The Reproduction and Recruitment of the sand dollar *Arachnoides placenta* (L.) (Echinoidea: Echinodermata) from differing habitats on the North Queensland coast

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Abstract

The reproductive periodicity, recruitment and population studies of the intertidal Indo-Pacific echinoid, *Arachnoides placenta* (Linnaeus), were investigated from April 2001 to September 2002 at sites along 650km of the north Queensland coast, Australia. Three locations were sampled, comprising Mission Beach; Pallarenda Beach Townsville; and the Mackay region. *A. placenta* is a dominant macro-organism at all sites sampled, individuals of all sizes are found across the entire stretch of the beach terrace but are rarely evenly distributed, displaying a preference for pools and ripples containing wet sand. Despite patchiness a significant decrease in density downshore was observed in 11 / 17 transects laid at Pallarenda Beach, 2001 ($p = <0.05$). Significant differences in density were observed between all sites ($p = 0.000$) and even over distances of metres ($p = 0.006$). A maximum density of 88 individuals m-^{2} was recorded at Mackay in 2002.

There was also clear temporal and spatial variation in the size-frequency of the population at Pallarenda Beach and significant differences in test diameter between sites ($p = 0.000$) which clearly shows no effect of latitude on test diameter. At Pallarenda Beach test diameter was observed to increase with distance downshore in 13 / 17 transects. Test diameter at Bucasia Beach, Mackay on the contrary decreased with distance downshore. No relationship between test diameter and population size was observed.

Significant differences in population density and size-frequency data even over scales of just metres suggest that discrete differences in abiotic or biotic factors, particularly sediment grain size, moisture and protection from wave action, between sites are enough to produce significant variations between populations.

Growth of *A. placenta* from settlement demonstrates an s-shaped growth curve that is typical of a number of echinoid species. From a size of approximately 10mm growth assumes a linear phase which slows at a size of 25mm, at which size individuals are estimated to be 3 or 4 years old.

The reproductive periodicity of *Arachnoides placenta* exhibited an overall seasonal cycle with a period of gamete growth and accumulation from December to February culminating in a March to May main spawning period. Gametogenic patterns at Pallarenda Beach indicate the breeding season of *A. placenta* coincides with the start of a decline in sea water temperatures that occurs from March (26 – 28 ^{o}C) which

reaches a minimum over the months of June – August (22 – 24 °C). Partial spawning was observed in some individuals to June/July with a few spawning until September at Pallarenda Beach, indicating the continuation of spawning until temperatures reached a minimum. Over the range studied, *A. placenta* experienced similar annual air/sea water cycles and relatively comparable rainfall cycles. Air temperatures varied a maximum of ±8 °C from those of Townsville, possibly accounting for minimal differences in gametogenesis between sites. Spawning was only synchronous between males and females during months of the major spawning period (March to July), during which female gonads returned to the recovering condition within a month or less of spawning. From July to November no female gonads were in the late mature stage and a very slow rate of gametogenesis was observed. In males, 30-100% of individuals in all populations had ripe gonads throughout both years except June and September 2002 in Mackay. A percentage of all male gonads were always in the spent stage, indicating recovery takes longer than a month.

Significant numbers of newly settled recruits occur within the sediment from March – May at all sites, which strongly correlates with the timing of the annual gametogenic cycle of adults. The density of recruits downshore at Pallarenda Beach in 2001 demonstrate a clear patchy distribution, however a significant decrease in individuals downshore was observed in three out of six months of sampling ($p = <0.05$). Newly settled recruits prefer the middle to lower section of the beach terrace until a size of around 10mm is reached, when these individuals show a preference for the inhabiting the upper –middle section of the beach terrace. Such size-related positions on the beach terrace point to optimal grain-size preference possibly related to feeding and movement. There does not appear to be an adult-larval attraction during settlement.

Chapter 1: General Introduction and Literature Review

1.1. Introduction

The intention of this study is to describe and compare the annual reproductive cycle, recruitment, and population size frequency distributions of a lesser-known echinoid, *Arachnoides placenta*, from five sites on the North Queensland coast. This study will also aim to evaluate the environmental and biotic factors important in regulating the individual and population-level traits of the species between habitats and locations. This species forms a dominant part of the intertidal fauna of many sandy shores on the north Queensland coast, but despite this, little has been documented on the species. Useful unpublished information on the population biology, reproduction and recruitment biology is provided by the authors Aung (1975), Campbell (1995) and Koizumi (1997), however there are numerous inconsistencies between the timing of reproduction and recruitment between written theses. I therefore hope this study will shed some new light on work already documented on the reproduction and recruitment of *A. placenta* by Aung (1975) and clear some of the current conflicts within the literature on the same subject, by Campbell (1995) and Koizumi (1997).

By means of a pilot study, *A. placenta* proved to be suitable for a study of reproduction, recruitment and population size frequency distributions, as preliminary observations showed individuals at each location were easily recognised and found in great abundance. There were a number of low tides throughout both years exposing populations on a regular basis, allowing collection and sampling over a minimum of six days per month.

This study of *A. placenta* is also appropriate in that it will also provide data on one member of the irregular echinoids, a group that has had considerably little published documentation in the past. Irregular echinoids are commonly the most abundant macro-organisms of sandy shores (Salsman and Tolbert 1965), and like *A. placenta* play an important role in reworking sediments and recycling nutrients in the benthic community of sandy shores (Bell and Frey 1969). Despite the relative abundance of irregular echinoids, documented research has focused on only a handful of species, mainly the Clypeasteroids. The other burrowing irregular echinoids, the Spatangoids, or heart urchins, have been widely ignored in the literature in comparison to the extensive literature describing the population ecology of regular echinoids.

1.2. Review of the Literature

For the following review of the literature on the Echinoidea, I have decided to place an emphasis on the ecology and physiology of irregular echinoids with particular focus on the sand dollar *A. placenta*.

1.2.1. Intertidal Distribution

1.2.1.1. Aggregations and Patchiness

The distribution of echinoderms has been termed notoriously patchy and appears to be particularly true of echinoids in general (Buchanan 1966, Ebert 1968b, Merrill and Hobson 1970). Intertidal and subtidal sandy shores are constantly influenced by varying biological and physical conditions, which in turn are believed responsible for the patchy population distributions. Contributing physical conditions include water movement, nature of the sediment, distribution of food and the temperature and salinity of interstitial sea water and biological factors include competition with individuals of the same species (and other organisms), predation risk and chemical cues (Hines and Kenny 1967, Bell and Frey 1969, Dix 1969, Pearse and Arch 1969, Birkeland and Chia 1971 etc.). The formation of aggregations in a number of sand dollars produces a higher selective advantage when breeding (Moore 1956, Salsman and Tolbert 1975, Lane and Lawrence 1980, Timko 1975). *A. placenta* is abundant throughout the year and forms patches at Pallarenda Beach (Aung 1975, Campbell 1995, Koizumi 1997). There is no correlation between population density and seasonal spawning (Aung 1975, Koizumi 1997) Individuals do not appear to aggregate to feed as the species can be found grouped throughout different substrata (from muddy to clean sand and from wet to practically dry sand bars), however the species occurs more often in areas of medium-fine wet sediment in which the availability of food is likely to be in greater abundance (Aung 1975, Campbell 1995). The clumping of *A. placenta* is *not* purely a response to physical factors (Aung 1975). *A. placenta* larvae have also been observed to form aggregations away from adults when settling (Aung 1975, Koizumi 1997) which may be important in protecting juveniles from predation (Meadows and Campbell 1972). No evidence of long-term aggregations have been documented for populations of *A. placenta* although population numbers remain in high numbers throughout the year. Cocanour (1969) also found no evidence of long-term patchiness amongst populations of *Echinarachnius parma*. Observations on the sea urchin *Diadema setosum* in the Solomon Islands also indicate that aggregations of the species are not stable in size, shape, position or individual composition. *D. setosum* is probably an omnivorous scavenger, feeding on silt, detritus and algae scraped off rocks. It is assumed that movements and changes in the aggregations of this species are partly due to grazing activities in the area (Pearse and Arch 1969). Species that do form long-term stable patches include the sand dollars *Dendraster excentricus* (Highsmith 1982).

Patchiness of food source may be one explanation for clumping. Small depressions in the sand can act as silt traps in which groups of sand dollars are often associated e.g. *Mellita quinquiesperforata* (Lane and Lawrence 1980). Other authors (Salsman and Tolbert 1965, Weihe and Gray 1968) have noted that there is a tendency for *M. quinquiesperforata* to become more abundant behind bars where water was calmer and silt accumulated. *A. placenta* similarly gathers in or around pools of water or between ripples on the intertidal shore (Aung 1975, Koizumi 1997, pers obs).

In numerous organisms chemical factors are important in forming aggregations (Meadows and Campbell 1972). Chemical attraction plays a significant part in the clumping of adults of the sea urchin *Evechinus chloroticus* (Dix 1969) and adult aggregations commonly play a role in influencing larval settlement near adult populations (Highsmith 1982, Burke 1984). It is not believed an adult-larval chemical attraction exists for *A. placenta* particularly as newly-settled recruits have been reported to aggregate away from adult inhabitants (Aung 1975, Koizumi 1997).

1.2.1.2. Across-shore Size Distribution and Directional Movement

As the beach slopes toward the sea, gravitational receptors enable intertidal invertebrates to orient themselves on the shore. Gravity responses of this sort appear to be a widespread attribute of intertidal animals (Meadows and Campbell 1972). The changes in response to gravity that occur as intertidal invertebrates including molluscs, crustaceans and echinoderms become immersed, or move from wet to dry sand, also assists in the maintenance of position in the intertidal zone (Meadows and Campbell 1972). Like other sand dollars *Arachnoides placenta* is a rather sedentary animal, but is however capable of moving 3-4 metres at low tide (pers. obs.) although it is not as yet known what the movement is a response to.

The position of individuals on the shore in response to factors including slope, current, sediment preferences and predation have been documented in a number of sand dollar species, including *Echinarachnius parma* (Cabanac and Himmelman 1996, 1998), *Mellita quinquiesperforata* (Lane and Lawrence 1980) and *A. placenta* (Aung 1975, Campbell 1995, Koizumi 1997). Different responses to slope and current were observed in adults and juveniles of the sand dollar *Echinarachnius parma* in the northern Gulf of St. Lawrence, Canada (Cabanac and Himmelman 1998). A strong preference for upslope movement was observed for both size groups, however when individuals were placed in a flume and observed for directional movement, large sand dollars (45-55mm in length) showed a preference for upstream movement while small individuals (20-30mm) moved up and downstream in approximately the same frequency. Larger individuals of *E. parma* appear to be better adapted than juveniles in exploiting shallow water as they are less likely to be transported by water turbulence (Cabanac and Himmelman 1998). Cocanour (1969) noted movement of *Echinarachnius parma* into deeper waters with increasing age. The sand dollar *Mellita quinquiesperforata* was also observed to move into deeper waters after having settled in a shallow inshore area (Lane and Lawrence 1980). Across the intertidal shore of Pallarenda Beach, Townsville, adults of *A. placenta* (<15mm) were more abundant on the higher shore while recruits (<10mm) were more abundant on the mid-shore (Koizumi 1997). However, at the same location Campbell (1995) and Aung (1975) found a greater abundance of recruits on the higher shore. A position higher on the shore may prevent mortality in small juveniles, as the sediment is coarse and larger marine predators are likely to be less abundant (Campbell 1995). The presence of juveniles higher up the shore is also observed for the sand dollar *Dendraster excentricus* (Merrill and Hobson 1969). Aung (1975) proposes that the fine shifting sand found on the lower beach would affect the survival of juvenile *Arachnoides placenta* accounting for their position in the coarser sediment higher on the intertidal shore.

In the Gulf of St. Lawrence, Canada, Cabanac and Himmelman (1996) observed the presence of two major size groups within a population of the sand dollar *Echinarachnius parma*. Larger ones (40-60mm) predominated in shallow water and small ones (≥ 4mm) occurred at greater depths.

1.2.1.3. Substrate preference

The adults and juveniles of a number of echinoid species exhibit a variety of preferences for different substrata (Buchanan 1966, Ferber and Lawrence 1976, Bertram and Strathmann 1998 etc.). Particle size has a significant effect on burrowing behaviour, burrowing rate, abundance and distribution of irregular echinoids across the habitat including the spatangoids *Lovenia elongata* and *Meoma ventricosai* (Nichols 1959, Chesher 1969, Lawrence and Ferber 1971). Adult species of *A. placenta* are most abundant in fine to medium particle size and substrate, although the occurrence of *A. placenta* in substrata containing coarse sand close to the spring line at Pallarenda Beach indicates a wide range of tolerance to different particle sizes (Aung 1975). The spatangoid *Lovenia elongata* also has broad tolerances to different types of substrata, from mud with stones to mixed sand and mussel shells (Lawrence and Ferber 1971) but generally has a preference for medium to fine sands (Ferber and Lawrence 1976). Buchanan (1966) reported different rates of growth in different substrata for the spatangoid *Echinocardium cordatum*.

Sediment that is too silty does not appear to suit the morphology and behaviour of the feeding mechanism of most clypeasteroids, spatangoids and sea urchins. The anterior ambulacral feeding mechanism of most irregular echinoids is better adapted to dealing with loose clean sand, which is passed far more efficiently to the mouth than fine particles (Buchanan 1966). When fine silt is introduced into the spine tract of the spatangoid *Echinocardium cordatum* there is an immediate tendency for it to fall between the blades of the spines and reach the floor of the ambulacrum so that the entire tract becomes choked and congested. In turn, feeding and movement becomes greatly impaired (Buchanan 1966). Very fine particles are also documented to block feeding apparatus by becoming trapped in mucous strands normally used to carry small to medium sand grains to the mouth (Buchanan 1966). There are exceptions to this rule however, as the spatangoids *Schizaster canaliferus* (Schinner 1993) and *Brissopsis lyrifera* (Hollertz, Sköld and Rosenburg 1998, Hollertz and Duchêne 2001, Hollertz 2002) are documented to inhabit areas of fine silt. *Schizaster canaliferus* populations are limited to silt and clay sediments in protected sub-littoral areas the Adriatic Sea. Burrowing activity in this species is only functional in fine sediment (Schinner 1993). The spatangoid *Brissopsis lyrifera* also lives in clayey sediment along the Atlantic coast and is regarded as a non-selective deposit feeder that feeds on the micro-organisms and organic matter adhering to the particles. It burrows through the sediment down to a few centimetres below the surface and a small respiratory funnel connects the heart urchin to the surface (Nichols 1959, Hollertz and Duchêne 2001). For water circulation spatangoids maintain ciliary currents around the test created by fascioles, which are dense bands of clavulae with cilia along the stem (Nichols 1959). Such morphological adaptations permit certain spatangoids to feed in such a non-selective manner and live at greater depths than most sand dollars (Nichols 1959). Evolutionary changes from that of the early clypeasteroids including modification of the lantern into a crushing mill, extreme flattening of the test, and proliferation of food-gathering tube feet have allowed clypeasteroids to become epifaunal inhabitants of environments characterised by fine, shifting substrates, a habitat previously inaccessible to most other irregular echinoids (Mooi 1990).

As mentioned, larvae of *Arachnoides placenta* have been documented to recruit away from adults at Pallarenda Beach producing a pattern of zonation (Koizumi 1997). This has also been observed by Bertram and Strathmann (1998) for the planktotrophic larvae of the sea urchin *Strongylocentrotus droebachiensis*. It is possible that larvae of these species have a different preference for grain size or sediment condition to adults. Post-settlement larvae are assumed to disperse further than adults, allowing settlement at sites distant from and dissimilar to the maternal site (Bertram and Strathmann 1998).

1.2.2. Feeding, Burrowing and Locomotive Behaviour

1.2.2.1. Introduction

Feeding, burrowing and locomotory behaviour of a number of larval and adult echinoids appears closely related to substratum characteristics, in particular to smaller particle sizes (Bell and Frey 1969, Aung 1975). As a result, this section is considered to overlap with the substrate preference of echinoids (section 1.3.).

1.2.2.2. Burrowing and locomotive behaviour

A number of physical and biological factors can play a role in the burrowing and locomotory behaviour of echinoids. Sand dollars, including *A. placenta* (pers. obs.), can actively move, right themselves when overturned, can bury themselves and can move around obstacles when required (Bell and Frey 1969, Chia 1969, Cabanac and Himmelman 1998).

Most intertidal echinoids have a preference for sediment grain size when burrowing. For example, the burrowing process of the spatangoid *Lovenia elongata* was found to be most rapid in natural sand of medium-fine composition (Ferber and Lawrence 1976). The distribution of the sand dollar *Mellita quinquiesperforata* is apparently explained by the organism's ability to burrow into a given substrate, which is related predominantly to particle size (Bell and Frey 1969).

In response to reduced moisture within the sediment *A. placenta* will bury itself deeper, particularly on sand bars where individuals have been found buried at an angle at depths of 5 centimetres (Aung 1975). Similarly Johnson (1965) noted that 70% of the marine invertebrates living within the sediment of intertidal sands at Tomales Bay, California were buried at depths greater than 5 cm to avoid the risk of dehydration. Temperature variations within the sediment above this depth were observed to be more variable and increasingly higher, which may be similar to temperatures encountered in 5 cm of sediment on dry sand bars, on which *A. placenta* become stranded at low tide.

