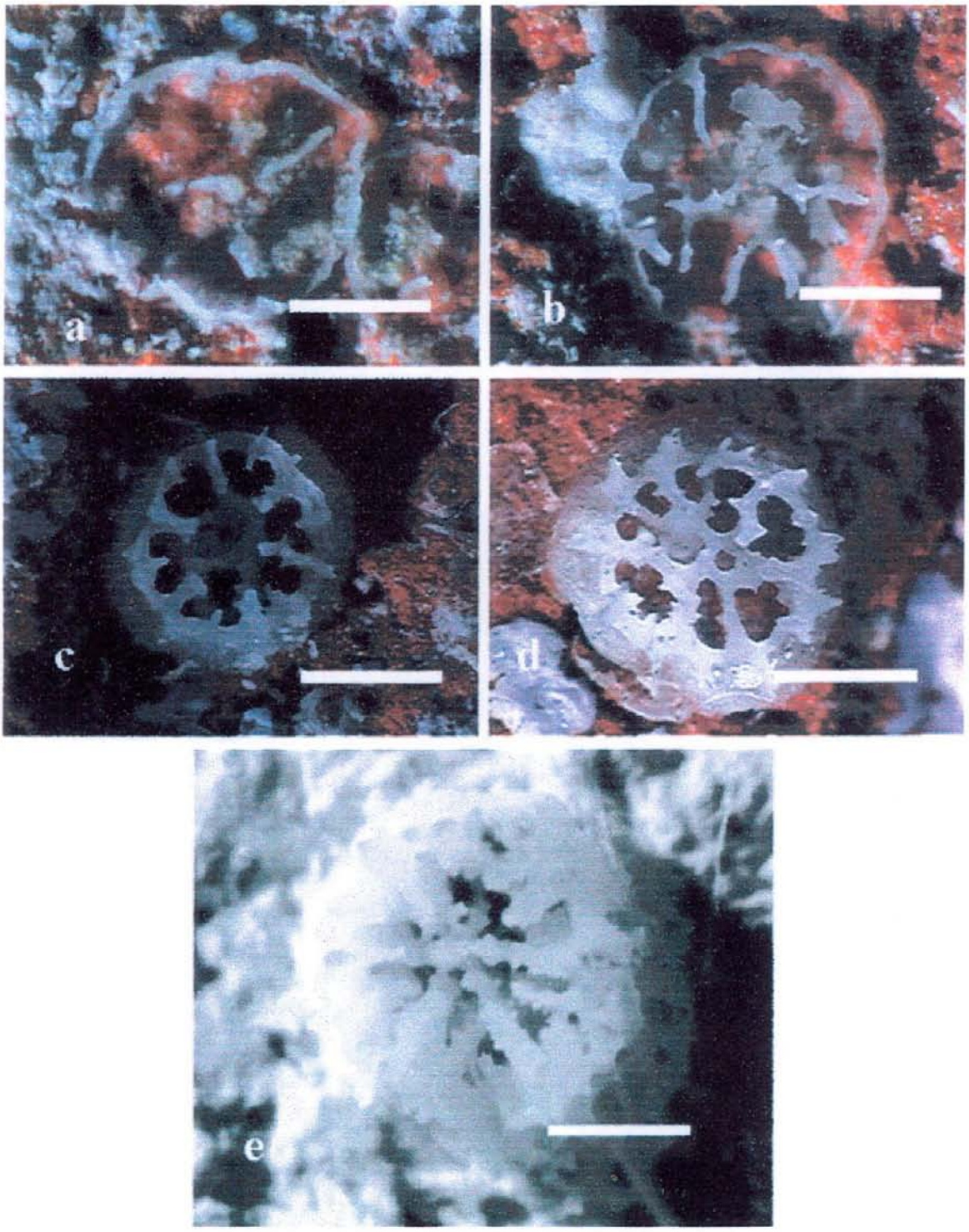


Figure 2.6 a. *Goniastrea aspera* 2 weeks b. *G. retiformis* 7 days c. *G. retiformis* 3 months. Scale bar = 500 microns

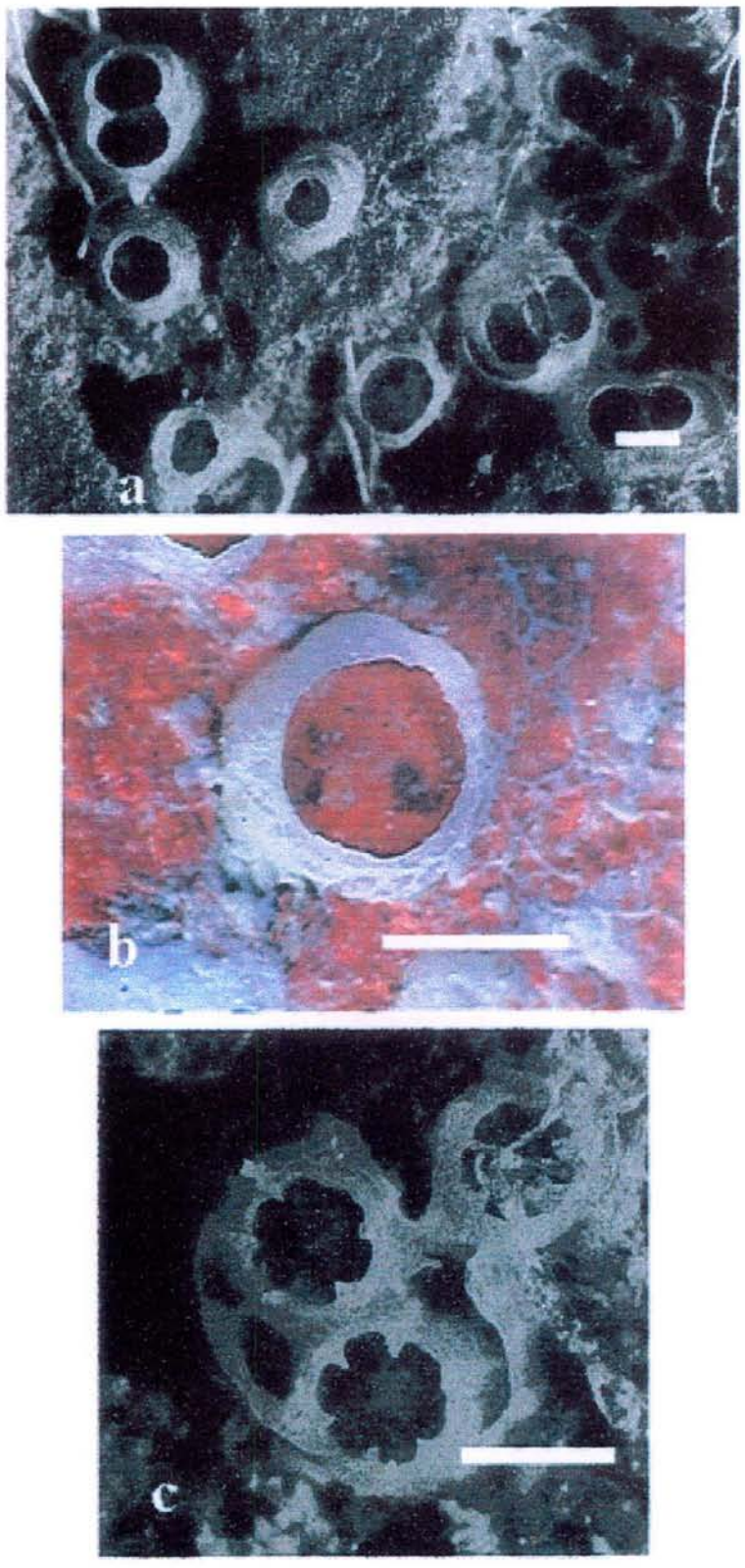


Figure 2.7 a. *Leptoria phyrgia* 3 days b. *L. phyrgia* 1 month c. *L. phyrgia* 6 months.

Scale bar = 500 microns

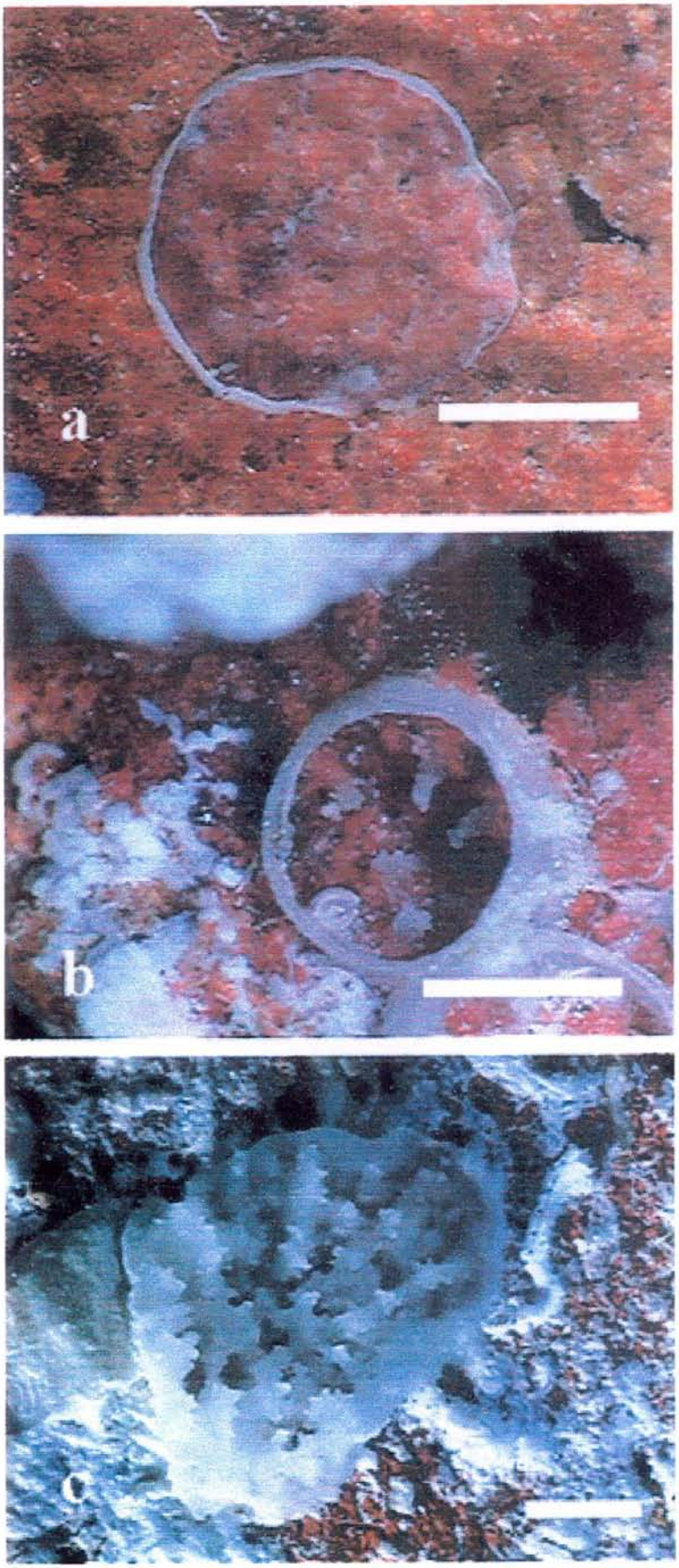


Figure 2.8 a. *Platygyra daedalea* 10 days b. *P. daedalea* 2 months c. *P. daedalea* 3 months d. *P. daedalea* 4 months e. *P. daedalea* 4 months. Scale bar = 500 microns

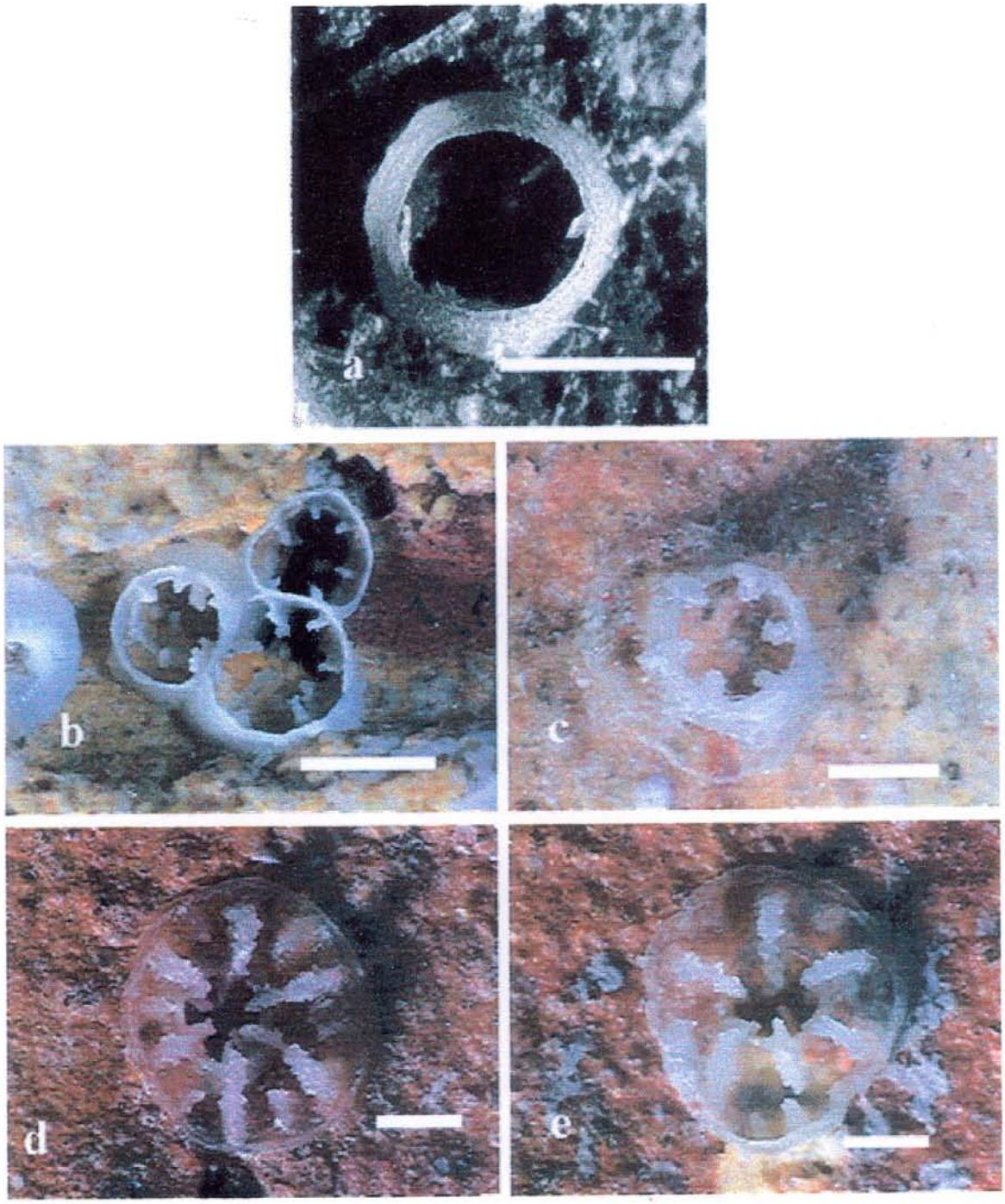


Figure 2.9 a. *Fungia horrida* 3 days b. *F. horrida* 2 weeks c. *F. horrida* 3 weeks d. *F. horrida* 3 months e. *F. horrida* 4 months f. *F. horrida* 5 months. Scale bar = 500 microns

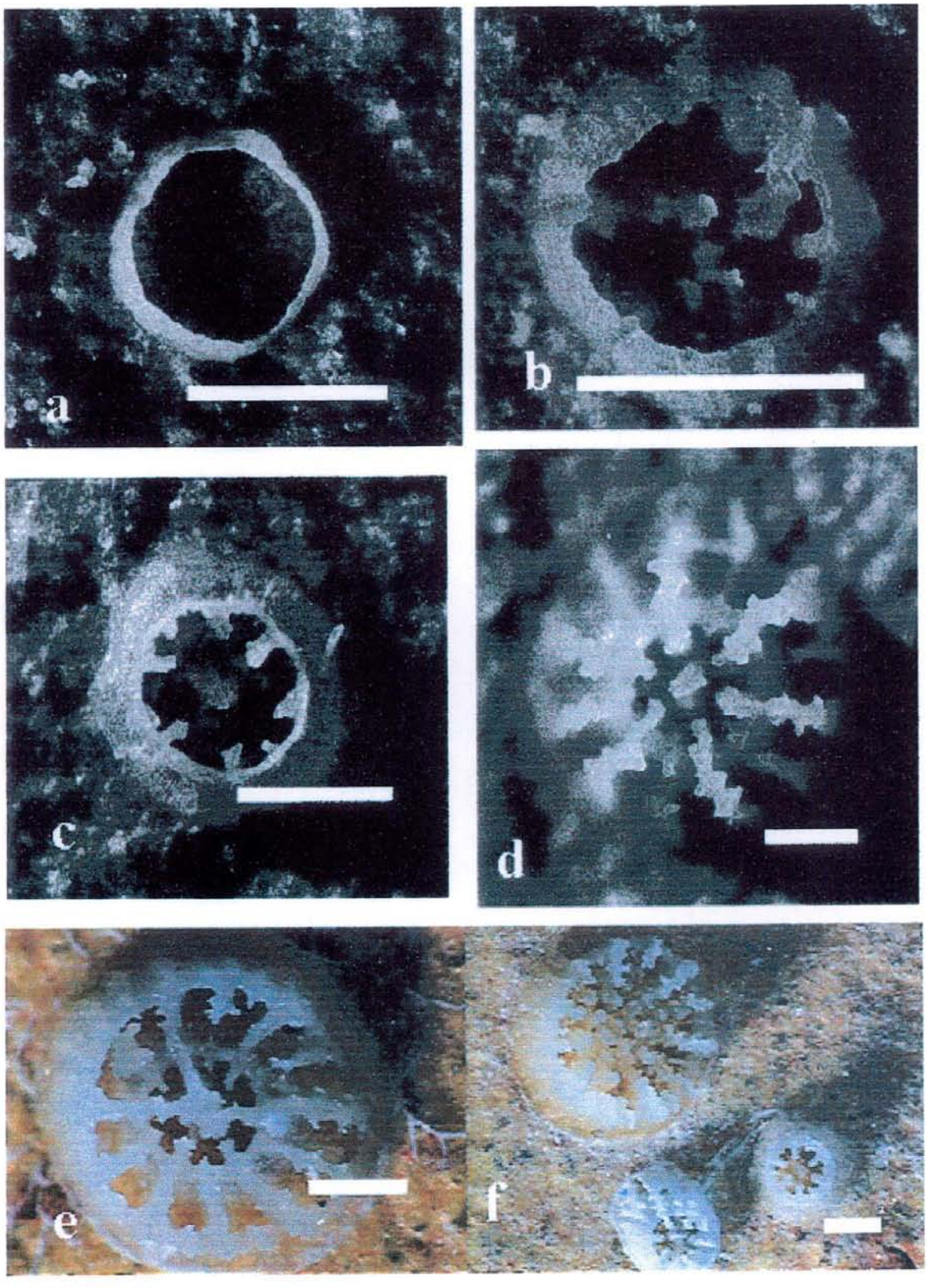


Figure 2.10 a. A wild *Fungia* spp. spat on pumice Scale bar = 500 microns

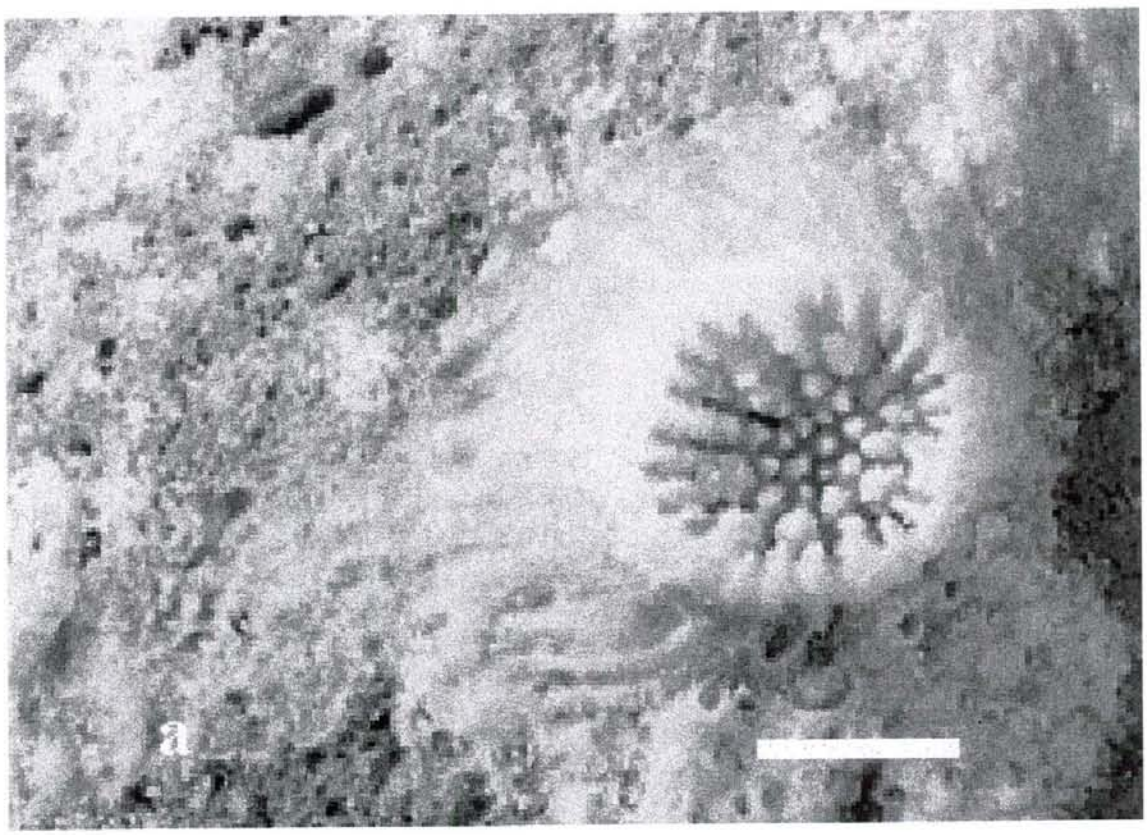


Figure 2.11 a. *Hydnophora excesa* 3 days b. *H. excesa* 3 months c. *Merulina ampliata* 2 weeks d. *M. ampliata* 1 month. Scale bar = 500 microns

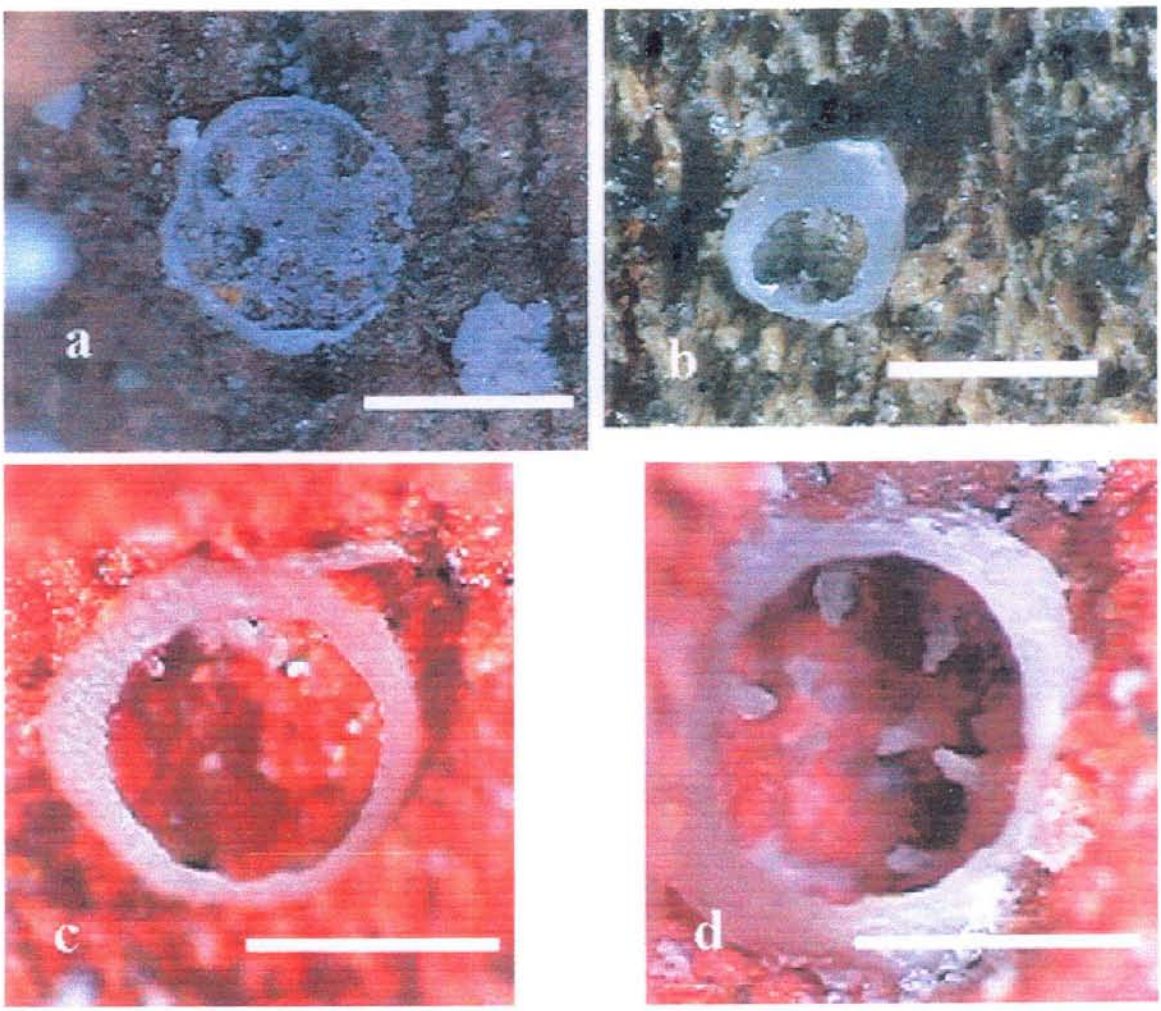


Figure 2.12 a. *Seriatopora hystrix* 12 h b. *Stylophora pistillata* 12 h c. *Pocillopora damicornis* 12 h d. *S. hystrix* 1 day e. *S. pistillata* 1 day f. *P. damicornis* 1 da g. *S. hystrix* 2 days h. *S. pistillata* 2 days i. *P. damicornis* 2 day j. *S. hystrix* 4 days k. *S. pistillata* 4 days l. *P. damicornis* 4 days. Scale bar = 500 microns

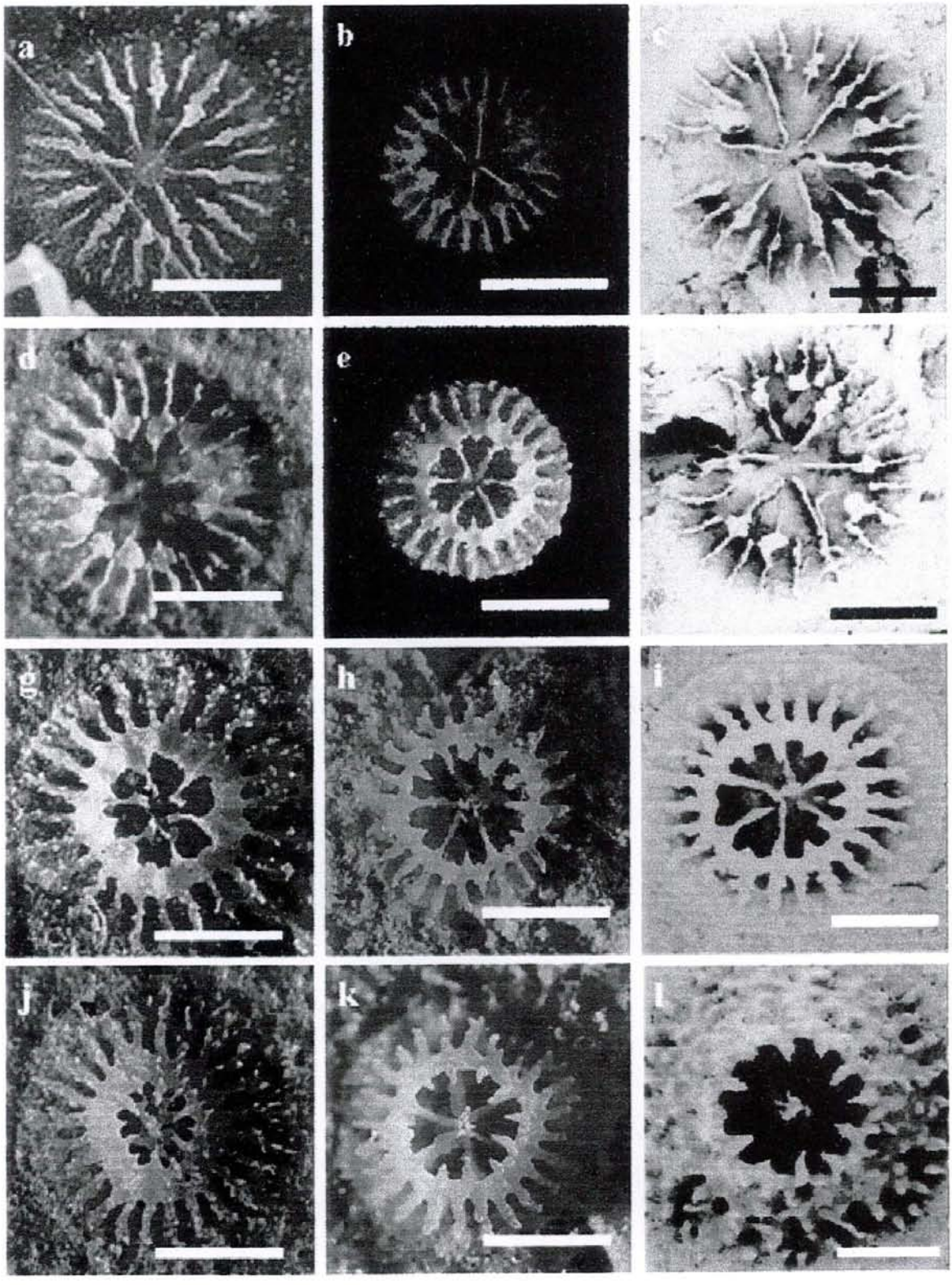


Figure 2.13 a. *Seriatopora hystrix* 2 months b. *Stylophora pistillata* 2 months c. *Pocillopora damicornis* 2 months. Scale bar = 500 microns

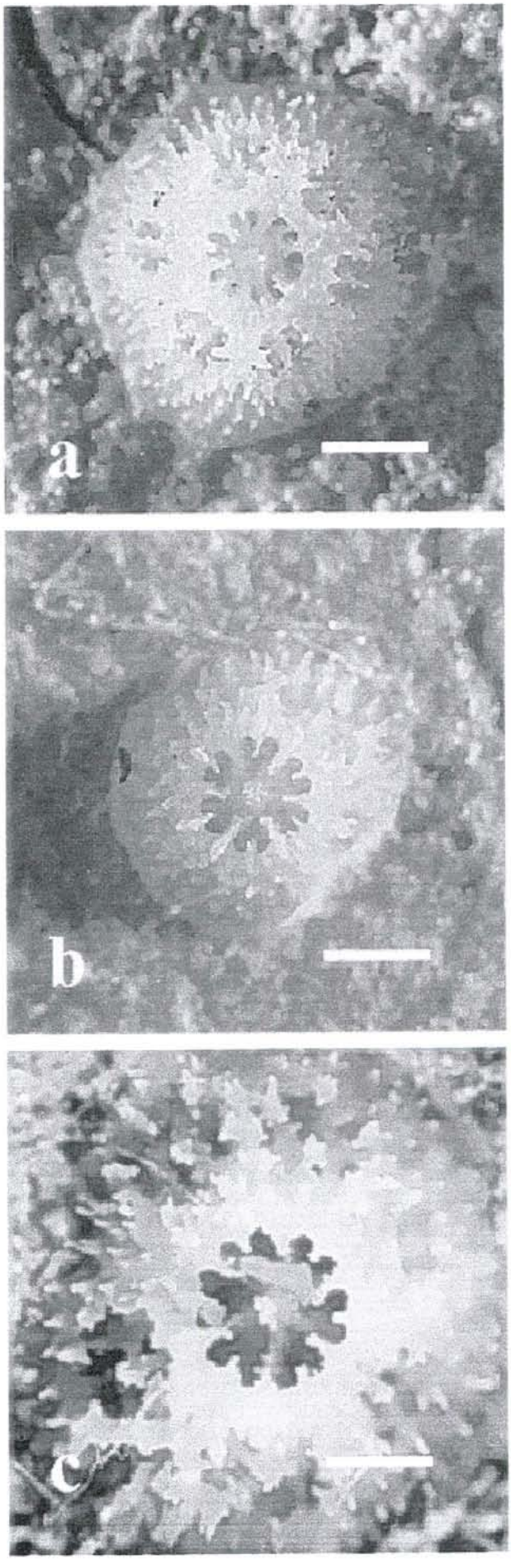


Figure 2.14 Mean diameter of the primary corallite (± SE) as a function of age since larval release in *Seriatopora hystrix*, *Stylophora pistillata* and *Pocillopora damicornis* recruits.

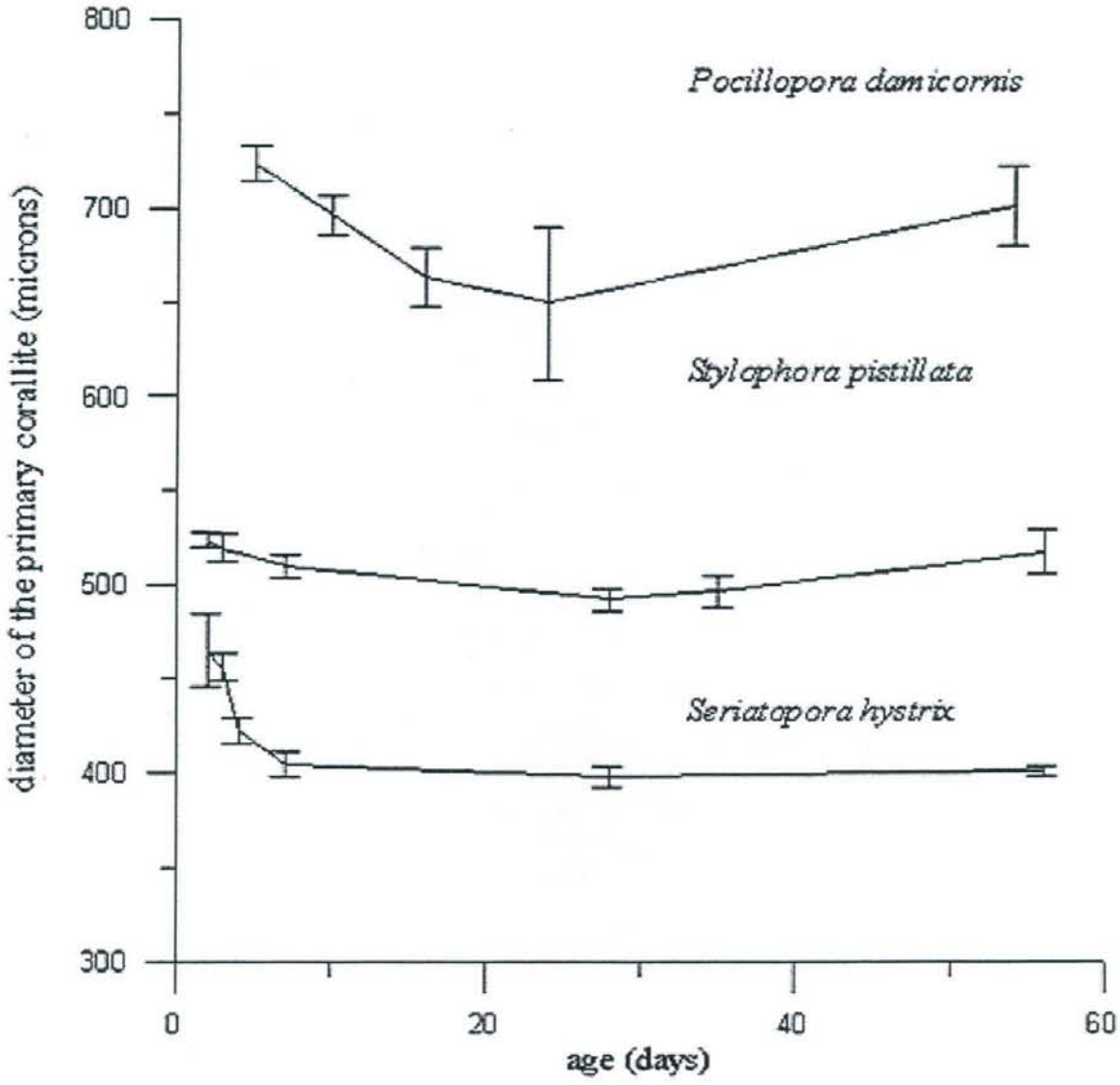


Figure 2.15 Mean diameter of the basal disc (± SE) as a function of age since larval release in *Seriatopora hystrix*, *Stylophora pistillata* and *Pocillopora damicornis* recruits.

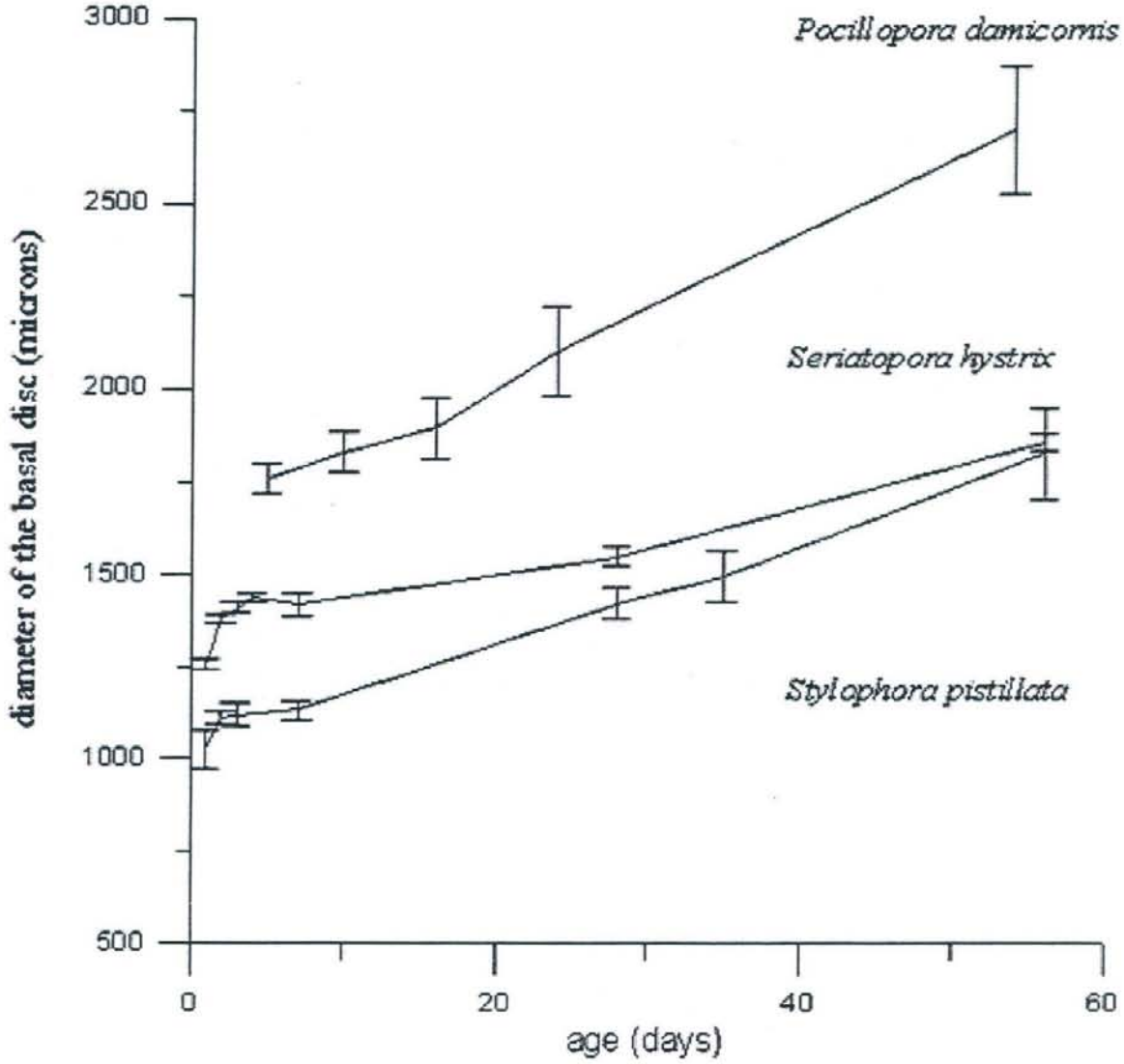


Figure 2.16 a. *Porites australiensis* 3 days b. *P. australiensis* 2 weeks c. *P. australiensis* 3 weeks d. *P. australiensis* 3 months e. *P. australiensis* 3 months f. *P. australiensis* 5 months. Scale bar = 500 microns

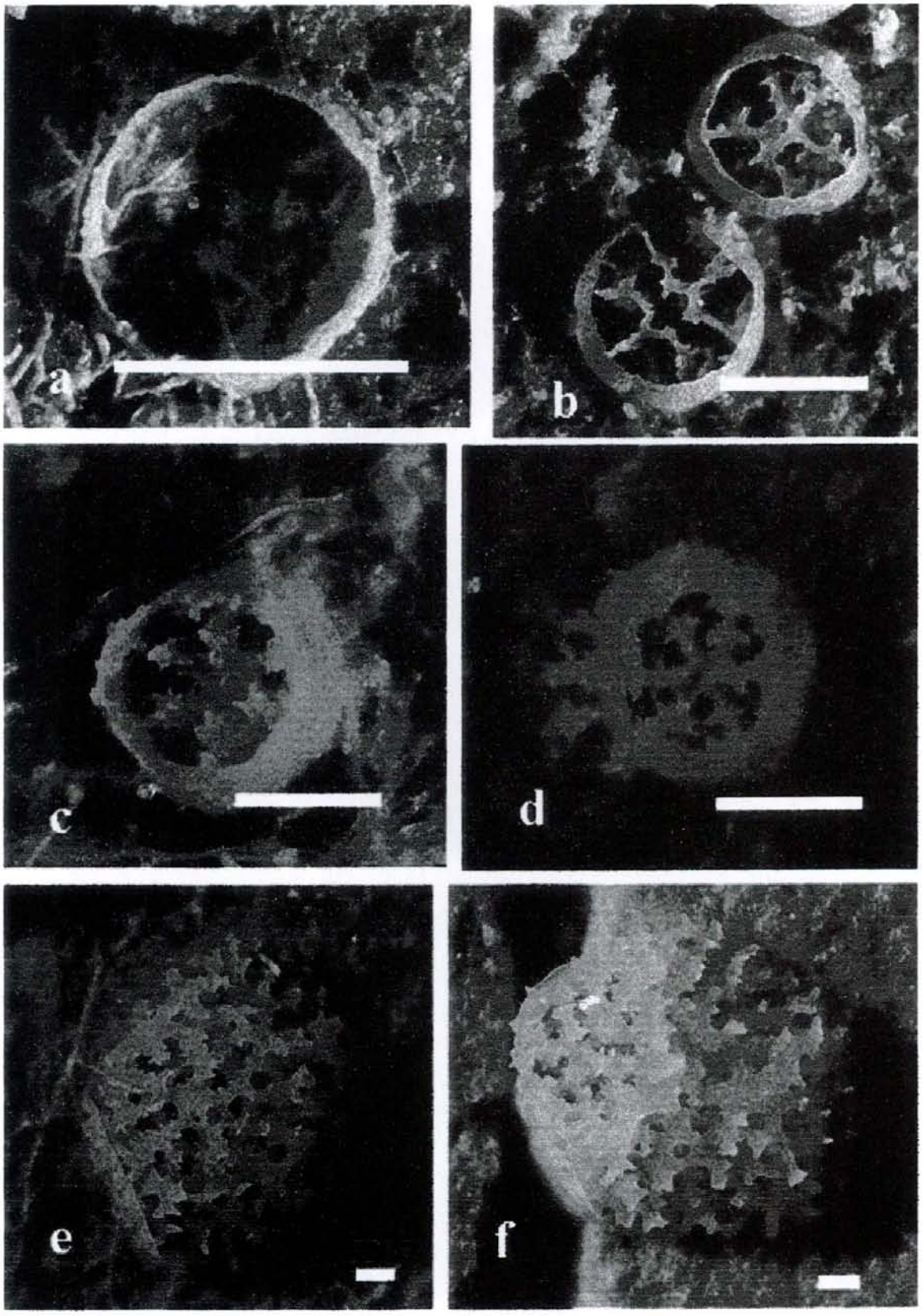


Figure 2.17 a. *Porites cylindrica* 3 days b. *P. cylindrica* 3 months c. *P. cylindrica* 3 months Scale bar = 500 microns. *P. cylindrica* 8 months. Scale bar = 1000 microns.

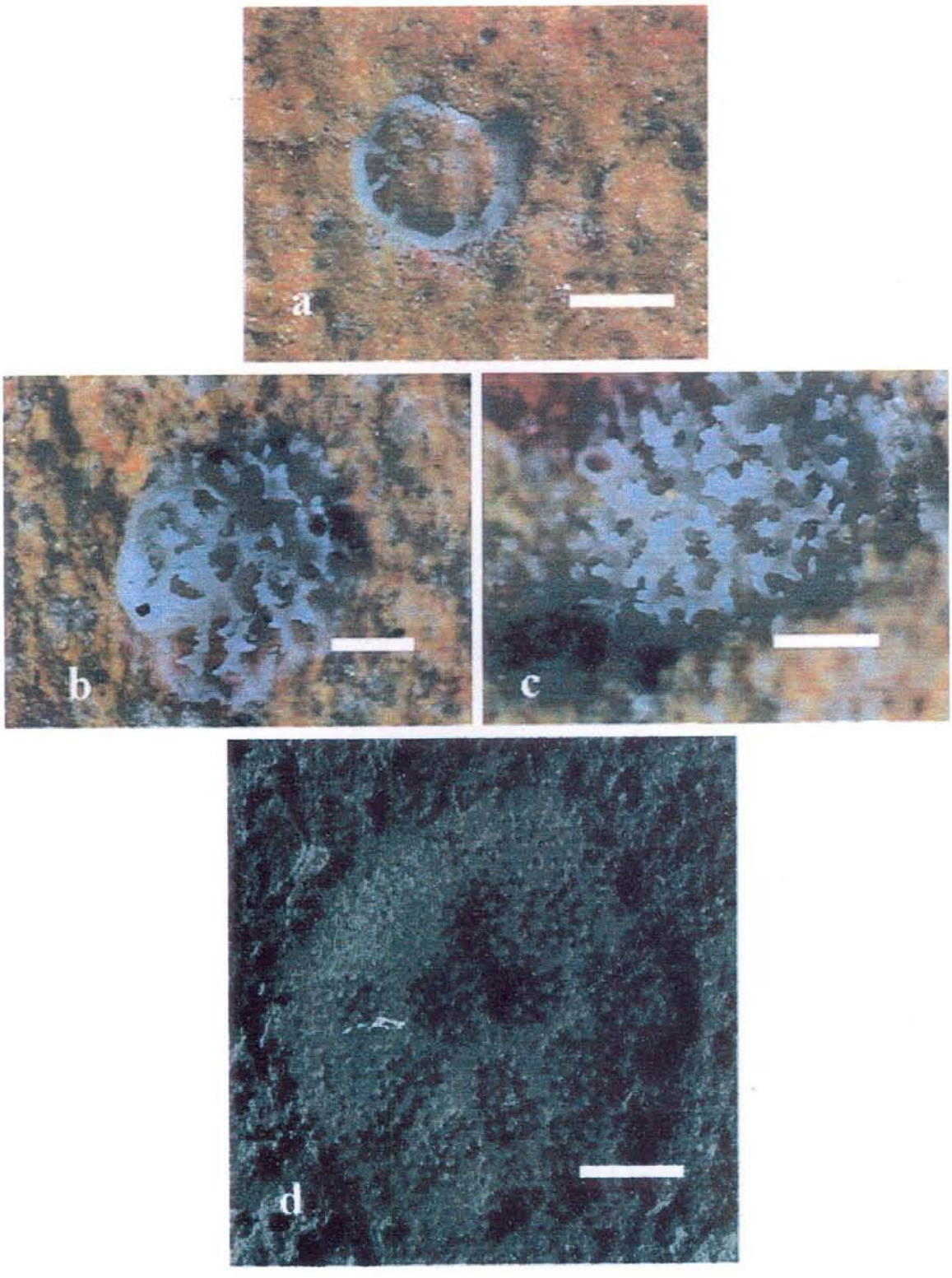


Figure 2.18 a. *Porites* sp. 2 months b. *Porites* sp. 2 months. Scale bar = 500 microns

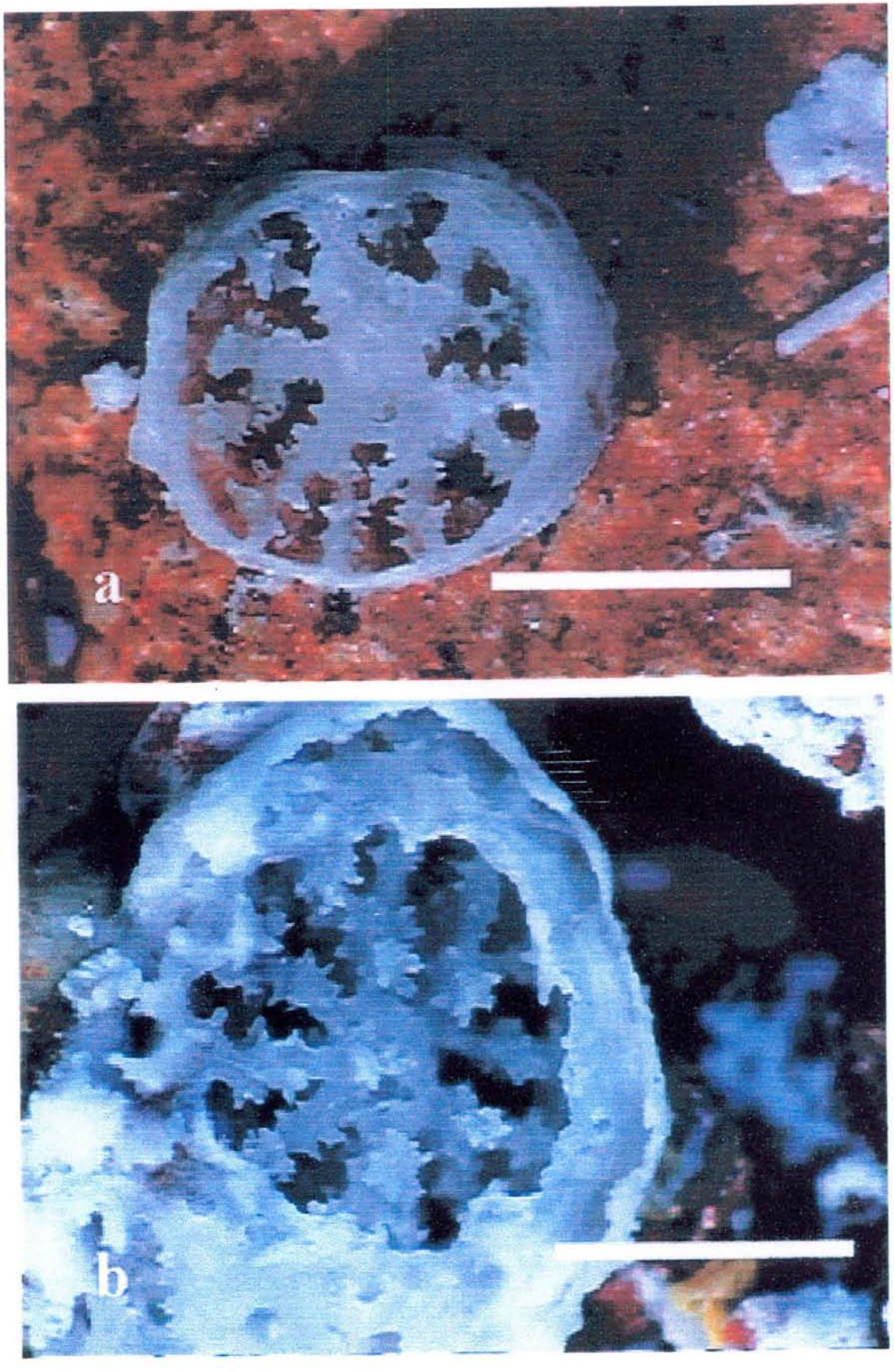
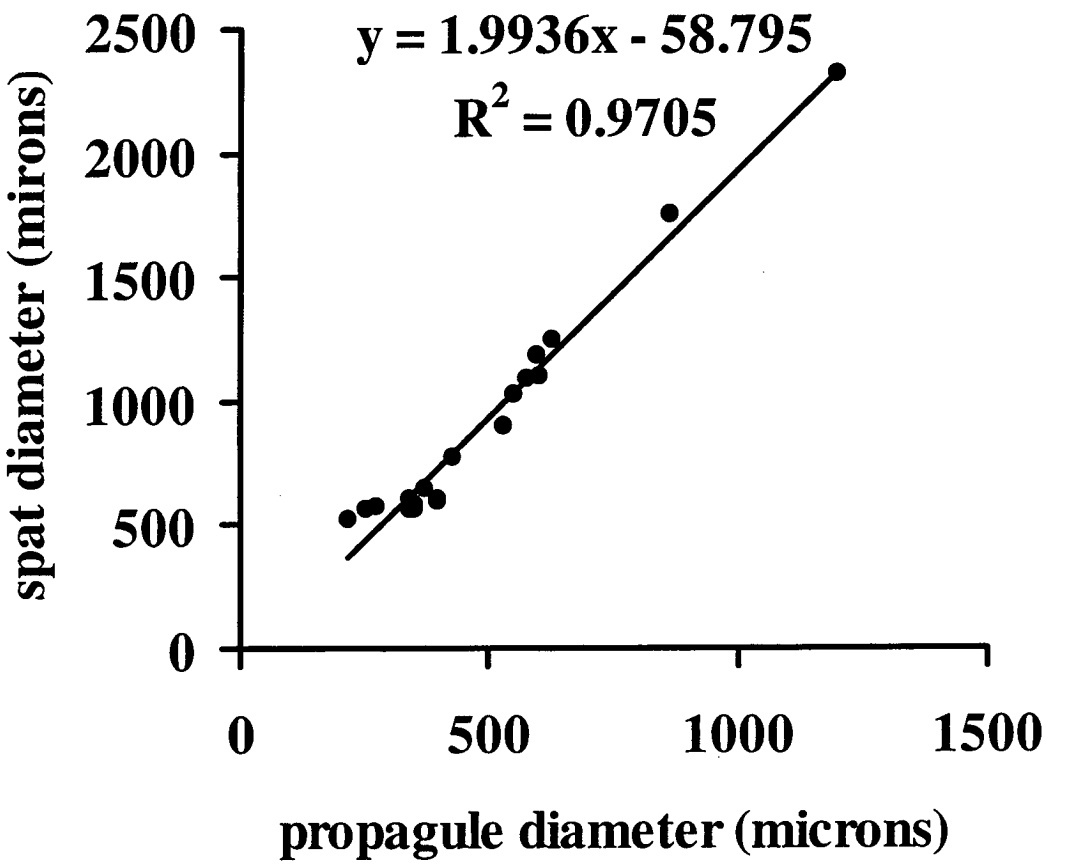


Figure 2.19 The relationship between propagules size at release and spat size at settlement.



CHAPTER 3. The depth zonation of coral assemblages

3.1 Introduction

The zonation of coral assemblages is one of the most prominent features of coral reefs worldwide (e.g. Goreau 1959, Stoddart 1969). Predictable assemblages occur consistently in a particular reef habitat, often over a wide geographical area (e.g. Done 1982). Community characteristics such as relative abundance and species diversity, vary predictably between these zones (e.g. Loya 1972, Sheppard 1982).

Zonation in coral assemblages has traditionally been attributed to different physiological tolerances of species along physical gradients, such as light and water movement (e.g. Rosen 1975, van den Hoek et al. 1978, Done 1983), which vary predictably with depth. Biological interactions between organisms such as competition (e.g. Sheppard 1979, Huston 1985) and predation (e.g. Neudecker 1979) have also been recognized as contributing to coral zonation.

Implicit in these early explanations of coral zonation is the assumption that larvae settle relatively uniformly over a wide depth range and that the depth distribution of adult corals emerges as a result of differential patterns of post-settlement mortality. Most recent studies of coral recruitment have tended to focus on comparing the number rather than the taxonomic composition of recruits between depths and thus have not been able to test this assumption. For example, coral recruitment is generally highest, though more variable, on the reef flat with a trend for recruitment to decrease with increasing depth on the GBR (Harriott 1985, Wallace 1985b, but see Sammarco 1991). Elsewhere in the Pacific (Birkeland et al. 1981) and the Caribbean (Rogers et al. 1984), densities of coral

recruits are highest at intermediate depths where the abundance of important competitors is reduced and conditions are less severe. While a few studies have shown that habitat selection by larvae or limited dispersal may influence the spatial distribution of adults within reef zones (e.g. Lewis 1974, Morse et al. 1988, Carlon and Olson 1993, Baird and Hughes 2000), the potential contribution of larval behavior to the depth zonation of adults has largely been ignored. This is despite evidence that the depth distribution of juveniles is often similar to that of adults (e.g. Bak and Engel 1979, Rogers et al. 1984, Colgan 1987, Baird and Hughes 1997).

Kawaguti (1941) was the first to suggest that differences in the degree of phototaxis between coral larvae might influence the depth distribution of adults. Similarly, Mundy and Babcock (1998) demonstrated that light intensity and spectral quality affected the settlement density of larvae from zone-specific coral species. Furthermore, when juveniles of these zone-specific species were transplanted outside the adult habitat they survived as well as juveniles from the adult habitat, indicating that differential patterns of mortality were not sufficient to explain the depth distribution of these species (Mundy and Babcock 2000). These results strongly suggest that larval choice at settlement may influence the depth distribution of these species. Nevertheless, a direct link between coral larval habitat selection and adult depth distributions remains to be established.

In this chapter, I firstly compare the depth distribution of recruits from seven coral taxa to that of the adults at 4 sites on the fringing reef surrounding Lizard Island in the period following the mass spawn in 1997. The patterns strongly suggest that adult depth distributions are determined at settlement in many taxa at this location. I then describe

an experiment to test the hypothesis that adult depth distributions are established at settlement by determining whether larvae settle preferentially on substratum conditioned in the parental habitat.

3.2 Materials and methods

3.2.1 Coral settlement patterns and the depth distribution of adults at Lizard Island

To examine variation in the distribution and abundance of coral recruits, 12 – 15 settlement panels were deployed in each of three depth zones (the reef crest (1 m), the reef front (2-4m), and the reef base (8-12m)) at four locations on the fringing reef surrounding Lizard Island on the northern Great Barrier Reef (14° 41'S, 145° 28'E) i.e. at South Island, Lizard Head, North Reef and Washing Machine (Fig. 3.1). The panels were deployed in November 1997, 7 - 10 days before the annual mass spawning period of corals on the GBR (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986). The panels were unglazed clay paving tiles (11 x 11 x 1 cm) attached individually by a bolt drilled into the substratum and inclined horizontally approximately 3-5 cm above the substratum (Fig. 3.2). Clay tiles are effective in sampling coral recruits and enable rapid and precise microscopic censusing (Harriott and Fisk 1987, Mundy 2000). Panels were retrieved after eight weeks with the result that spat will be between 0 – 6 weeks old. This duration maximizes taxonomic resolution and minimizes loss of recruits through mortality (see Chapter 2). On removal the tiles were bleached in NaOH solution, rinsed and sun dried. All tile surfaces were censused using a stereo dissector microscope. Coral recruits were counted and identified as one of the following taxa according to the

criteria established in Chapter 2: acroporids, *Isopora*, *Seriatopora*, *Stylophora*, *Pocillopora*, Poritidae, and remaining recruits were classified as "others".

The distribution and abundance of adult corals (counts of colonies >1cm in diameter, and percent cover) were estimated using 7-10 10m, line-intercept transects at each depth and each reef. On each transect, colonies lying underneath the tape were identified, and the intercept was measured to the nearest centimeter.

Patterns in the distribution and abundance of coral recruits and adult corals were examined using a two-factor, fully orthogonal ANOVA (Factors: location - 4 levels, fixed; depth - 3 levels, fixed). Assumptions of normality and homogeneity of variances were examined via a plot of residuals.

3.2.2 Habitat selection by larvae and the depth distribution of adults

To examine the influence of habitat selection by larvae on the depth distribution of adults, six species of scleractinian corals (Fig 3.3) were chosen on the basis of their depth distribution at the fringing reef on the south-east side of Pelorus Island (18°46'S, 146°15'E) in the central Great Barrier Reef. *Goniastrea aspera* and *G. retiformis* form massive colonies generally found only on the reef flat (Veron 2000). *Fungia horrida* and *F. repanda* are locally restricted to unconsolidated substratum at the base of the reef slope. *Platygyra daedalea* and *Leptoria phrygia* are massive brain corals common over a broad depth range (Veron 2000). All species are broadcast spawners at this locality and the larvae have a similar minimum planktonic period of 4 days (See Chapter 5). The depth distributions of these species was confirmed using 6 replicate 15 x 0.5 m belt transects laid at each of three depths; the reef flat (2 m), the mid slope (6 m), and at the

base of the reef slope (12 m). Transects passed over the sites where tiles were conditioned and from where the adults were collected. The number of colonies of each species in each transect was recorded (Table 3.1).

Larvae for each species were cultured as described in Chapter 2.2. The larvae were maintained until the majority were motile, a period of between 32 – 48 hours depending on the species. To test whether larvae could recognize tiles conditioned in the parental habitat, between 300 – 1500 larvae, depending on availability, were introduced into two replicate aquaria containing 3 replicate clay paving tiles (35 x 35 x 10 mm) from each of 3 treatments; tiles conditioned at 2 m (shallow tiles), tiles conditioned 12 m (deep tiles), and unconditioned tiles. Tiles of different treatments were arranged evenly within the gird. Tiles were conditioned by bolting them to concrete blocks in a horizontal position for 8 weeks at Pelorus Island. Larvae were left for 10 days to allow the majority to metamorphose, after which tiles were removed and censused in a water bath under a stereo-dissector and the number of metamorphosed larvae recorded. The total number of larvae metamorphosed in each aquaria was calculated and the mean proportion of larvae on different tiles was compared in a two-way orthogonal ANOVA (Factors: Species - fixed, 6 levels; and tiles - fixed, 3 levels i.e. 2m, 12m and unconditioned tiles). Differences in the absolute number of larvae introduced into the aquaria required that a comparative measure of metamorphosis be obtained using log-transformed data according to Equation 3.1 as in Heyward and Negri (1999).

$$Lp_i = \ln((a+0.5)/(n-a+0.5))$$

Where Lp_i = logit transformed probability of metamorphosis, a = total number of larvae metamorphosed, and n = total number of larvae.

To compare the structure of the fouling communities on conditioned tiles, 6 tiles from each depth were censused and the number of crustose coralline algae (CCA), bryozoans, polychaetes, bivalves and foraminiferans were recorded.