Juveniles and adults of the sand dollar *Echinarachnius parma* differ in their tendency to bury themselves in response to water turbulence acting on the shore (Cabanac and Himmelman 1998). In a study on an east Canadian shoreline, a considerable 95 percent of *E. parma* juveniles were buried within sediment in comparison to only 30 percent of adults. The increased tendency of juveniles (<28mm in length) to bury themselves could be an adaptation to avoid water turbulence. It appears juveniles have a preference for a substratum that allows them to bury themselves but does not shift excessively during storms (Cabanac and Himmelman 1998). Similarly seventy-seven to eighty-five percent of tagged large *E. parma* remained at a release site after a storm, while most tagged small sand dollars (20-30mm) which were released, disappeared, indicating the efficiency of the larger body form in resisting transport by waves. The disappearance of smaller individuals is most likely related to water turbulence and, as suggested by Cabanac and Himmelman (1998), even gentle wave action is adequate to transport small sand dollars.

Irregular echinoids have often been recorded as the most abundant macro-organism on intertidal or subtidal sandy substrata (Salsman and Tolbert 1965, Muffley 1981) and through feeding and burrowing can significantly change the nature of the substratum, by reworking the sediment to exclude other organisms. Such activities are known to exclude other individuals of the same population or different species from the surrounding area, and may reduce competition while feeding or reduce predation rates (Woodin 1976, Bell and Frey 1969). *Dendraster excentricus* reduces densities of various infaunal species like the tanaeid crustacean *Leptochelia dubia*, which requires a stable substratum for the suspension feeding of diatoms and algae around the mouth of its burrow (G. Brenchly pers. comm. cited in Highsmith 1982). *D. excentricus* manages to achieve such a reduction in infaunal species in the sediment it inhabits, while remaining vertical at high tide and burrowing at low tide (G. Brenchly pers. comm. cited in Highsmith 1982, Barnes and Ruppert 1994). The feeding and burrowing mechanisms of the sand dollar *Mellita quinquiesperforata* also substantially modifies the substrates in which it lives (Bell and Frey 1969).

1.2.2.3. Feeding Mechanisms

Irregular echinoids are generally considered to be selective deposit feeders (Barnes and Ruppert 1994). Two feeding mechanisms have been suggested for feeding in sand dollars, both of which assume a preference for small sized particles: 1) the sieve hypothesis, in which aboral spines act as a sieve to select certain particles, and 2) the podial deposit feeding hypothesis, where podia of the oral surface are the primary food collecting organs.

Authors which support the sieve hypothesis include Chia (1969) for the sand dollar *Dendraster excentricus*, Lane (1977), Ghiold (1979), Lane and Lawrence (1982a), Mooi and Telford (1982) and Ghiold (1983) for the sand dollar *Echinarachnius parma*. The sand dollar collects fine particles which drop between spines on the aboral surface, picked up in ciliary currents and are swept to the oral surface where they enter food grooves It is a central feature of the sieve hypothesis that the particles must be small (< 100μm) in order to move through the interspine spaces and to be transported by ciliary current. Individuals are also known as ciliary-mucoid feeders for this reason. Despite playing a role in food transport, podia are assumed to play a secondary role in particle selection. Aung (1975) states that *A. placenta* feeds in accordance with the sieve hypothesis, using the dense spine covering of the animal, which acts as a particle size selector. Despite this however almost nothing is known about the feeding mechanisms of *A. placenta*. Nichols (1959) documents a size frequency distribution of the gut contents of the spatangoids*, Echinarachnius flavescens, E. pennatifidum*, and *Spatangus* *purpureus*, indicating that particle size selection does occur in feeding and in which the species are possibly using a sieve mechanism for feeding. Lawrence and Ferber (1971) also observed particle size selection in the feeding of the sand dollar *Lovenia elongata*. The sand dollars *Mellita quinquiesperforata* (Lane and Lawrence 1982a) and *M. sexiesperforata* (Goodbody 1960) are also believed to feed using the sieve hypothesis.

Ellers and Telford (1984) however are critical of the sieve hypothesis. Particles found in the gut of the sand dollar *Echinarachnius parma* were considered too large to have been utilised by the proposed sieve mechanism. The ciliary born currents suggested to play a role in the sieve hypothesis are more likely to ventilate and keep the surface free of sand, thus at most making a trivial contribution to feeding (Mooi and Telford 1982, Ellers and Telford 1984). The authors support the podial deposit-feeding hypothesis instead, in which particular food items are selected by specialised long barrel-tipped podia which pick selected sand grains out of the substrate and are passed from podium to podium until they reach the food grooves, where they are aggregated into mucous cords. The cord is passed into the mouth using another set of specialised podia and a powerfully muscled lantern which contains teeth, crushes diatoms and fractures sand grains (Ellers and Telford 1984, Telford et *al*. 1985). In disagreement with Lane and Lawrence (1982a), Telford et *al*. (1985) documents *Mellita quinquiesperforata* to predominantly feed using podia.

Marine benthic invertebrates including some echinoderms select smaller grain particles (Ghiold 1979) and those covered with an organic coating (Taghon 1982).

Pomory et *al.* (1995) consider grain size selection to be more closely related to the ability to handle grains during feeding, rather than during movement, despite the fact that sand dollars and heart urchins encounter sand grains during both movement and feeding.

1.2.2.4. Food Preference

An age difference in diet has been documented in echinoids, larval food in particular has often been reported to be entirely different to that of adults for example, the sea urchin *Strongylocentrotus intermedius* for example feeds primarily on detrital material immediately after metamorphosis in contrast to older stages (Fuji 1967, Kawamura 1973).

Examination of gut contents in sand dollars (Lane and Lawrence 1982a), indicate that some clypeasteroids ingest inorganic and organic detritus and living material. Inorganic material included sand grains, silt, frustles of different diatoms, tintinnid lorica, sponge spicules and fragments of copepod carapaces. Organic particles included pollen grains, bits of plant material and a variety of dead dinoflagellates (Lane and Lawrence 1982a). The food of the sand dollar *Dendraster excentricus* invariably consists of small sand grains, diatoms and detritus which are conveyed primarily along the food groove system to the mouth by mucoid ciliary action of the spines and tube feet (Chia 1969). It is believed the sieve hypothesis is the suggested method of feeding by *D. excentricus* (Chia 1969, Telford, Mooi and Ellers 1985).

1.2.3. Population Density

The density of populations of the sand dollars *Dendraster excentricus*, *Mellita grantii* and *Mellita quinquiesperforata* may fluctuate from year to year with highest densities occurring after a successful recruitment of juveniles and decreasing thereafter due to mortality (Birkeland and Chia 1971, Ebert and Dexter 1975, Lane and Lawrence 1980). Distribution patterns and densities of adult sand dollars may also be affected by behaviour and migration according to Ebert and Dexter (1975) who state changes in densities in sand dollar populations are due to lateral migration in and out of study areas. Merrill and Hobson (1970) reported migration of entire patches of *D. excentricus*.

The pacific coast sand dollar *Dendraster excentricus* may achieve extremely high densities (1000/m^2) due to their overlapping inclined position in the sand. These high densities are thought to be behavioural adaptations which increase food capture and fertilisation success while in the inclined position (Timko 1975). For those sand dollars which are not inclined, clumping of individuals within populations has also been noted (Section 1.1) (Moore 1956, Salsman and Tolbert 1975, Weihe and Gray 1968, Bell and Frey 1969) but is not always indicative of reproductive activity (Cocanour 1969, Lane and Lawrence 1980).

1.2.4. Reproductive Biology

1.2.4.1. Reproductive physiology

Aung (1975) observed that sexual maturity for *Arachnoides placenta* is reached at a diameter of 15 - 20 mm test diameter. Mature *A. placenta* possess genital papillae with the external opening of the gonoduct at a gonopore, which project from the aboral surface (Chia 1977). Chia (1977) listed 31 species of echinoids with genital papillae, of which 28 species are sexually dimorphic with the papillae present in males and distinctly smaller or absent in females. Genital papillae have also been reported in the echinoderm classes Cocentricycloidea, Holothuroidea and Ophiuroidea, of which 21 species of holothurians have genital papillae (O'Loughlin 2000). Chia (1977) suggested that genital papillae present an adaptive advantage for gamete dispersal, particularly for sperm, in echinoids which are mucus ciliary feeders.

In other species, the heart urchin *Echinus esculentus* in the English Channel and the Firth of Clyde reaches sexual maturity at a size of 94mm and 166mm respectively, corresponding to 1.5 to 2.5 years of age (Nichols et *al.* 1985). The sea urchin *Paracentrotus lividus* reaches sexual maturity at 35 mm (Lozano et *al.* 1995). Another sea urchin *Strongylocentrotus droebachiensis* becomes mature at an age of 2.75 years when individuals are larger than 19mm in size (Raymond and Scheibling 1987).

1.2.4.2. Factors influencing breeding cycles and spawning

Most of the documentation on the breeding cycles of echinoids points to a predominant role of temperature in the regulation of gametogenesis, reproduction and larval development (Hines and Kenny, 1967, Dix 1970, Aung 1975, Cochran and Engelmann 1975, Ebert 1983, Spirlet et *al.* 1998 etc.), although photoperiod seems important for some echinoid species (Cochran and Engelmann 1975, Pearse et *al*. 1986, McClintock and Watts 1990, Spirlet et *al.* 1998). However, the actual factors triggering spawning episodes in echinoids are not known with certainty (Lopez et *al.* 1998).

A number of echinoid species are documented to spawn in association with rising or falling sea water temperature cycles. The sand dollar *Echinarachinus parma* has a distinct annual cycle inversely related to temperature with a spawning period from November to December in captivity at Lamoine, Maine (Cocanour and Allen 1967). The sea urchin *Evechinus chloroticus* also displays spatial and temporal variability in spawning in New Zealand, occurring near the time of highest sea-surface temperatures (~15 ^{o}C) (Brewin et *al.* 2000).

Field studies by Gonor (1973) and Bay-Schmith and Pearse (1987) indicate that the reproductive cycle of the sea urchin *Strongylocentrotus purpuratus* is also dictated by seasonally changing photoperiod, with only a slight or no effect by temperature. Gametogenesis and spawning in the subtidal sand dollar *Clypeaster ravenelli* are also highly synchronised with increasing day length during the winter in the northern Gulf of Mexico but not significantly correlated with changes in sea water temperature (Vernon et *al*. 1993). Rainfall is one other factor that is known to affect spawning. Higher than average rainfall was associated with smaller than average gonads in the sea urchin *Lytechinus variegatus* (Moore and Lopez 1972).

Some authors (Himmelman 1975, Stanwell-Smith and Peck 1998, Starr et *al.* 1990) have also observed a direct coupling of echinoid spawning with phytoplankton blooms. Pulses of phytoplankton may result in pulses of microphytobenthos, resulting in an enhanced supply of carbon to the benthos (mainly in the form of diatom aggregates) during bloom period. Echinoids may also utilise phytoplankton blooms in a different way, spawning independently of the plankton production, but in which larval survival is enhanced in the presence of abundant planktonic resources (Lopez et *al.* 1998).

Arachnoides placenta in northern east Australia keeps a synchronised annual pattern, but in response to which factor, is unknown (Aung 1975, Campbell 1995, Koizumi 1997). Koizumi (1997) observed males to spawn throughout the year without corresponding to a season, whereas the development of ovaries was more seasonal. There is however some dispute as to the spawning period of *A. placenta* in Queensland. According to Koizumi (1997) *A. placenta* spawns relatively continuously between June and September, and possibly later at Pallarenda Beach. This data varies from that of Hines and Kenny (1967) and Aung (1975) who consider spawning to occur between May and July at Lucinda, which is only located a distance of 150km north of Townsville.

Timing of spawning can also vary between locations for the same species. For instance, the sea urchin *Echinometra mathaei* spawns in the summer and early fall in the Gulf of Suez (Pearse 1969b). However, at Rottnest Island individuals become ripe and spawn throughout the year, suggesting that the environmental factor that synchronises and seasonally restricts reproduction in the species is absent at Rottnest Island (Pearse and Phillips 1968). *Evechinus chloroticus* in New Zealand spawns in summer or early autumn depending on its location (Dix 1970).

1.2.5. Recruitment Biology

1.2.5.1. Introduction

Recruitment of marine invertebrates with a planktonic stage, like the Echinoidea, can be broadly divided into three components: 1) pre-settlement processes comprising larval production and larval development, mortality and transport, 2) settlement and metamorphosis, and 3) post-settlement growth and mortality of juveniles (Cameron and Schroeter 1980, Harrold et *al*. 1991). In particular, a prominent feature of most echinoid populations is the high degree of spatial and temporal variability in larval distribution, settlement and recruitment, varying from metres between adjacent habitats to hundreds of metres between regions (Pedrotti and Fenaux 1992, Balch and Scheibling 2000a,b). Recruitment is therefore understandably accepted to be the single most important factor in limiting adult populations, including the Echinoidea (Boolootian, 1966).

1.2.5.2. Larval morphology

Once fertilization occurs in echinoids, pelagic planktotrophic echinopluteus larvae form. Like most echinoids, the echinopluteus of *Arachnoides placenta* is a complex, pelagic, feeding larva characterised by anteriorly directed arms that are supported by calcareous skeletal rods (Okazaki 1975, Chen and Chen 1992, Hart and Strathmann 1994). The larva is bilaterally symmetrical with the arms arranged as left-right pairs. The arms are hollow extensions of the body wall that contain blastocoelic space and bear the ciliated bands, which are used to capture food, such as small algal cells. This ciliated band traces a convoluted loop around the whole of the larval body. The echinopluteus also possesses a complete gut consisting of a tubular oesophagus, bulbous stomach, short tubular intestine and an anus opening on the posterior ventral side (Burke 1981, Hart and Strathmann 1994).

It is estimated that the larval period in *Arachnoides placenta* takes approximately two weeks, during which time they feed on microscopic algae (Aung 1975, Chen and Chen 1992). Laboratory raised sea urchin larvae including *Lytechinus pictus* spend longer in the water column, taking approximately 21 days to reach metamorphosis (Cameron and Hinegardner 1974). Similarly, larvae of the New Zealand sea urchin *Evechinus chloroticus* occur in the water column in the Austral summer months of November through to April. Larvae reach competency as early as 21 days in the laboratory (Lamare and Barker 2001). Metamorphosis in *A. placenta* subsequently takes place after settlement on the substratum occurs, where transformation to the adult stage takes place (Aung 1975).

A newly metamorphosed echinoid has no mouth and does not begin feeding immediately but these develop a few days later depending on the species and conditions (Hinegardner 1969). Complete metamorphosis from feeding larvae to feeding adult takes 5 or 6 days in the sea urchin *Lytechinus pictus* which includes the development of the adult internal organs as well as the formation of the adult mouth and anus (Cameron and Hinegardner 1974).

1.2.5.3. Factors influencing Larval Development

Two important factors that play an important role in larval development include sea water temperature and food availability (Rupp 1973, Chen and Chen 1992, Metaxas and Young 1998, Stanwell-Smith and Pack 1998). Most echinoderms are sensitive to water temperatures higher than normal ambient, subsequently affecting the survival and distribution of adults as well as their gametes and larval stages that exist in the plankton (Rupp 1973). High temperatures are observed to significantly affect the larval development of *Arachnoides placenta* producing small juveniles (Chen and Chen 1992). Fertilization and cleavage of embryos in the sea urchin *Echinometra mathaei* is also significantly affected by higher than ambient sea water temperatures (Rupp 1973).

Larval development rates of larvae in tropical habitats are considerably faster than those of temperate and Antarctic climates (Stanwell-Smith and Peck 1998). In the Antarctic sea urchin *Sterechinus neumayeri* larval development was recorded to be 2-10 times slower than rates for temperate and tropical species (Stanwell-Smith and Peck 1998). Spawning in this species probably corresponds with a rise in sea water temperatures in November benefiting larvae with increasing phytoplankton levels (Stanwell-Smith and Peck 1998).

Echinoid larvae may also be able to maximise their food intake by actively remaining in areas of increased food concentration. Larvae of the sea urchin *Echinometra lucunter* enhance the chance of survival by vertically migrating to food patches that form at haloclines (Metaxas and Young 1998). Meidel et *al*. (1999) observed larval food rations to have a strong effect on the rates of development, growth and metamorphosis of the sea urchin *Strongylocentrotus droebachiensis*. In the same investigation results suggested parental nutrition had a small effect on the larval development of the species.

Larval sea urchins that are faced with a lack of food are capable of developmental plasticity Bertram and Strathmann 1998). For example *Strongylocentrotus droebachiensis* like other echinoid larvae grow larger larval feeding appendages in response to scarcer food. In areas of abundant food, fast development of the echinus rudiment occurs, which is retained in the juvenile and adult echinoid, including *S. droebachiensis* (Starr et *al.* 1993, Meidel et *al.* 1999). Maternal investment also has a significant and detectable effect on larval growth rate, however effects are small in comparison to larval nutrition (Bertram and Strathmann 1998, Meidel et *al.* 1999).

1.2.5.4. Factors influencing Larval Supply

The supply of larvae to benthic populations is regulated by a complex interaction of biotic (e.g. larval behaviour, food availability, predation) and abiotic factors (currents, temperature, salinity), which control larval production, development and survival (Balch and Scheibling 2000b). In view of their considerable ecological and economical importance, the population ecology of many echinoids has been studied at length (Moore 1956; Ebert 1967, 1968b; Salsman and Tolbert 1975; Lane and Lawrence 1980 Lozano et *al*. 1995 etc.), however the importance of early life history events in determining the population structure and dynamics, remain poorly understood for most species of echinoids. In a review of the existing documentation on larval supply, settlement and recruitment in echinoderms, Balch and Scheibling (2000b) determine there is strong evidence for regulation of echinoid larval settlement by currents and hydrodynamic forcing.