3.3 Results

3.3.1 Coral settlement patterns and the depth distribution of adults at Lizard Island

Pronounced differences in the abundance of adult coral taxa were apparent between depth zones. Acroporid cover was significantly higher on the reef crest than on the reef front or reef slope ($F_{(2, 102)} = 126.9$, $p = 0.000$, Tables 3.2, 3.3). Acroporid cover varied 50 fold between depth zones ranging from a mean cover of 24.5% ± 18.5 on the crest to 0.5% ± 0.01 on the slope (Table 3.3). Isoporans were largely restricted to the reef crest, with 31 of the 32 colonies occurring in this depth zone and only one colony occurring on the slope (Table 3.4). Isoporan abundance varied 12 fold between locations around Lizard Island, with the number of colonies particularly low at North Reef where only one colony was recorded (Table 3.4). Similarly, *Pocillopora* cover was significantly higher on the reef crest ($F_{(2, 102)} = 12.24$, $p = 0.000$, Tables 3.2, 3.3). *Pocillopora* cover ranged 7 fold between depths ranging from 3.5 % ± 0.6 on the reef crest to 0.5% ± 0.16 on the reef slope (Table 3.3). Few *Seriatopora* colonies were found on the transects at Lizard Island (max. % cover = 0.2%, Table 3.3). Of the 6 colonies recorded, 5 occurred on the reef front and one on the reef crest (Table 3.4). *Stylophora* was more abundant on

the reef crest with 25 of the 44 colonies recorded in this depth zone (Table 3.4). *Stylophora* abundance declined with depth with 13 colonies on the reef front and 6 on the reef slope (Table 3.4). Poritid cover was significantly higher on the reef front ($F_{(2, 102)} = 1.99$, $p = 0.000$, Tables 3.2, 3.3). Poritid cover varied 7 fold between depth zones ranging from 3.4% ± 0.09 on the reef front to 0.5% ± 0.01 on the reef crest (Table 3.3). Similarly, the cover of "other" scleractinian taxa was significantly higher on the reef front ($F_{(2, 102)} = 1.02$, $p = 0.000$, Tables 3.2. 3.3). "Other" cover varied 8 fold between depth zones ranging from 11.6% ± 1.43 on the reef front to 1.5% ± 0.34 on the crest (Table 3.3).

The depth distribution of acroporid recruits was not consistent between locations at Lizard Island ($F_{(6, 128)} = 9.7$, $p = 0.000$, Table 3.5). Acroporid recruitment declined with depth at all locations except Washing Machine, where the abundance of recruits was similar at all depths (Fig 3.4). In contrast, isoporan recruits were largely restricted to the reef crest (Fig. 3.5), where 9 of the 10 recruits were recorded (Table 3.6). *Pocillopora* recruitment declined with depth at all locations (Fig 3.6), however, the decline was more pronounced at South Island ($F_{(6, 128)} = 3.0$, $p = 0.008$, Table 3.5). Overall 84 of the 100 *Pocillopora* recruits occurred on the reef crest, 8 on each of the reef front and the slope (Table 3.6). *Seriatopora* recruits were rare and the depth distribution was not consistent between locations ($F_{(6, 128)} = 4.4$, $p = 0.000$, Table 3.5). *Seriatopora* recruitment was generally higher on the reef crest (Fig. 3.7), where 25 of the 55 recruits occurred, however, the highest abundance of recruits occurred on the slope at North Reef (Table 3.6). *Stylophora* recruitment declined with depth at all locations, except North Reef, where recruitment was low at all depths (Fig. 3.8). The abundance of poritid recruits did not vary significantly between depths (Fig. 3.9, Table 3.5). Overall,

poritid recruitment was highest at Lizard Head ($F_{(3, 128)} = 5.4$, $p = 0.002$, Table 3.5). The abundance of "other" recruits was low and did not vary significantly between depths or locations (Fig. 3.10, Table 3.5).

3.3.3 Habitat selection by larvae

Larval substratum preferences for tiles subjected to the different conditioning treatments were generally consistent with those predicted on the basis of the depth distribution of the adults (Table 3.7). Zone-specific species showed a clear and pronounced preference for tiles conditioned in the parental habitat. For example, the reef flat species *Goniastrea aspera* and *G. retiformis* (Table 3.1), settled on shallow tiles in densities 4 times greater than on deep tiles (Fig. 3.11). *Fungia horrida,* which was locally restricted to the base of the reef slope (Table 3.1), was six times more abundant on deep tiles and *Fungia repanda* settled exclusively on deep tiles (Fig. 3.11). In contrast, *Leptoria phrygia* settled in equal densities on shallow and deep tiles which is consistent with its broad depth distribution at this location (Table 3.1, Fig. 3.11). While the larvae of *Platygyra daedalea* settled preferentially on shallow tiles, this preference was much less pronounced than in either of the reef flat species (Fig 3.11). However, in all the zone-specific species with the exception of *Fungia repanda*, some larvae settled on both deep and shallow tiles (Fig. 3.11) indicating that larval preference for the adult habitat is not absolute. Unconditioned tiles were largely avoided by the larvae of all species except *Fungia horrida* where 13% ± 1.7 of the larvae settled on unconditioned tiles (Fig. 3.11).

Most of the fouling organisms had a clear preference for the deep tiles, the only exceptions being the bryozoan *Thalamoporella* which was equally abundant on deep and shallow tiles, CCA which was 5 times more abundant on the shallow tiles, and

foraminiferans which were twice as abundant on the shallow tiles (Table 3.8). All of the other fouling organisms were more abundant (e.g. polychaetes, anascan bryozoans), or found exclusively (e.g. ascophoran bryozoans) on the deep tiles (Table 3.8).

3.4 Discussion

3.4.1 Depth distribution of coral taxa around Lizard Island

Clear differences between depth zones were evident in the distribution patterns of all the adult taxa. Isoporans, *Pocillopora* and *Seriatopora* were found almost exclusively on the reef crest. The abundance of acroporids and *Stylophora* was highest on the reef crest, intermediate on the reef front and lowest at the reef slope. In contrast, the area cover of poritids and "other" taxa were highest on the reef front. In some of these taxa these distribution patterns were largely reflected in the patterns of settlement. In particular, isoporan and *Pocillopora* recruitment occurred almost exclusively on the reef crest where the vast majority of adults were found. Similarly, recruitment of *Acropora* declined with depth, reflecting the distribution of the adults. These results strongly indicate that larvae in these taxa have some influence over where they settle. However, the peak in area cover of poritids and "other" taxa on the reef front was not reflected in the distribution of the recruits which varied little between depth zones. Consequently, post-settlement processes are likely to have an influence on the depth distribution of these taxa. However, the scale of spatial and temporal variability in the patterns in settlement remain to be established and consequently the results must be treated with caution.

3.4.2 Larval habitat selection

Larval substratum preferences were generally consistent with those predicted on the basis of the depth distribution of the adults. Zone-specific species showed a clear and pronounced preference for tiles conditioned in the parental habitat. These results strongly suggest that the depth distribution of these species is influenced, in part, by patterns established at settlement. However, in all species, with the exception of *Fungia repanda*, some larvae settled on both deep and shallow tiles (Fig. 3.11) indicating that larval preference for the adult habitat is not absolute. This suggests that either chemical signals other than those characteristic of optimum settlement surfaces may induce metamorphosis or the cues that induce metamorphosis in these species are not 100% depth specific. Either way, some settlement will occur on sub-optimal substrata (Johnson et al. 1997). Consequently, even in zone-specific species some larval settlement is likely over a broad depth range suggesting that differential patterns of post-settlement mortality may also be involved in establishing the depth distribution of adults. While Mundy and Babcock (2000) found no difference in rates of mortality between depths of transplanted juveniles in the 8 months of their study, they suggested that infrequent catastrophic events or difference in rates of mortality in later life may contribute to the depth distribution of adults. Furthermore, settlement patterns in the field are likely to be affected by larval response to other features of the environment. For example, the ability of larvae to recognize depth-specific differences in the quality and intensity of light (Mundy and Babcock 1998) may result in few larvae of shallow water species spending time exploring substrata at depths beneath those optimal for the adults. Thus, while they may settle on tiles conditioned at depth *in vitro*, few may reach deep habitats in the field. Few single features of the environment are likely to provide larvae with all the information necessary to locate optimal settlement surfaces. For

example, light intensity is very variable within depth zones and the shading effect of canopy-forming species such as *Acropora hyacinthus* is comparable to the reduction in light intensity that occurs between 1 and 10 m depth (Stimson 1985). Consequently, many features of the environment may be used by larvae to navigate to and select suitable settlement surfaces.

Unconditioned tiles were largely avoided by the larvae of all species (Fig. 3.11). This avoidance of unconditioned tiles is consistent with observations that surface contact with chemical cues associated with the substratum are necessary to induce metamorphosis in many invertebrate larvae (Pawlik 1992).

Larval settlement in many coral species is controlled by chemosensory recognition of a cue associated with crustose coralline algae (CCA) (Morse et al. 1996, Heyward and Negri 1999). The difference in the density of settlement of the reef flat species between shallow and deep tiles was very similar to the difference in abundance of CCA on tiles at these two depths with CCA being 4 times more abundant on the shallow tiles (Table 3.8). Larval requirement for contact with CCA may therefore explain the substratum preferences of these species. In contrast, the marked preference of the fungiids for deep substratum suggests they are responding to the presence of other organisms, many of which were found in higher abundance (e.g. polychaetes, anascan bryozoans), or even exclusively (e.g. ascophoran bryozoans) on the deep tiles (Table 3.8). However, none of these organisms have been demonstrated to induce metamorphosis in coral larvae. Alternatively, inducement of settlement in the fungiids may be influenced by zone-specific CCA species, or bacteria, as has been proposed to explain the depth-specific recruitment of *Acanthaster planci* (Johnson et al. 1991). Unfortunately, the taxonomic

resolution of CCA used in this study does not allow this hypothesis to be examined. Similarly, bacterial flora were not examined, but would have been part of the biofilms present on the plates.

The larvae of coral species with a wide depth distribution settled relatively evenly on both shallow and deep tiles. In contrast, most of the fouling organisms had a clear preference for one or other of the conditioned tiles, the only exception being the bryozoan *Thalamoporella* which was equally abundant on deep and shallow tiles (Table 3.8). This suggests that *Platygyra daedalea* and *Leptoria phrygia* respond to some other feature of the biological environment that is similar on both shallow and deep tiles. An other potential sources of induction in coral larvae are bacteria which have been implicated in the induction of settlement of many marine organisms (see review by Johnson et al. 1997) including corals (Negri et al. 2001). Bacterial assemblages typically include microbes that provide a chemical signature characteristic of a particular settlement surface, as well as microbes common to many surfaces (Johnson et al. 1997). Consequently, bacteria provide a characteristic and consistent cue to enable larvae with specific habitat requirements to distinguish between habitats. For larvae of generalist species, a proportion of the bacterial assemblage will provide consistent cues in a wide range of habitats (Johnson et al. 1997). The settlement patterns of larvae from the generalist species used in this study strongly support these suggestions.

The substratum preferences demonstrated experimentally in the larvae of these six species, and the settlement patterns of taxa such as the *Isopora*, *Pocillopora* and *Acropora* in the field, strongly suggest that the depth distribution of the adults is influenced, in part, by patterns established at settlement. Furthermore, the fact that the

larvae of these species responded differently to similar settlement surfaces suggests that settlement cues may species specific and more diverse than has been previously suggested. Furthermore, settlement cues are likely to vary between individuals of the same cohort.

Table 3.1 Depth distribution of the six study species used to test larval substratum preferences. Values are the total number of colonies found within six 15 x 0.5 m belt transects conducted at each depth at Pelorus Island.

	Depth (m)		
Species	2	6	12
Fungia horrida	1	0	21
Fungia repanda	0	4	28
Goniastrea aspera	67	4	0
Goniastrea retiformis	54	6	0
Leptoria phrygia	15	13	14
Platygyra daedalea	17	23	18

Table 3.2 ANOVA testing for difference in the mean area cover of adult taxa around Lizard Island. The Bonferroni corrected level of significance used was 0.0125

variable	Source	df	Mean Square	F	p
acroporids	REEF	3	509.1	0.1	0.960
	ZONE	2	648335.2	126.88	0.000
	R * Z	6	4287.1	0.84	0.543
	Error	102	5109.9		
Pocillopora	REEF	3	3088.8	4.79	0.004
	ZONE	2	7892.4	12.24	0.000
	R * Z	6	833.8	1.29	0.267
	Error	102	644.6		
poritids	REEF	3	2029.1	1.99	0.120
	ZONE	2	8748.5	8.58	0.000
	R * Z	6	2447.5	2.4	0.033
	Error	102	1019.8		
other	REEF	3	2956.9	1.02	0.388
	ZONE	2	114704.5	39.46	0.000
	R * Z	6	3366.5	1.16	0.335
	Error	102	2906.5		
	Total	114			

Table 3.3 Abundance of adult coral taxa on the fringing reef around Lizard Island. Values are the mean percent cover and one se from 7-10 line intercept transects. SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine.

one	Reef	acroporid		*Isopora*		*Pocillopora*		*Seriatopora*	
		mean	se	mean	se	mean	se	mean	se
Crest	SI	23.3	4.94	2.6	1.15	5.5	1.65	0.0	0.00
Crest	LH	24.1	3.27	2.2	0.67	3.4	0.82	0.0	0.00
Crest	NR	23.5	2.23	0.1	0.13	3.7	0.91	0.0	0.00
Crest	WM	28.4	4.47	1.1	0.63	0.7	0.51	0.1	0.11
Crest mean		24.5	1.85	1.5	0.40	3.5	0.60	0.0	0.02
Front	SI	5.2	1.99	0.0	0.00	2.8	1.10	0.0	0.00
Front	LH	2.6	0.85	0.0	0.00	0.7	0.41	0.1	0.08
Front	NR	5.3	1.96	0.0	0.00	1.6	1.11	0.2	0.15
Front	WM	1.0	0.24	0.0	0.00	0.1	0.08	0.6	0.53
Front mean		3.6	0.79	0.0	0.00	1.3	0.44	0.2	0.14
Slope	SI	0.5	0.20	0.0	0.00	0.5	0.32	0.0	0.00
Slope	LH	0.4	0.23	0.0	0.00	0.2	0.20	0.0	0.00
Slope	NR	0.4	0.18	0.0	0.00	0.9	0.41	0.0	0.00
Slope	WM	0.8	0.26	0.1	0.06	0.3	0.34	0.0	0.00
Slope mean		0.5	0.11	0.0	0.01	0.5	0.16	0.0	0.00
Grand mean		9.3	1.19	0.5	0.15	1.8	0.28	0.1	0.05

Table 3.3b Abundance of adult coral taxa on the fringing reef around Lizard Island. Values are the mean percent cover and one se from 7-10 line intercept transects. SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine.

zone	Reef	*Stylophora*		poritid		other		total	
		mean	se	mean	se	mean	se	mean	se
Crest	SI	0.2	0.13	0.2	0.16	1.3	0.63	33.0	5.65
Crest	LH	1.2	0.50	0.4	0.19	1.3	0.58	32.6	3.60
Crest	NR	0.0	0.00	1.1	0.48	1.3	0.78	29.7	2.30
Crest	WM	1.8	0.57	0.5	0.23	2.3	0.82	35.0	3.63
Crest mean		0.7	0.21	0.5	0.16	1.5	0.34	32.4	1.98
Front	SI	1.3	1.33	7.0	3.05	12.9	2.95	29.3	4.34
Front	LH	0.1	0.05	3.3	1.05	10.2	3.48	17.0	3.75
Front	NR	0.1	0.10	2.2	0.61	8.0	1.91	17.3	3.97
Front	WM	0.3	0.17	1.4	0.54	14.8	3.02	18.1	3.45
Front mean		0.5	0.35	3.5	0.90	11.6	1.43	20.6	2.07
Slope	SI	0.0	0.00	1.1	0.35	1.1	0.18	3.1	0.49
Slope	LH	0.0	0.03	2.6	0.64	2.1	0.79	5.3	1.20
Slope	NR	0.1	0.06	0.6	0.22	3.4	1.10	5.4	1.35
Slope	WM	0.2	0.13	0.5	0.18	2.7	0.69	4.6	0.70
Slope mean		0.1	0.04	1.2	0.23	2.3	0.40	4.6	0.51
Grand mean		0.4	0.14	1.7	0.33	5.1	0.66	18.9	1.43

Table 3.4 The number of adult corals in seven coral taxa on the fringing reef around Lizard Island. Values are the total number of colonies on 7-10 line intercept transects. SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine.

zone	Reef	acroporid	*Isopora*	*Pocillopora*	*Seriatopora*	*Stylophora*	poritid	other	n
crest	SI	74	12	28	0	3	1	5	10
crest	LH	115	9	23	0	8	4	8	10
crest	NR	88	1	21	0	0	10	9	10
crest	WM	111	9	5	1	14	4	13	7
crest total		388	31	77	1	25	19	35	37
front	SI	19	0	11	0	3	17	25	10
front	LH	25	0	4	1	1	21	48	8
front	NR	32	0	10	1	2	15	47	10
front	WM	14	0	3	3	7	15	99	10
front total		90	0	28	5	13	68	219	38
slope	SI	9	0	3	0	0	17	25	10
slope	LH	6	0	1	0	1	41	32	10
slope	NR	6	0	5	0	1	10	31	10
slope	WM	14	1	7	0	4	10	28	9
slope total		35	1	16	0	6	78	116	39

Table 3.5a ANOVA testing for difference in the mean abundance of recruits around Lizard Island. Data were $\log_{10}(x + 1)$ transformed.

Variable	Source	df	Mean Square	F	p
acroporid	REEF	3	1.32	14.8	0.000
	ZONE	2	5.02	56.3	0.000
	R * Z	6	0.87	9.7	0.000
	Error	128	0.09		
Isopora	REEF	3	0.01	1.6	0.195
	ZONE	2	0.05	7.3	0.001
	R * Z	6	0.01	1.1	0.391
	Error	128	0.01		
Pocillopora	REEF	3	0.04	1.0	0.378
	ZONE	2	1.37	37.2	0.000
	R * Z	6	0.11	3.0	0.008
	Error	128	0.04		
Seriatopora	REEF	3	0.14	5.0	0.003
	ZONE	2	0.11	3.9	0.022
	R * Z	6	0.12	4.4	0.000
	Total	140			

Table 3.5b ANOVA testing for difference in the mean abundance of recruits around Lizard Island. Data were $\log_{10}(x + 1)$ transformed.

Variable	Source	df	Mean Square	F	p
Stylophora	REEF	3	0.25	4.4	0.005
	ZONE	2	1.34	23.7	0.000
	R * Z	6	0.40	7.1	0.000
	Error	128	0.06		
poritids	REEF	3	0.20	5.4	0.002
	ZONE	2	0.13	3.3	0.039
	R * Z	6	0.11	2.9	0.011
	Error	128	0.04		
others	REEF	3	0.00	0.2	0.915
	ZONE	2	0.04	1.5	0.226
	R * Z	6	0.07	2.4	0.028
	Error	128	0.03		
	Total	140			

Table 3.6 Abundance of coral recruits on the fringing reef around Lizard Island. Values are the total number of recruits. SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine.

zone	location	acroporid	*Isopora*	*Pocillopora*	*Seriatopora*	*Stylophora*	poritid	others	n
crest	SI	611	2	43	8	51	9	2	12
crest	LH	339	3	12	1	16	12	3	10
crest	NR	872	0	15	8	5	2	5	12
crest	WM	114	4	14	8	53	16	1	10
crest total		1936	9	84	25	125	39	11	44
front	SI	76	0	0	1	0	3	3	12
front	LH	186	0	4	1	7	16	2	12
front	NR	466	0	3	2	8	5	6	12
front	WM	174	1	1	3	10	3	6	12
front total		902	1	8	7	25	27	17	48
slope	SI	59	0	1	0	0	8	14	12
slope	LH	49	0	2	1	3	11	7	12
slope	NR	118	0	2	22	12	3	1	12
slope	WM	178	0	3	0	19	3	5	12
slope total		404	0	8	23	34	25	27	48
Grand Total		3242	10	100	55	184	91	55	140

Table 3.7 ANOVA testing for significant differences in the mean number of larvae of six coral species settling on tiles subjected to three experimental treatments: conditioning at 2m, conditioning at 12 m and unconditioned. The data were transformed according to Equation 3.1

Source	df	Mean Square	F	p
Species	5	3.22	27.12	0.000
treatment	2	45.33	381.64	0.000
spp * treat	10	5.31	44.69	0.000
Error	18	0.12		
Total	35			

Table 3.8 The total number of various calcareous organisms on 6 tiles from 2m and 12m. The final column shows the proportional abundance of the taxon on 12m tiles when compared to 2m tiles.

Higher taxa	taxon	shallow	deep	difference
Foraminifera	foraminiferan	176	100	0.6
Polychaete	serpulid a	51	177	3.5
	serpulid b	111	195	1.8
	serpulid c	23	307	13.3
Bivalvia	Bivalvia	1	21	21.0
Ascophora	Ascophora a	0	2	
	Ascophora b	0	2	
Tublioporata	Lichenoporidae a	0	11	
	Lichenoporidae b	1	5	5.0
Anasca	*Thalamoporella*	23	25	1.1
	Articulata	0	6	
CCA		455	78	0.2
Total Polychaeta		185	679	3.7
Total Ascophora		0	4	
Total Tublioporata		1	16	16.0
Total Anasca		23	31	1.3
Total bryozoa		24	51	2.1

Figure 3.1 Lizard Island showing the four locations used in the study.

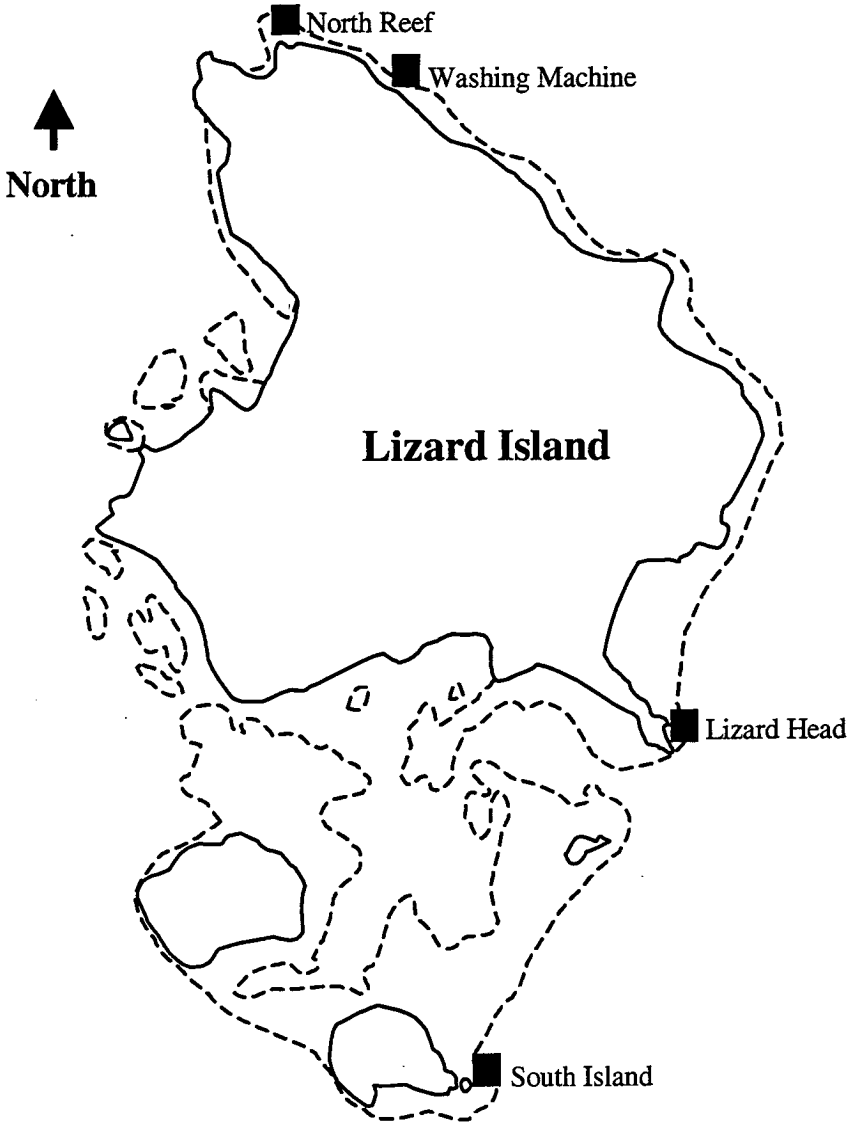


Figure 3.2 A recruitment panel on the reef crest at Lizard Island.

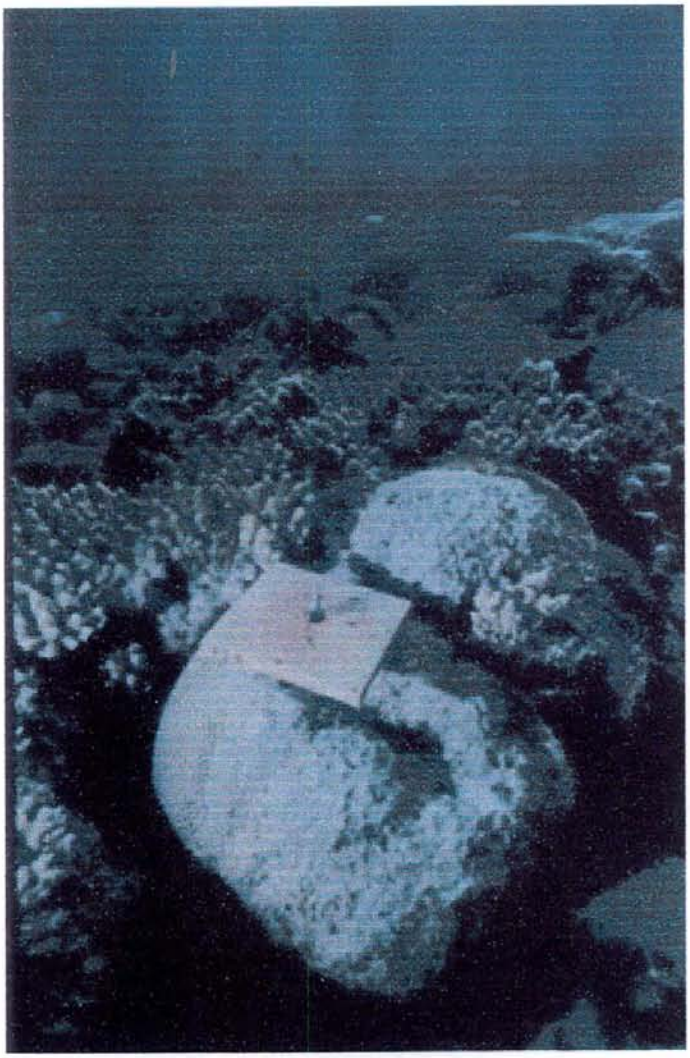


Figure 3.3 Study species (a) *Goniastrea aspera* (b) *G. retiformis* (c) *Fungia repanda* (d) *F. horrida* (e) *Platygyra daedalea* (f) *Leptoria phyrgia*

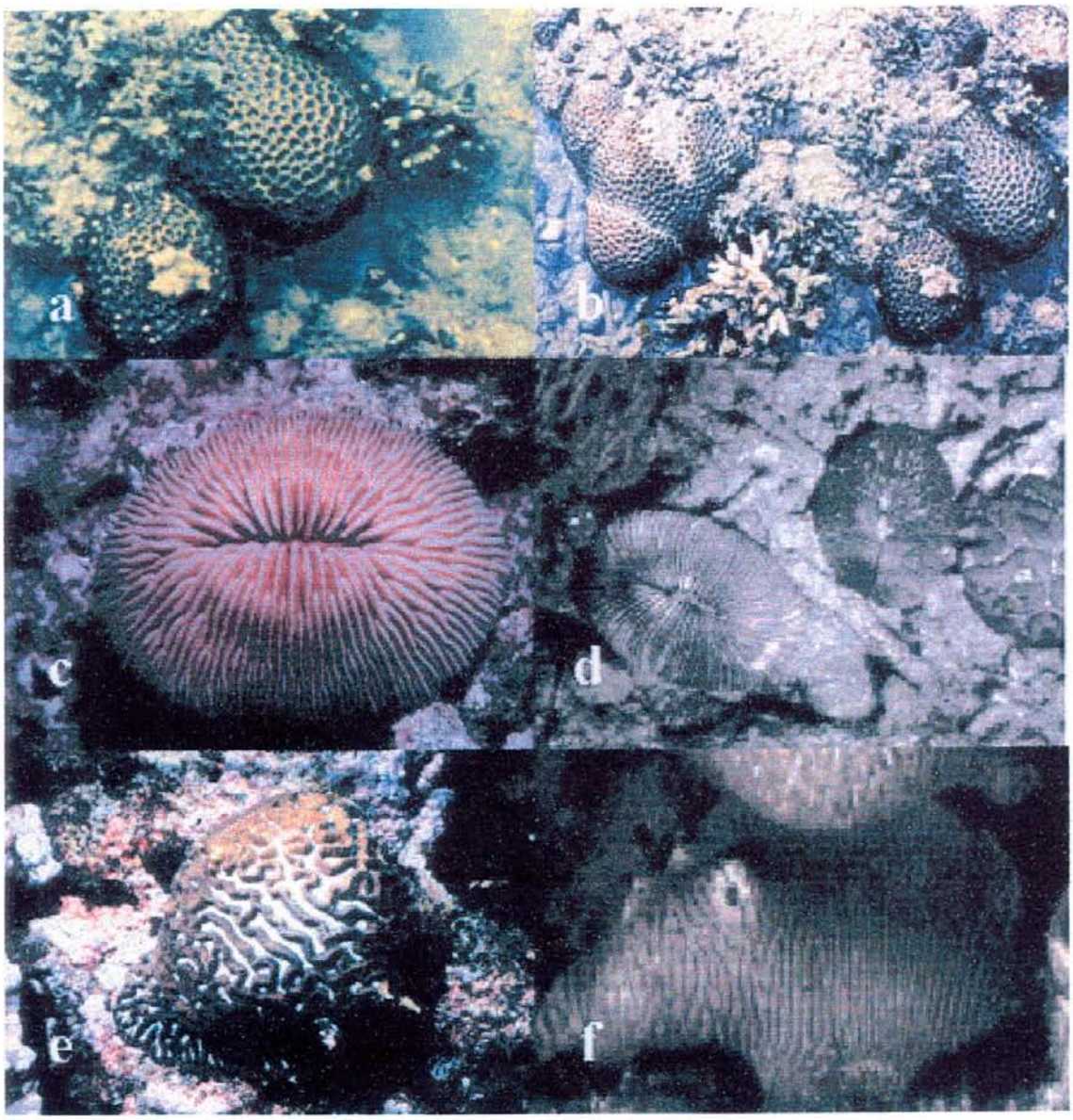


Figure 3.4 Mean number (± one se) of acroporid recruits per panel around Lizard Island (SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine).

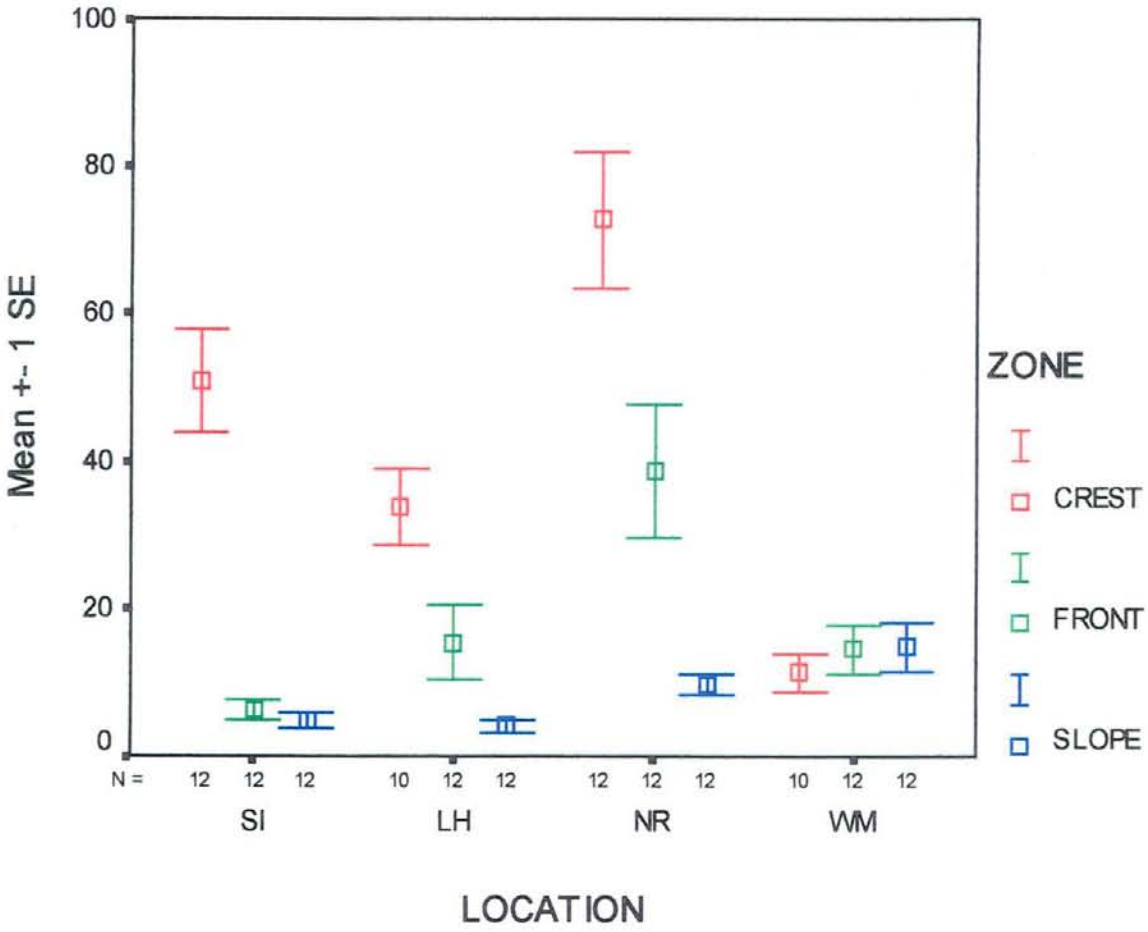


Figure 3.5 Mean number (± one se) of *Isopora* recruits per panel around Lizard Island (SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine).

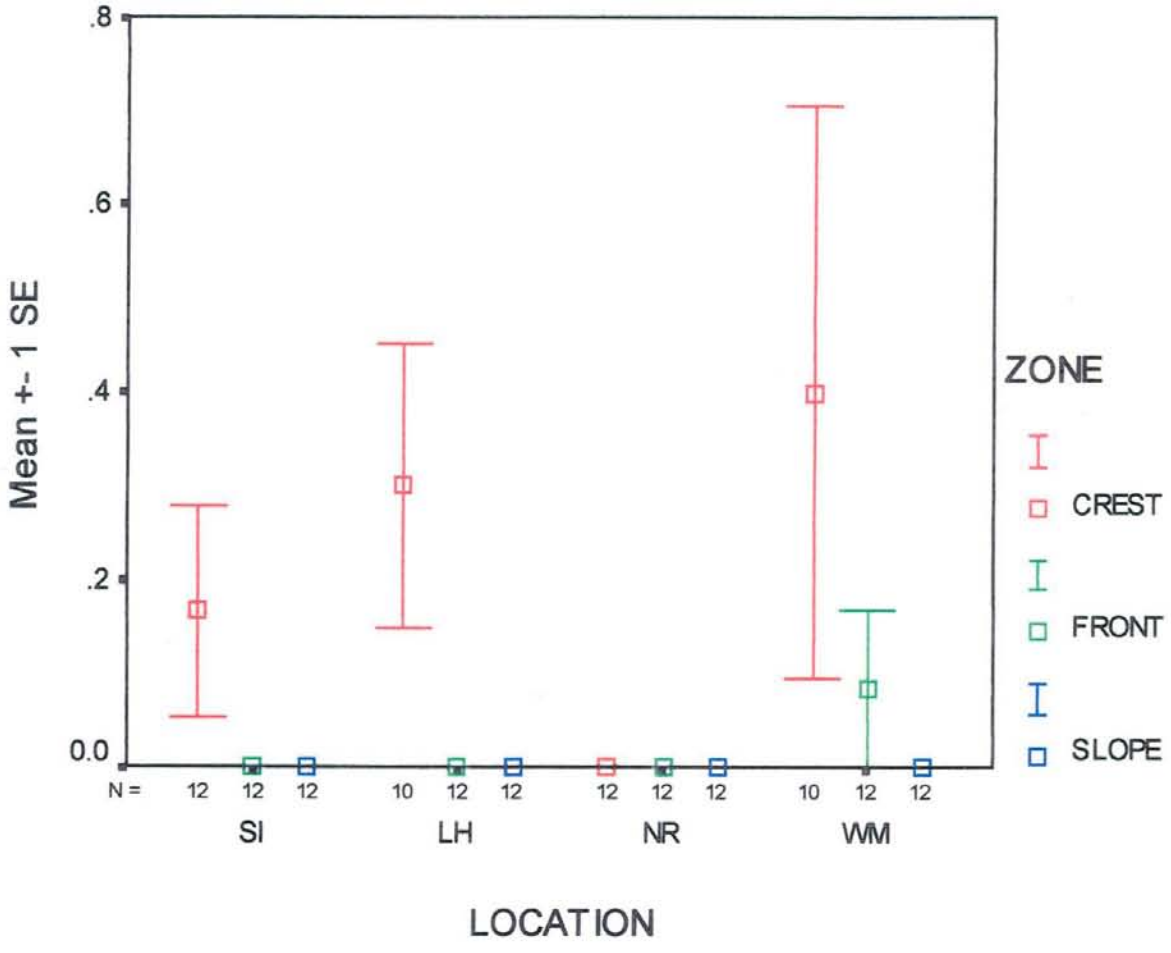


Figure 3.6 Mean number (± one se) of *Pocillopora* recruits per panel around Lizard Island (SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine).

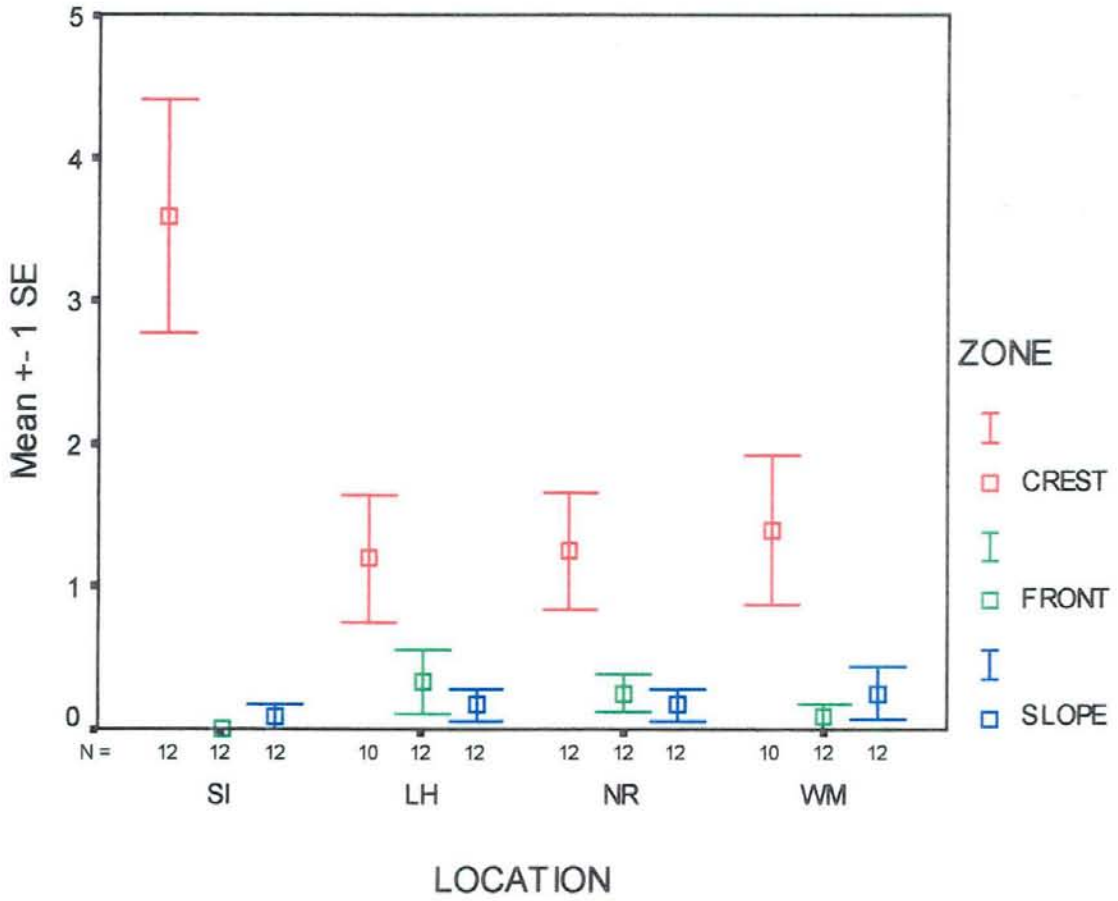


Figure 3.7 Mean number (± one se) of *Seriatopora* recruits per panel around Lizard Island (SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine).

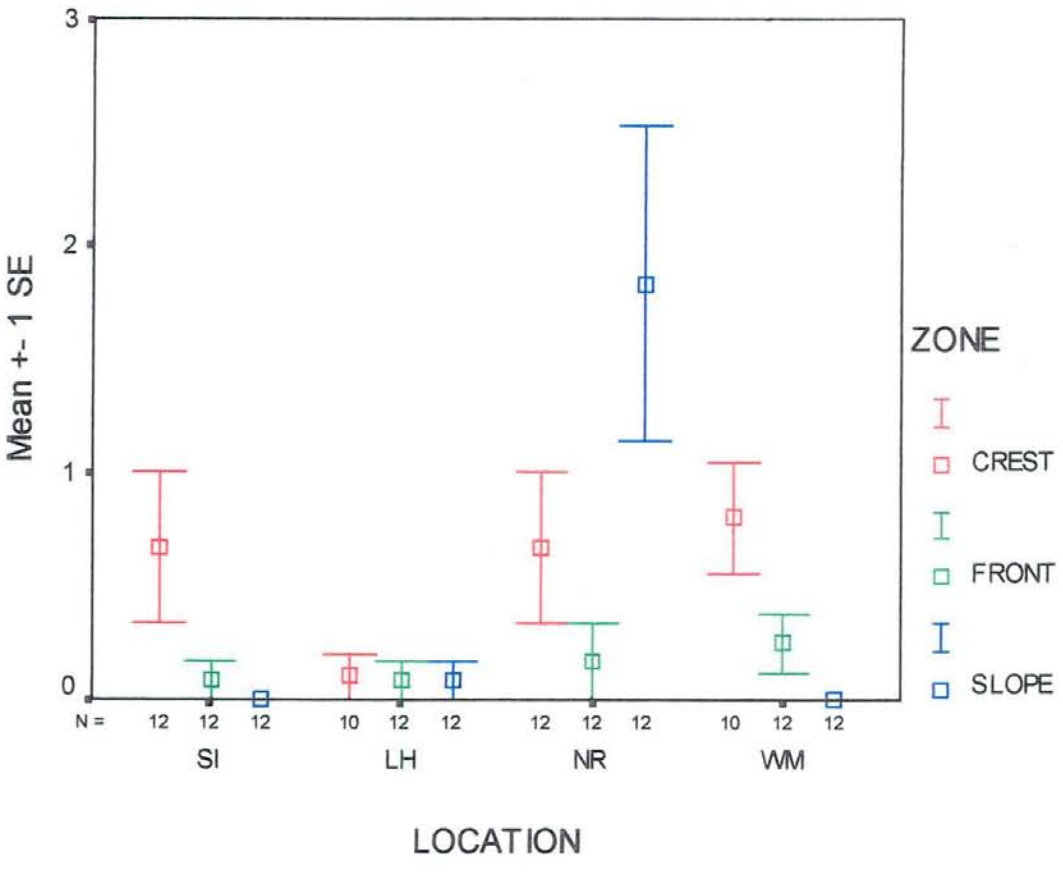


Figure 3.8 Mean number (± one se) of *Stylophora* recruits per panel around Lizard Island (SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine).

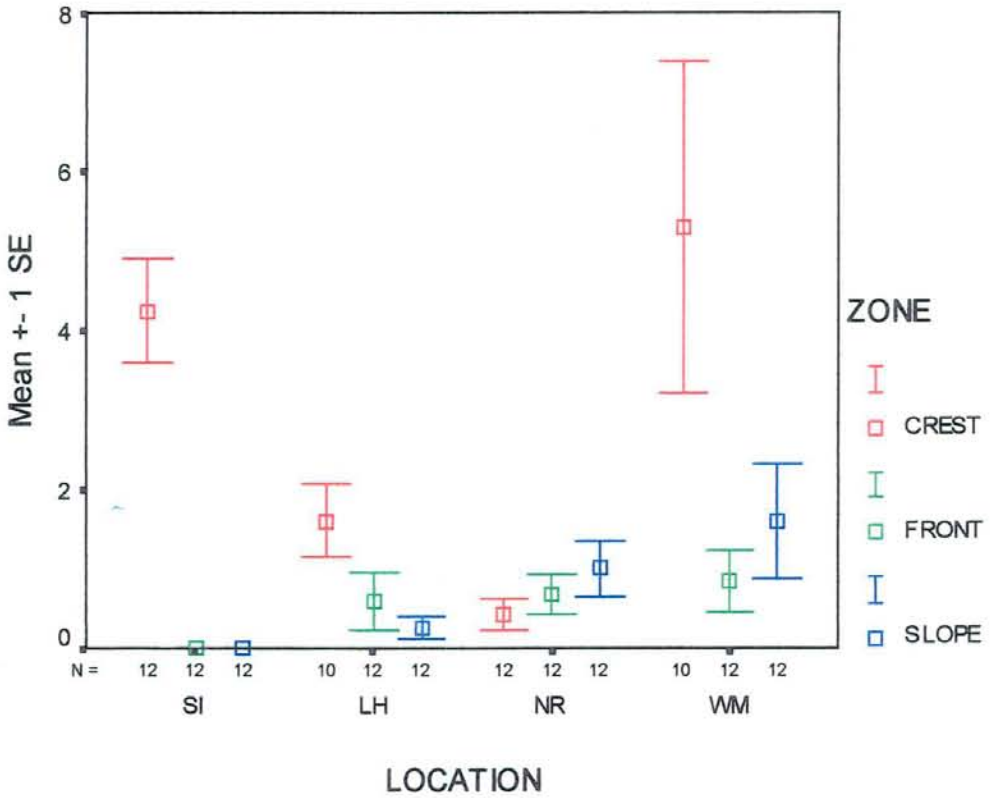


Figure 3.9 Mean number (± one se) of poritid recruits per panel around Lizard Island (SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine).

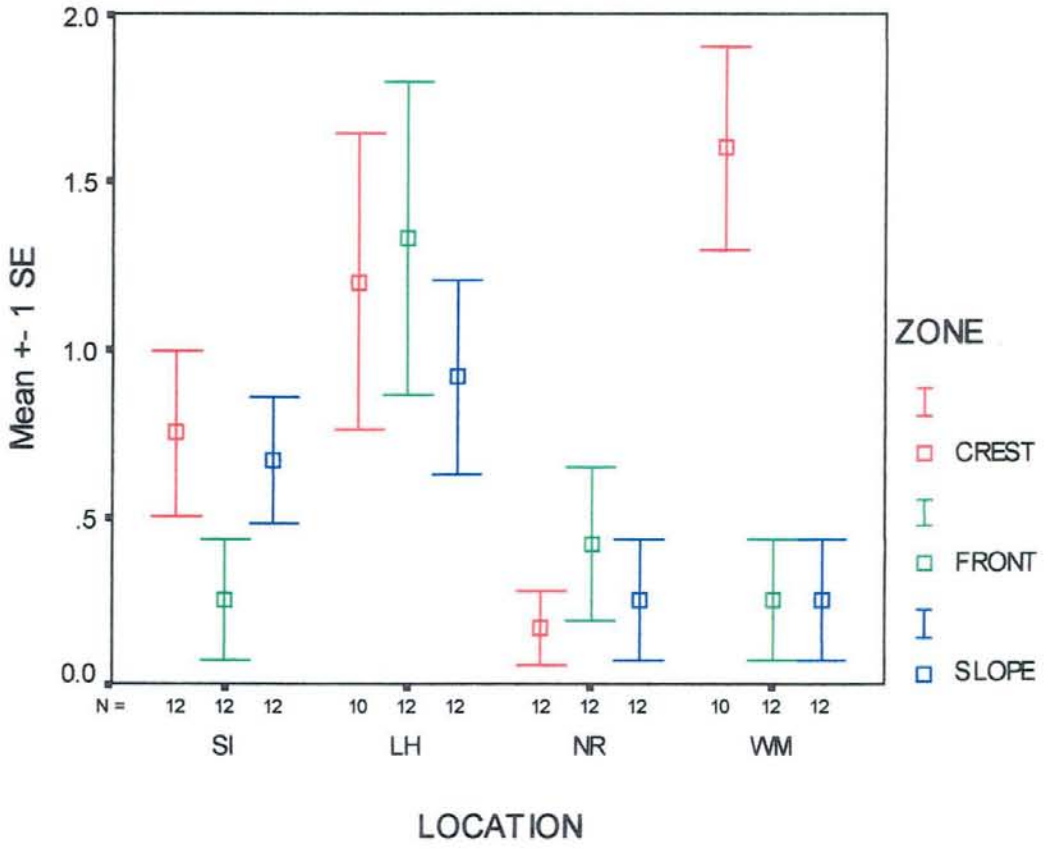


Figure 3.10 Mean number (± one se) of "other" recruits per panel around Lizard Island (SI = South Island; LH = Lizard Head; NR = North Reef; WM = Washing Machine).

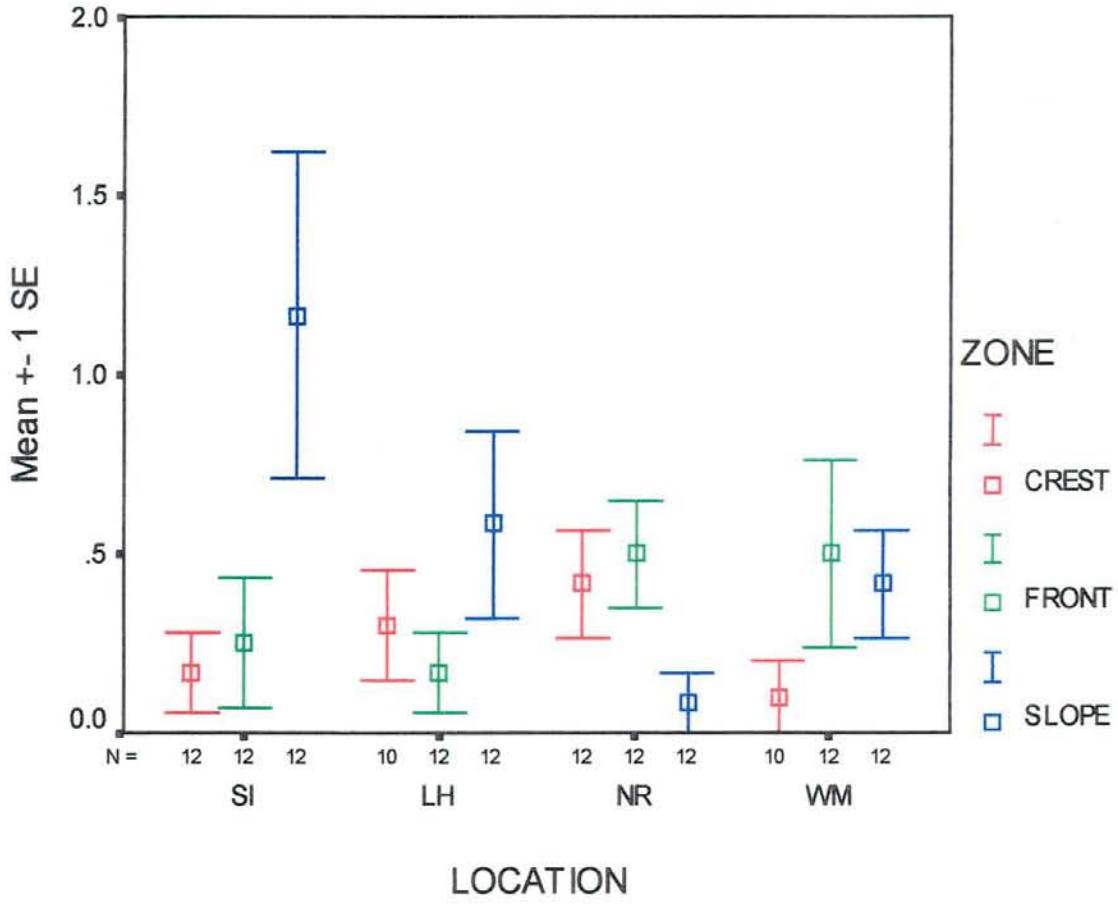
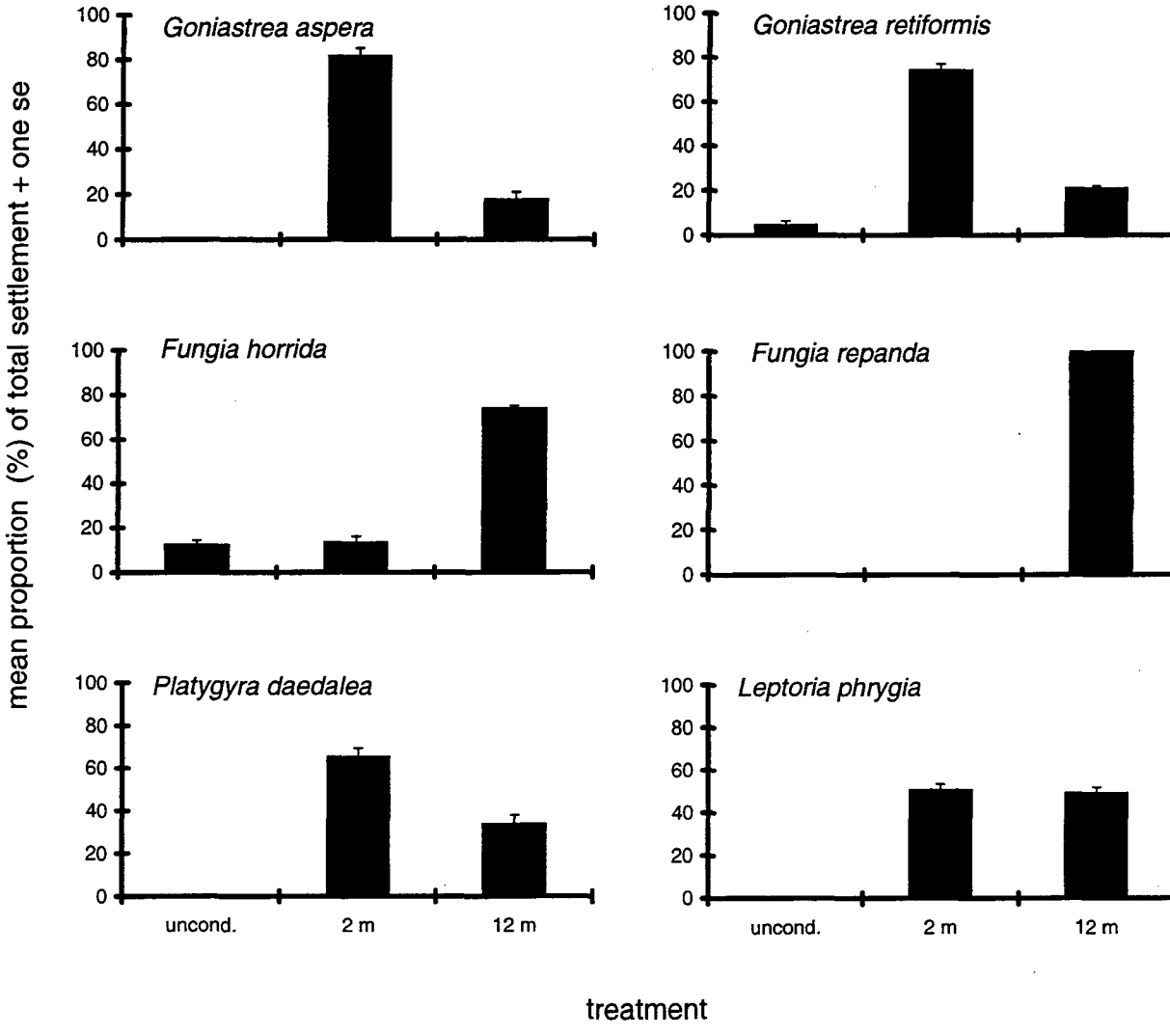


Figure 3.11 The relative abundance of recruits of 6 coral species on tiles conditioned at 2 m, 12 m and on unconditioned tiles expressed as the mean proportion + one standard error of total spat settled in two replicate aquaria.



CHAPTER 4. Induction of metamorphosis in larvae of the brooding corals *Stylophora pistillata* and *Acropora palifera*

4.1 Introduction

Settlement and metamorphosis in many marine invertebrate larvae is induced by chemical and other environmental cues (for reviews see Scheltema 1974, Pawlik 1992). Recent investigations of the settlement cues of coral larvae have concentrated on the role of crustose coralline algae (CCA) in inducing metamorphosis (e.g. Morse et al. 1988, Morse et al. 1996, Heyward and Negri 1999). For example, the larvae of seven species in two genera of Caribbean agariciids settle and metamorphose in response to chemosensory recognition of a morphogen associated with the cells walls of CCA (Morse and Morse 1991). Similar metamorphic requirements of larvae in many species of Pacific corals from the families Acroporidae and Faviidae suggest the existence of a common chemosensory mechanism predating the phylogenetic divergence of these families (Morse et al. 1996). The requirement for this cue in these larvae is highly stringent and specific (Morse et al. 1996). Larvae do not metamorphose in the absence of CCA and when presented with a choice of algae, live corals, various inert substrata typical of those used in studies of coral settlement, fouled panels and CCA, settlement and metamorphosis occurred exclusively on certain species of CCA (Morse et al. 1996 but see Heyward and Negri 1999). The larvae of both brooding and broadcast spawning corals require these cues for the induction of metamorphosis which persists for the duration of larval competence (Morse and Morse 1990, Morse et al. 1996).

However, not all coral larvae appear to require CCA to induce metamorphosis. Recent experimental work by Heyward and Negri (1999) indicated that cues associated with substrata other than CCA, such as coral rubble, can induce metamorphosis in the larvae of broadcast spawning corals. Similarly, Negri et al. (2001) have used bacteria isolated from the surface of CCA to induce metamorphosis in coral larvae. Lewis (1974) recorded higher densities of the larvae of *Favia fragum* on unconditioned glass surfaces than on surfaces which had developed a biological film. In addition, many early studies of larval behavior in Indo-Pacific brooding species, including the pocilloporids *Stylophora pistillata*, *Seriatopora hystrix* and *Pocillopora damicornis* report settlement on surface which had not been conditioned (Atoda 1947 a & b, 1951; Harrigan 1972). A number of ecological traits suggest pocilloporids larvae may be less specific in their substratum preference. Pocilloporids are generally the first to recolonise reefs following disturbance and dominate early successional assemblages on primary reef substrata (Connell 1973; Loya 1976a). For example, 87% of the colonies and 90% of the cover on 1.6 years old larvae flows were *Pocillopora meandrina* (Grigg and Maragos 1974). Similarly, 70% of the juveniles recruits on pumice were pocilloporids (Jokiel 1990). Furthermore, pocilloporid recruits are more abundant than species with specific substratum requirements, such as the *Acropora*, on substrata with little CCA, such as the shaded substrata under *Acropora hyacinthus* tables (Baird and Hughes 2000). Finally, the phorbol ester TPA can induce metamorphosis in larvae of *Stylophora pistillata* (Hennig et al. 1996)

The extensive circumstantial evidence cited above led me to hypothesize that pocilloporid larvae may not require CCA to induce metamorphosis. To test this

hypothesis I examined the induction of metamorphosis in planulae of the pocilloporid, *Stylophora pistillata,* and the acroporid *Acropora palifera.*

4.2 Materials and methods

Stylophora pistillata forms compact bushes with thick club-shaped branches and is common in shallow water exposed to strong wave action (Fig. 4.1; Veron 2000). On the Great Barrier Reef (GBR), *S. pistillata* releases brooded planulae in the 3rd lunar quarter for an extended period over the summer months (Tanner 1996). *Acropora palifera* ranges in morphology from encrusting plates, massive colonies with thick ridges, to columnar or arborescent colonies and is common in most reef environments (Fig. 4.1; Veron 2000). On the GBR, *A. palifera* releases brooded planulae for an extended period over the summer months (Kojis 1986).

Five to 8 colonies of *Stylophora pistillata* and *Acropora palifera* were collected from 2 – 5 m depth at Pelorus Island, in the central GBR (18°46'S, 146°15'E) in November 1996 and maintained individually in 40 L flow-through aquaria. *S. pistillata* planulae swim to the water surface following release allowing them to be collected in containers lined with 300 μm plankton mesh positioned beneath the aquaria outflow. In contrast, *A. palifera* planulae swim to the bottom to explore the substratum and consequently, the planulae were collected with a 4 mm diam. siphon. Larvae were washed in 0.2 μm-filtered seawater containing 0.2 μg/ml of the anti-bacterial rifampicin then placed in assay containers.

To examine the induction of metamorphosis in *Acropora palifera* and *Stylophora pistillata*, planulae were introduced into cups containing various materials to see how

the planulae would respond. These materials included: a glass cover slip; small chips of an unconditioned clay tile of the type commonly used to sample coral recruits on the reef (e.g. Mundy 2000); chips from a similar tile which had been conditioned by placing it on the reef flat at 2 m depth for 8 weeks; small pieces of coral rubble collected from the reef flat; 3 species of CCA *Peyssonnelia sp.*; *Hydrolithon sp.*; *Porolithion sp.*; and the brown algae *Lobophora sp.* These materials were all placed in 15 ml of 0.2 μm filtered-seawater (FSW) in 20 ml polystyrene disposable cups. Two types of control were used; 0.2 μm FSW alone and unfiltered seawater. Assays where performed by placing 5 larvae in two replicate cups in each of the above 10 treatments.

Reef rock encrusted with colonies of *Peyssonnelia sp.*, *Hydrolithon sp.* and *Porolithion sp.* was collected from the habitat of the study species. CCA were carefully cleaned of macroscopic epibionts and chipped off the substratum. Chips were washed in 0.2 μm-FSW containing 2 μg/ml rifampicin to eliminate bacteria associated with the surface of the CCA. Approximately 1 mm^3 of CCA was placed in each of the relevant cups. *Lobophora sp.*, a brown algae, was similarly collected and small pieces were torn from the thallus, treated with rifampicin, and placed in the assay containers.

The planulae were given 64 h following their introduction to the assay containers to complete metamorphosis. Metamorphosis was defined as the deposition of a skeleton, which was clearly visible through the juvenile coral tissue. In these species, a skeleton begins to be secreted within 12-24 hours of settlement (Baird and Babcock 2000, and see also Chapter 2). One-way ANOVA was used to test for significant differences in the mean number of larvae metamorphosed in each treatment.

4.3 Results and discussion

The induction of metamorphosis in the planulae of *Stylophora pistillata* was neither stringent nor specific to CCA. Some settlement occurred in all treatments, except *Lobophora sp.* (Fig. 4.2). Settlement was, however, significantly higher in unfiltered seawater and a high proportion of planulae also settled on the glass cover slip (Fig. 4.2, Table 4.1). While CCA did not prevent metamorphosis, the proportion of planulae settling was generally low and ranged from 20% in *Hydrolithon sp.* and *Porolithion sp.* to 40% in *Peyssonnelia sp.* (Fig. 4.2). Few planulae settled on the conditioned and unconditioned chips, and coral rubble (Fig. 4.2). Settlement occurred on the substrata when provided. In the CCA treatments and other treatments which did not include substrata, planulae settled on the side of the assay containers.