The relationship between the transport of larval stages and hydrodynamic processes has been presented for a number of echinoid species, and are documented to affect larval supply to the benthos at various spatial scales (e.g. Cameron and Rumrill 1982, Emlet 1986, Estes and Duggins 1995, Prince 1995, Lamare 1998). Both local hydrodynamics and large scale oceanographic forces play an important role in the arrival of planktonic larvae at suitable settlement sites, and are key determinants of recruitment success. A latitudinal cline in settlement has been observed in the sea urchins *Strongylocentrotus purpuratus* and *Strongylocentrotus franciscanus* along the coast of California, which has been associated with the general oceanographic processes that occur along the stretch of coast sampled (Ebert 1983). Estes and Duggins (1995) attribute large-scale oceanographic processes causing differences in episodic recruitment in the sea urchins *Strongylocentrotus droebachiensis*, *S. purpuratus* and *S. franciscanus* to regions in southeast Alaska between 1972 and 1990. Spatial and temporal variability in the recruitment of the sea urchin *Echinometra mathaei* at Rottnest Island, Western Australia is highly correlated with both differences in local hydrodynamics as well as large scale interannual variation in ocean currents (Prince

1995). A positive relationship between recruitment and the shoreward transport of larvae has also been documented for irregular echinoids, including the sand dollar *Dendraster excentricus* (Cameron and Rumrill 1982). Larvae of populations of the same species inhabiting a small fiord however are documented to be advected offshore by wind-driven circulation (Emlet 1986). Lamare (1998) compared the larval abundances of the sea urchin *Evechinus chloroticus* between a fiord in Doubtful Sound and an outer-fiord site, both in New Zealand. Higher abundances of larvae were recorded within the fiord in comparison to the outer fiord site which is probably due to the greater offshore advection and dispersal of larvae associated with coastal currents. High levels of water retention within fiords, consistent with circulation patterns of estuaries, are responsible for reduced larval exchange as populations are closed or semi-closed, which subsequently influence the recruitment process of marine invertebrates that inhabit such areas. This case is probably in contrast to the majority of *E. chloroticus* population sites in Doubtful Sound which occur along the open coast and are almost certainly open in terms of larval supply. Open marine invertebrate populations are more likely to have irregular and/or low recruitment mainly due to a decoupling of reproduction and recruitment (Hughes 1990). It is important in open systems therefore that currents deliver the larvae of marine organisms to coastal areas with suitable habitats for settlement, as the likelihood of settling is greatly reduced once larvae are advected far offshore (Balch and Scheibling 2000a,b).

Increased temperature increases or enhances settlement in a number of echinoids by accelerating larval development and reducing the length of time that larvae are exposed to planktonic predators (Ebert 1983). These findings suggest that temperature alone does not reliably explain recruitment patterns as changes in sea temperature may simply reflect shifts in local hydrodynamics or other environmental factors, such as salinity, food availability or predator abundance. These factors in turn may enhance or limit larval survival (Balch and Scheibling 2000b).

Predation within the plankton has long been recognised as a major component of larval mortality although few studies have examined predation of echinoderm larvae (Ebert 1983). Experiments on the predation of larvae of the sand dollar *Dendraster excentricus*, and the sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* demonstrated that planktonic invertebrate predators such as crustaceans, chaetognaths, medusae and ctenophores, selectively feed on embryos and larval stages, while small planktivorous fish chose larger plutei to feed on (Rumrill et *al*. 1985). In addition, as larvae approach the substrate they also become exposed to a large group of suspension feeding benthic invertebrates including mussels, ophiuroids, ascidians, anemones and tunicates, depending on the substrate the larvae settle on (Balch and Scheibling 2000b).

1.2.5.5. Settlement of Recruits

Settlement of benthic marine invertebrates is generally defined as the attachment of larvae to the substratum and consequent metamorphosis into the juvenile form (Woodin 1986, Balch and Scheibling 200b). Recruitment is usually defined operationally as occurring some time after settlement when individuals can be reliably counted and some post-settlement mortality or migration may have occurred (Keough and Downes 1982, Harrold et *al*. 1991, Balch and Scheibling 200b). Settlement in *A. placenta* is reported by Aung (1975) to occur at an approximate size of 0.5mm test diameter at Townsville, North Queensland. A newly metamorphosed individual of the sea urchin *Lytechinus pictus* is also approx. 0.5mm in test diameter (Cameron and Hinegardner 1974). Hines and Kenny (1967) state metamorphosis at Lucinda, Queensland occurs during September when winter sea temperatures are between 20^{o}C and 22^{o}C. This conflicts with the observations of Koizumi (1997) who noted the first appearance of *A. placenta r*ecruits earlier, in mid-August 1997, at three locations between Rowes Bay and Pallarenda Beach, Townsville.

Larvae of *A. placenta* require a minimum of 7 days for metamorphosis (Chen and Chen 1992). Recruits are of meiofaunal size (0.1 – 1.0cm), covered with spines and are found very close to surface of the substratum (Aung, 1975; Campbell, 1995; Koizumi, 1997). Smaller individuals tend to become resuspend in the water column with low disturbance (Aung, 1975; Koizumi, 1997). According to Koizumi (1997) at locations on the shore where the adult population was considerably dense, a large number of recruits occurred. Because of the planktonic nature of the larvae of *Arachnoides placenta*, it is most likely that the tides and currents that disperse the larvae significantly influence the distribution and settlement of individuals, in turn affecting the distribution of adult populations later on (Koizumi 1997).

1.2.5.6. Factors influencing Metamorphosis and Post-Settlement Processes

Like many other intertidal organisms *Arachnoides placenta* depends strongly on the recruitment of free-swimming larval stages to maintain adult populations (Koizumi

1997). In echinoid larvae, two stimuli are needed to initiate metamorphosis, 1) a chemical cue and 2) a surface for tube foot attachment (Cameron and Hinegardner 1974, Gosselin and Jangoux 1998). The substratum is tested by sensory-secretory primary podia that project from the larva. They are able to adhere to the substratum in order to allow evagination of the echinoid rudiment (i.e. metamorphosis) (Gosselin and Jangoux 1998). Larvae of other sediment dwellers, such as polychaetes and bivalves also require the presence of sediment for settlement to occur (Woodin 1986).

Metamorphosis in sea urchins is influenced by factors including: water temperature, water motion, food source, the bacterial film on sediment grains and chemical cues produced by adults (Cameron and Hinegardner 1974, Hinegardner 1969, Highsmith 1982). For example, larvae of the sand dollar D*endraster excentricus* are rapidly induced to metamorphose by a chemical believed to be a peptide secreted into the sand by adults (Highsmith 1982, Burke 1984). In captivity a bacterial film on the surface of containers induce metamorphosis in the larvae of a number of sea urchin species including *Lytechinus pictus* and *Arbacia punctulata* (Cameron and Hinegardner 1974). Larvae of *D. excentricus* will delay metamorphosis for 25 days or more if such substrates are not present (Highsmith 1982) and larvae of the sea urchin *Paracentrotus lividus* may remain capable of metamorphosis for up to 2 months (Vaitilingon et *al*. 2001).

The role of post-settlement processes in influencing echinoid populations remains a poorly researched aspect of echinoid life history. Most species of benthic marine invertebrates suffer very high mortality within the first days to months after settlement (Balch and Scheibling 2000b). A general trend documented in thirty studies of marine invertebrate populations shows that survivorship of newly settled recruits decreases exponentially during the first days or weeks of juvenile until at the age of four months old, virtually all recruit cohorts were reduced to less than 20% of initial numbers, from which time mortality remained low (Gosselin and Qian 1997). Various factors including predation, disease, storms and reduced salinities are associated with high post-settlement mortality, and thus play an important role in regulating recruitment rates and patterns (Balch and Scheibling 2000b). While predation is the most documented cause of mortality, abiotic factors might be more important in intertidal habitats for example, where conditions fluctuate to extremes in just over a few hours. The settlement success of small recruits of the sand dollar *Mellita quinquiesperforata* for example is strongly influenced by turbulence and surf on the intertidal shore (Lane and Lawrence 1980). This may be the main factor affecting the success of the settlement of numerous sand dollar species as larvae settle primarily in shallow benthic areas where turbulent surf conditions could easily cause re-suspension and mortality. Unlike adults, which bury during turbulence, juveniles do not or cannot bury as deep due to a lighter test. As a result, very young juveniles are especially susceptible to resuspension. Early juveniles may be more vulnerable to desiccation stress than adults when emersed, as individuals probably lose water faster than adults due to a greater surface to volume ratio (Lane and Lawrence 1980, Gosselin and Qian 1997). Desiccation during low tide is also the suggested cause of mortality in the sand dollar *Encope grandis* (Ebert and Dexter 1975). High water temperatures and persistent low salinity levels also cannot be tolerated in the juveniles of a number of juvenile echinoid species (Himmelman et *al*. 1984), including *A. placenta* (Chen and Chen 1992).

1.2.6. Growth of newly settled recruits and adults

Growth rate is a critical parameter of the population dynamics of all echinoid species (Lamare and Mladenov 2000). Within the last two centuries, the diversity of growth models have gradually increased (e.g., von Bertalanffy 1938, Richards 1959), however not one of these models appear to complement each other. Choosing a growth model for both sea urchins and irregular echinoids therefore often remains subjective (Grosjean et *al*. 2003). Recently a new functional growth model has been applied to the sea urchin *Paracentrotus lividus* (Grosjean et *al.* 2003).

Growth rates of sea urchin and sand dollar species, including *Arachnoides placenta*, *Echinarachnius parma*, *Dendraster excentricus*, *Mellita grantii* and *Paracentrotus lividus* have been measured using either size frequency analysis, growth rings or marked animals in the field (Hines and Kenny 1967, Birkeland and Chia 1971, Ebert and Dexter 1975, Cabanac and Himmelman 1996, Grosjean et *al*. 2003). A rapid growth rate of smaller immature individuals (approximately 12 months old) and a slow growth rate in adults are reported for a number of echinoids including *A. placenta* (Hines and Kenny 1967, Nichols et *al*. 1985, Lamare and Mladenov 2000). Thompson (1979) concluded that the primary allocation of nutrients to growth resulting in the rapid growth of small individuals of the sea urchin *Strongylocentrotus droebachiensis* might result from selective pressures resulting from higher mortality, competition of small individuals, as well as the predictability of the food supply. Newly settled recruits (0.5 - 1mm test diameter) however, initially exhibit a slow rate of growth for the first six to twelve months, the reasons for which are not clear. It may involve the completion of functional development of all aspects of feeding digestion and assimilation associated with a new way of life (Lane and Lawrence 1982b, Lamare and Mladenov 2000).

Environmental factors such as availability of food, sea water temperature, (which vary seasonally), and injury may explain the variable growth rates observed between individuals of the same age and different year classes of the same population (Lares and McClintock 1991). Seasonal differences on body growth as well as negative growth are reported for the sand dollars *A. placenta* (Hines and Kenny 1967) and *Echinarachnius parma* (Cocanour 1969). The effect of prolonged lower than normal temperatures, could also explain slowed growth during that period (Lane 1977). Lewis (1958), Moore et *al.* (1963) and McPherson (1965) document a 2 – 3 year lifespan and a maximum size of 90 – 100mm for the sea urchin *Tripneustes ventricosus*. A marked decrease in growth was observed with increased temperature (Moore et *al*. 1963), but also a sharp drop in growth occurred at lowest optimal temperatures (McPherson 1964). Negative growth recorded for adult populations of the sand dollar *Mellita quinquiesperforata* also appears to be indirectly correlated with high summer water temperatures (Lane and Lawrence 1980).

Newly settled *A. placenta* recruits are recorded to grow from 0.5 mm to 7mm in the first year and subsequently increase by 4mm in the second year and third year after metamorphosis (Hines and Kenny 1967). *Arachnoides placenta* at Lucinda, North Queensland, with a diameter of 36mm has a lifespan of approximately 5 years (Hines and Kenny 1967). Newly settled urchins of *Evechinus chloroticus* had a similar growth rate, growing to a mean size at one year of 10.5mm test diameter in the field with mean growth rates of 0.12mm week^{-1}. Growth of newly settled *E. chloroticus* does however appear to be non-linear with slow growth for a period of 197 days post-settlement after which accelerated growth follows in which individuals grew a faster 1.7mm month^{-1} over the next 65 days (Lamare and Mladenov 2000). Initial growth in the sea urchin *Paracentrotus lividus* from 0.6 mm to 2 mm is estimated to take up to 3 to 4 months (Lopez et *al.* 1998). Such non-linear growth is generally associated with a major shift in diet, previously observed in newly settled sea urchins. The Richard's growth model (Richards 1959) shows a strong relationship between diameter and age (also known as the Richards S-shaped growth curve). The Richard's growth model provides the closest prediction of size of *E. chlorotius* at 1 year (Lamare and Mladenov 2000) and describes the growth of the sand dollar *Echinarachnius parma* (Cabanac and Himmelman 1996) and the sea urchin *Echinus esculentus* (Nichols et *al*. 1985). There is an eventual decline in growth rate with time so that a maximal body size is attained. Ebert (1967, 1968a, b) suggest that echinoids grow to a limit allowed by the environment and adjust as the environment fluctuates. A decrease and eventual cessation of somatic growth resulting from utilisation of nutrients for gametogenesis has been suggested (Moore and Lopez 1966, Moore et *al.* 1963). It might be expected that an inverse relationship between numerical density and size of individuals. Higher densities would reduce the amount of food available to each individual, producing an optimal size of adults within the population that is inversely related to density (Lane and Lawrence 1982b).Growth in grazing populations of sea urchins rely on a number of factors including the quality of sea water and food availability (Nichols et *al*. 1985).

1.2.7. Factors influencing Adult Populations

1.2.7.1. Adult Mortality

Mortality in echinoids can result from changes in salinity and high sea water temperatures (Aung 1975, Lane and Lawrence 1980), wave action and sedimentation of silt (Aung 1975), predation (Ebert 1975) and senescence (Salsman and Tolbert 1965, Birkeland and Chia 1971).

Senescence is the main source of mortality in intertidal *Dendraster excentricus* populations (Birkeland and Chia 1971) and *Mellita quinquiesperforata* (Salsman and Tolbert 1965). It is believed also that sand dollars undergo substantial mortality every year in the summer wet season mainly as a result of heavy rainfall and river discharge, reducing the salinity of sea water (Lawrence 1973, Aung 1975). Heavy rainfall is understood to be responsible for the mortality of medium to large size individuals of *Arachnoides placenta* at Pallarenda Beach, North Queensland, during the wet season of January to March 1975. Despite this however, smaller individuals continued to persist in great abundance on the intertidal shore (Aung 1975). Lawrence (1973) suggested high levels of rainfall was also the cause of a decrease in the population size of the sea urchin *Lytechinus variegatus* in Florida and juveniles of *L. variegatus* have been reported to appear in greater numbers in comparison to adults in years of low rainfall (Moore and Lopez 1972). Ebert (1966) also observed small individuals of *Stongylocentrotus purpuratus* were more tolerant of extreme conditions than adults.

1.2.7.2. Predation of adults

There has been little documented work on the role that predation plays on irregular echinoderm populations. Sand dollars are prey for a few animals including some large crabs, sea stars, herring gulls and fishes (Moore 1966, Merrill and Hobson 1969, Birkeland and Chia 1971). The crabs *Loxorrhynchus grandis* and *Cancer* spp. and an active asteroid predator, *Astropecten braziliensis armatus*, predates on the sand dollar *Dendraster excentricus*, the latter mostly at night (Merrill and Hobson 1969). Limbaugh (1955) reports finding tests of *Dendraster excentricus* in the stomach of pile perch. In the field sand dollars and sea urchins have been observed to have chips or cuts in the test, which may be from gull predation (Moore 1966, Birkeland and Chia 1971).

1.2.7.3. Parasitic and Commensal Associations

A number of endo- and ecto-parasitic relationships have been observed between echinoid and mollusc species, in particular gastropods of the family Eulimidae. *Hypermastus placentae* are the only eulimid gastropods found in association with *Arachnoides placenta*. This gastropod temporarily associates with its host and penetrates the test to feed using an extendable proboscis (Crossland et *al*. 1993). Feeding observations show that *Hypermastus placentae* feed on the gonad tissue and possibly the coelomic fluid. Gastropod density however, was considerably less than the density of *A. placenta* (Crossland et *al.* 1991, 1993). *H. placentae* only parasitized hosts with a test diameter larger than 20 millimetres. Aung (1975) observed that *Arachnoides placenta* reached sexual maturity at 15 - 20 mm diameter indicating the preference of *Hypermastus placentae* for mature gonadal tissue.

In temperate regions, the burrowing bivalve *Montacuta substriata* remains near the surface of the sand close to the entrance of the burrow of the spatangoid *Spatangus purpureus* and attaches itself to and parasitizes *S. purpureus* when it leaves its burrow (Gage 1966). A close relative, *Montacuta ferriginosa* is geopositive, and burrows further into the sediment where it parasitizes another heart urchin *Echinocardium cordatum* (Gage 1966). Such parasitic or commensal relationships may result in the death of a host or produce a decrease in growth rate as a result of bodily damage. *A. placenta* for example may affect an individual’s ability to spawn as a result of *H. placentae* feeding on its gonadal tissue. In turn, such factors may influence a decline in a population.

The aim of this project is threefold: 1) to describe in detail the reproductive cycle, patterns of recruitment and size frequency of individuals from the onset of metamorphosis at determined sites on the Queensland coast; 2) to propose, and where possible test, hypotheses relating to the timing of spawning and recruitment pulses within *A. placenta* populations; and 3) to discuss the findings with reference to current theories in echinoid reproduction, recruitment and demography.