Settlement of *Stylophora pistillata* was 3 times higher in the assay that included a glass cover slip compared to the control which contained 0.2 μm FSW only (Fig. 4.2). This suggests that the physical properties of the glass surface may influence rates of metamorphosis. Similarly a higher proportion of planulae settled on the glass slide than on any of the other materials, suggesting *S. pistillata* larvae prefer smooth surface over rough surfaces. A preference for smooth surfaces in *S. pistillata* may explain the higher relative abundance of *S. pistillata* and other pocilloporid recruits on smooth substratum in the ocean (Loya 1976a, Wallace and Bull 1982, Harriott and Fisk 1987)

Some settlement of *Stylophora pistillata* occurred even in sterile sea water (Fig. 4.2). This indicates that *S. pistillata* does not necessarily require the formation of a biofilm to induce settlement, which is a precursor to settlement in most other marine invertebrate larvae (Scheltema 1974). However, as the highest settlement occurred in the treatment

which contained un-filtered seawater, settlement may nonetheless be enhanced by a biofilm or by other organisms, such as bacteria, or other molecules present in the un-filtered seawater. Morse (1990) has described how the sensitivity of the morphogenic response to CCA in larvae of the abalone *Halotis rufescens* is greatly amplified by low concentration of various amino acids in seawater. The high proportion of planulae settling in the seawater treatment suggests a similar pathway may induce metamorphosis in *S. pistillata.* While the specific morphogenic trigger for *S. pistillata* remains unclear from these experiments, the settlement patterns in the various treatments indicate that many factors such as the physical properties of the surface, the presence of water born cues or other organisms, are involved in the metamorphosis of *S. pistillata* planulae.

In contrast to the patterns of settlement in *Stylophora pistillata*, settlement of *Acropora palifera* planulae occurred only in the treatments containing CCA (Fig. 4.2), demonstrating that a specific and stringent requirement for CCA is present in both brooded and broadcast spawned *Acropora* larvae confirming that the mechanism is independent of the mode of reproduction in this genera (Morse et al. 1996). However, even in the CCA treatments only a low proportion of planulae settled, ranging from 20 % in *Hydrolithon sp.* and *Porolithion sp.* to 50 % in *Peyssonnelia sp.*, which suggests that the response is not very stringent (Fig. 4.2). Similarly, Morse et al. (1996) reported that the stringency for CCA varied between *Acropora nasuta* and *A. digitifera. A. palifera* planulae maintained in the other treatments continued swimming or crawling for the duration of the experiment, except in the *Lobophora sp.* treatment in which planulae quickly became inactive and remained motionless on the bottom of the assay containers.

Interestingly, there was no settlement in the treatments containing a portion of a conditioned clay paving tile. These tiles have been very successful in collecting coral recruits in the field (e.g. Hughes et al. 1999 & 2001). We suggest this apparent contradiction occurred because only a small fragment of the conditioned tile could fit in the assay containers. Consequently this fragment may not have included a high enough abundance of CCA, or other organism, to induce metamorphosis in *Acropora palifera.*

No settlement of either species occurred in the treatment containing the brown algae *Lobophora sp.* (Fig. 4.2). The planulae of both species in this treatment quickly stopped swimming and sunk to the bottom of the assay containers where they remained motionless for the duration of the experiment. The behavior of the planulae in this treatment suggest *Lobophora sp.* may contain secondary metabolites which inhibit settlement in coral larvae. Similarly, Morse et al. (1996) found that the larvae of a number of acroporid species did not settle in assays which included *Lobophora variegata.* Many algae contain secondary metabolites with anti-fouling properties (Hay 1987) and the maceration of *Lobophora sp.* in these experiments may have released these secondary metabolites into the assay containers. It remains to be established whether this allelopathic effect is a feature of *Lobophora sp.* in the field.

Stylophora pistillata and other pocilloporids are important early successional species in coral assemblages in many parts of the world. For example, Loya (1976a) found *S. pistillata* was the only species to colonize the primarily substrata provided by a new sea water pipe for at least one year. Loya (1976b) has attributed the success of *S. pistillata* as a pioneer to early reproduction, high fecundity, a long breeding season and a fast

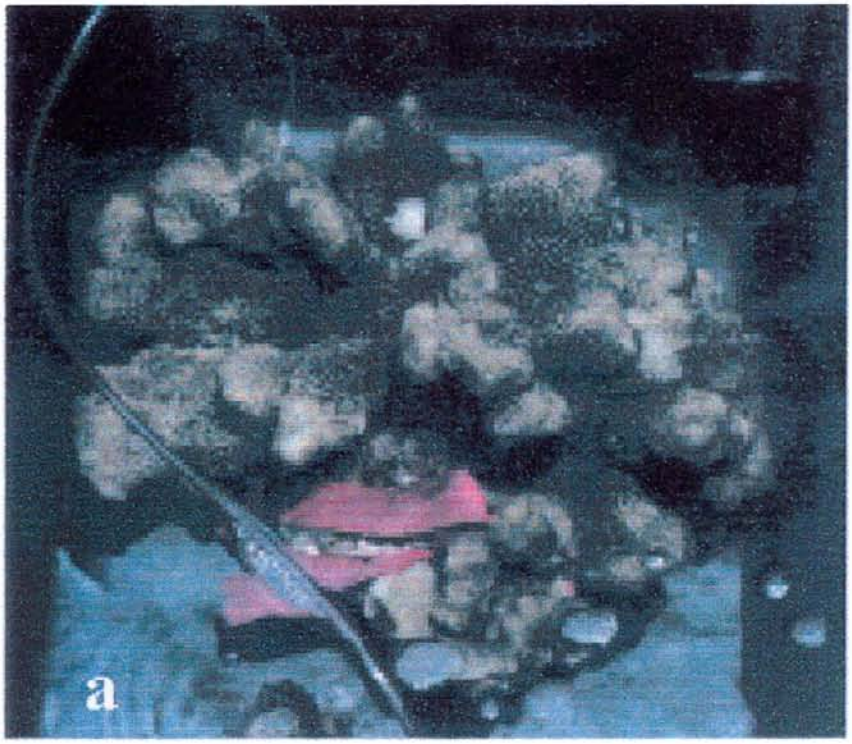
growth rate. While these life history traits are undoubtedly important, our results suggest that the success of *S. pistillata* may depend the fact that planulae do not require chemical cues, such as CCA to induce metamorphosis. Dead corals and primary substrata in the marine environment are quick to be colonized by filamentous algae in all reef environments, however, succession from filamentous algae to CCA assemblages may take much longer (Klumpp and McKinnon 1992). For example, CCA had covered only 10% of the surface area of settlement tiles after 9 weeks on the reef crest (Baird and Hughes 2000). Consequently, species which require chemical cues to induce metamorphosis may need to wait up to 9 weeks for new substrata to become suitable for settlement. In contrast, *S. pistillata* planulae can colonize substrata as soon as it becomes available, allow it to pre-empt species which may be better competitors as adults.

The difference in settlement requirements between *S. pistillata* and most other corals examined suggests there will be an inherent bias towards pocilloporids on primary substrata such as those used in settlement studies and account for the observation that pocilloporid recruits are consistently more abundant as recruits when compared to their relative abundance in adult assemblages (Hughes et al. 1999). Nonetheless, the effectiveness of these substrata in attracting recruits with as little as 10 days conditioning (e.g. Hughes et al. 2001), suggests either that cues provided by CCA are effective even at low cover, or the presence of an amplifier pathway similar to that described in the larvae of the abalone *Haliotis rufescens* (Morse 1990).

Table 4.1 ANOVA testing for significant differences in the mean number of planulae of *Acropora palifera* and *Stylophora pistillata* metamorphosed in 10 different treatments. Five larvae were placed in two replicate cups in each treatment.

Source	df	Mean Square	F	Sig.
species	1	8.1	13.5	0.002
treatment	9	2.5	4.2	0.004
spp. * treat.	9	2.1	3.5	0.009
Error	20	0.6		
total	39			

Figure 4.1 Study species. (a) *Acropora palifera* (b) *Stylophora pistillata*



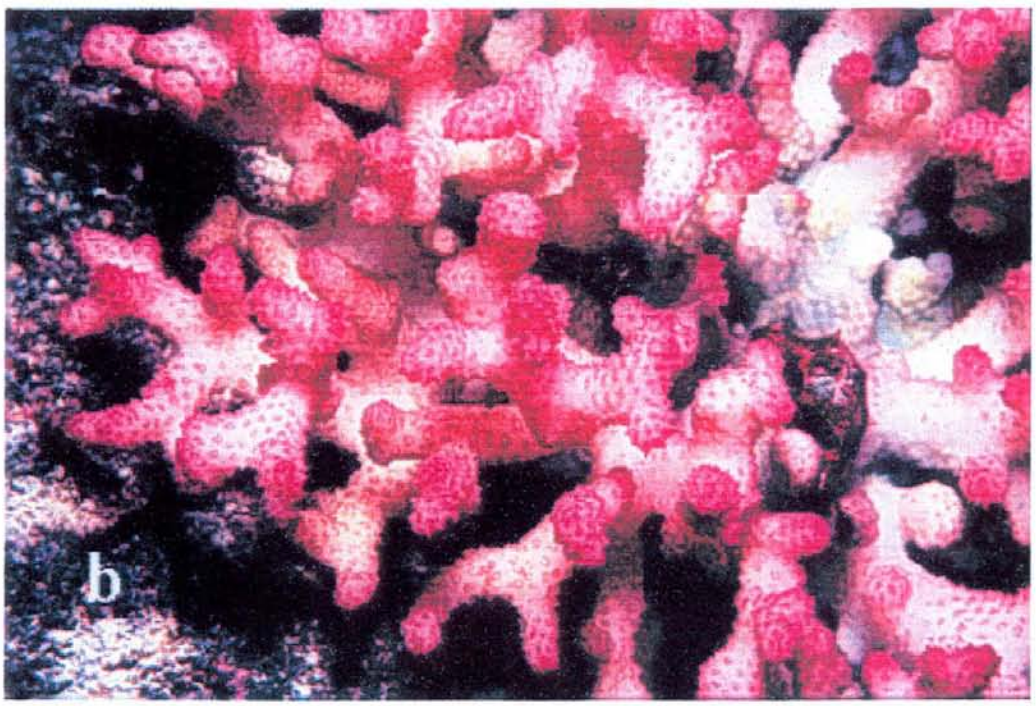
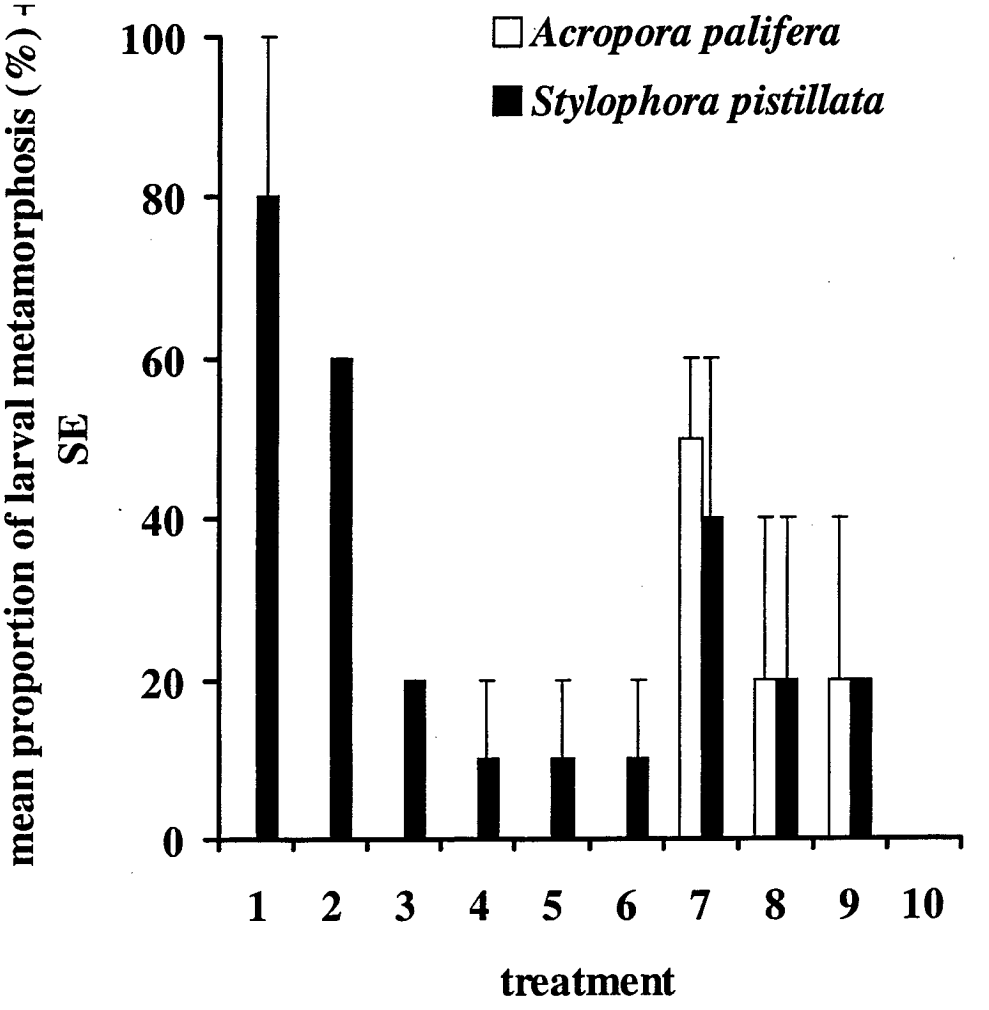


Figure 4.2 The mean proportion of larvae completing metamorphosis (%) + one standard error after 64 h. Assays involved 5 individuals in each of two trials (n = 2). Treatments were: 1 = unfiltered seawater; 2 = cover slip; 3 = 0.2 μm FSW; 4 = unconditioned tile; 5 = conditioned tile; 6 = clean coral rubble; 7 = *Peyssonnelia sp.*; 8 = *Hydrolithon sp_1*; 9 = *Porolithion sp.*; 10 = *Lobophora sp.* In each treatment, except unfiltered seawater, the material was placed in 15 ml of 0.2 μm filtered seawater in 20 ml polystyrene cups.



CHAPTER 5 The length of the larval phase in corals

5.1 Introduction

One of the major goals in marine ecology is to determine the patterns of connection between populations. The majority of reef organisms have a complex life history with a sedentary adult stage followed by a planktonic larvae (e.g. Scheltema 1986). The prevailing paradigm for marine organisms is massive export of propagules from the reef of origin followed by wide dispersal with the result that reef populations are connected by the exchange of larvae over large spatial scales (Palumbi 1994; Caley et al. 1996). However, recent research has indicated a surprising proportion of larvae may be retained locally, even in species with long larval duration. For example, Jones et al. (1999) used mark and recapture of larvae to estimate that 15-60 % of the recruits of the coral reef fish, *Pomacentrus amboinensis*, were of local origin on Lizard Island. Similarly, Swearer et al. (1999) determined that recruitment to an island population of a widely distributed coral-reef fish was often the result of local retention on leeward reefs. Other evidence to suggest at least some degree of self-recruitment in marine populations includes unexpectedly sub-divided genetic structure of some marine populations (Plaines 1993; Ayre and Hughes 2000), the persistence of endemic species with pelagic larvae on small isolated islands (Hourigan and Reese 1987), the persistence of populations following marine introductions (Baltz 1991), the persistently high concentration of coral larvae within the reef lagoon for up to 5 days following spawning (Willis and Oliver 1988) and the relationship between larval production and larval supply in reef fish (Meekan et al. 1993) and corals (Hughes et al. 2000).

For most of the last century it was generally accepted that the majority of coral recruits were of local origin (e.g. Done 1982). The basis of this assumption was that most of the corals studied at this time brooded larvae which were ready to settle within hours of release (Harrison and Wallace 1990). However, this assumption was challenged by the finding that the vast majority of corals were broadcast spawners releasing gametes into the water column for external fertilization and development (Harrison et al. 1984, Shlesinger and Loya 1985, Willis et al. 1985, Babcock et al. 1986), with settlement commencing between 4 and 6 days after the release of gametes (Babcock and Heyward 1986). On the basis of these observations, and the fact that coral propagules are, at least initially, positively buoyant, most authors concluded that the majority of planulae would be dispersed away from the reef of origin (e.g. Harrison et al. 1984, Babcock and Heyward 1986). This conclusion was supported by plankton tows following the coral mass spawn on the Great Barrier Reef which showed that the majority of propagules accumulated at the surface and were then dispersed offshore within 12 h (Bull 1986; Willis and Oliver 1988). Furthermore, aerial observations revealed that in calm conditions coral propagules aggregated into surface slicks which were transported off the reef (Oliver and Willis 1987, Willis and Oliver 1990). Sampling around drogues placed in slicks indicated that larvae could travel 26 km down current within 2 days (Willis and Oliver 1988). Nonetheless, significant concentrations of planulae were also entrained in back reef eddies and within the reef lagoons for up to 5 days (Willis and Oliver 1988).

The assumption that most coral larvae would be exported form the reef of origin was initially challenged by Sammarco and Andrews (1987) who recorded high rates of coral recruitment in areas close to Helix reef, where hydrographic models predicted eddies

would form to trap coral larvae. However, as the source of the recruits could not be identified, the conclusions of this study were rightly challenged (Willis and Oliver 1990). However, recent work on the GBR has again raised the possibility that self-recruitment may be higher than expected in some coral populations. Ayre and Hughes (2000) estimated the population structure of a number of brooding and broadcast spawning corals on the GBR and found that, contrary to the prediction of regular dispersal between reefs, there was "considerable genetic subdivision among sites within reefs suggesting that larval dispersal is surprisingly limited even in species with a relatively long larval duration". In addition, Hughes et al. (2000) demonstrated that recruitment of corals was consistently higher on reefs in regions where a high proportion of corals were gravid indicating that there was a strong relationship between local production of larvae and recruitment. In this chapter, I perform a series of experiments in an attempt to reconcile these apparent contradictions.

The larval phase of corals can be divided into a pre-competent stage, characterized by rapid morphological and physiological development, and a competent stage, where the larva is able to settle but may delay doing so in the absence of the necessary cues (Scheltema 1986). Coral larvae have relatively poor powers of locomotion when compared to most other marine invertebrate larvae (Chia et al. 84; Fadlallah 1983) and therefore the patterns of dispersal will be largely determined by the interaction between larval competence periods and the prevailing hydrodynamic conditions. The hydrodynamic environment around reefs have typically been examined with the use of mathematical models. For example, Williams et al. (1984) predicted that after 4 days 90% of particles would be exported from the reef of origin and stated that "within a few days, if not hours, of hatching planktonic larvae are likely to be flushed out of the natal

reef and into the mainstream shelf current". In contrast, Black et al. (1991), predicted the formation of eddies in the lee of reefs that could persist for up to a week, thereby providing a mechanism by which some larvae might be retained, and concluded that reefs did have the potential to be self-seeded. However, while these models provide information necessary to determine the extent of dispersal, they are not in themselves sufficient. To predict the potential for localised recruitment it is necessary to determine not only how many larvae may be retained in the vicinity of reefs for how long but also what proportion of the larvae will settle within this period (Butler and Keough 1990). Indeed, it is the proportion of the larvae that is critical. A simple estimate of the time until first settlement is inadequate to address this issue. Similarly, while mathematically models can predict the proportion of larvae exported, the time it will take larvae to travel between reefs, and the proportion of larvae trapped by reefs downstream, the ultimate degree of connection between reef populations will depend on features of the biology and ecology of larvae including, larval survivorship within the plankton, the proportion of surviving larvae that remaining competent to settle and the condition of recruits following settlement. In this chapter, I provide empirical data on the key issue of changing settlement competencies through time.

Opinion is also divided on the potential of corals for long distance dispersal and its biogeographical significance particularly with respect to the origin and maintenance of coral assemblages in remote and isolated regions (Harrison and Wallace 1990). For example, Heck and McCoy (1978) challenged Dana' s (1975) hypothesis of an Indo-Pacific origin for corals in the Eastern Pacific largely on the basis of a lack of evidence for teleplanic dispersal. Surprisingly, Heck and McCoy's (1978) criticism remains valid and the assumption of regular long distance dispersal in corals is based almost entirely

on adult distribution patterns and biogeography. Certainly, most coral species have a wide geographical range and there are relatively few endemic coral species (Veron 1995). However, empirical support for the assumption is limited. The potential for long distance dispersal depends primarily on how long coral larvae can remain in the plankton whilst retaining the ability to settle and metamorphose. Richmond (1988) modeled the dispersal potential of coral larvae on the basis of initial energy content and energy consumption and predicted a maximum competence period of 20 days in *Acropora tenuis*. However, the specific assumptions used in the model and this prediction remain untested. Another way to estimate the dispersal potential of larvae is to observe the duration of active swimming. For example, Harrison et al. (1984) kept coral larvae alive for 7 – 90 days and the larvae of *Pocillopora damicornis* can swim for 212 days (Harrigan 1972). However, longevity is not necessarily a reliable indicator of larval dispersal potential because once the energy reserves of the larvae drop below a certain threshold, settlement and metamorphosis will no longer be possible. Empirical estimates of coral larval competence are few. Richmond (1987) demonstrated that 3 of 5 surviving larvae of *P. damicornis* could metamorphose after 103 days. However, this value of this data is limited because the proportion of the cohort that survived was not provided. Similarly, some larvae of *Cyphastrea seriala*, *Goniastrea australiensis* and *Acanthastrea lordhowensis* metamorphosed after 26, 56 and 78 days respectively (Wilson and Harrison 1998). However, in this experiment larvae were continually exposed to the chemical cues required to induce metamorphosis. Thus, the proportion of these cohorts remaining competent under the more realistic scenario that they were deprived of chemical cues (i.e. adrift in the plankton), cannot be established and consequently, the value of this data as an estimate of the long distance dispersal potential of these species is unclear.

In this Chapter, I address the patterns of coral dispersal by examining larval competence under two distinct scenarios. In the first experiment, I examine how larvae behave if retained near the reef of origin (i.e. in the presence of cues required to induce metamorphosis). Here, my aim was to asses the likelihood of localised dispersal by quantifying the proportions of planulae settling over time from single cohorts from a number of species. In the second experiment, I examine how larvae behave in the event they are dispersed away from the reef of origin. Here, I assess the potential of coral larvae to disperse over long distances by quantifying how long larvae remain competent.

5.2 Materials and methods

5.2.1 Study species

Seven broadcast spawning corals and two brooding corals were used in the following series of experiments (Table 5.1). *Acropora gemmifera* forms sturdy, digitate to corymbose colonies and occurs inter-tidally and sub-tidally on reef tops and upper slopes (Fig. 5.1 d, Wallace 1999). *Acropora humilis* forms sturdy, digitate to corymbose colonies and occurs inter-tidally and just sub-tidally on reef tops and upper slopes to about 5m (Fig. 5.1 b, Wallace 1999). *Acropora pulchra* forms open arborescent, thicket like colonies and occurs on reef flats and shallow habitats or inter-tidal reef lagoons (Fig. 5.1 c, Wallace 1999). *Acropora millepora* forms corymbose colonies and occurs on inter-tidal reef flats or in shallow sub-tidal areas to 3m (Fig. 5.1 a, Wallace 1999). *Acropora valida* forms small rounded corymbose colonies or thick tables and occurs inter-tidally on outer reef flats and sub-tidally on the reef edge (Fig. 5.1 e, Wallace 1999). *Acropora valida* is the most widely distributed species of *Acropora*, and is found from the west

coast of Africa to the Eastern Pacific, and is present and abundant at most localities throughout this range (Fig. 5.2 e). *A. humilis* is another widely distributed and abundant *Acropora* found from the east coast of Africa to French Polynesia and is one of only 3 *Acropora* to occur in Hawaii (Wallace 1999). In contrast, *A. gemmifera, A. pulchra* and *A. millepora* are generally restricted to the central Indo-Pacific with only a few scattered records of these species west of Sumatra (Fig. 5.2). *Goniastrea retiformis* colonies are massive or columnar and usually the dominant species on inter-tidal reef flats (Fig. 5.1 f, Veron 2000). *Platygyra daedalea* forms massive to encrusting colonies and is common in a wide range of habitats, especially back reef margins (Fig. 5.1 g, Veron 2000). *Seriatopora hystrix* colonies are bushy with thin, delicate branches (Fig. 5.3 a). *S. hystrix* is found from Africa in the West to Samoa in the East (Veron and Pichon 1978). *Stylophora pistillata* forms compact bushes with thick branches and is found from Africa in the West to Pitcairn Island in the East (Fig. 5.3 b, Veron and Pichon 1978).

5.2.2 The potential of larvae for localised recruitment

To establish the potential for localized recruitment, I quantified the proportions of larvae settling over time from single cohorts of these species. Broadcast spawning larvae were cultured as described above (Chapter 2.2; see also Table 5.1 for date and time of gametes release) and when the majority were motile, 330 to 1200 larvae, depending on availability (Table 5.2), were individually counted into two replicate aquaria containing two clay paving tiles (5 x 5 x 1 cm) conditioned for 6 weeks in the adult habitat as a settlement substratum. The experiments were performed in the laboratory under constant temperature (26 – 28 ^{O}C) and the tanks were positioned under a combination of blue actinic and white light with a 12 h light then 12 h dark photo-period. The tiles were removed and replacements introduced on days 4, 7 10 & 14 following fertilization. All

tile surfaces were censused in a water bath using a stereo-dissecting microscope and the number of larvae completing metamorphosis was counted. Metamorphosis was defined by the deposition of a skeleton which was visible through the tissue of the developing polyp. To establish the potential for localised recruitment in *Seriatopora hystrix* and *Stylophora pistillata*, the brooded larvae were collected as described above (Chapter 2.2) and 60 larvae introduced into each of two clear plastic jars per species containing unfiltered seawater. The number of larvae which had settled on the side of the jars was counted every 6 h. Unlike the Acroporidae and Faviidae, the larvae of many pocilloporids e.g. *S. pistillata* do not require conditioned surfaces to induce metamorphosis (see Chapter 4).

5.2.3 Larval development

The rate of embryogenesis in four species, *Acropora gemmifera*, *A. millepora*, *A. valida*, *Platygyra daedalea*, was quantified from samples of between 20 – 50 embryos every 6 hours following egg release for 72 hours. The number of larvae in each of the following stages of development were counted: egg; 2-cell stage; 4-cell stage; 8 to multicellular blastula; early gastrula; late gastrula; early larva; motile larva; elongate larva (Fig 5.4).

5.2.4 The potential for long-distance dispersal in broadcast spawning larvae

To investigate the potential of corals for long distance dispersal, I estimated the proportion of the larval cohort remaining competent to settle through time of the broadcast spawning species, with the exception of *Acropora humilis* (Fig. 5.1). Larval cohorts were maintained in 3.5 L polystyrene containers containing 0.2 μm filtered seawater to deprive them of the cues required to induce settlement (e.g. Morse et al.

1996) at densities of approximately 1000 larvae per liter. At various intervals after spawning, samples of between 5-100 of the surviving larvae were pipetted from the cultures and introduced into replicate 500 ml plastic buckets containing a single conditioned clay tile (Table 5.3). These larvae were left for 72 hours after which the tiles were removed and the number of larvae successfully completing metamorphosis recorded. No metamorphosis was recorded on the sides of the containers. The experiments were performed in the laboratory under the same conditions as described above.

Larval survivorship was measured by estimating the change in the number of larvae remaining in the culture containers through time. Three replicate 50 ml water samples were collected following agitation of the culture on each occasion the 0.2 um filtered seawater was changed (Table 5.4). When the number of larvae remaining dropped below 200 they were counted individually.

The mean size of the larvae through time was estimated from samples of between 12-30 larvae. Size of the larvae was measured as the half the sum of larval length and breadth in order to enable a comparison to egg size which was measured as the diameter of the spherical eggs.

5.3 Results

5.3.1 The potential of larvae for localised recruitment

Striking differences were apparent in the patterns of settlement between the species. In *Acropora valida*, *A. humilis* and *Goniastrea retiformis* the highest proportion of larvae settled (peak settlement) on, or before, day 4 (Fig. 5.5). This pattern was particularly prominent in *A. valida* and *G. retiformis* where 61% ± 5.9 and 61% ± 0.8 of the cohort had settled on, or before, day 4 respectively (Fig. 5.5). In contrast, peak settlement of *A. millepora*, *A. gemmifera* and *Platygyra daedalea* occurred between 4 - 7 days after spawning (Fig. 5.5). In *A. pulchra* peak settlement of 8% ± 1.4 occurred on day 10 (Fig. 5.5). At least some larvae from each species had settled within four days of spawning, ranging from 6% ± 1.2 in *A. pulchra* to 61% ± 5.9 in *A. valida* (Fig. 5.5).

Considerable variation in the age at settlement was apparent between individual larvae within all cohorts. For example, some *Acropora pulchra* and *A. millepora* larvae settled 10 days after others in the cohort (Fig. 5.5). This variation was less pronounced in *A. valida* and *A. gemmifera* where settlement was concentrated in the week following spawning (Fig. 5.5).

Profound differences were also evident in the total proportion of the cohorts that settled in each species. In the faviids, *Platygyra daedalea* and *Goniastrea retiformis*, 90% of the larvae had settled within the 14 day duration of the experiment (Fig. 5.6). The proportion of *Acropora* settling ranged from 20% in *A. pulchra* to 70% in *A. valida* and *A. millepora* (Fig. 5.6).

The larvae of the brooding species *Seriatopora hystrix* and *Stylophora pistillata* settled very rapidly. Within 6 hours of release, 50% of the larvae had settled (Fig. 5.7). Within 24 hours of release, 65% of *S. hystrix* and 68% of *S. pistillata* larvae had settled (Fig. 5.8). A small proportion of the larvae settled sporadically over the next week and the total proportion of the cohort that settled approached 80% in each species (Fig. 5.8).

5.3.2 Larval development

The rates of embryogenesis were similar among the three *Acropora* species examined in detail (Fig. 5.9 & 5.10). Cleavage commenced with 2 h and after 12 h the majority of embryos had reached the early gastrula stage (Fig. 5.9 & 5.10). After 24 h embryogenesis was largely complete in all *Acropora* (Fig. 5.9 & 5.10). Motile larvae were first observed after 36 h and between 48 h – 54 h, 50% of the cohort became motile (Fig. 5.9 & 5.10). After 72 h, all *Acropora* larvae were motile (Fig. 5.9 & 5.10). Qualitative observations of *A. humilis* and *A. pulchra* indicated a similar rate of development. In contrast, the larvae of *Platygyra daedalea* developed more quickly than the *Acropora*. Embryogenesis was largely complete within 12 h when 94% of the embryos were late gastrula and 6% non-motile larvae (Fig. 5.10). Fifty percent of the cohort was motile after 18 h and all larvae were active after 36 h (Fig. 5.10). A similar rate of development was observed in *G. retiformis*. Consequently, larvae of the faviids were motile in half the time it took for the *Acropora*. The larvae of *Seriatopora hystrix* and *Stylophora pistillata* were motile on release.

The rate of larval development of the broadcast spawning species was highly correlated with the size of the eggs on release. A regression of the time to onset of larval motility against egg size was highly significant with smaller eggs becoming motile more quickly

(Fig. 5.11). However, despite the fact that the larvae of species with smaller eggs developed more rapidly, they did not appear to settle in abundance any earlier and there was no correlation between peak settlement and egg size (Fig. 5.12). For example, *Acropora* species have similarly sized eggs (Table 5.1) yet peak settlement occurred on day 4 in *A. valida*, on day 7 in *A. millepora* and *A. gemmifera*, and on day 10 in *A. pulchra* (Fig. 5.5). Furthermore, despite the eggs of the *Acropora* being considerably larger than those of the faviids, some larvae of all species had settled on or before day 4 (Fig. 5.5).

5.3.3 The potential for long-distance dispersal in broadcast spawning larvae

In the *Acropora*, the proportion of the cohort competent to settle rose to a peak of over 50% between days 7 and 11 although the peak was less pronounced in *A. valida*, in which 55% ± 5.0 of the cohort was competent to settle after 3 days (Fig 5.18). In *A. gemmifera* and *A. pulchra* competence dropped rapidly from this early peak to less than 20% after 14 days (Fig 5.18). No *A. pulchra* larvae survived beyond 14 days (Fig 5.18). Ten percent ± 0.0 of *A. gemmifera* remained competent to settle on day 34 after which no more larvae settled despite some larvae surviving for 60 days (Fig 5.18; Table 5.4). In contrast, over 50% of the cohorts of *A. millepora* and *A. valida* remained competent to settle for 30 days (Fig. 5.13). Few *A. millepora* larvae settled after this with only 5% ± 2.0 competent on day 60 (Fig. 5.13). No further settlement was recorded in *A. millepora* despite some larvae surviving for 110 days (Table 5.4). In contrast, the larvae of *A. valida* had an extraordinary capacity to delay metamorphosis with 30% ± 5.2 of surviving larvae settling on day 60, 10% ± 2.5 on day 90 and 5% on day 110 (Fig. 5.13). Some *A. valida* larvae remained alive for 130 days although no more larvae settled (Table 5.4).

Peak competence occurred on day 3 in *Goniastrea retiformis*, when 67% ± 5 of the surviving larvae settled, after which it dropped rapidly to 27% ± 4.5 on day 11 (Fig. 5.14). The proportion of the cohort competent to settle then increased to 45% ± 3.75 on day 21 after which it fell again to 10% ± 0 on day 36 (Fig. 5.14). No further settlement was recorded despite some larvae surviving for 60 days (Fig. 5.14; Table 5.4). In contrast, the proportion of the cohort of *Platygyra daedalea* competent to settle rose gradually to peak at 52% ± 2.5 on day 14 then dropped rapidly to 2.5% ± 2.5 on day 34 (Fig. 5.14). No more *P. daedalea* larvae settled although some larvae survived for 60 days (Fig. 5.14; Table 5.4).

High rates of mortality were evident in all species during the first month after which less than 10% of larvae remained alive in all species (Fig. 5. 20). Mortality rates were particularly high in the first 3 days of life in *Acropora pulchra* and *Platygyra daedalea* where 50% of the cohort died (Fig. 5.15). After 60 days, survivorship of *A. valida* larvae was 3 times higher than in the other species in which larvae were still alive (Fig. 5.15). Larvae were lost in a number of ways. A small number of larvae metamorphosed while still in the water column usually on the water surface (Fig 5.21a). Many larvae stuck to the bottom and side of the container where they quickly lost color and structure. Many others appeared to dissolve, forming fatty slicks on the surface of the water. A small number were lost when the water was being changed.

The size of surviving *Acropora valida* and *A. millepora* larvae varied little during the first month of life (Fig. 5.17). Later samples indicated that the larvae of these species could shrink to about 60% of their size at release and still settle (Fig. 5.17). The larvae

of *A. gemmifera* began to shrink after 14 days and after 60 days were approximately 66% of the size at release (Fig 5.22). In contrast, there was a relatively steady reduction in the size of faviid larvae over time and again few larvae survived once they had reached 70% of the size at release (Fig. 5.18).

5.4 Discussion

5.4.1 The potential for localised recruitment

The patterns of settlement within the cohorts of the broadcast spawning corals suggest that many coral larvae have a considerably shorter pre-competence period than the 4 - 7 days generally referred to in the literature (e.g. Harrison & Wallace 1990), a figure which is based on the time it took larvae to *begin* to settle (Babcock & Heyward 1986). For example, over 60% of the larvae of *Acropora valida* and *Goniastrea retiformis* had metamorphosed within 4 days of gamete release (Fig. 5.5). Furthermore, some settlement on, or before, day 4 was recorded in all species (Fig. 5.5). The discrepancy may be caused by many factors including difference in experimental conditions, such as temperature and light under which larvae were maintained, and genetic differences between cohorts, which in most cases, including the current study, originate from a small number of parents. Furthermore, as only one cohort was examined per species, the possibility of annual difference in the estimates of the proportion of cohorts settling through time cannot be eliminated. However, I believe the most likely cause of the difference was the comparative state of conditioning of the settlement substrata. The larvae of many broadcast spawning coral species require specific chemical cues to induce settlement and metamorphosis (e.g. Morse et al. 1988, Morse et al. 1996, Heyward and Negri 1999, Negri et al. 2001). In this experiment, the tiles were conditioned for 8 weeks at 3 m depth. Furthermore, all tiles were placed horizontally to

allow an even coating of crustose coralline algae to develop. A similar approach was not adopted in previous experiments (e.g. Harrison et al. 1984, Babcock & Heyward 1986). I conclude that when the necessary chemical cues to induce metamorphosis are present, the larvae of many species will settle more rapidly than previously considered providing corals with considerable potential for self-recruitment. Furthermore, larvae of the broadcast spawning species became motile between 18 - 36 hours, depending on the species, and a high proportion of larvae were motile within 24 – 48 hours (Fig. 5.9 & 5.10). Coral larvae typically begin to explore the substratum shortly after becoming motile (Harrison and Wallace 1990). If these larvae can swim strongly enough to influence their position within the water column, this may further enhancing the potential for self-recruitment. However, there was a large range in the response between individuals of the same species with some larvae settling up to 10 days later than others in the cohort, indicating that under most conditions there will also be export of propagules (Fig 5.5).

The ultimate number of larvae that recruit locally will depend on what proportion of the cohort remain within reach of the natal reef and for what length of time. Hydrodynamic models predict that rate of diffusion of propagules from the reef or origin depends critically on their buoyancy. For example, Gay & Andrews (1994) simulations predict a high proportion of negatively buoyant particles will be trapped indefinitely. In contrast, positively buoyant particles will be rapidly transported from the reef of origin in surface currents controlled by the wind (Gay & Andrews 1994). However, plankton tows have demonstrated that under conditions of light winds high densities of positively buoyant coral propagules persist within the reef lagoon and in eddies behind reefs for 5 days, although it is not known whether the larvae are of local origin or from an upcurrent reef

(Willis and Oliver 1988). The potential influence of larval settlement patterns on the degree of self-recruitment and genetic population structure of the species is best considered by examining the cumulative proportion of settlement through time (Fig. 5.6). This allows for the proportion of the cohort retained, and the proportion exported, under different scenarios of particle retention to be estimated. If we initially consider the, perhaps unlikely, scenario of 100% of larvae being retained in the vicinity of the reef of origin for 4 days, 60% of the larvae of *Acropora valida* and *Goniastrea retiformis* would recruit locally with the remainder of the cohort exported into the plankton (Fig 5.6). Similarly, 30% of *A. humilis* and *P. daedalea*, 15% of *A. millepora* and *A. gemmifera* and 6% of *A. pulchra* would be retained under these conditions (Fig 5.6). These species difference will be quantitatively similar no matter what the actual proportion of larvae retained. Such differences in the frequency distribution of settlement between species are likely to result in pronounced differences in the genetic structure of coral populations. Longer residence times will result in a higher proportion of larvae retained. Longer residence times will also result in the differences between the species in the proportion retained being reduced. For example, if larvae are retained for 7 days over 40% of larvae would be expected to recruit to the reef of origin in all species except *A. pulchra* (Fig 5.6).

Differences between these species in the proportion of cohorts settling through time (Fig. 5.6) lead to predictions of genetic population structure remarkable similar to those identified by Ayre and Hughes (2000) who used allozyme electrophoresis to examine the population structure of 14 coral species on the GBR. Two broadcast spawning species, *Acropora millepora* and *A. valida* were common to our studies. Under a scenario of particle retention of 4 days, 60% of larvae *A. valida* would recruit locally

compared to 12% of *A. millepora*. From this data one would predict (1) a more highly structured population within reefs and (2) lower rates of connection between reefs in *A. valida* than in *A. millepora*. This is precisely the pattern identified by Ayre and Hughes (2000). *A. valida* populations were more highly structured within reefs than *A. millepora* ($F_{(st)}$: 0.28 Vs 0.1) and there were lower levels of connection between the reefs as indicated by the number of migrants per generation (N_{em}: 12.3 Vs 24.8).

The brooded larvae of *Seriatopora hystrix* and *Stylophora pistillata* were competent to settle shortly after release, a feature which was also observed in the larvae of the octocoral *Heteroxenia fuscescens* (Benayahu et al. 1989). Consequently, the proportion of the brooded larvae of *S. hystrix* and *S. pistillata* retained on the reef of origin will be high under most conditions. For example, 50% of larvae would be retained with residence times of 6 hours and after 4 days 80% of larvae will be retained (Fig. 5.8). Atoda (1949b & 1951) found peak settlement of *S. hystrix* and *S. pistillata* occurred on the first day following release and while this result is consistent with data presented here, the finer resolution of the current study reveals that peak settlement in these species occurs within 6 hours of planulae release (Fig. 5.7). Nonetheless, planulae continued to settle for up to a week after release and some export of propagules is to be expected (Fig. 5.7). The population structures of these species predicted by such a short a pre-competence period are in strong agreement with those measured by Ayre and Hughes (2000). The populations of *S. hystrix* and *S. pistillata* were highly structured between sites within reefs ($F_{(st)}$: 0.28 & 0.18 respectively) and there was little migration between reefs (N_{em}: 1.4 & 2.5).

The ultimate patterns of connection between reef populations will depend on a number of factors including (a) the number of propagules exported (b) the proportion of larvae that survive to reach downstream reefs (c) the number of these propagules captured by downstream reefs and (d) the proportion of surviving larvae that remain competent to settle. For example, Black (1993) has predicted that while over 90% of the neutrally buoyant larvae of the crown-of-thorns starfish (COTS) will be transported off the reef of origin during their 7-10 day pre-competent period, less than 1% of exported propagules will be captured by reefs downstream within the 2-3 weeks that COTS larvae remain competent. While the actual number of larvae captured by a reef downstream depends on many factors, such as the distance between the reefs, the shape of the source reef and the size of the source reef, Black et al. (1991) predicted that few larvae will travel between reefs because currents direct larvae around downstream reefs, rather than capturing them. Extreme caution should be exercised when extrapolating the dispersal of coral larvae from a model designed to predict the dispersal of COTS. As discussed above, the proportion of larvae retained in a given time period is critically dependent on the buoyancy of the propagules (Gay & Andrews 1994). Most coral eggs are positively buoyant and rise to the surface from where they are transported off the reef of origin in surface currents within 12 h (Willis and Oliver 1990). However, coral larvae may become neutrally, or even negatively buoyant, soon after completing embryogenesis by "dumping" the lipid globules that aggregate in the coelenteron (Aileen Morse pers. comm.). Furthermore, coral larvae that are motile may be able to act as negatively buoyant particles. In addition, not all coral eggs are positively buoyant. For example, *Fungia* and *Pachyseris speciosa*, release neutrally buoyant eggs (pers. obs.) and *Goniastrea favulus* releases eggs which are negatively buoyant (Babcock 1984). Consequently, the rate of entrapment of coral larvae by reefs downstream is likely to be

similar to the rate of entrapment of COTS larvae. Furthermore, if the high rates of mortality in the larval cultures (e.g. 10% survival after 1 month Fig. 5.15) are similar to that in the plankton, then combined with low capture rates by reefs downstream, few exported propagules are likely to recruit successfully to populations downstream. In addition, larvae arriving on downstream reefs are likely to be smaller, particularly if they have spent over one month in the plankton (Fig. 5.16), resulting in smaller recruits (see Fig. 2.19). Post-settlement survivorship in corals is lower in smaller recruits (e.g. Loya 1976b, Rylaarsdam 1983). Consequently, post-settlement survivorship may be lower in recruits that develop from larvae that have spent an extended period in the plankton, further reducing the contribution of recruits which originate on distant reefs to the local population. Thus, even when a high proportion of the cohort is dispersed from the natal reef the majority of juveniles may still be of local origin, particularly on reefs isolated by a lack of connecting currents or distance.

5.4.2 Larval development

Survivorship of the larvae in culture was generally low, particularly in the initial 28 days (Fig. 5.15). While some mortality was the result of mechanical damage and loss of larvae during water changes, the water changes were necessitated by the large number of larvae lysing apart within the cultures. In addition, a small number of larvae metamorphosed while in the plankton, often on the water surface, and such metamorphosed larvae were not motile (Fig. 5.16 b). High mortality within larval cohorts, in the absence of any obvious cause, and the planktonic metamorphosis of some individuals suggests that the age at which metamorphosis occurs may be genetically pre-determined in each individual. Alternatively, this may indicate differences between eggs in quality and quantity of maternal energy supplied.

The length of time coral larvae spend in the plankton may be further extended if larvae can derive nutrition from within the plankton. While coral planulae are generally assumed to be non-feeding (Fadlallah 1983), this assumption has not been rigorously tested. The fact that surviving *Acropora* larvae did not begin to shrink until after 1 month (Fig 5.21) suggests that these larvae may have been able to supplement initial energy reserves with energy derived from another source, at least for the first month. The only possible source of nutrition in the cultures, in which the water was filtered to 0.2 μm, is dissolved organic material (DOM), which is an important source of nutrition in many marine invertebrate larvae (Manahan 1990). In the plankton, coral larvae may feed in a number of ways. For example, the larvae of *Caryophyllia smithi* trail strings of mucus which trap particles for ingestion (Tranter et al. 1982). *Pocillopora damicornis* planulae can develop tentacles which may be capable of capturing particles (Richmond 1981). Larvae with partially differentiated tentacles were observed in *Acropora millepora* (Fig 5.21 b). In contrast to the planktonic metamorphosis described above, (Fig 5.21 a) these larvae remained motile. Lipid globules in the coelenteron of *Stylophora pistillata* planulae were considered evidence of planktonic feeding (Rinkevich and Loya 1979). However, similar lipid globules were present in the coelenteron of all the broadcast spawning larvae I examined, following embryogenesis, and probably result from the aggregation of lipid vacuoles, which are abundant in the eggs of many coral species (e.g. Arai et al. 1993). Finally, the eggs and larvae of some coral species contain zooxanthellae on release, and others are capable of taking up zooxanthellae while in the plankton (e.g. Krupp 1983). Zooxanthellate larvae may be capable of utilizing photosynthetic products from their symbionts, as was demonstrated in *Pocillopora damicornis* (Richmond 1981). If the energy production of symbiosis exceeds consumption, planktonic duration may be extended beyond that determined by

initial energy reserves. Clearly these are aspects of the biology and physiology of planulae that require further exploration.

The size of propagules was highly and inversely correlated with the of rates of development in broadcast spawning corals (Fig. 5.11). However, there was no correlation between size and the pre-competence period as suggested by Ayre and Hughes (2000). The minimum pre-competent period was less than 4 days in all species (Fig 5.5), despite significant difference in the size of eggs (Table 5.1). Size was also a poor predictor of the day of peak settlement which differed markedly between the species, occurring on or before day 4 for *Acropora valida* and *A. humilis*, day 7 for *A. millepora* and *A. gemmifera* and day 10 for *A. pulchra*, despite little difference between the size range of eggs in these species (Fig. 5.12). Nor was the size of larvae correlated with the pre-competent period in the pocilloporids, where peak settlement in *Stylophora pistillata* and *Seriatopora hystrix* occurred within 6 hours, despite differences in the mean size of larvae between the species (Table 5.1).

5.4.3 Long distance dispersal and coral biogeography

The ability of coral larvae to remain competent for extended periods has important implications for the biogeography and evolution of corals. These data indicate that teleplanic dispersal may be a regular phenomenon in hard corals, as has been demonstrated in some octocorals (Zaslow et al. 1996), and confirms the assumption of many previous authors (e.g. Vaughan 1907, Potts 1985). For example, Veron's (1995) theory of Surface Circulation Vicariance states that evolutionary change in corals is driven by changing patterns of ocean currents that alternately switch between being barriers to dispersion and vehicles of transport. This theory depends entirely on long distance dispersal being a regular feature of coral life histories. The results presented

here confirm the potential of the theory. For example, the capacity of *Acropora valida* to complete metamorphosis after 110 days represents a sufficient interval to allow larvae to disperse across the Eastern Pacific divide which Richmond (1987) has estimated would take a passive larvae 90 days and suggests it is no coincidence that *A. valida* is the only *Acropora* in the Eastern Pacific (Wallace 1999). Furthermore, the data support Grigg et al.'s (1981) contention that the recent recolonization by *Acropora* of the Hawaiian Islands could have occurred via larval transported from Johnson Atoll which they estimated would take 50 days in the Subtropical Countercurrent. Again *A. valida* is one of 3 species of *Acropora* present in the Hawaiian archipelago (Veron 2000). While the limited capacity of some corals to delay metamorphosis (e.g. *A. millepora, A. gemmifera* and the faviids) may restrict them from the more remote locations in the Indo-Pacific, the ability of a proportion of the cohorts to delay metamorphosis for 30 - 60 days is still extraordinary and far exceeds Richmond's (1981) prediction of 20 days for *A. tenuis* and supports Potts' (1985) theory of retarded speciation in the scleractinia. Competence intervals of 30 – 60 days will result in sufficient long-distance dispersal between coral populations to prevent divergence and maintain a consistent suite of life history characters over a vast geographic range.

Many authors have suggested that rafting of juvenile corals on flotsam and jetsam may be an important feature in the biogeography of corals (e.g. Jokiel 1984, Jackson 1986, Rosen 1988). For example, Jokiel (1990) proposed rafting may be important for corals following the discovery of high numbers of coral recruits on pumice washed up on the beach front of tropical eastern Australia. Rafting theories were largely influenced by the assumption of a maximum competence period of 3 - 5 weeks and the failure to predict the distributions of many marine invertebrate taxa from larval life spans. The maximum

competence periods present here (Fig 5.18 & 5.19) make it unnecessary to invoke rafting to explain coral distributions because they are sufficient to enable at least some larvae to complete even the longest journeys in the Pacific Ocean, such as across the Eastern Pacific divide. However, any attempt to predict species distributions from larval duration will fail because successful colonization depends on many features of the life history of a species (Harriott 1992). In particular, larvae must have the ability not only to disperse to an isolated location but also the ability to maintain the population once established i.e. there is a combination of life history characteristics that define the successful colonizer. For example, *Acropora valida* which is the most widespread coral species, and one of the most abundant, has an extraordinary capacity to delay metamorphosis and a high proportion of larvae settle quickly. Consequently, *A. valida* larvae have the capacity to disperse to isolated locations, and maintain a population in remote locations once established. A similar settlement pattern was evident in the other widespread *Acropora* used in this study, *A. humilis*. Unfortunately, the competence period of *A. humilis* was not examined as the cultures were destroyed. However, it is difficult to draw any firm conclusions on the basis of 6 species, particularly as all of the *Acropora* species used have relatively wide geographic distribution (Fig 5.3). Ideally, the experiments would have included some species with a genuinely restricted distribution, however, there are few endemic *Acropora* on the GBR and these are rare and restricted to habitats which are difficult to access. Future work on settlement and competency should aim to examine endemic species. While rafting may, none the less, be an important feature in the dispersal of some corals, in particular the pocilloporids (see Chapter 4), I agree with Veron (1995) who states that it will have a relatively minor influence in most coral genera, which are relatively infrequent colonizers of flotsam and jetsam (Jokiel 1990).

These data present a significant opportunity to increase our understanding of the patterns of connection between coral populations on the GBR. Mathematical models designed to predict patterns of connections have been relatively unsuccessful in predicting the distribution and abundance of coral larvae around reefs (Oliver et al. 1992). This is perhaps partly due to the failure to incorporate relevant features of the biology of coral larvae. Furthermore, the data presented here indicate that the biological assumptions used were more than often incorrect. For example, models typically assumed that larvae take between four to six days to begin to settle (e.g. Williams et al. 1984) which is likely to be an underestimate for many broadcast spawning species (Fig. 5.5) and most brooders. Furthermore, there are large differences in rates of development between species, and between individuals of the same species (Fig. 5.5). Another assumption used when modeling patterns of connection between reefs was that coral larvae could only survive for between 2-3 weeks in the plankton (e.g. Williams et al. 1984). Again for many coral species this is an underestimate (Fig 5.18 & 5.19). A number of features of the biology of the larvae need be considered in future modeling efforts including: the proportion of cohorts settling through time; larval survivorship; and the proportion of larvae that remain competent through time. Furthermore, further work on coral larval behavior and swimming speeds is required, particularly with respect to the ability of coral larvae to influence their vertical distribution (Harrison and Wallace 1990).

Table 5.1 Date and time of spawning and mean egg size (maximum diameter) of the 7 corals species examined.

Family	Species	Date of spawn	Time of spawn	Mean egg size (microns)	se
Acroporidae	*Acropora humilis*	10/12/98	21:30	532	20.8
Acroporidae	*Acropora gemmifera*	08/12/98	21:00	604	6.9
Acroporidae	*Acropora millepora*	18/11/97	22:00	549	5.5
Acroporidae	*Acropora pulchra*	18/11/97	22:00	575	9.5
Acroporidae	*Acropora valida*	23/11/97	23:00	596	11.2
Faviidae	*Goniastrea retiformis*	19/11/97	21:30	371	3.6
Faviidae	*Platygyra daedalea*	09/11/98	19:00	396	3.6
Pocilloporidae	*Seriatopora hystrix*	1/12/96	6:00	625	7.9
Pocilloporidae	*Stylophora pistillata*	4/12/96	6:00	549	7.1

Table 5.2 The number of larva introduced into two replicate aquaria to estimate the proportion of the cohort settling through time in seven species of broadcast spawning corals.

species	larvae	n
Acropora gemmifera	1000	2
Acropora humilis	330	2
Acropora millepora	800	2
Acropora pulchra	500	2
Acropora valida	500	2
Goniastrea retiformis	1200	2
Platygyra daedalea	1000	2

Table 5.3 The age of larva (days since fertilization) and the number of larvae introduced into replicate plastic buckets (n) to test for settlement competence in seven species of broadcast spawning corals

species	age	number of larvae	n
Acropora gemmifera	4	100	2
Acropora gemmifera	7	75	2
Acropora gemmifera	14	20	2
Acropora gemmifera	34	20	2
Acropora gemmifera	60	10	2
Acropora millepora	4	100	2
Acropora millepora	8	50	2
Acropora millepora	11	40	2
Acropora millepora	14	40	2
Acropora millepora	21	20	2
Acropora millepora	27	20	2
Acropora millepora	60	20	2
Acropora millepora	90	10	2
Acropora millepora	110	5	2
Acropora pulchra	4	100	2
Acropora pulchra	8	40	2
Acropora pulchra	11	40	2
Acropora pulchra	14	40	2
Acropora valida	3	100	2
Acropora valida	6	50	2
Acropora valida	9	40	2
Acropora valida	16	40	2
Acropora valida	22	40	2
Acropora valida	31	40	2
Acropora valida	60	40	2
Acropora valida	90	20	2
Acropora valida	110	10	1
Acropora valida	130	6	1
Goniastrea retiformis	3	100	2
Goniastrea retiformis	7	100	2
Goniastrea retiformis	11	100	2
Goniastrea retiformis	21	40	2
Goniastrea retiformis	27	20	2
Goniastrea retiformis	36	20	2
Goniastrea retiformis	60	8	2
Platygyra daedalea	4	100	2
Platygyra daedalea	14	20	2
Platygyra daedalea	34	22	2
Platygyra daedalea	60	10	2

Table 5.4 Summary of larval competence.

Species	Peak competence	Maximum competence	longevity
Acropora gemmifera	7	34	60
Acropora millepora	11	60	110
Acropora pulchra	11	14	14
Acropora valida	9	110	130
Goniastrea retiformis	3	36	60
Platygyra daedalea	14	34	60

Figure 5.1 Broadcast spawning corals used in experiments (a) *Acropora millepora* (b) *A. humilis* (c) *A. pulchra* (d) *A. gemmifera* (e) *A. valida* (f) *Goniastrea retiformis* (g) *Platygyra daedalea*

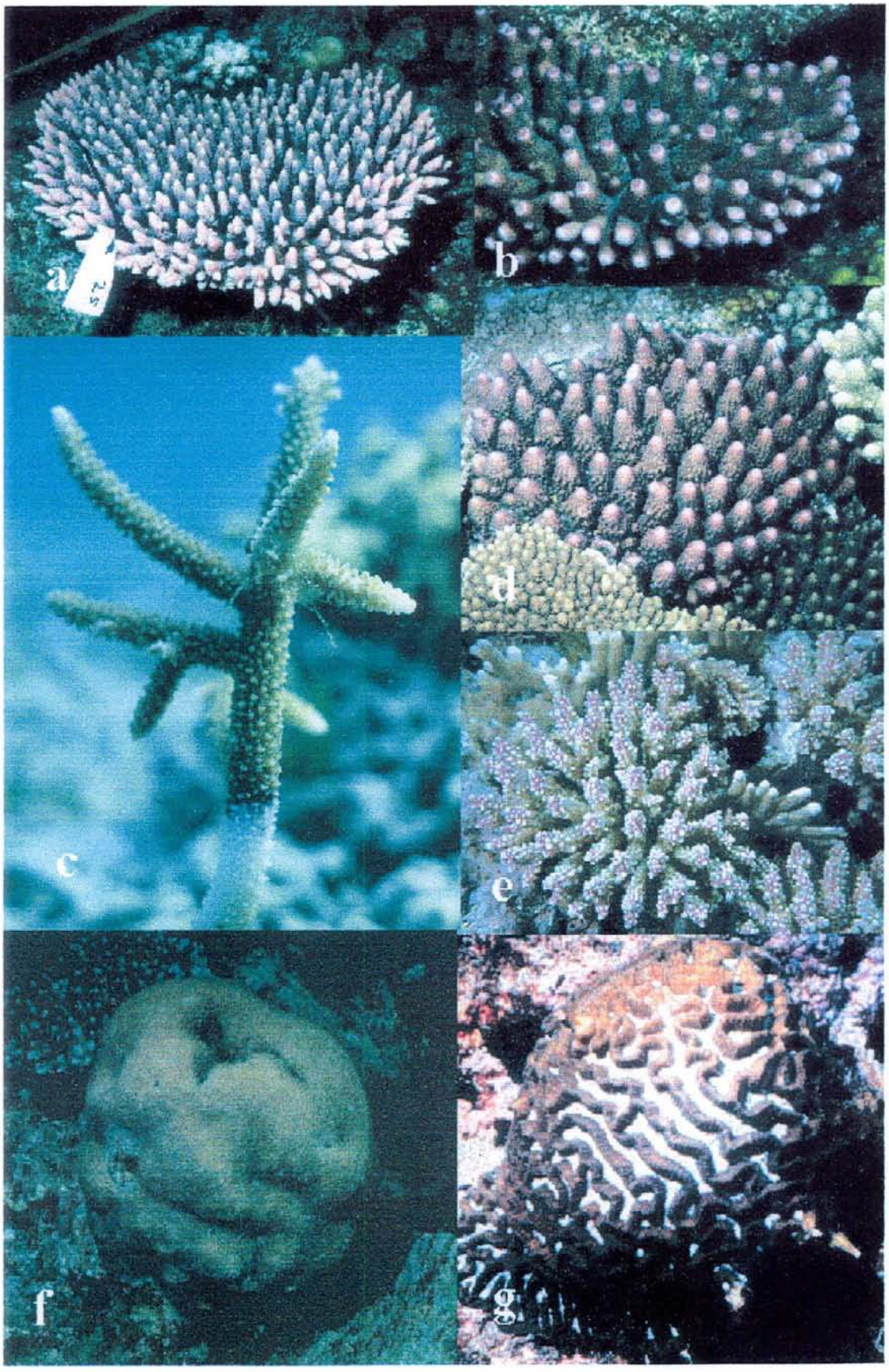


Figure 5.2 Geographical distributions of (a) *Acropora gemmifera* (b) *A. humilis* (c) *Acropora millepora* (d) *A. pulchra* (e) *A. valida*. Data from the Museum of Tropical Queensland *Acropora* database courtesy of Dr Carden Wallace. Range is the longitudinal range in degrees. The number of sites is the number of site records in the data base.

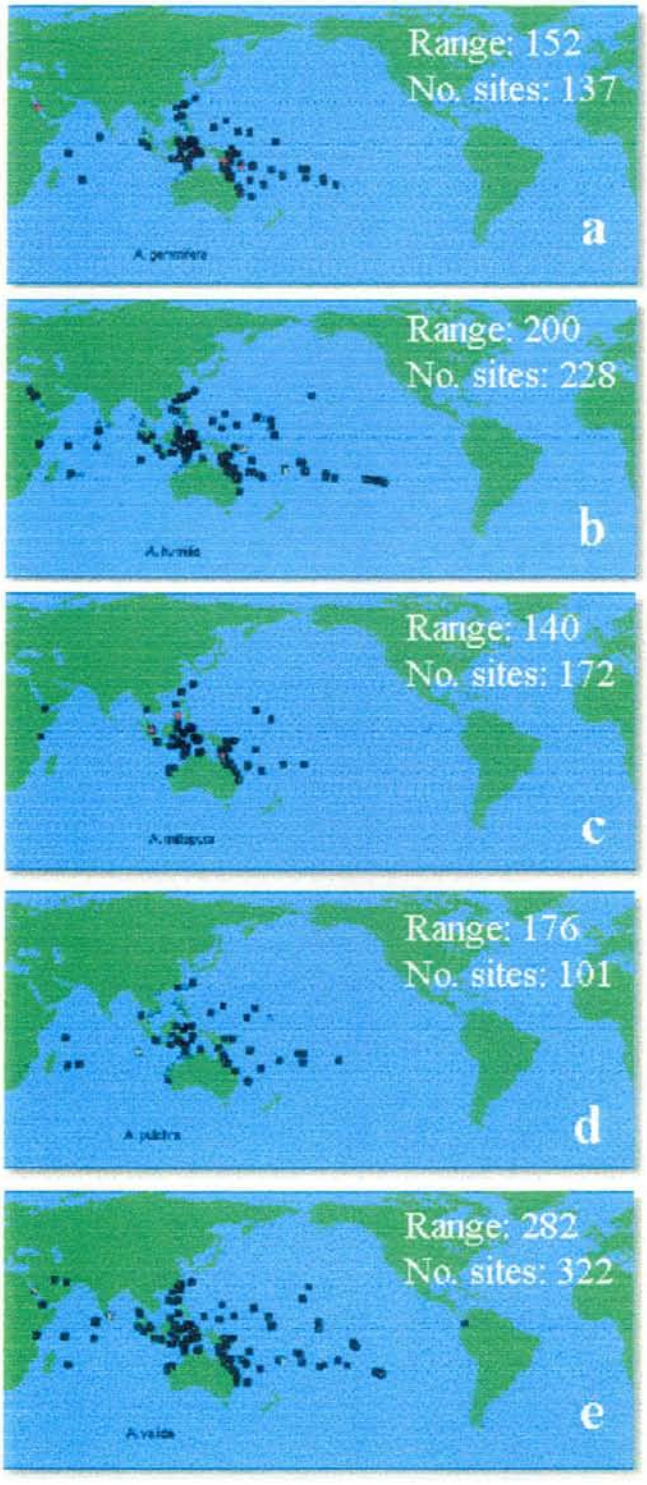


Figure 5.3 Brooding corals used in experiments (a) *Seriatopora hystrix* (b) *Stylophora pistillata*

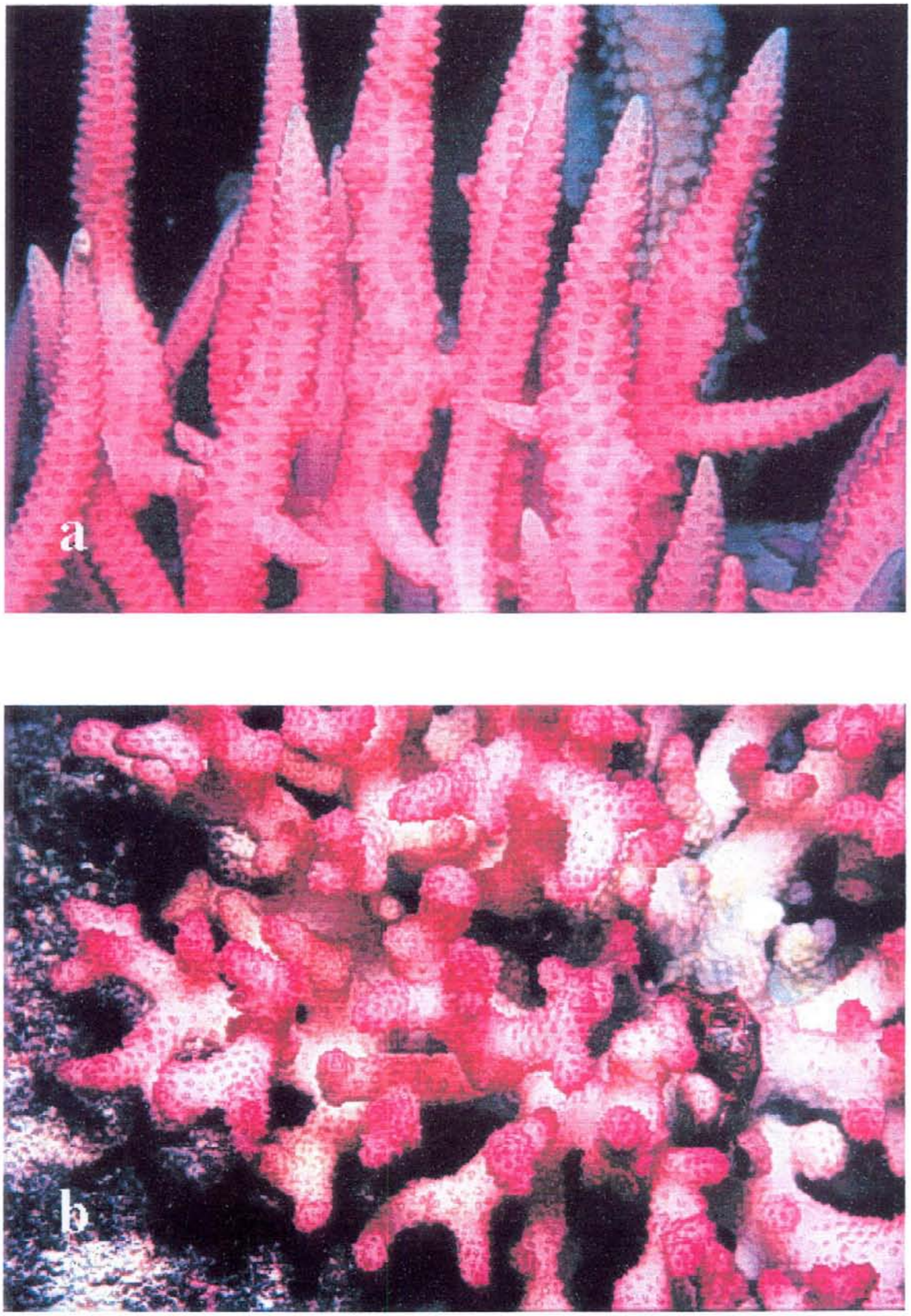


Figure 5.4 Stages in the embryonic development of the broadcast spawning coral *Acropora millepora* (a) egg (b) 2-cell stage (c) 4-cell stage (d & e) multicellular blastula (f) early gastrula (g) late gastrula (h) non-motile larvae (i) motile larvae. Scale bar = 500 microns.