Chapter 2 provides a biological background of *A. placenta* and describes the study sites. Chapter 3 investigates the density, spatial distribution and size frequencies of pre-mature indivduals and adults at all sites from April 2001 to September 2002. As mentioned previously, *A. placenta* populations are constantly exposed to a wide range of biotic and abiotic variables that are associated with intertidal shores. Variations in population characteristics including density, spatial distribution, size frequencies, age structure relating to abiotic and biotic habitat specific factors at each site will be investigated in Chapter 3. Biotic factors responsible for influencing echinoid population characteristics, which will be investigated at all sites, include differential recruitment success and post settlement survival (Ebert 1983), differences in the quality or quantity of available food resources and the levels of predation at each habitat (Harrold and Pearse 1987). Intertidal sands, which commonly comprise grains of different sizes across the shoreline, also play an important role in affecting the spatial distribution of a species (Meadows and Campbell 1972) and will also be investigated in this chapter. The effect of abiotic factors on population demographics will also be investigated at all sites, including the effects of sea water temperature, air temperature and rainfall on asymptotic body size and variations in the initiation, timing, intensity and duration of reproductive events. The structure of echinoid populations are also documented to differ even in similar areas of close proximity as a result of what may be considered minor but significant abiotic or biotic variations between sites. Two sites within close proximity on the same beach at Mackay within Chapter 3 should determine whether the population structure of *A. placenta* is influenced in a similar manner.

Chapter 4 examines the reproductive cycle of *A. placenta* and the factors that play a potential role in the seasonality of the species' reproductive cycle. Factors that have been documented in other echinoids to influence gametogenesis include photoperiod (Giese 1959; Byrne et *al.* 1998), sea water temperature (Cocanour and Allen 1967, King et *al.* 1994, Kelly 2000) and day length (Byrne et *al.* 1998). The role that each of these factors play at each site on the reproductive cycle of *A. placenta* will be investigated in this chapter.

Chapter 5 determines how recruitment amongst populations of *A. placenta* differs spatially and temporally at each site and how variations in abiotic and biotic factors might alter recruitment. Factors that regulate pre- and post-settlement processes in both irregular echinoids and sea urchins include a complex interaction of both near-shore currents, sea temperature, salinity, food availability, predation and wave action (Highsmith 1982, Butman 1987, Balch and Scheibling 2001). The effect of these factors on the recruitment biology of *A. placenta* will be investigated in this chapter.

Chapter 2: Biological Background of *Arachnoides placenta* and a Description of the Study Sites

2.1. Biological Background

2.1.1. Introduction

The irregular echinoids (Superorder Gnathostomata) comprise the sand dollars (clypeasteroids) and heart urchins (spatangoids). Most of the prominent features of irregular echinoids are adaptations for inhabiting, and burrowing into sand (Barnes and Ruppert 1994). Most sand dollars have a greatly flattened body that is more or less circular in appearance. The aboral and oral surface of clypeasteroids are covered in short fine spines, which play a primary role locomotion and feeding. There is a significant difference in the test of sand dollars, depending on whether they inhabit intertidal or subtidal habitats. *Arachnoides placenta* for example, is an intertidal sand dollar specialised to bury deep into the sediment at low tide should an individual become stranded on a sand bar. The periphery of the test of this species is thin and adapted to easily bury into thixotropic sediment (fig. 2.1.). On the same shore however, the sand dollar *Laganum depressum* is a subtidal species, replacing *A. placenta* subtidally (Aung 1975, Saunders 1986). *L. depressum* is not known to become exposed at low tide, and does not bury into the sand, primarily as it is not subjected to the risk of desiccation encountered by intertidal clypeasteroids (Saunders 1986). The morphology of *L. depressum* is clearly reflected in the habitat in which it exists as its test is much thicker and greatly rounded by comparison (pers. obs.). On a global scale, the majority of sand dollars are subtidal species and like *L. depressum* have a thicker and more rounded test (Ghiold 1979, Harrold and Telford 1982, Cabanac and Himmelman 1998).

In *A. placenta* the oral centre containing the mouth is located centrally within the test (fig.2.1.a, c). The periproct and anus are within the posterior ambulacrum (fig 2.1.b, d), on the aboral surface near the periphery of the test. The aboral surface also bears petaloids which contain tube feet that are specialised for gas exchange (Boolootian 1966). The oral surface possesses clear radiating grooves which contain small podia that provide the major source of mucus used in the ciliary-mucus feeding mechanism utilised by most clypeasteroids (Mooi 1986a). The other major types of podia present amongst clypeasteroids include accessory podia, which are largely sensory and

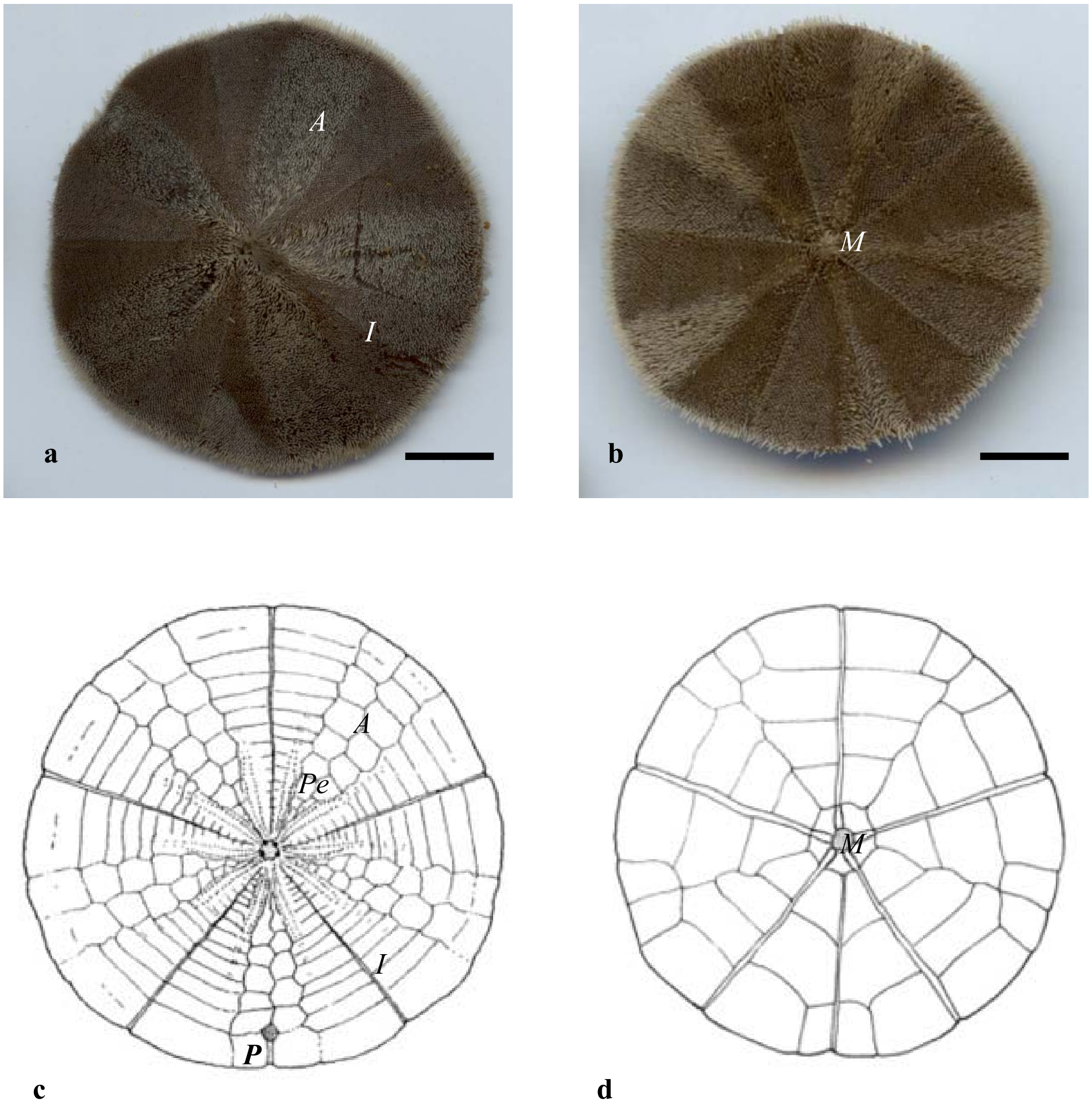

Figure 2.1. *Arachnoides placenta*. A typical sand dollar with a greatly flattened body displaying a circular circumference (**a**) Convex aboral surface of test covered in spines, which are used for locomotion and keeping sediment off the body surface. The aboral centre is located centrally from which radiate ambulacra (*A*) and interambulacra (*I*) (**b**) Flattened oral surface, also covered in spines. Oral centre containing mouth (*M*) is also centrally located. (**c**) Life size drawing of aboral surface without spines. Periproct (*P*) is located ventrally in the posterior ambulacrum (*PA*) and surface bears conspicuous petaloids (*Pe*) (**d**) Life size drawing of oral surface without spines. Distinct grooves radiate from mouth (*M*), which play a primary role in feeding. Scale bars = 10mm. Drawings by J. Collins (by permission).

manipulatory, and barrel-tipped podia which collect food and pass it to the food grooves (Mooi 1986a). Mucus cells are not associated with the military spines of any member of the Arachnoididae, although the sacs found at the tip of such spines had a previously supposed mucus-secretory role (Mooi 1986b).

2.1.2. Classification of *A. placenta*

Arachnoides placenta (Linnaeus 1758), the subject of this thesis, was first listed in Systema Naturae as *Echinus placenta*. The nomenclature of the species has since been changed on a number of occasions and today is known as *Arachnoides placenta*. The genus *Arachnoides* belongs to the order *Clypeasteroidea*, family *Arachnoididae*. The subfamily consists of two genera with three species, comprising *A. placenta* (Linnaeus), *Arachnoides tenuis* (Clark), endemic to Western Australia and *Fellaster zelandiae* (Gray) endemic to New Zealand (Clarke 1921, 1946). In agreement with Rowe and Gates (1995) *A. placenta* is classified as follows:

PHYLUM	Echinodermata
CLASS	Echinoidea
SUBCLASS	Euechinoidea
SUPERORDER	Gnathostomata
ORDER	Clypeasteroidea
SUBORDER	Clypeasterina
FAMILY	Arachnoididae
GENUS	Arachnoides
SPECIES	*placenta* (Linnaeus 1758)

2.1.3. World Distribution

The major limiting factor in the latitudinal distribution of *A. placenta* appears to be temperature. On a global scale, Amoy, South China (24^{o} 30’ N) is probably the extreme northern distribution limit of the species (Chang 1932). Its southern distribution limit is probably Port Curtis (Gladstone, Queensland, Australia 23^{o} 52’ S) (Aung 1975) (fig. 2.2.).

Figure.2.2. Global distribution of *Arachnoides placenta* (Aung 1975)

2.1.4. Australian Distribution

Arachnoides placenta exists from Torres Strait (Clark 1921) to Southern Queensland on the east coast of Australia (Clark 1946) and West around the Northern Territory to Augustus and Champagny Islands in Western Australia (Clark 1921). South of Augustus Island *A. placenta* is limited by the species *Arachnoides tenuis*, the only other species of the genus *Arachnoides* (Clark 1946).

2.1.5. Queensland Distribution

According to Clarke (1946) *A. placenta* extends along the mainland coast and continental islands of Queensland and islands of the Great Barrier Reef from Thursday Island, Cape York down to Caloundra, Moreton Bay. The echinoderm collection of the Australian Museum, consists of *A. placenta* samples from Bowen, Repulse Bay, Port Darwin, Whitsunday Passage and Port Curtis (Aung 1975). Aung also from 1974 – 1975 collected samples of *A. placenta* from Lizard Island, Cairns, Cape Bowling Green, Bluewater, Shelley Beach, Saunders Beach, Magnetic Island, Mackay, Sarina and Cape Palmeston. Aung (1975) has since observed the disappearance of *A. placenta* from Caloundra and Moreton Bay (1946) and suggests Port Curtis, some 500km north of Moreton Bay and a fraction south of the Tropic of Capricorn, is now the most southern limit of distribution of the species.

2.1.6. Previous studies on *Arachnoides placenta*

A limited number of studies have been conducted in the past on *Arachnoides placenta*. The first documented research of the species was by Feliciano in 1933, who investigated the early development of the organism in the Philippines. However, he failed to rear larvae under laboratory conditions and his figures according to Aung (1975) were most probably inaccurate as a result of poor specimen preservation. Hines and Kenny (1967) studied the growth rate of *A. placenta* by following the size frequency distribution of individuals at Lucinda, North Queensland, and Aung in 1975 investigated the larval and reproductive biology of the species at Pallarenda Beach, Townsville. Chia in 1977 described the structure and function of the genital papillae of *A. placenta*.

In the last twelve years, work has covered the species-specific parasitism of the eulimid mollusc *Hypermastus* on *A. placenta* (Crossland et *al.* 1991; 1993), the effects of high temperature on larval development and metamorphosis of *A. placenta* (Chen and Chen 1992), and studies on various aspects of the biology and population structure of the species (Campbell 1995; Koizumi 1997). Most recently, Lawrence et *al*. (1998) has documented observations on the bilateral petaloid symmetry of *A. placenta*.

2.1.7. Occurrence

Arachnoides placenta is found mainly on the upper to middle sections of intertidal sandy shores at or below MLWN (mean low water neap tide) but sometimes occurs higher. The species occurs in high densities on medium to fine sand substrata and is often comprises the dominant epibenthic macrofaunal component of the intertidal community (Hines and Kenny 1967; Aung 1975; Muffley 1981; Campbell 1995; Koizumi 1997). *A. placenta* prefers habitats which are permanently damp or wet, occurring in or around intertidal pools of sea water left at low tide (Campbell 1995, Koizumi 1997, pers. obs.). In the absence of such pools the animals are found to lie between sand ripples at low tide. Animals stranded on sand bars usually burrow deeper (2-5cm depth). A distinct sand trail left by their progress just beneath the surface can be observed (fig 2.5.c).

A. placenta occurs from low spring tide to mean sea level and prefers a gently sloping sand flat to steep sloping beaches (Campbell 1995; pers. obs.). Although this species is mainly confined to the intertidal zone, the literature records some specimens having been found from depths of between 16 to 57 metres at certain locations (Aung 1975). Specimens in the Australian Museum collected from the Whitsunday Passage and Repulse Bay near Mackay were reportedly collected from a depth of 16 metres (Aung 1975). In Townsville, *A. placenta* is replaced subtidally by the sand dollar *Laganum depressum* (Aung 1975; Campbell 1995; Koizumi 1997; pers obs.). Significant numbers of *L. depressum* tests found washed up at the high water mark at Bucasia Beach, North Mackay and Casuarina Beach, Cape Hillsborough National Park suggest that *L. depressum* similarly occurs subtidally (pers obs.).

2.2. The Intertidal Sandy Shore with Site Descriptions

2.2.1. Introduction

The following section provides a description of a typical intertidal sandy shore. The intertidal shores of each site will subsequently be described and compared to that of this typical intertidal shore.

2.2.2. A common description of the intertidal sandy shore

Intertidal sandy shores all consist of an upper coarse sand beach that normally slopes steeply from sand dunes to about mean sea level (MSL). At this point a sharp break in slope occurs as the beach slope flattens to form a broad beach terrace consisting of finer sediment, that usually remains wet at low tide. During periods of heavy rain these springs will be brackish (Crossland et *al*. 1991). Small sand banks often form on the beach terrace in response to waves and currents forming slightly raised regions that dry out during extreme low water tides. In other places the terrace does not dry out forming a glassy wet surface. Shallow pools, moats and often prominent ripples caused by currents, contain pools of seawater towards the top of the beach terrace (pers. obs; Aung 1975, Campbell 1995). A typical intertidal beach is a very dynamic system, responding to changes in wave height and direction forced by the prevailing wind. Longshore drift of sediments can be seasonal, and is often associated with the gradual migration of sand bars. Storms on the other hand can have an immediate effect and cause considerable changes in the beach profile (Bird 1971). However along the Queensland coast, the Great Barrier Reef affords shorelines much protection from oceanic wave conditions (Crossland et *al*. 1991). Intertidal sandy shores, such as the ones sampled in this study, are usually composed of coarse sand upper beaches with a mean grain size of about 250 microns. On all the mainland beaches the sediment has a significant component of biogenic material consisting of broken shells, foraminfera, corals and calcareous algae. The main inorganic component consists of riverine sands that are primarily derived from decomposed granite (Bird 1971).