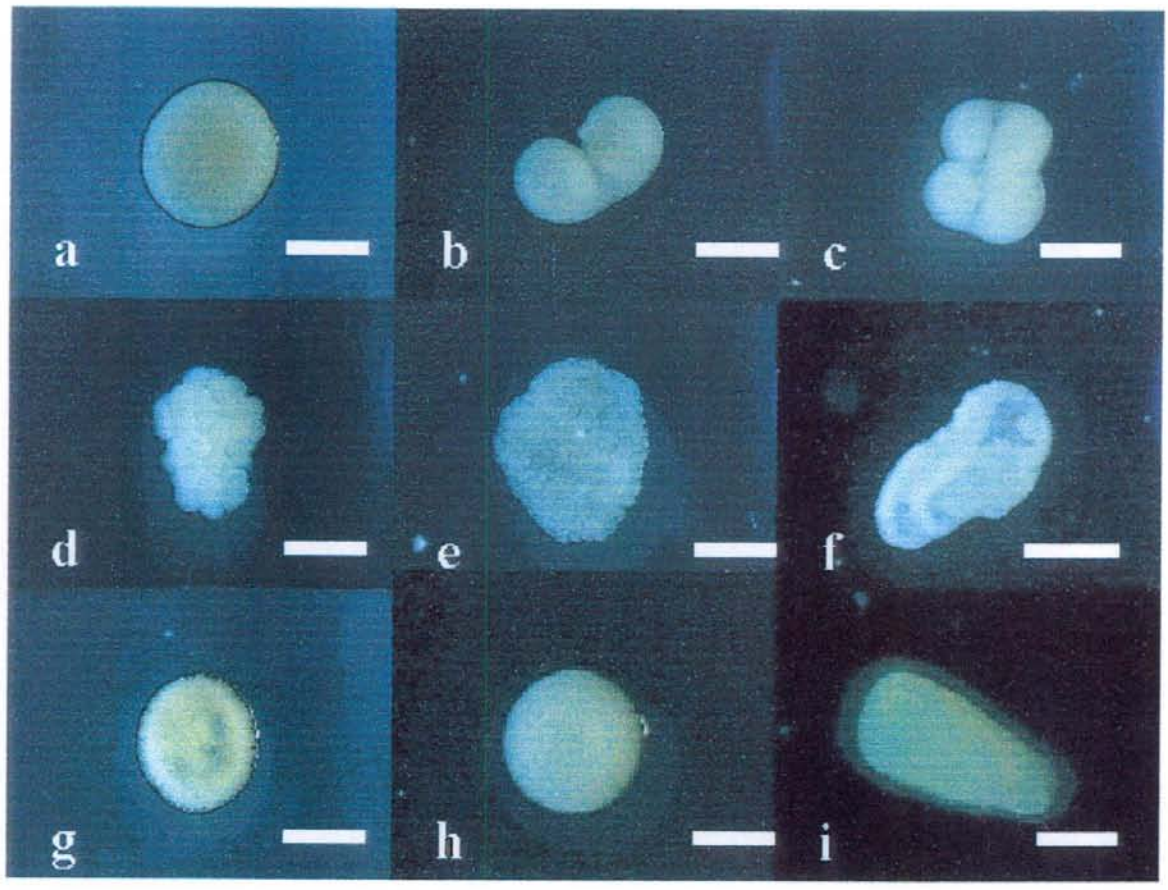


Figure 5.5 The proportion of the larval cohort of seven species of broadcast spawning corals settling through time. Values are the mean proportion + one se of the total number of larvae in the cohort settling in each time period.

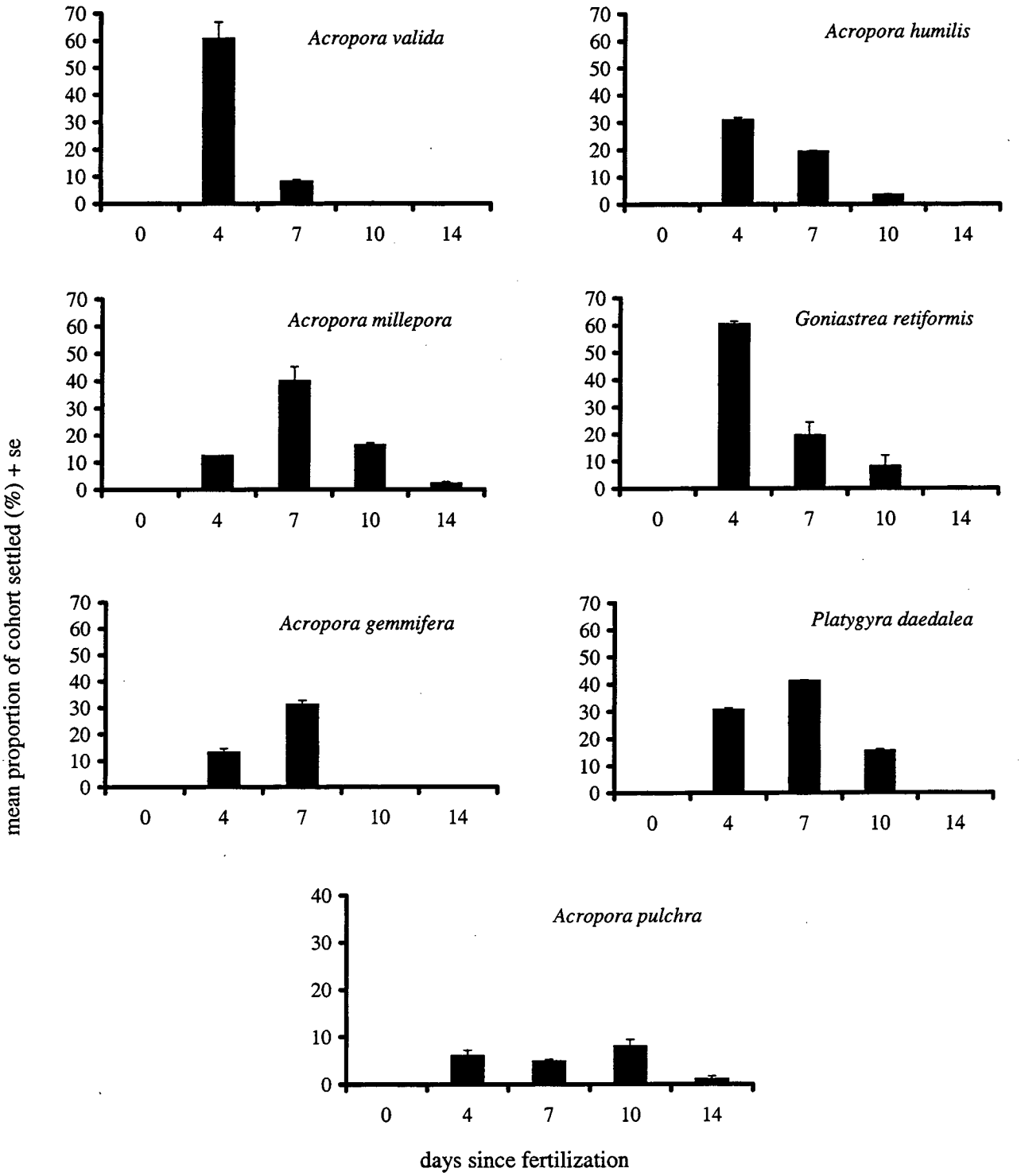


Figure 5.6 The cumulative proportion of the larval cohort of seven species of broadcast spawning corals settling through time.

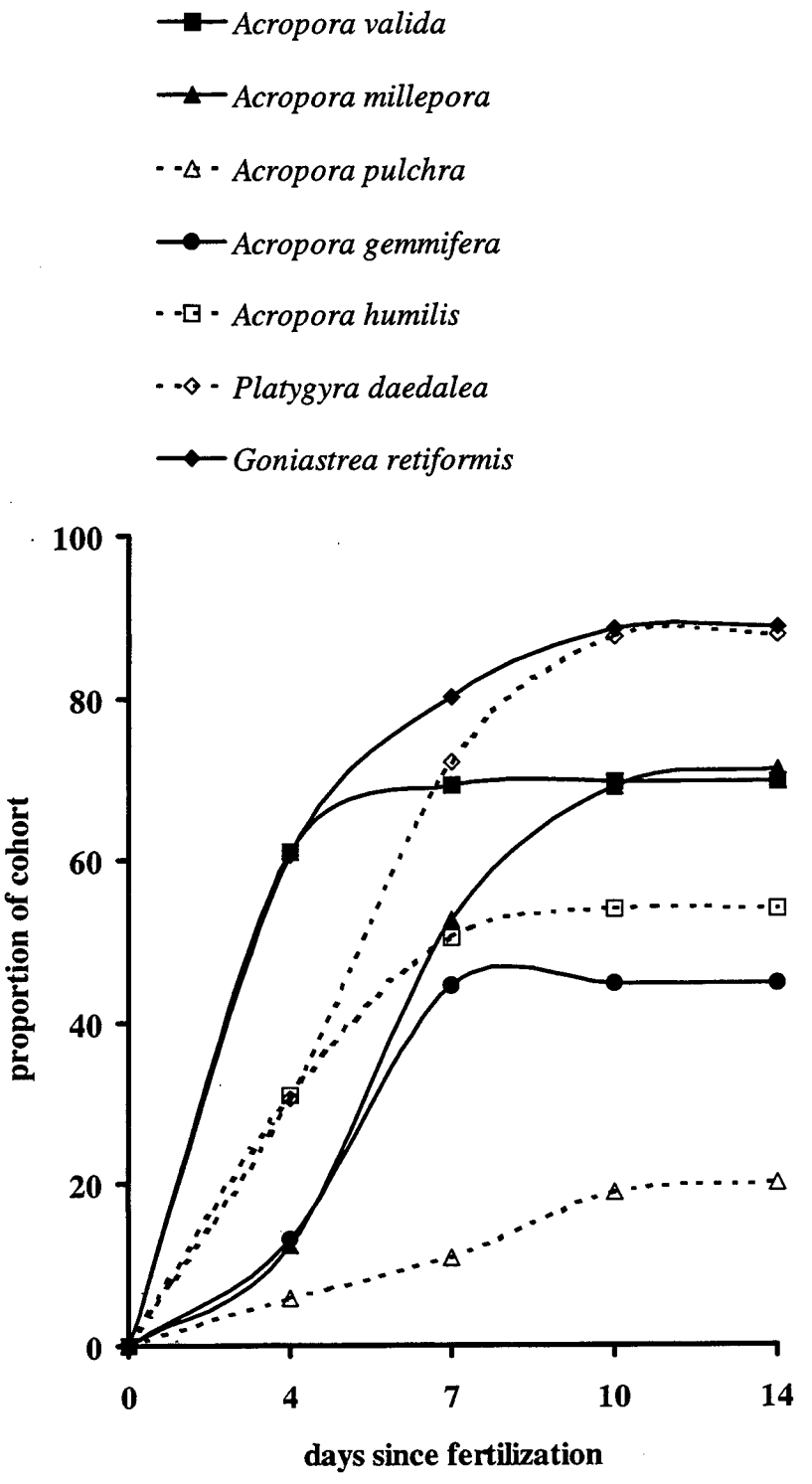


Figure 5.7 The proportion of the larval cohort of *Seriatopora hystrix* and *Stylophora pistillata* settling through time. Values are the mean proportion + se of the total cohort settling in each time interval (n=2).

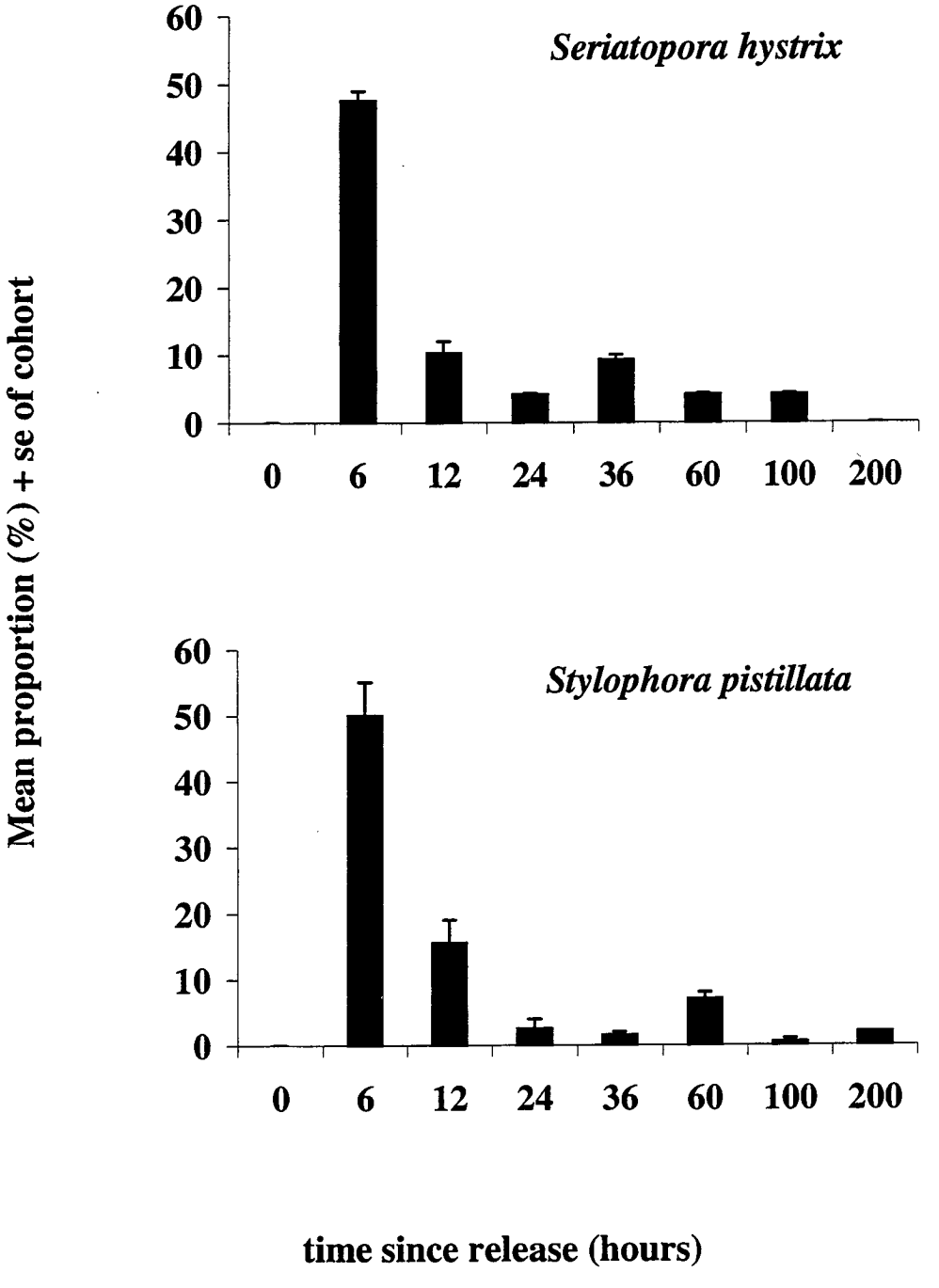


Figure 5.8 The cumulative proportion of the larval cohort of *Seriatopora hystrix* and *Stylophora pistillata* settling through time.

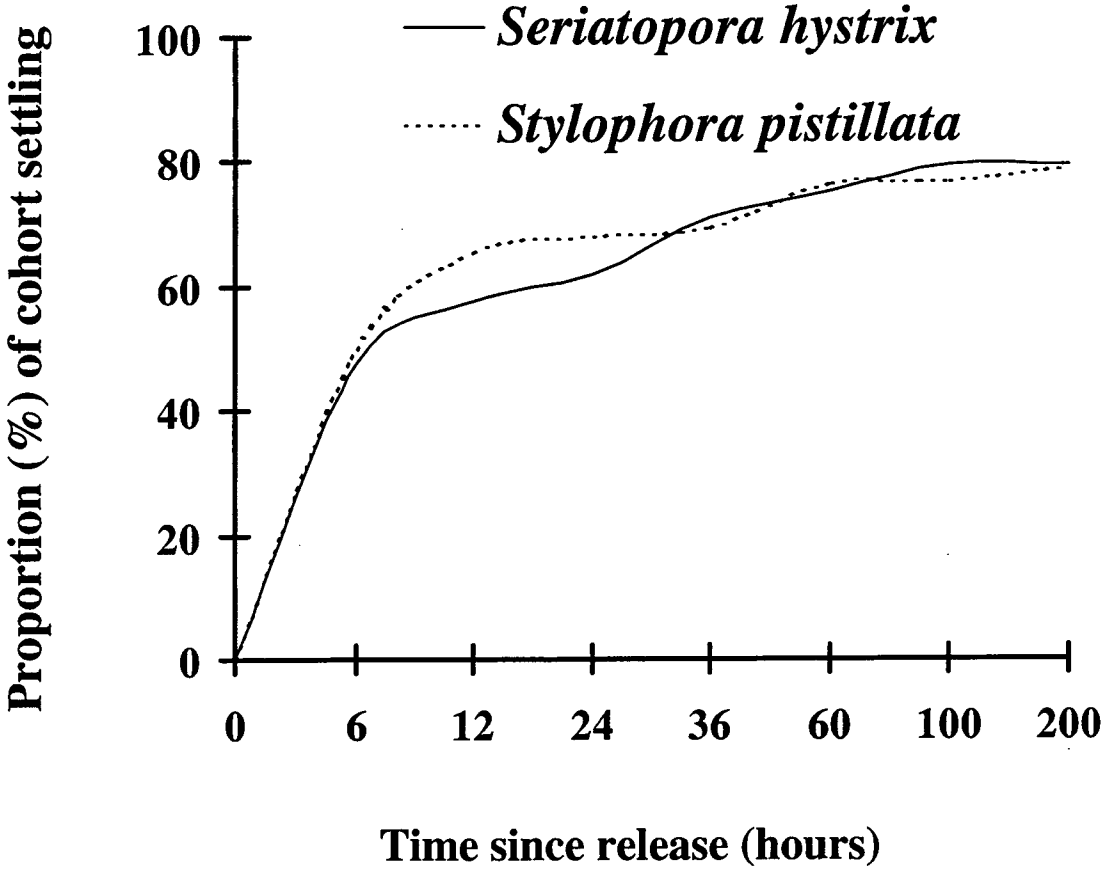


Figure 5.9 The rate of embryogenesis in *Acropora gemmifera* and *A. millepora*.

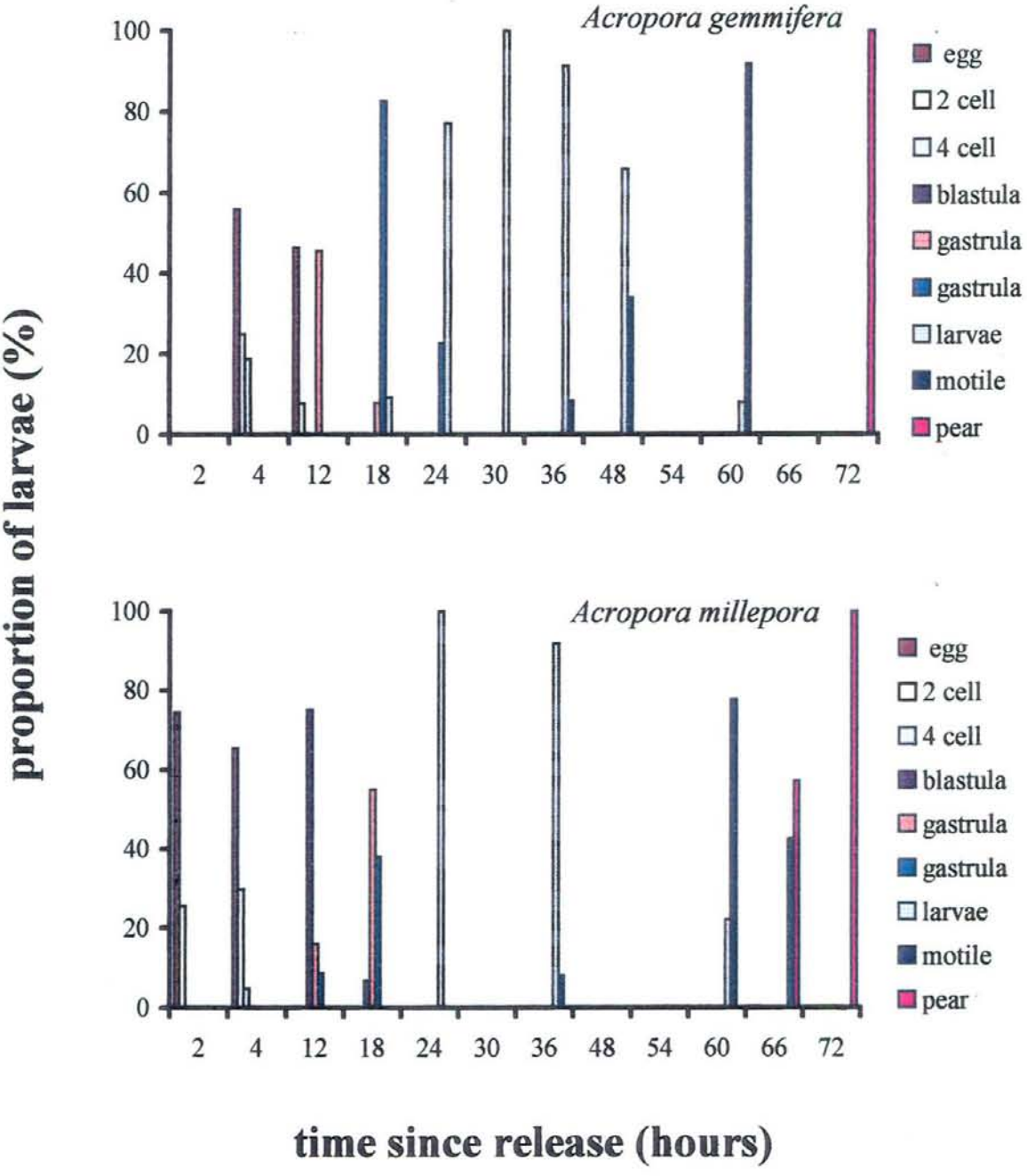


Figure 5.10 The rate of embryogenesis in *Acropora valida* and *Platygyra daedalea*.

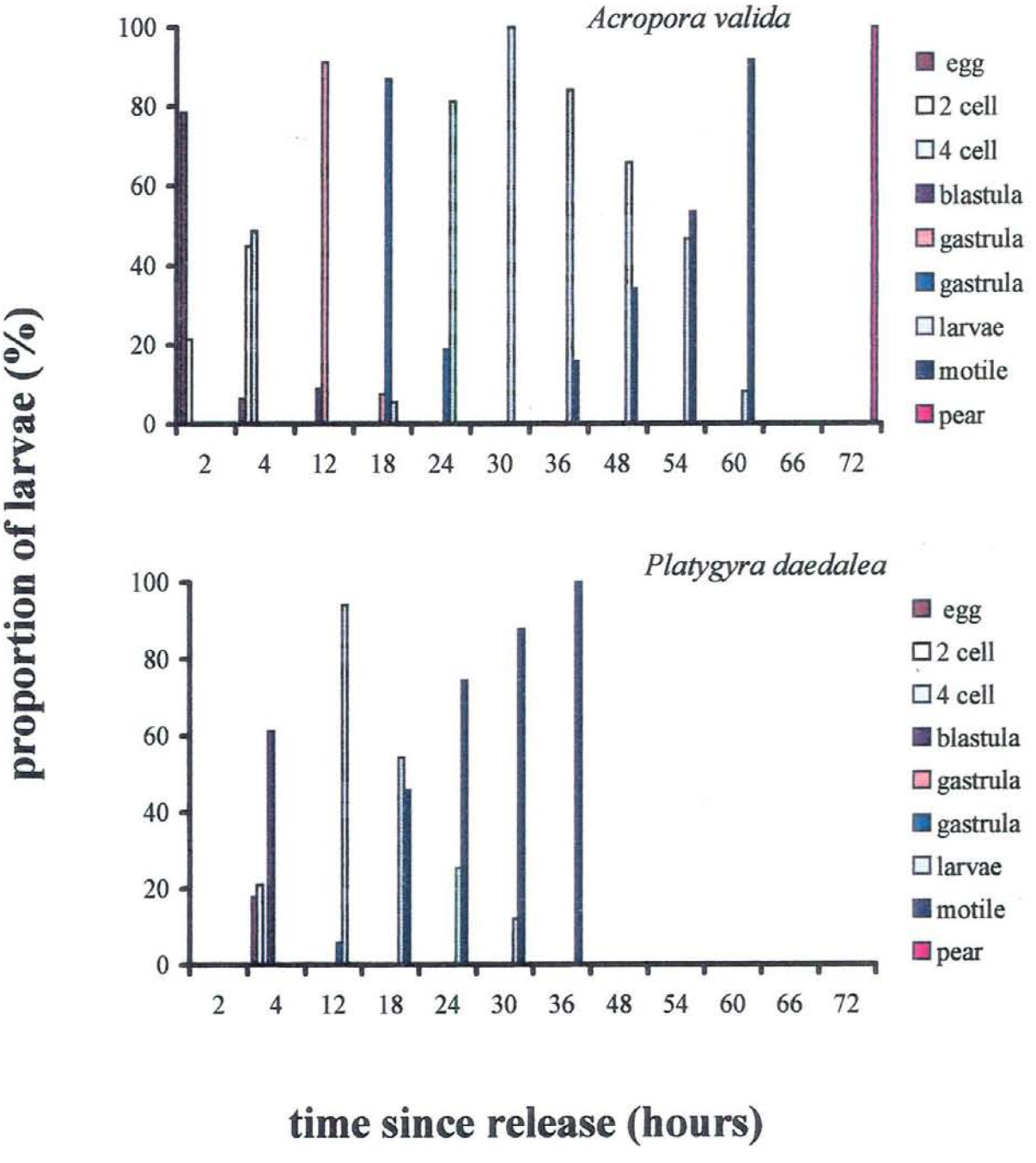


Figure 5.11 Larval size and development: time since larval release when half the cohort were motile.

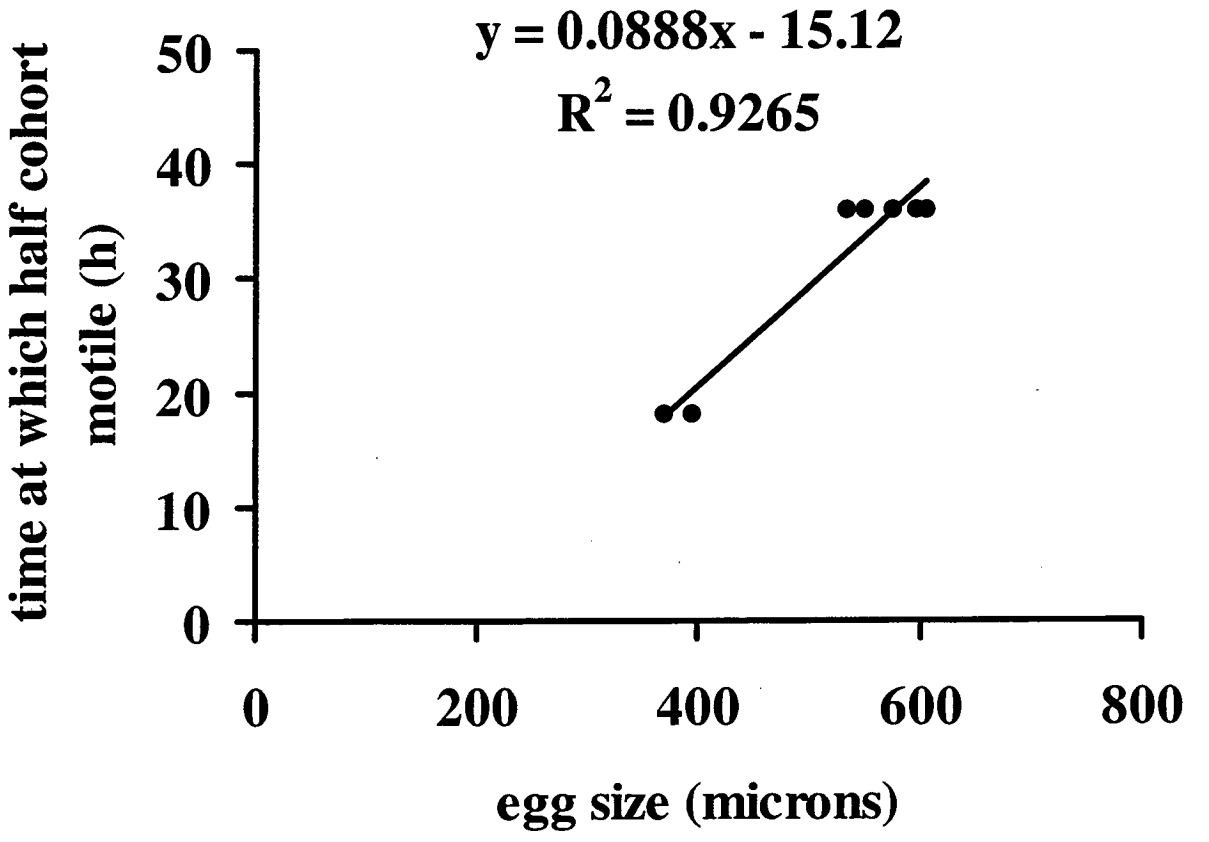


Figure 5.12 Larval size and development: day after release of peak settlement regressed against egg size.