2.2.3. Site descriptions

Arachnoides placenta was collected from intertidal shores at Mission Beach (17^{o} 52'S, 146^{o} 06'E), Pallarenda Beach, Townsville (21^{o} 02'S, 149^{o}10'E); Bucasia Beach,

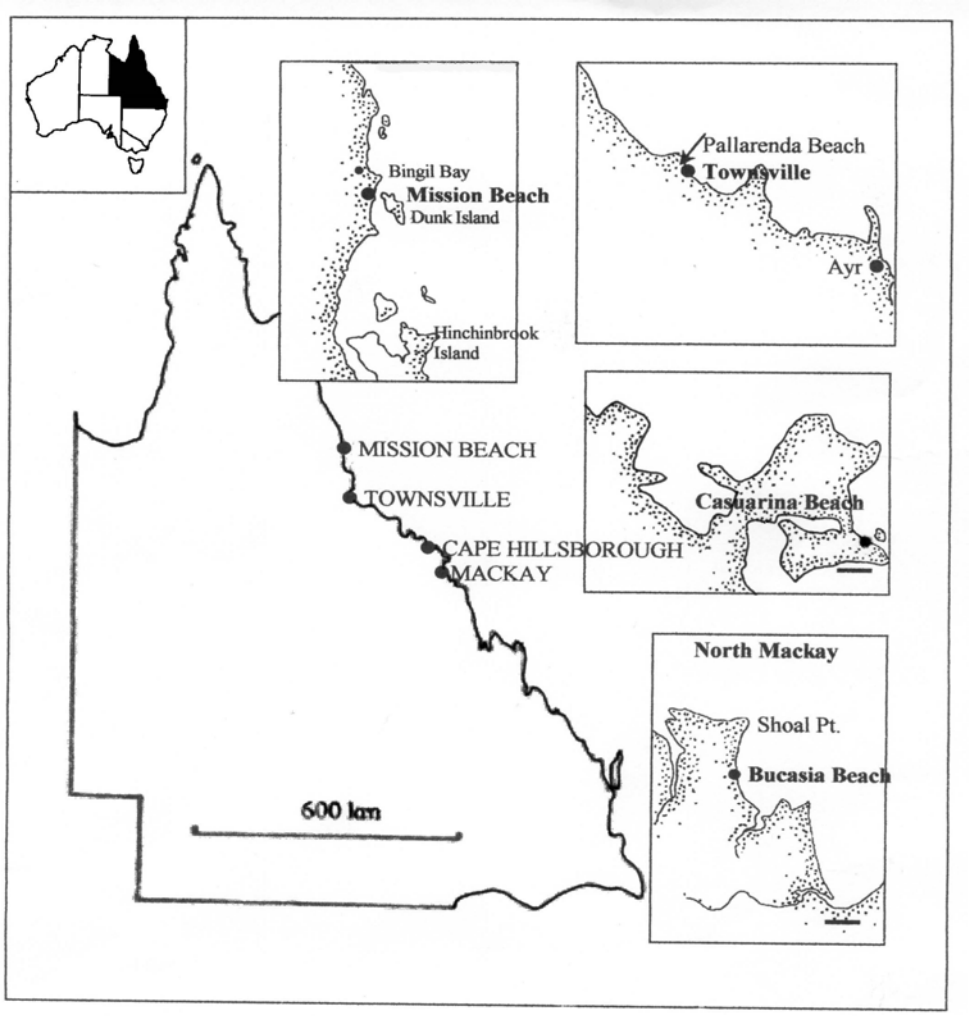

Figure 2.3. Location of sampling sites, Mission Beach; Pallarenda Beach, Townsville; Casuarina Beach, Cape Hillsborough National Park and Bucasia Beach, North Mackay, North Queensland, Australia

North Mackay (21^o 15'S, 149^o 18'E), and Casuarina Beach, Cape Hillsborough National Park (20^o 54'S, 149^o 04'E), twenty kilometres north of Mackay (Fig. 2.3.).

2.2.3.1. *Mission Beach*

Mission Beach is situated thirty seven kilometres south of Innisfail and stretches approximately 3 kilometres in length. The beach is usually protected from strong wave action as a result of protection provided by Dunk Island as well as the Great Barrier Reef. Mission Beach varies a considerable degree to that of a typical intertidal shore, in that the entire shoreline comprises a gently sloping beach, with only an inconspicuous change in shoreline gradient marked by the presence of a line of salt water drainage springs which define the division of the upper shore and beach terrace (Fig. 2.4.a). The shoreline also has no sand dunes and sand bars or large pools of water and primarily consists of medium - fine grain sand. At extreme low tide the beach terrace extends only a very short distance of 40 metres along which the sediment grain size decreases from medium to fine sand grain size. At low tide *A. placenta* ranges from the middle section of the beach terrace to the waters edge.

2.2.3.2. *Pallarenda Beach, Townsville*

Pallarenda Beach is situated at the north-western end of Cleveland Bay approximately 6km NNW of Townsville, Queensland (Fig. 2.4.b) and is defined as a typical intertidal sandy shore. The beach is exposed to low or moderate wave energy conditions as a result of protection provided by Magnetic Island and the Great Barrier Reef. The extreme tidal range in the area is approximately 4.07m. The littoral zone of the study site is composed of a steep coarse-sand upper beach that extends seaward for approximately 30 m from the high-water mark. At extreme low spring tides the lower beach forms a beach terrace that extends a further 80-100 m to the low water at extreme low water tides. A line of small upper beach salt water drainage springs form a distinct horizon that marks the junction of the steeper upper beach and gently sloping beach terrace. From the top of the beach terrace, the sediment of the intertidal shore of Pallarenda Beach shows a very gradual seaward change from medium-coarse to fine sand. The upper beach terrace is composed primarily of coarse sand mixed with larger pieces shell rubble and often very high densities of juvenile pippis (3-4mm in size) (*Paphies altenae*, Family Mesodesmatidae). At the seaward extremity very fine

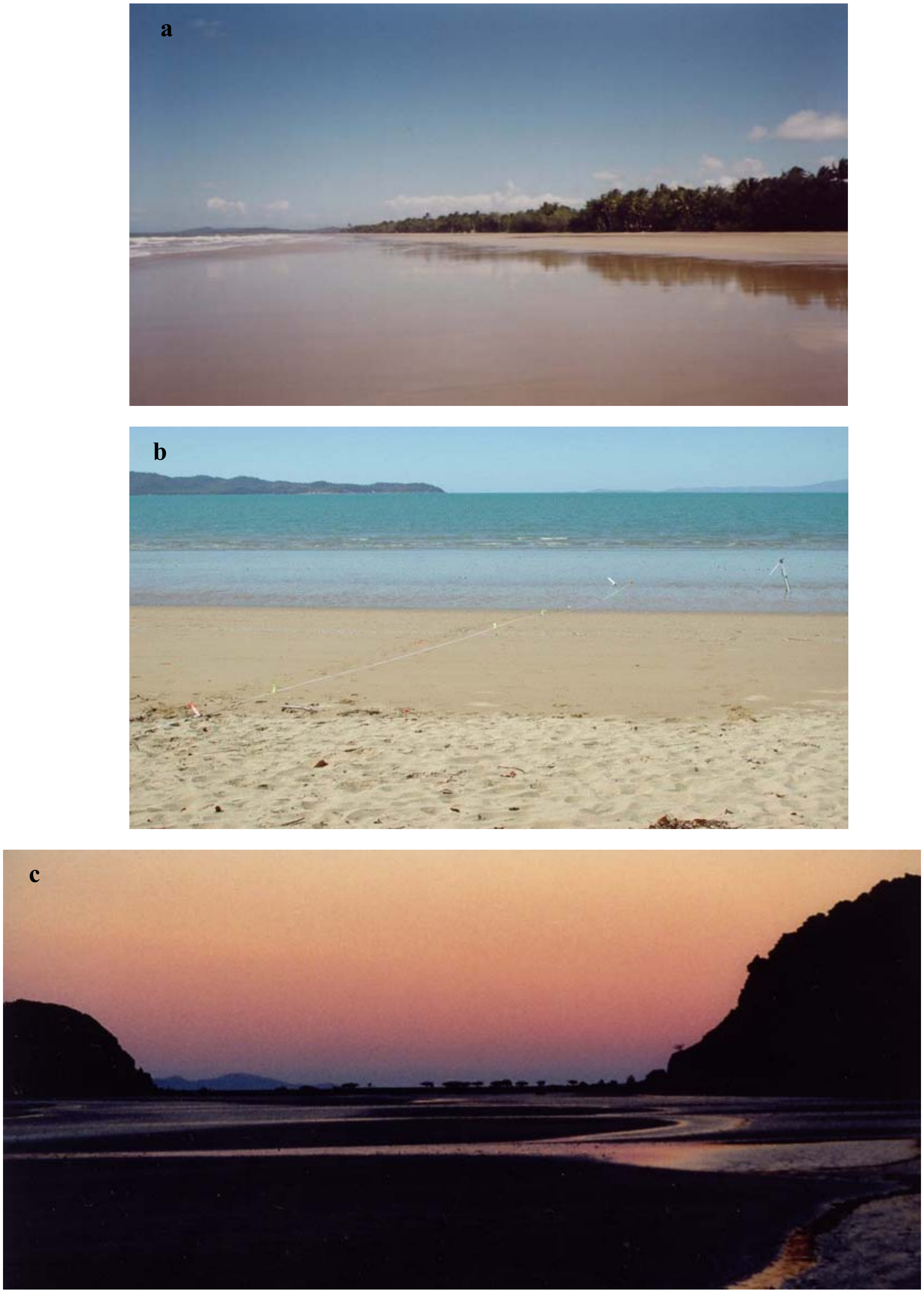

Fig. 2.4 a Mission Beach, showing gently sloping shoreline with drainage springs towards the upper shore. Predominantly fine wet sediment with no ripples. **b** Pallarenda Beach, Townsville, at low tide showing steep coarse-sand upper beach, followed by a line of drainage springs and a flatter sand terrace. The latter section consists of wet rippled sediment with abundant sand dollars. **c** Casuarina Beach, Cape Hillsborough NP at dusk, a gently sloping shore with some ripples, sand bars and troughs across the beach.

thixotropic sediment exists with the appearance of sea grasses, some 60-70 m from the spring horizon. The shoreline varies considerably in the formation of unstable sand bars and large pools of water, which often vary in shape and location from one low tide to the next. *A. placenta* occurs in abundance from the line of drainage springs to the extreme low tide mark.

2.2.3.3. *Casuarina Beach, Cape Hillsborough National Park*

Casuarina Beach is a very flat shore bordered by volcanic rock formations on the peninsula of Cape Hillsborough National Park, affording the beach much protection from the effect of strong wave action (Fig.2.4.c). The shoreline does not conform to the description of a typical intertidal shore. From the upper shore the flat beach consists of medium to fine grain sediment with a few ripples. There is no evidence of where the upper shore ends and where the beach terrace commences as salt water drainage springs occur in an inconsistent pattern across the shore and no change in gradient is evident. Where drainage springs commence on the shore, slightly raised sand bars large shallow troughs of water that form behind each. Water from these troughs also run between the sand bars to the shore. At the extreme low water mark the shore stretches for approximately 100 metres from the sand bars, towards which the sediment progressively gets finer and sea grasses appear at the lower confines of the shore. Considerable sections of the beach from where the drainage springs commence are rippled or contain pools of water, and it within these areas that the majority of sand dollars exist.

2.2.3.4. *Bucasia Beach, North Mackay*

Bucasia Beach in North Mackay is approximately 4 km in length (Fig. 2.3.). Two sites with considerable differences in shoreline topography were chosen for the sampling of sub-populations. The first site is close to the mouth of a creek at one end of the beach and the second approximately 500 metres from the first site, is close to an old swimming enclosure. The creek end site also fits the description of a typical intertidal sandy shore (fig. 2.5.a) comprising a number of very steep sand dunes at the top of the shore which extend approximately 20 metres to the mean sea level. From this point the shore forms an extensive beach terrace which extends a considerable distance of approximately 180 metres seaward at all low tides. Like other sites, a line of saltwater drainage springs represents the noticeably sharp break in gradient between the steep

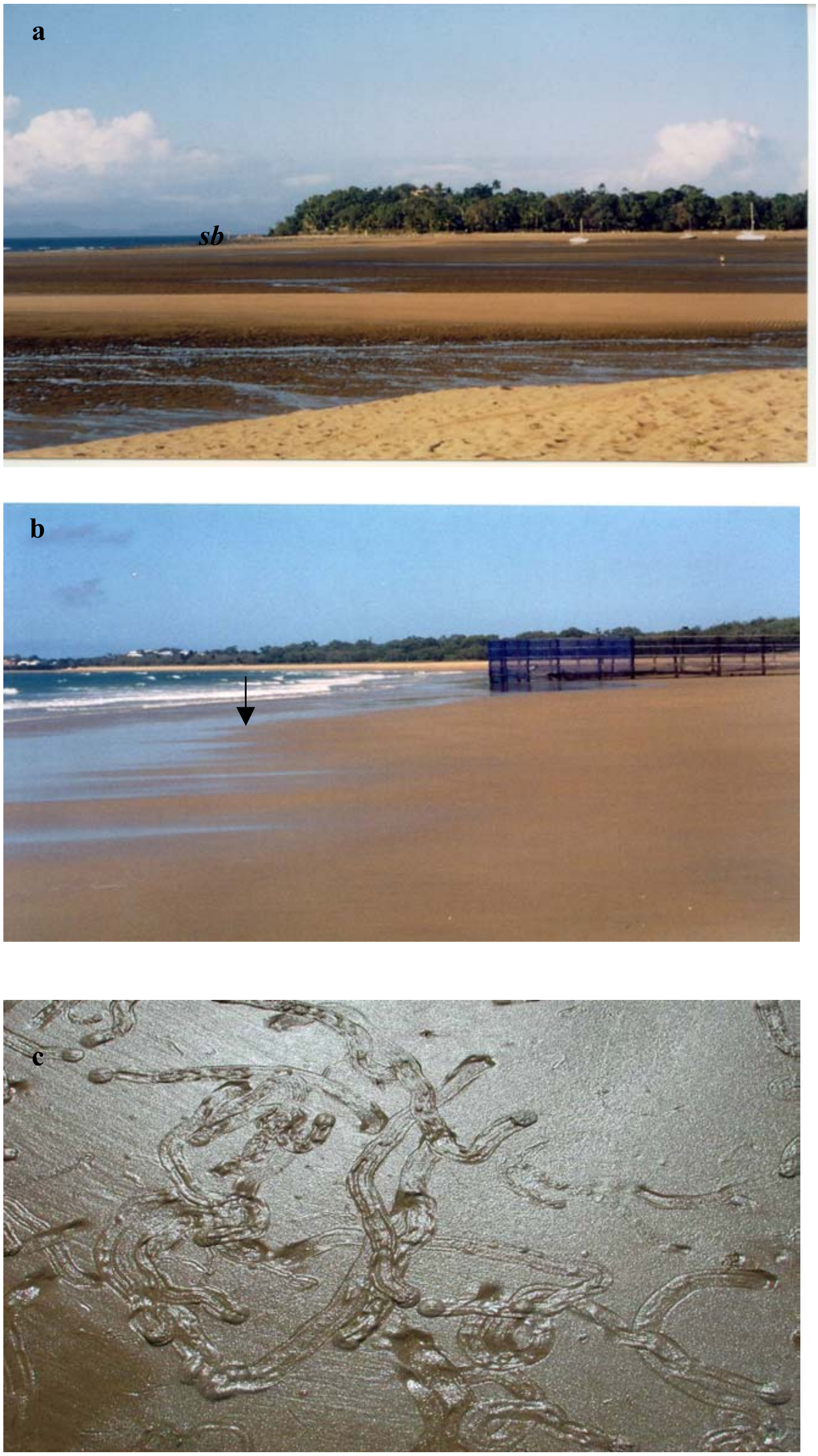

Figure 2.5. a Creek end site, Bucasia Beach. Sections of wet rippled coarse sediment between high sand bars at low tide. A line of boats mark the line of Eimeo creek, which cuts parallel across the shore to create a sand bar (*sb)*. **b** Swimming enclosure site. The sand here is flat and consists of moderate to fine sediment. Sand dollars occur lower on the shore (↓). **c** Trails left in the sediment by *A. placenta* at low tide.

coarse sediment of the upper shore and gently sloping beach terrace. The upper section of the beach terrace, which comprises coarse wet sand from the merging of salt water streams which drain from the spring line, still slopes quite steeply for approximately 10 metres and subsequently flattens out for the remainder of the beach. The beach terrace itself is split up and also surrounded by a number of prominent sand bars, which divide large sections (approximately 30 metres across) of very coarse to medium grain sediment that is prominently rippled. The sand bars are particularly stable and any changes in formation occur over a long period of time. The sediment of the beach terrace also consistently comprises coarse sand grains which in most other intertidal sandy shores progresses from medium to fine grain sediment. A dense population of *A. placenta* occurs within the rippled areas and along the edges of the sand bars. Beyond the beach terrace the shore is transected horizontally by the creek and surrounding sand bars which extend a further 20m downshore. There is no evidence of *A. placenta* within the sediment from this point. The sand bars that enclose the beach terrace of this site most likely provide more protection to the beach terrace than is typical of other intertidal sandy shores.

The swimming enclosure site (fig. 2.5.b) contrasts greatly to the creek end site and would not be described as a typical intertidal sandy shore. The upper shore slopes gently from the sand dunes to mean sea level and comprises mean to fine grain sediment. No distinction between sediment grain size or shoreline gradient is evident between the upper shore and beach terrace which in typical intertidal sandy shores is defined as a sharp break in gradient and a noticeable change in sediment from coarse to fine sand. An inconsistent line of salt water drainage springs however marks the mean sea level and the start of an undefined beach terrace. At extreme low tides the shore extends a short distance of approximately 50 metres from the mean sea level, which is approximately half the area of sediment exposed during extreme low tide on the beach terrace of a typical intertidal sandy shore. The beach terrace of the swimming enclosure site also comprises no sand bars, distinct ripples or pools of water at low tide. *A. placenta* occurs from the middle to the lower section of the beach terrace.