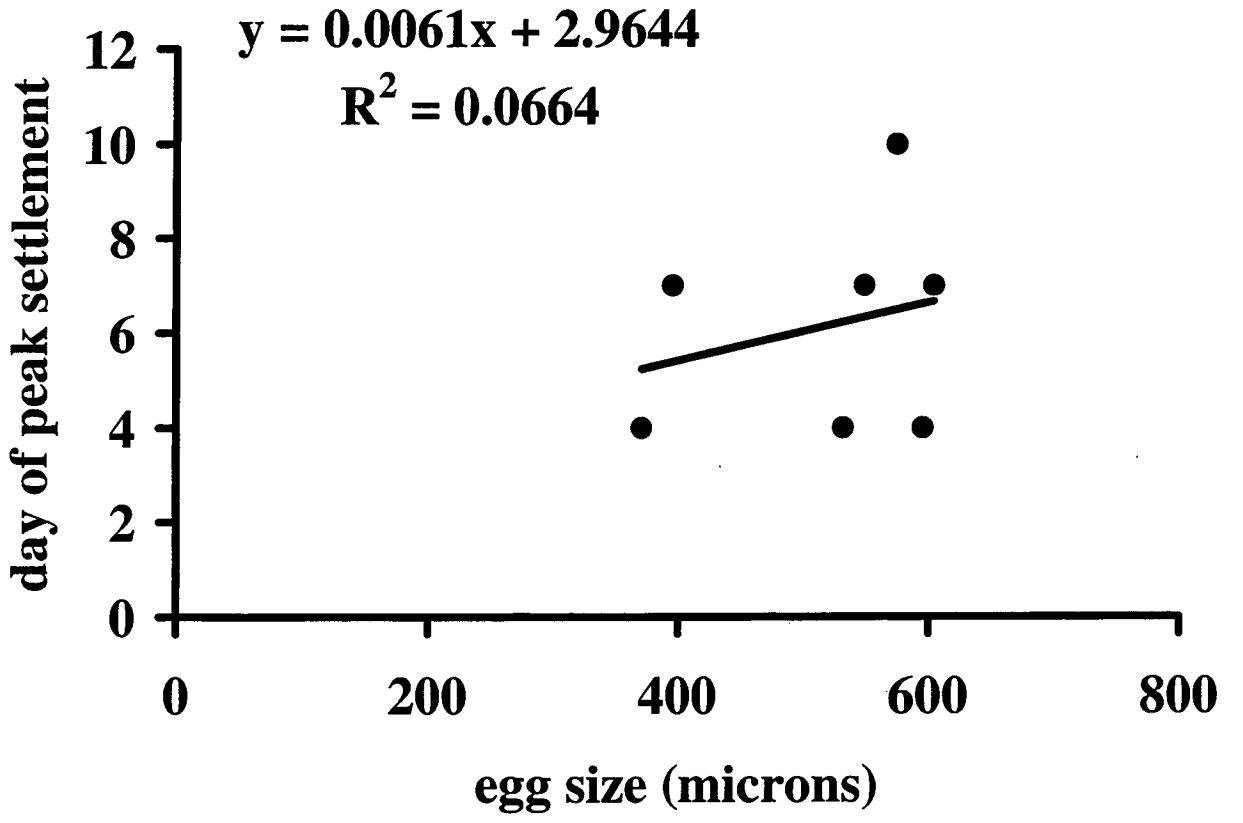


Figure 5.13 The proportion of the surviving larval cohort in four species of *Acropora* remaining competent to settle through time. Values are the mean proportion ± se of two subsamples of larvae from the cohorts at each time. The number of larvae used at each time is included in Table 5.3.

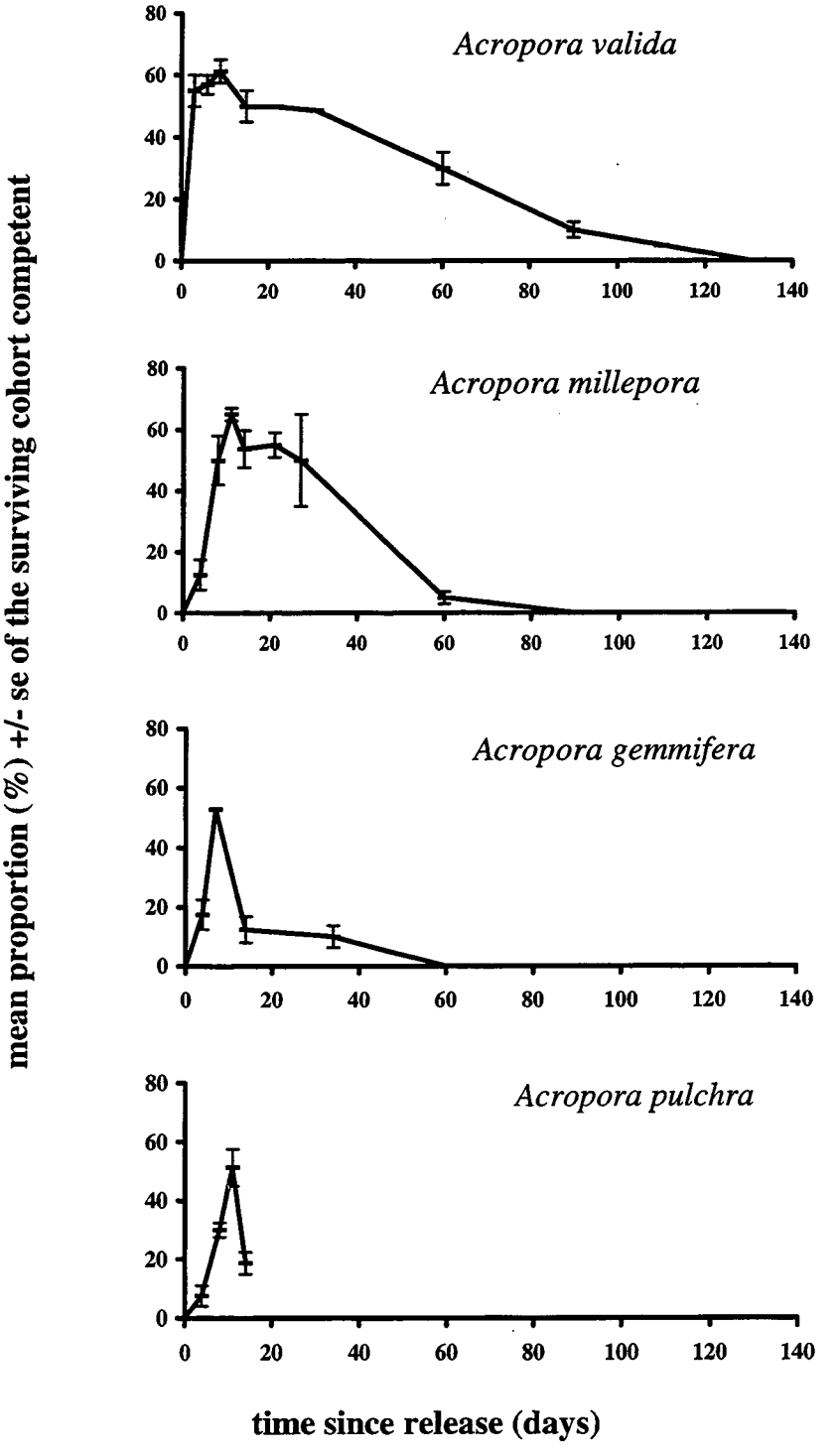


Figure 5.14 The proportion of the surviving larval cohort in two faviid species remaining competent to settle through time. Values are the mean proportion ± se of two subsamples of larvae from the cohorts at each time. The number of larvae used at each time is included in Table 5.3.

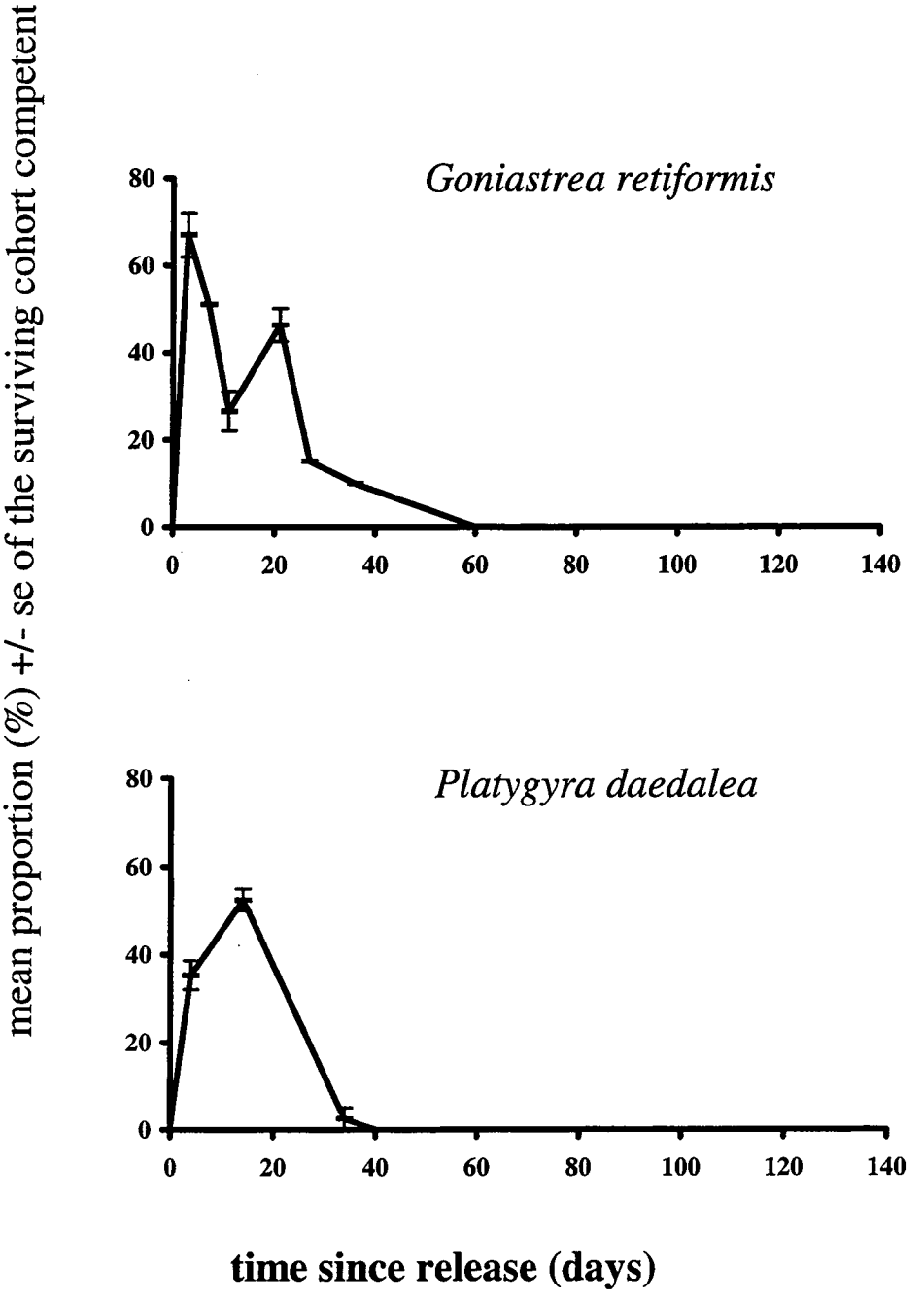


Figure 5.15 Survivorship in larval cohorts in 6 coral species. Values are the estimated number of larvae alive in each cohort at each time period based on 3 replicate samples.

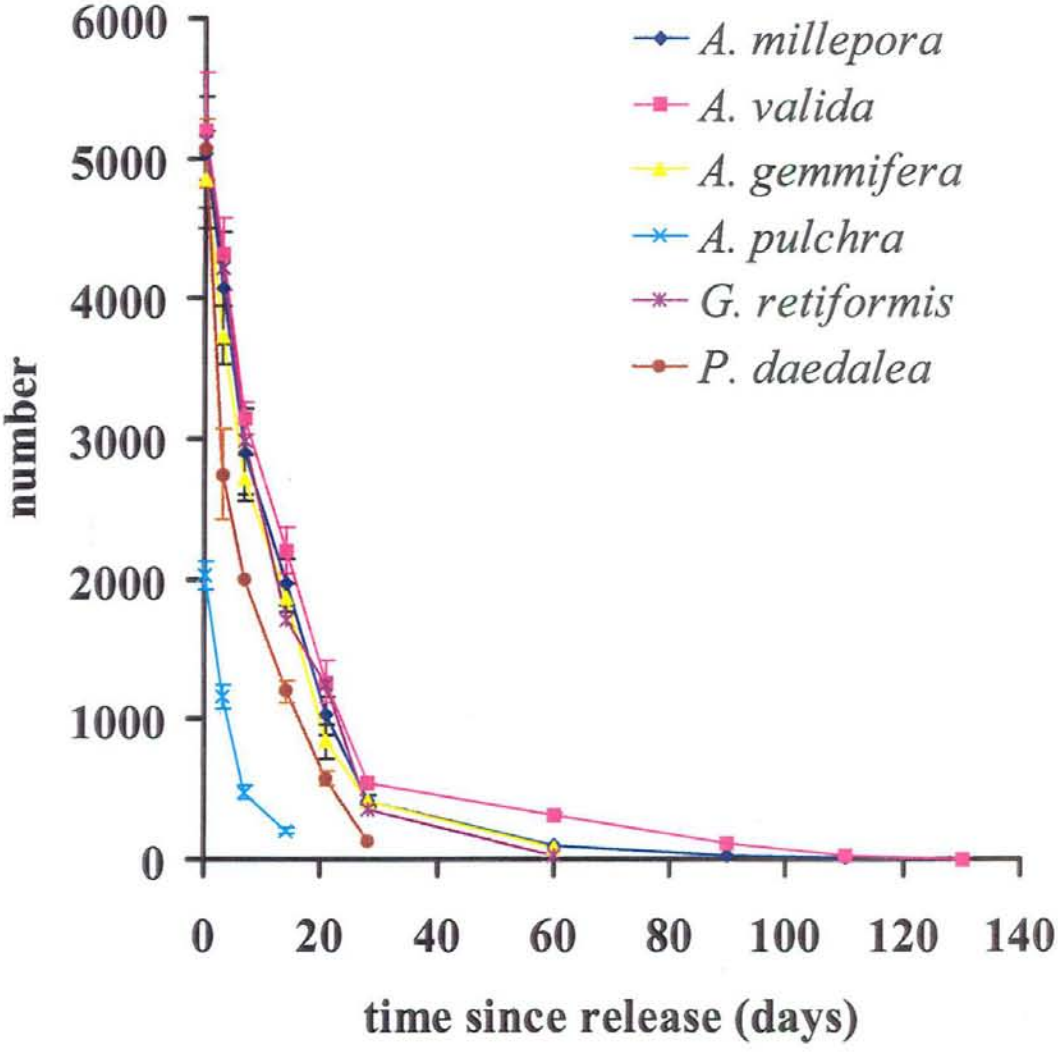
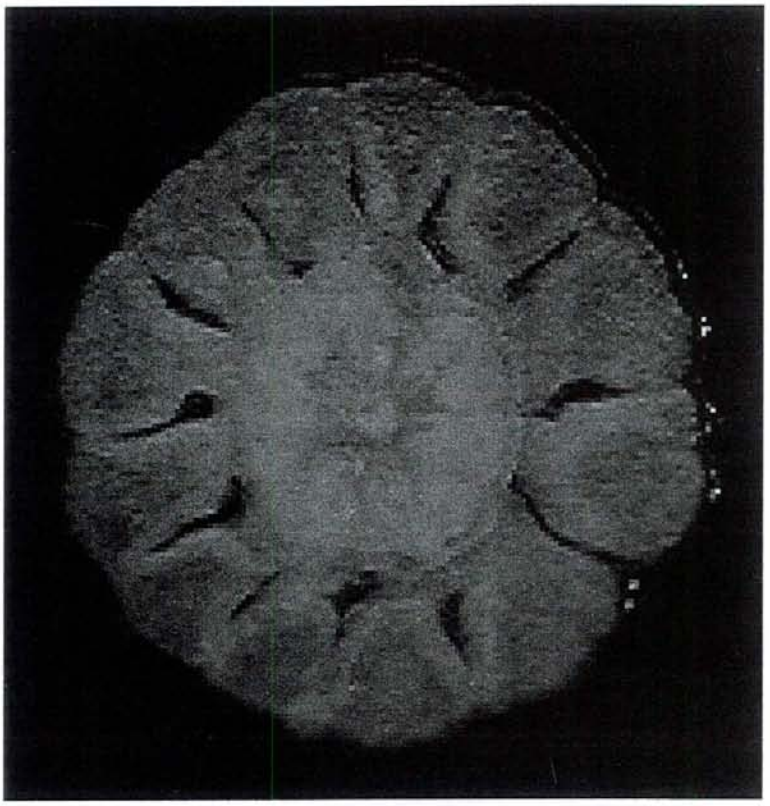


Figure 5.16 (a) Planktonic metamorphosis of *Acropora valida* larvae 1 week old (b) Scanning electron micrograph of an *A. millepora* larvae with tentacles 2 weeks old.



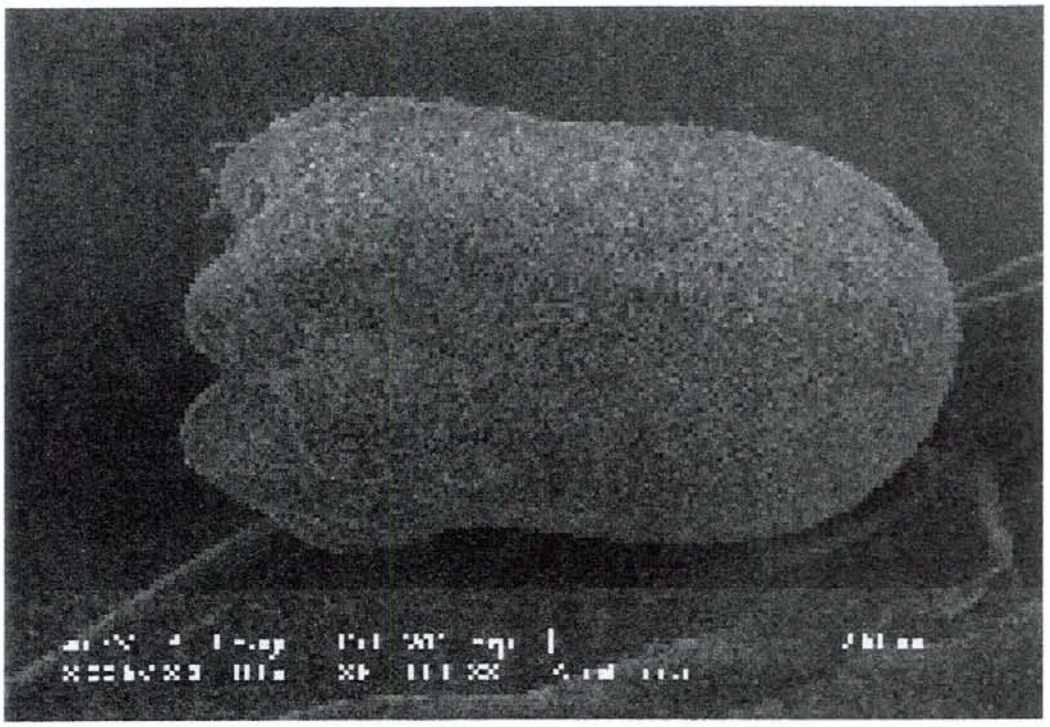


Figure 5.17 The size of larvae through time in 4 species of *Acropora*. Values are the mean diameter ± se in microns

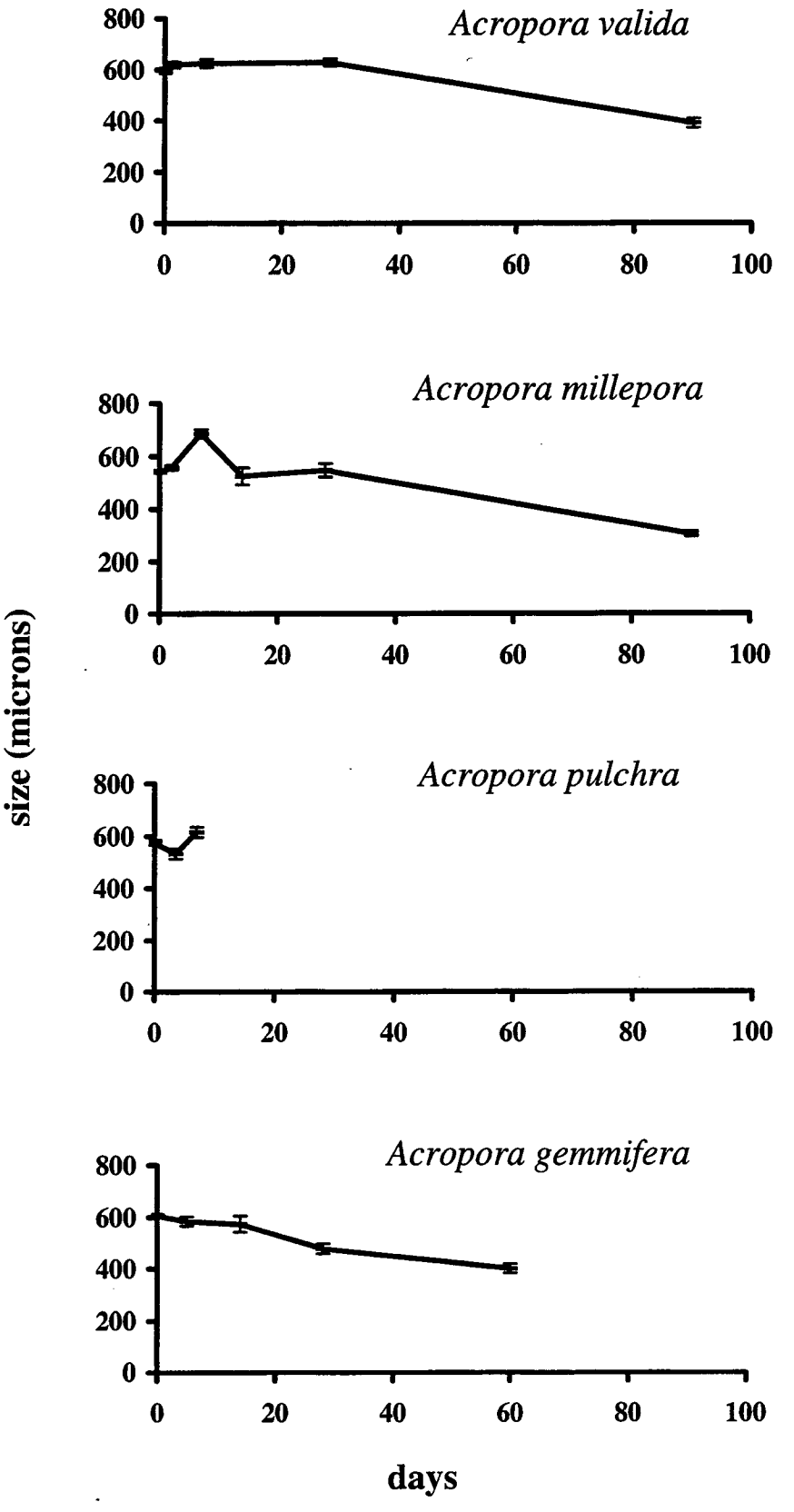
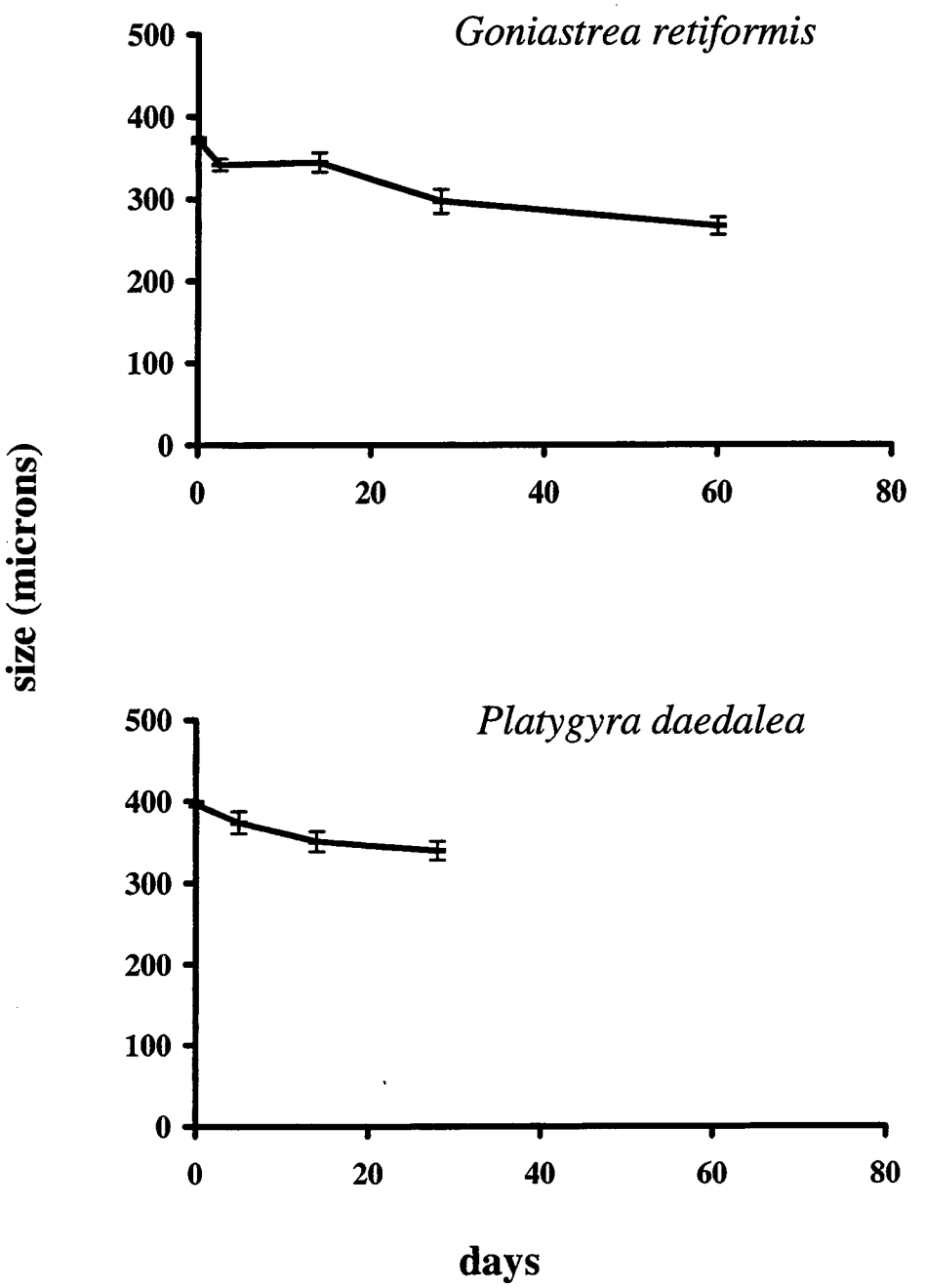


Figure 5.18 The size of larvae through time in 4 two faviid species. Values are the mean diameter ± se in microns



CHAPTER 6 General conclusions

In this thesis, I demonstrate that larval biology plays a fundamental role in many aspects of the ecology of coral species and that coral larvae, despite being superficially simple organisms, have the capacity to sense and respond to their environment in complex ways. In Chapter 2, I describe a modest increase in the taxonomic resolution of early coral recruits. In Chapter 3, I demonstrate that habitat selection by larvae may have a strong influence on the depth distribution of some coral species. In Chapter 4, I explore differences between species in the induction of metamorphosis and discuss how these differences are linked to the life history strategies of species. In Chapter 5, I demonstrate that when presented with the necessary cues to induce metamorphosis, the larvae of many broadcast spawning species will settle more rapidly than has previously been considered. However, when deprived of these cues, coral larvae have a extraordinary capacity to delay metamorphosis. In this final chapter, I will consider some of the implications of these findings and suggest some areas for future research.

The advances in taxonomic resolution of young corals outlined in Chapter 2 were modest, highlighting the slow nature of skeletal development for many coral species in their first few months as well as difficulties associated with the taxonomy of small colonies. For these reasons it is unlikely that the number of taxa distinguishable will be greatly increased with further study. The loss of taxonomic resolution between 6 and 16 weeks sets further limits to the taxonomic resolution achievable and cautions against over-optimistic identifications that would lead spurious conclusions. The advances in taxonomic resolution, do however, provide exciting opportunities to increase our understanding of a number of areas in reef ecology. For example, the ability to

distinguish between recruits of brooding and spawning species provides an opportunity to test the hypothesis that brooding is a more successful life history strategy than spawning in higher latitudes (e.g. Harriott and Simpson 1996, Hughes et al. 2001). The ability to identify *Stylophora* recruits is also particularly significant. This genus is mono-specific in many regions of the Indo-Pacific (Veron 2000). Consequently, the processes that regulate the abundance of *Stylophora pistillata* in these regions can now be examined. Finally, Chapter 2 provides some firm guidelines by which to standardize the study of coral settlement, primarily by identifying the ideal length of time to leave settlement panels at sea. Studies of coral settlement and recruitment are becoming more numerous for a variety of reasons. Firstly, reef scientists and managers have become more aware of the importance of monitoring processes such as recruitment rather than just changes in adult abundance in order to understand how reef ecosystems function (Karlson 1999). Secondly, early stages in the life history of corals are often more susceptible to certain environmental perturbations, such as eutrophication and sedimentation, than adults (Ward et al. 1996, Gilmour 1999). Consequently, measuring changes in patterns of settlement and recruitment will provide an early warning of potential damage to reefs or impacts on resilience after disturbance.

Coral larvae selectively respond to cues present on substratum conditioned in their parental habitat in the absence of any depth-related physical parameters (Chapter 3). Therefore, contrary to the generally held assumption that post-recruitment processes play the major role in determining adult distribution patterns, habitat selection by larvae clearly contributed to the depth distribution of adult corals in this study. Furthermore, the fact that different species behave in different way to similar habitat suggests that a wider range of cues may be involved in the induction of metamorphosis in coral larvae

than has previously been considered. Indeed, in Chapter 4, I demonstrate that larvae of *Stylophora pistillata* are induced to metamorphose by water born cues. I argue that many aspects of the ecology of pocilloporids, such as their importance in early successional communities, suggest that larvae of other species in this family may behave similarly. The challenge now is to identify what is inducing these larvae to settle. This information may prove useful for restoring reefs that have been affected by disturbance and for creating artificial reefs. Such efforts are of growing interest and importance (Oren and Benayahu 1997), because 58% of the world's reefs are threatened by human activity (Bryant et al. 1998) and that coral reef area continues to decline according to the latest report on the status of the world's coral reefs (Wilkinson 2000).

In Chapter 5, I describe how aspects of larval biology, such as settlement patterns and the capacity to delay metamorphosis, have a profound influence on the population structure of species. In particular, I argue that while there is considerable potential for dispersal, a high proportion of recruits are likely to be of local origin. The scale of dispersal will have important implications for marine meta-population models, marine reserve design and evolution of marine organisms (Karlson 1999). For example, limited dispersal will provide a greater potential for local adaptations to be maintained in local populations, particularly in species with rapid settlement and short generation times such as *Stylophora pistillata* (Loya 1976a) and some alcyonacean corals (Benayahu and Loya 1985). Consequently, the potential of some corals to adapt to environmental perturbation, such as global warming, may be much higher than is generally recognized (e.g. Hoegh-Guldberg 1999).

The scale of dispersal and the patterns of connection between reefs, also have important implications for the design of marine reserves (Roberts 1997). For example, if a high proportion of recruits originate from the natal reef, it may be more important to protect areas within each individual reef, rather than protect a small proportion of entire reefs, particularly in regions where reefs are far apart. The data on frequency distributions of settlement, larval competence periods, and larval survival present an excellent opportunity to improve our understanding of patterns of connectivity between reefs on the Great Barrier Reef by combining these aspect of larval biology with current models of water movements.

Finally, the data on larval competence presented in Chapter 5 make it clear that many coral larvae have an extraordinary capacity to delay metamorphosis. It remains to be established how this is achieved. In particular, the energy source needs to be identified and the difference between the species explained. Future work should aim to quantify ontogenetic change in the biochemical composition and metabolism of larvae, and to determine whether greater initial energy reserves or a slower rate of utilization account for the observed differences in the planktonic duration. The experiments on larval competence were conducted under conditions where the larvae were deprived of most potential sources of nutrition, except perhaps dissolved organic material. Consequently, the values for competence may underestimate what larvae can achieve in the plankton. Future work should seek to establish whether coral larvae can supplement initial energy reserves by (1) feeding in the plankton (2) uptake of dissolved organic material or (3) transfer of metabolites from maternal zooxanthellae or zooxanthellae acquired within the plankton. Furthermore, the length of the larval phase needs to be examined in a wider range of species. In particular, the planktonic duration of endemic species should

be compared to that of cosmopolitan species to examine to what extent larval duration determines species geographical distributions.

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APPENDIX ONE: Publications during the course of Ph D candidature

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