Chapter 3: Population Density, Size Frequency structure and Growth rate of *Arachnoides placenta*

3.1. Introduction

Animals on intertidal shores are constantly exposed to a wide range of biotic and abiotic variables linked to such an environment (Meadows and Campbell 1972). Population characteristics including density, spatial distribution, size frequencies, age structure and juvenile recruitment as well as somatic and reproductive growth and mortality may be influenced by habitat specific factors. The structure of populations of echinoids may differ even in similar areas of close proximity and may be based on differential recruitment success and post settlement survival (Ebert 1983), differences in the quality or quantity of available food resources, or levels of predation (Harrold and Pearse 1987). Population demographics may also be influenced by abiotic factors. For example both asymptotic body size and variations in the initiation, timing, intensity and duration of reproductive events are reported to be set by local environmental conditions in echinoid populations (Ebert 1968, Pearse 1969, Dix 1970, Moore and Lopez 1972, Gonor 1973, Lessios 1981, King et *al.* 1994). Variations in growth rates as a result of variable and biotic factors inherent to particular habitats, have been reported in geographically isolated populations in sea urchins (McPherson 1965, Lawrence and Kafri 1979). Growth rate in itself is a critical parameter of the population dynamics of a species (Meadows and Campbell 1972). In particular, intertidal sands vary in sediment composition, often comprising sand grains of different sizes, which play an important role in affecting the spatial distribution of intertidal invertebrates (Meadows and Campbell 1972).

This study investigates the density, spatial distribution and size frequency of populations of *A. placenta* at Pallarenda Beach in 2001 and 2002. In 2002 Mission Beach, Cape Hillsborough and Bucasia Beach at Mackay were also sampled to determine and document the potential effect of different sites on population density, size of individuals and somatic growth.

3.2. Materials and Methods

3.2.1. Sampling size frequencies and mean density of individuals

A systematic sampling program was devised to measure the distribution, size frequency structure and density of individuals across the intertidal shores of Pallarenda Beach, Mackay, Cape Hillsborough and Mission Beach from 2001 to 2002. To remove the effect of newly settled recruits and small juveniles, only individuals that could be seen with the naked eye were sampled as they were easily collected by hand and could be collected without having to sieve the sediment. Chapter 5 provides detailed studies on the recruitment of the species and population studies of recruits and smaller individuals (<10mm) which were collected through sieving the sediment.

In the first year (April 2001 - January 2002), monthly samples of *A. placenta*, were collected and recorded at low tide solely at Pallarenda Beach. In the following year (February - September 2002), populations from Pallarenda Beach, Mission Beach, and the Mackay region were sampled sequentially on a monthly basis. The first year of sampling at Pallarenda Beach provided long-term data for which other sites sampled in the following year could be compared. The greatest length of time between any two sampling dates of the same site never exceeded three months. Intertidal distribution was recorded at Bucasia Beach creek end site and Pallarenda Beach in 2001 and 2002. The size frequency structure of populations, including animals <10mm, were recorded at all sites in both years.

For the collection of size frequency structure and population density data, three transects up to 150 metres apart were placed perpendicular to the shore at low tide from the high water mark to the waters edge. Based on a pilot study conducted at Pallarenda Beach and previous maximum recordings of *52* individuals m^{-2} by Aung (1975) at Pallarenda Beach, it was appropriate to use a one metre square quadrat to determine the density of pre-mature and mature individuals at each site in this study. Similarly based on a pilot study and previous maximum recording of 276 juvenile *A. placenta* at Pallarenda Beach (Aung 1975), a 30cm square quadrat was used to collect individuals not seen by the naked eye, by sieving the sediment. The population density and spatial distribution of these smaller individuals will be further investigated in Chapter 5.

Quadrats were placed at either side of each transect at three-metre intervals from the upper shore (fig. 3.1) in which the mean density (m^{-2}) of both quadrats and/or test

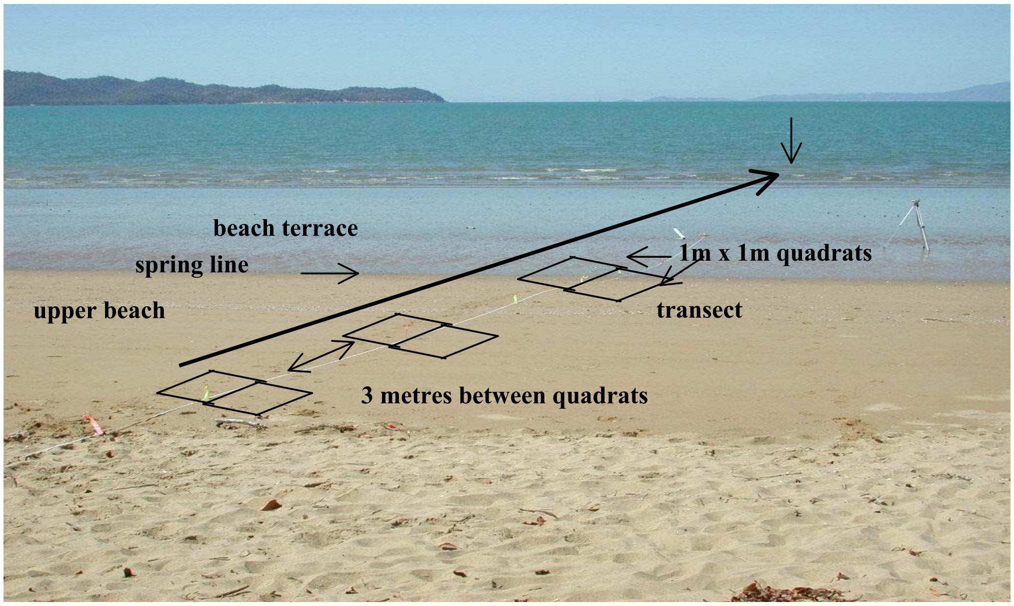

Figure 3.1. Sampling method used to record and collect population size frequency and density of *A. placenta* (>10mm) downshore (not to scale)

diameter of individuals ≥ 10mm were recorded to the nearest 0.5mm from each quadrat. Indivduals were returned to the same location to minimise the effect of sampling on the population. Approximately one thousand individuals were sampled every month. The population density of *A. placenta* at Mission Beach was relatively low, with a maximum of 4 individuals m^{-2}. In this instance, sand dollars were sampled for size frequency data without the use of a transect and quadrats and were collected at random from upper, middle and lower sections of the shore during low tide. Growth rates were determined from size frequency distributions.

3.2.2. Statistical analysis

Minitab (ver. 13.32) was used to carry out one-way ANOVAs and linear regression analyses on the effect of distance from the high water mark on 1) individual density m^{-2} and 2) size frequencies of populations at Pallarenda Beach and Bucasia Beach in 2001.

3.3. Results

3.3.1. Intertidal Distribution

A. placenta is a dominant macro-organism at Mission Beach, Pallarenda Beach, Bucasia Beach and Cape Hillsborough National Park. At Pallarenda Beach, all

individuals of sizes 10 – 50mm were found across the entire shoreline and existed amongst the sea grass and fine sediment found at low water spring tide levels, but were rarely evenly distributed around a bay or entire beach. Instead, individuals often aggregated into groups specifically around pools of water or depressions in the sand, in particular avoiding sand bars. Similar to observations made by Aung (1975), two types of intertidal distribution were observed for different *A. placenta* populations;
1. Populations in an extensive area, such as Mission Beach, Casuarina Beach and Bucasia Beach swimming enclosure site, comprising individuals that were generally separated by areas of low density or total absence of specimens, and 2. High densities occurring within large populations, like those at Pallarenda Beach and Bucasia Beach creek end site.

Fig. 3.2 and fig 3.3 show the patchy distribution of *A. placenta* down shore at Pallarenda Beach at low tide. Over a typical transect distance of 60 metres from the high water mark to the low water mark, patchiness in *A. placenta* appeared to be strongly related to sediment properties, which vary from very fine to coarse sand and troughs of water to practically dry sand bars. Individuals in particular formed clusters in between ripples and in and around pools of water left at low tide.

Despite a noticeable trend in patchiness downshore, there was a significant decrease in mean density downshore ($p = <0.05$) along eleven out of the seventeen transects laid downshore at Pallarenda Beach in 2001. Individuals were most dense at the top of the shore just below the line of salt water drainage springs at the junction of the upper beach and beach terrace. The sediment within this area consisted of coarse sand grains and shell fragments fed by a number of small drainage streams, which provided constant moisture to that section of the shore. On the upper to mid terrace, on which most of the individuals occurred, the sediment was composed of graduated medium to fine sand grains (medium size 125 –250μm) downshore. Pallarenda Beach is partly protected from wave action in Cleveland Bay however there is enough disturbance to produce variations in the structure of sand bars every day. On the contrary, there was no apparent effect of distance from high tide mark on population density at Bucasia Beach creek end site, a site that comprised very wet coarse and rippled sediment throughout the beach terrace, which was enclosed entirely by large stable sand bars, affording the protection from wave action.

A maximum density of 63.5 individuals (>10 mm test diameter) m^{-2} was recorded during September 2001 at Pallarenda Beach (Table 3.2) as a result of the arrival of a new mode of individuals (11-20 mm test diameter) into the main size group (>11mm test diameter). At other times, maximum density rarely exceeded 40 individuals m^{-2}. A maximum of 88 individuals m^{-2} (>10 mm test diameter) were recorded at Bucasia Beach creek end site (Table 3.2).

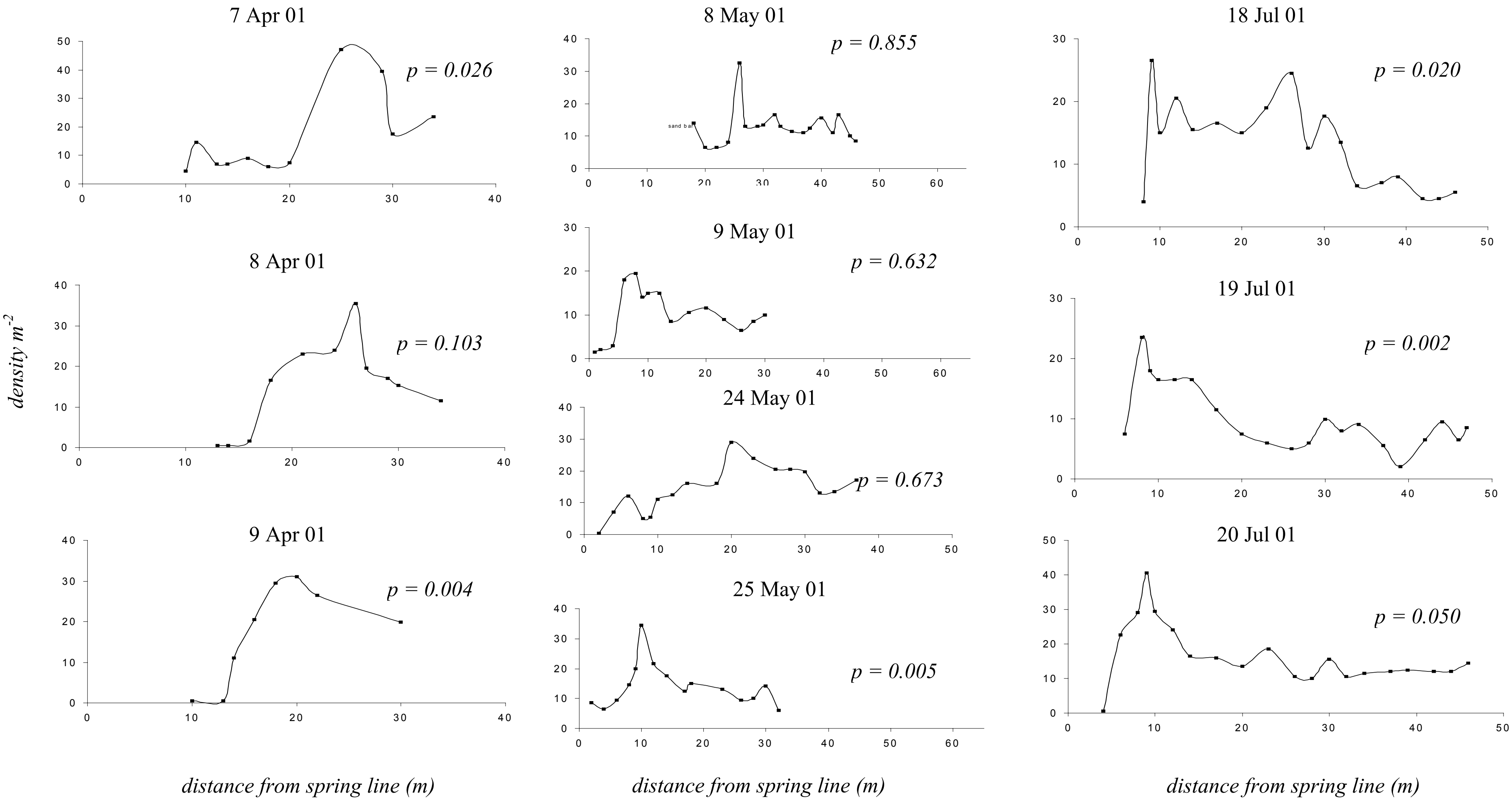

Figure 3.2. *Arachnoides placenta*. Mean density of individuals m^{-2} (>10 mm test diameter) from the spring line (upper limit of distribution) to the low water mark at Pallarenda Beach, Townsville, April - July 2001. *P*-values from ANOVA display effect of distance from springline on density m^{-2}

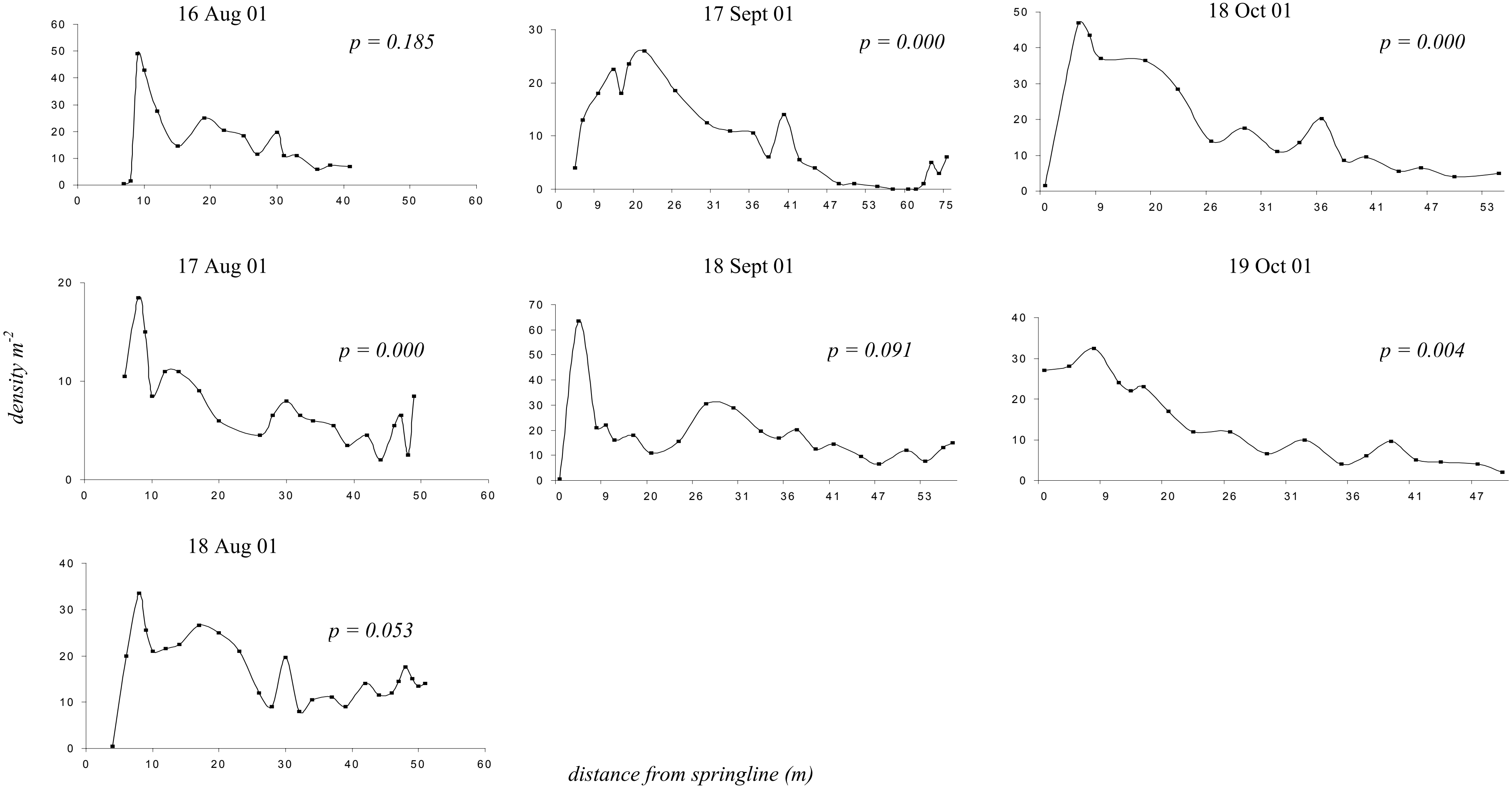

Figure 3.3. *Arachnoides placenta*. Mean density of individuals m^{-2} (>10mm test diameter) from the spring line (upper limit of distribution) to the low water mark at Pallarenda Beach, Townsville, August - October 2001. *P*-values from ANOVA display effect of distance from springline on density m^{-2}

3.3.2. Size Frequency Analysis

At Pallarenda Beach throughout 2001, there was clear temporal and spatial variation in the size frequency structure of the population of *A. placenta* (fig. 3.5). There was also a significant difference in test diameter (≥11mm) between sites (*p* = 0.000) (fig 3.4, 3.6), which clearly shows there was no effect of site on test diameter of populations. This is further supported by significant differences in test diameter between Bucasia Beach creek end site and Bucasia Beach swimming enclosure site (*p* = 0.001) (fig 3.4, 3.6).

The maximum test diameter of individuals varied from 54 mm at Mission Beach, 52 mm at Bucasia Beach creek end site, 48 mm at Pallarenda Beach, 44 mm at Cape Hillsborough to 38 mm at Bucasia Beach swimming enclosure site, as indicated by outliers (fig. 3.4).

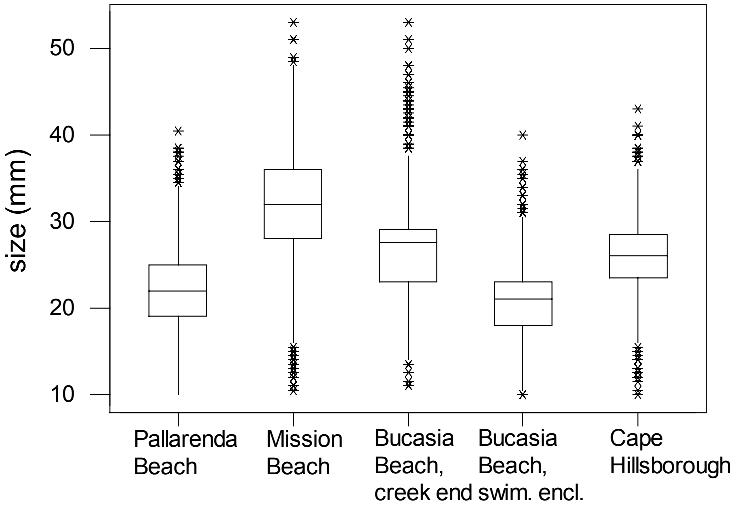

Figure 3.4. *Arachnoides placenta*. Box plot of mean size frequencies of populations (≥10mm test diameter) at Pallarenda Beach (n = 4420); Mission Beach (n = 1293); Bucasia Beach, creek end (n = 3057); Bucasia Beach, swimming encl. (n = 3290) and Cape Hillsborough (n = 1218), recorded January to September 2002. Stars indicate outliers.

The mean test lengths of individuals at these sites were also higher than the mean test length of sand dollars sampled at other sites. There was also no relationship between test diameter and density of individuals as illustrated in table 3.1.

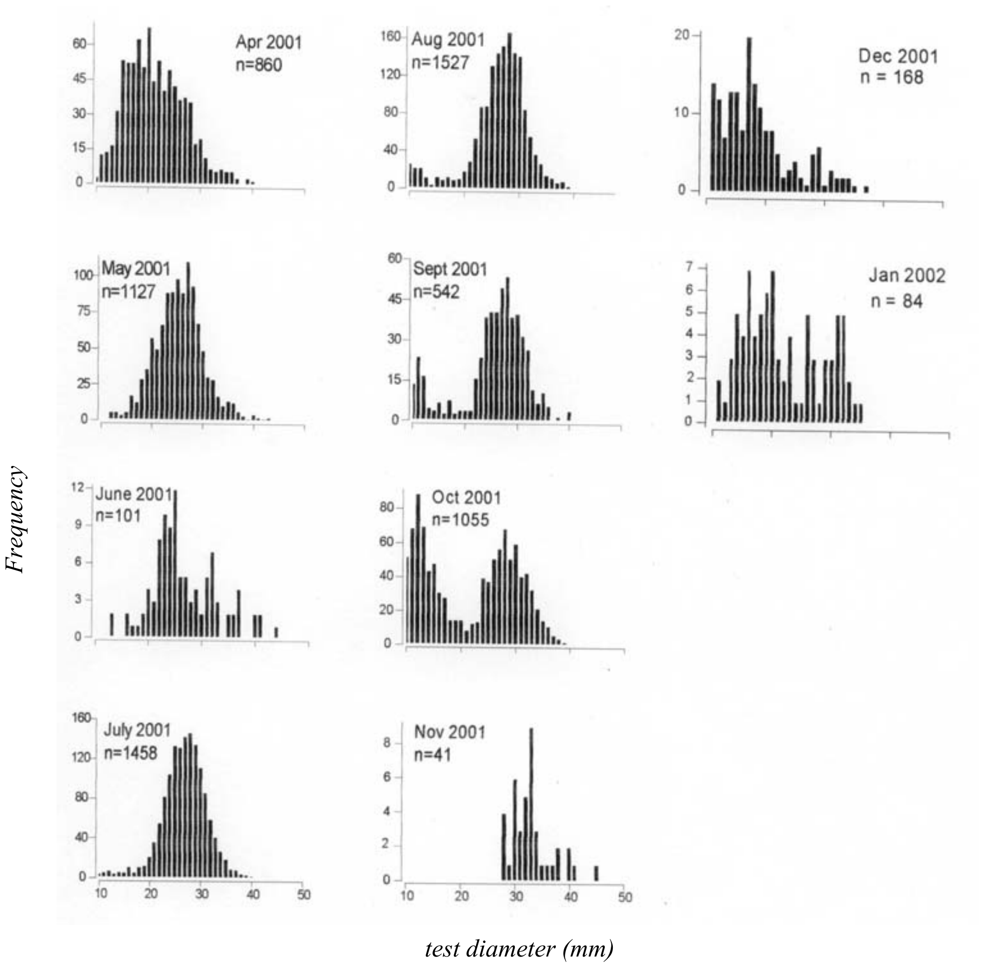

Figure 3.5. *Arachnoides placenta*. Population size frequencies (>10mm test diameter) Pallarenda Beach, April 2001 – January 2002.

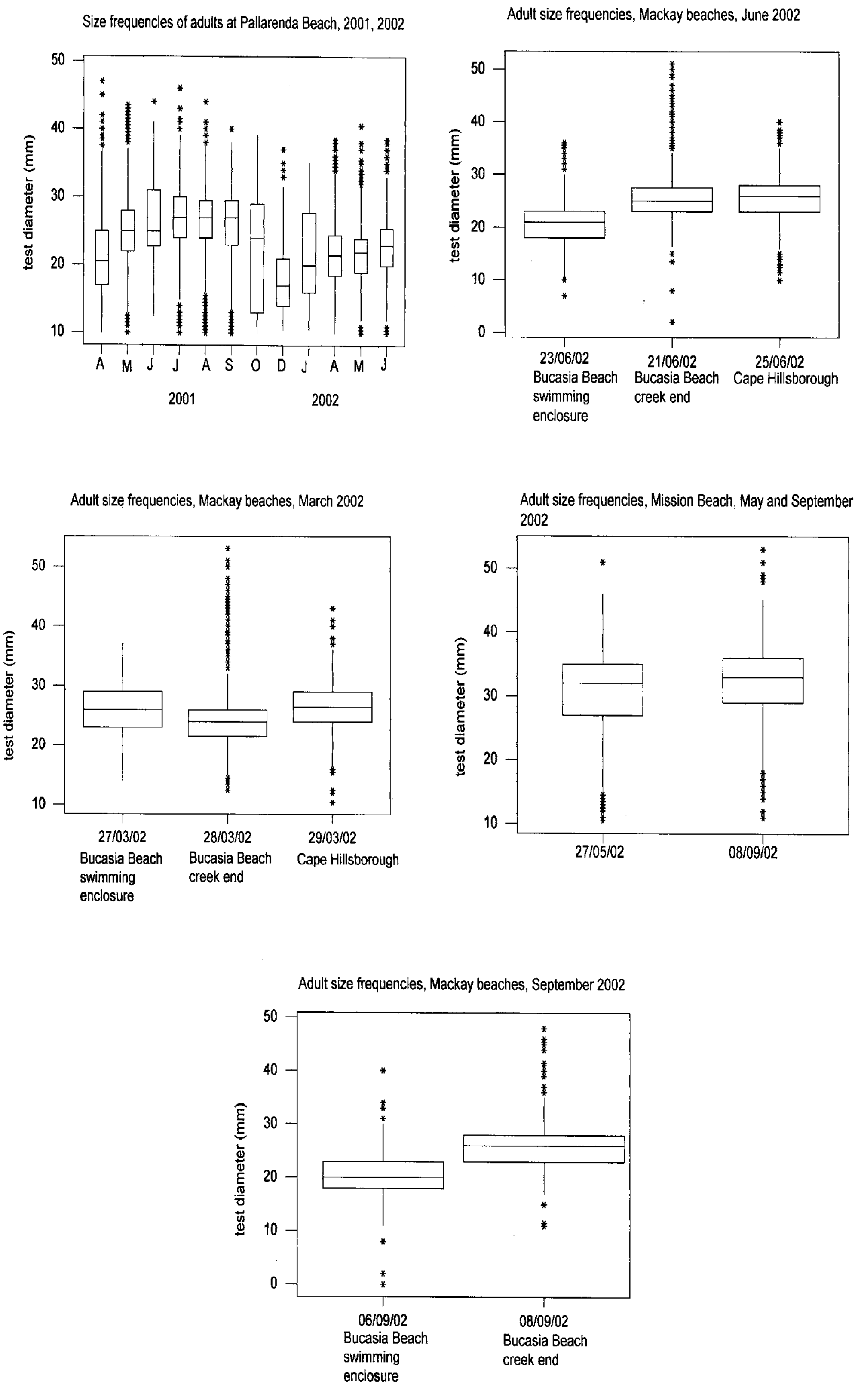

Figure 3.6. *Arachnoides placenta.* Mean monthly boxplots of population size frequencies (>11mm test diameter) at Pallarenda Beach, April 2001 – January 2002, Bucasia Beach and Casuarina Beach, March, June and September 2002 and Mission Beach May and September 2002

Site	Maximum density m^{-2}	Maximum test diameter (mm)	Mean test diameter (mm)
Bucasia Beach, creek end site	88	52	28
Pallarenda Beach	63.5	48	22
Casuarina Beach	12	44	27
Mission Beach	4	54	33

Table 3.1. *Arachnoides placenta*. Maximum density m^{-2} of individuals with comparisons of maximum and mean test diameter (mm) of populations at each site

Linear regression analyses of the effect of distance from the high tide mark on individual test diameter at Pallarenda Beach were highly significant (p = >0.005) for 13 out of 17 transects, each exhibiting an increase in the test diameter with distance downshore (fig 3.7, 3.8). The majority of individuals 11 – 20mm test diameter at Pallarenda Beach, were always situated within the upper confines of the shore (fig 3.7, 3.8). This size group of individuals were particularly abundant from August 2001 through to January 2002 within the sediment and is evident within the size frequency histograms (fig. 3.5). There was also a highly significant relationship between test diameter and distance downshore at Bucasia Beach creek end site in June 2001 (p = 0.000), and March 2002, (p = 0.006) (fig. 3.8), however test diameter in this instance decreased with distance downshore, contrary to the population sampled at Pallarenda Beach.

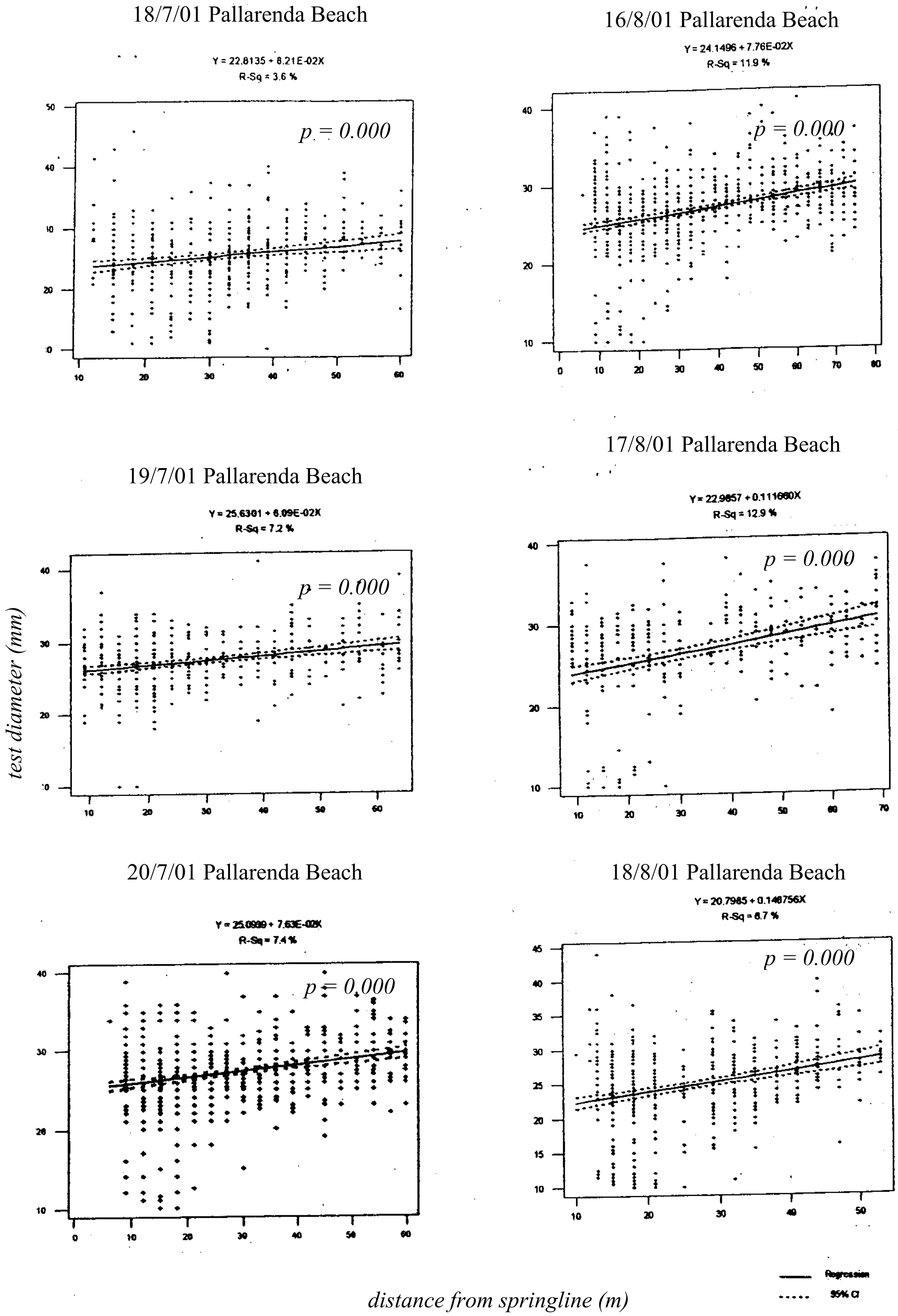

Figure 3.7. *Arachnoides placenta*. Regression analysis graphs of test diameter (mm) versus distance downshore (m), Pallarenda Beach, July and August 2001. *P*-values from regression ANOVA display effect of distance from springline on density m^{-2}

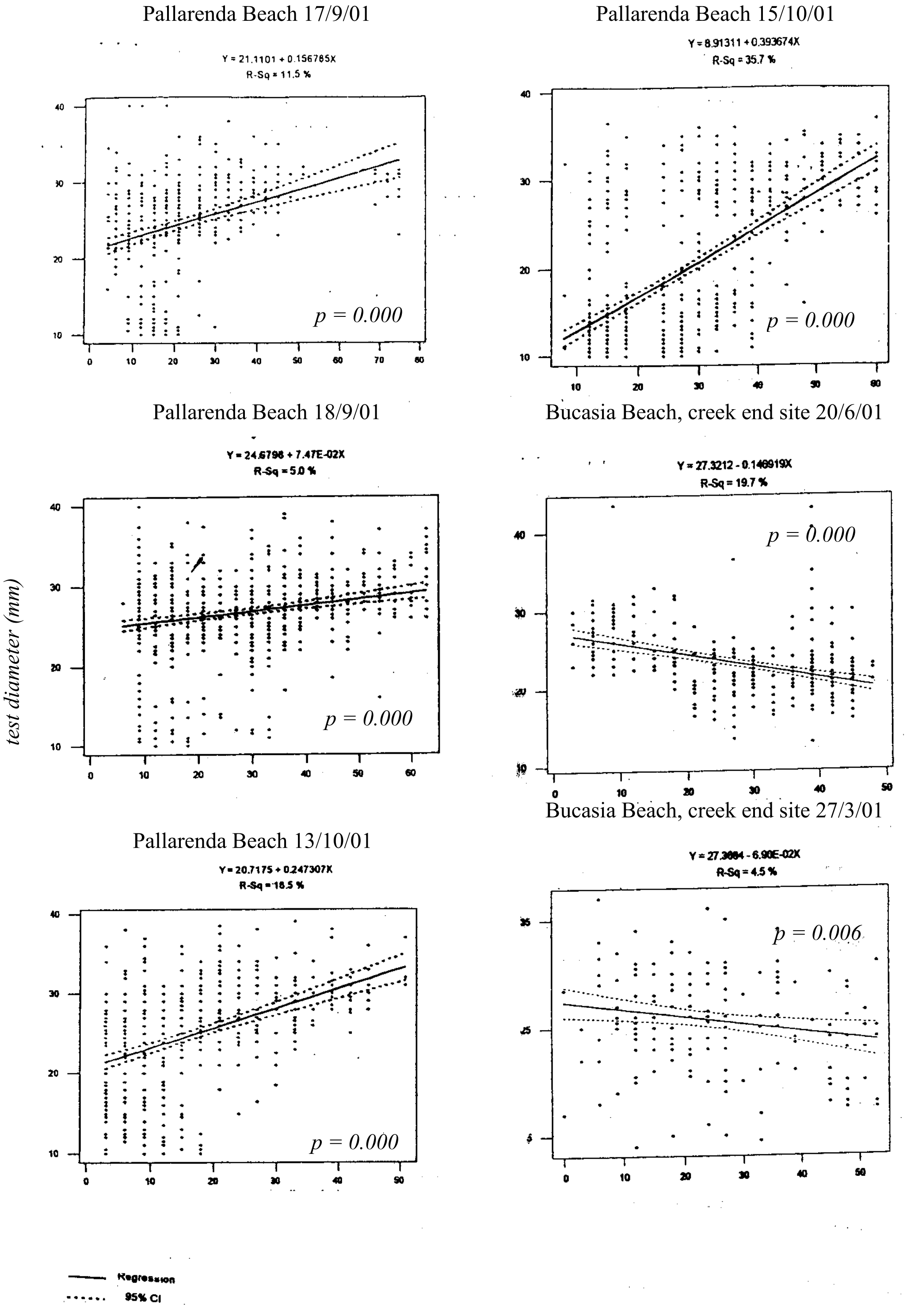

Figure 3.8. *Arachnoides placenta*. Regression analysis graphs of test diameter (mm) versus distance from springline (m) at Pallarenda Beach, September and October 2001, and creek end site of Bucasia Beach, June 2001 and March 2002. *P*-values from regression ANOVA displays effect of distance from springline on density m^{-2}

3.3.3. Growth

Growth rates of *A. placenta* were constructed based on shifts in the modes of the size distributions at Pallarenda Beach in 2001 and 2002 as the same month of different years displayed similar size groups. The growth from the onset of settlement demonstrated a clear S-shaped Richard's growth curve, or asymptotic growth curve (fig. 3.9). Outside of the major recruitment period at Pallarenda Beach in 2001 (May - July), there was some difficulty determining major cohorts of recruits of previous years as often less than 50 recruits per month were sampled, particularly of the size group 2.5 – 10mm, although recruits were found continuously within the sediment at Pallarenda each month. To account for the lack of sufficient individuals in this size group, two rates of growth are estimated for *A. placenta*. Size-frequencies of recruits in 2001 suggest that individuals grow either 4mm (growth estimate 1, fig. 3.9) or 5 - 6mm (growth estimate 2, fig. 3.9) in the first year. Within the recruit size frequency histograms August and September 2001 (see chapter 5, fig 5.3) there is slight evidence of a second mode of recruits of 5 –6mm and 6 –7mm respectively, within what initially has the appearance of a unimodal group of individuals, indicating the presence of recruits that settled in 2000.

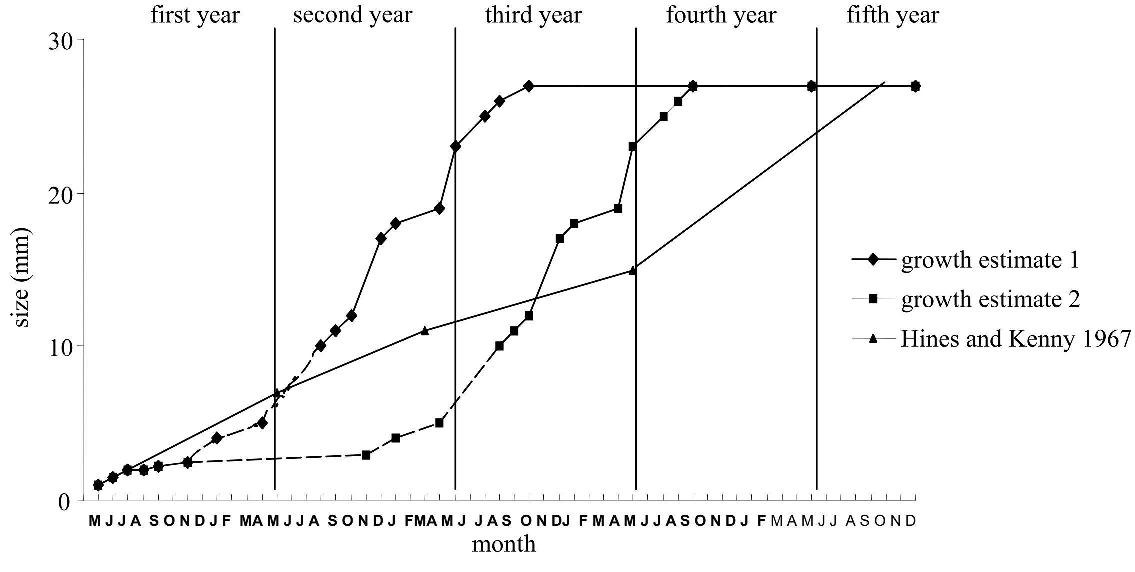

Fig. 3.9. *Arachnoides placenta*. Estimated growth rate of newly settled recruits at Pallarenda Beach (growth estimate 1 and growth estimate 2) 2001 – 2002 and Lucinda, North Queensland (Hines and Kenny 1967)

If this small cohort of year 2000 recruits is present (and is small due to poor recruitment or high levels of predation or mortality), individuals from the onset of settlement are estimated to grow 10mm in 32 months (growth estimate 2, fig. 3.9). If this cohort of recruits does not exist, or the recruits that settled in 2000 are larger than 10mm, then newly settled recruits are estimated to grow 10mm in 16 months (growth estimate 1, fig 3.9).

From a size of 10mm (and possibly smaller), it is apparent that growth assumes a linear growth phase. There is however a noticeable decrease in growth between January and April of the second (growth estimate 1, fig 3.9) or third year (growth estimate 2, fig. 3.9) at a size of approximately 20mm. Growth after this period however again maintains a sharp increase until a size of 25mm is reached. The largest numbers at Pallarenda Beach are of a unimodal size class of 20mm to 35mm test diameter, and reflect a stable size structure where there is an accumulation of large individuals. Individuals of this size are estimated to be three to four years of age. Figure 3.10 shows a sample of the different sizes of individuals collected, from a newly settled recruit of 0.5mm to a maximum adult size of 50mm.

Figure 3.10. Size range of *A. placenta* from settlement (0.5 mm) to largest individual recorded

3.4. Discussion

3.4.1. Intertidal Distribution

The patchiness in the distribution of *Arachnoides placenta* observed throughout the year at Pallarenda Beach in conjunction with evidence for a seasonal breeding cycle (Chapter 5) may suggest that individuals do not specifically aggregate in order to spawn, a behaviour reported for other echinoids, known to increase the success of gamete fertilisation in the water column (Moore 1956, Salsman and Tolbert 1975, Lane and Lawrence 1980). However, the high density of individuals and aggregations of *A. placenta*, particularly within Pallarenda Beach and Bucasia Beach creek end, may suggest that males and females are within close enough distance to each other already for spawning to occur successfully. Likewise densities of the sea urchin *Lytechinus variegatus* are probably high enough to promote fertilisation success of gametes without population aggregations (Beddingfield and McClintock 2000). Populations of *A. placenta* also aggregate throughout areas of different sediment grain sizes, indicating that the distribution of food may not be patchy across the shore, however further investigation would be required to determine whether this was true.

3.4.2. Temporal and spatial population density

There was significant spatial and temporal variation in the mean density of populations of *Arachnoides placenta*. The population density of larger individuals (>11mm) at Pallarenda Beach in particular varied quite distinctly throughout the year in relation to clear annual recruitment episodes and a maximum density at Pallarenda Beach of 63.5 individuals m^{-2} (> 11mm test diameter) was recorded during September 2001 (Table 3.1). This increase in density was the result of a pulse of recruits, which had settled during the major recruitment period in March to July 1999, and grown to >11mm test diameter by September 2001 (section 3.4.4.). The maximum mean density of individuals m^{-2} also varied significantly between sites ($p = 0.000$), indicating little or no effect of site on population density. In particular population densities varied significantly over scales of just metres (a common feature of echinoid populations) as observed between populations of the creek end site and swimming enclosure site at Bucasia Beach ($p = 0.006$), positioned only 500m apart. These results indicate that even discrete differences in abiotic or biotic factors between sites will produce significant variations in population densities from hundreds of kilometres to distances of just metres. This is evident also at the local scale as *Arachnoides placenta* is observed to form discrete patches in a seemingly homogenous habitat of sand, suggesting the species may be detecting differences between areas of sand habitat. Pomory et *al*. (1995) in particular, suggests that relative abundances of different sediment grain sizes may play a role in fine scale habitat preferences, which is a possible determinant of the local distribution of *A. placenta.* Patchiness has been reported for the sand dollars *Encope grandis*, *Mellita grantii*, *Dendraster excentricus* and *Mellita quinquiesperforata* (Bell and Frey 1969, Merrill and Hobson 1970, Ebert and Dexter 1975).

The temperate subtidal species *Dendraster excentricus* and *Mellita quinquiesperforata*, are also documented to have variable densities, but however form considerably greater densities m^{-2} than tropical intertidal species like *Arachnoides placenta* (Table 3.2). *D. excentricus* is documented to be found piled on top of each other in extended periods of calm seas, or assuming an inclined position on the lower shore to feed (Merrill and Hobson 1969, Timko 1975). The density of the sand dollars *Encope grandis* and *Mellita grantii* in Mexico which occur on subtidal and intertidal shores varied from a high of $380m^{-2}$ / $56m^{-2}$ to $0.1m^{-2}$ / $0.8m^{-2}$ respectively (Ebert and Dexter 1975) (Table 3.2). Adult densities of the tropical sea urchin *Lytechinus variegatus* are documented to reach 150 m^{-2} (Moore et *al*. 1963) which although is denser than individuals of *A. placenta*, is in no way comparable to subtidal temperate clypeasteroids. *A. placenta* and other intertidal clypeasteroids may be less abundant due to enhanced adverse conditions on the intertidal shore such as increased exposure to wind, wave action, storms, dehydration and predation, which in subtidal habitats are greatly reduced. The constantly shifting sand bars at Pallarenda Beach for example may smother smaller sand dollars or recruits, reducing population numbers.

Individuals were considerably denser on the upper to middle section of the beach terrace at Pallarenda Beach and the Bucasia Beach creek coinciding with medium to coarse grain sediment. The sediment of the upper section of shore in particular was also the wettest part of the beach terrace as a result of salt water running downshore from drainage springs, providing a favourable environment in which individuals were probably benefiting from reduced dehydration and possibly an increased food supply (although further investigation would be required to determine this). The lower shore

Species	Maximum density m^{-2}	Reference
Dendraster elongates	559.7	McGintie and McGintie, 1968
D. excentricus	80.1	McGintie and McGintie, 1968
D. excentricus	629 intertidal	Birkeland and Chia, 1971
D. excentricus	1386 subtidal	Merrill and Hobson, 1970
Echinarachnius parma	56 intertidal	Cocanour, 1969
Mellita quinquiesperforata	821.0 subtidal	Salsman and Tolbert, 1965
M. quinquiesperforata	37.0	Weihe and Gray, 1968
Arachnoides placenta	276.0 juveniles	Aung, 1975
A. placenta	52.0 adults	Aung, 1975
A. placenta Pallarenda	63.5 adults	Present study
A. placenta Pallarenda	229.5 juveniles[1]	Present study
A. placenta Mission Beach	4.0 adults	Present study
A. placenta Cape Hillsborough	12 adults	Present study
A. placenta Bucasia (creek end)	88.0 adults	Present study
A. placenta Bucasia (creek end)	108.0 juveniles[1]	Present study

Table 3.2. Population density of some irregular sand dollars, including *A. placenta* from four sample sites in the present study

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[1] estimated from 0.3^{m-2}

comprised fine sand with a silt component on which there was fewer sand dollars. Areas with either predominantly fine silt (<63µm) or large particles (>1mm) are usually not inhabited by sand dollars, as grain sizes are most likely too small or too big, and impede the processes of movement and feeding (Weihe and Gray 1968, Bell and Frey 1969, Lane 1977). The temperate sand dollar *Mellita quinquiesperforata* for example does not inhabit coarse grain sediment or mud as individuals cannot burrow into it (Bell and Frey 1969). Likewise *Mellita tenuis* is more capable of burying into larger particle sizes (> 500µm) and *Echinarachnius parma* is able to move particles as large as 30mm onto its aboral surface (Pomory et *al*. 1995) as opposed to smaller particles. The sand dollar *Lovenia elongata*, in the Red Sea has a preference for medium to fine sand in the field and in captivity (Ferber and Lawrence 1976). It appears that *A. placenta*, like a number of sand dollars, are more capable of handling larger sand grains as opposed to smaller grain sizes. Larger grain sizes are also more freely draining and may be avoided by *A. placenta* to avoid the risk of dehydration at low tide. Other factors such as hydrodynamics and organic load may also be important, however as all three factors are interrelated it is difficult to discern if they have an individual importance under field conditions (Pomory et al. 1995) and would require more investigation in this study.

Arachnoides placenta does have the ability to adjust its position on the beach, being able to move over an area of 2 – 3 m at low tide. It is thus assumed that its distribution (over tens of metres) on the beach reflects *A. placenta*'s preference in some way for optimal shoreline conditions. It is apparent that *A. placenta* (and other sand dollars) prefer areas on the beach terrace that are more sheltered by sand bars and those that contain numerous shallow pools and ripples as indicated by a higher density m^{-2} of individuals in such areas. Like the distribution of *A. placenta* within the enclosed sand bars at Bucasia Beach creek end site, aggregations of the sand dollar *Mellita quinquiesperforata* are more obviously abundant in more enclosed areas of sand flats in North Carolina, where water is calmer (Salsman and Tolbert 1965, Weihe and Gray 1968). The spatangoid *Lovenia elongata* from the Red Sea also has a preference for sublittoral areas of protected bays and lagoons sheltered from heavy wave action. Reduced dehydration at low tide and possibly increased food distribution within pools of water and rippled sediment on the beach terrace at low tide are the most likely explanation for the high densities and patchiness at both Bucasia beach creek end site and Pallarenda Beach, but require further investigation to determine this. Individuals only 500 metres away at Bucasia Beach swimming enclosure site and Mission Beach comprise smaller populations possibly due to increased exposure in the absence of sand bars, leaving the beach terrace more exposed to currents and wave action. The lack of pools and ripples may cause food to be available on the beach terrace of Mission Beach and Bucasia Beach swimming enclosure site accounting for lower population numbers, although this again would require further investigation. At all sites *A. placenta* exists in patches that move, so that at any one time an area of the beach may or may not have sand dollars. Ebert and Dexter (1975) attribute the disappearance of the sand dollars *Encope grandis* and *Mellita grantii* from an area mainly to movement of individuals, but also partly to mortality.

3.4.3. Population Size-frequency distributions

The significant difference in test diameter between (p = <0.005) and within sites, particularly over a distance of 500 metres at Bucasia Beach (p = <0.005) (fig.3.4), suggests that site has a significant effect on individual test diameter. Local factors such as sediment preferences, exposure to wave action and relates to distribution of food appear to play a role in the size distribution of *A. placenta*.

Ebert (1967, 1968a) proposes that echinoids grow to a limit allowed by the environment and adjust as the environment fluctuates. In support of this, Lane and Lawrence (1982b) suggest an inverse relationship exists between the numerical density of echinoids and the size of individuals, in which higher densities reduce the amount of food available to each individual producing an optimal size within the population. Lewis and Storey (1984) also attribute the smaller size of the sea urchin *Echinometra lucunter* in certain habitats, to less food availability. The population density of *A. placenta* however does not appear to relate to the size of individuals (table 3.1.) as sites with maximum test diameters (52 mm and 54 mm, from Bucasia Beach creek end site and Mission Beach) comprised greatly differing maximum densities of 88 m^{-2} and 4 individuals m^{-2} respectively. The differences in the density of *A. placenta* seem more attributable to specific variations in shoreline topography and exposure, which as previously mentioned, may influence the distribution of food and the extent of repair required for test maintenance (Ebert 1967, 1975). In these unfavourable environments there is often a shift from reproduction to somatic investment. Individuals in such environments that are not yet mature might show a smaller mean size, and mature individuals invest less towards gonadal growth and gametogenesis because of the need to allocate resources to maintenance and repair (Ebert 1975). Echinoids in more exposed areas particularly require regenerative powers to heal the wounded surface of the test and replace lost spines in order to maintain population numbers (Weihe and Gray 1968; Ebert 1975). For example in an area of strong current 93% of individuals of the sand dollar *Mellita quinquiesperforata* had test damage and a smaller mean diameter than individuals in areas of little current and wave action, where only 9% displayed test damage (Weihe and Gray 1968). Variations in hydrodynamic forces between sites may well explain the significant differences in the mean test diameter of subpopulations at Bucasia Beach existing only 500 metres apart (fig 3.4) but necessitates further research. It is most probable that the creek end site has larger individuals partly because the site comprises an extensive beach terrace surrounded by sand bars, which affords greater protection than the swimming enclosure site that slopes directly towards the low water mark and is therefore more exposed to the action of waves and currents.

However when echinoids are faced with favourable conditions and an abundant food supply, individuals delay gonadal investment in favour of a period of somatic growth before the onset of gametogenesis (Lozano et *al.* 1995). This may account for the occurrence of larger *P. lividus* inhabiting areas of reduced hydrodynamism (Lozano et *al*. 1995) and may provide one explanation for the larger size and greater density of *A. placenta* at Bucasia Beach creek end site and Pallarenda Beach. The sediment at both sites comprises wet, rippled areas throughout the area which act as small depressions (see chapter 2, fig. 2.5), and a localised food source of echinoids, including diatoms, blue-green algae and natural sand bacteria, and most likely provide an increased source of food to individuals on the beach terrace at low tide (Meadows and Campbell 1972). Despite the presence of larger individuals at Mission Beach, the intertidal shore contained no sand bars or rippled sediment and extended a maximum of only 30m from the upper shore at spring and neap tides (see chapter 2, fig 2.4). The lack of ripples and shallow pools at this site may reduce the abundance of food within the sediment available to individuals at low tide (but requires investigation to ascertain this), which consequently is sufficient only to sustain a smaller population of significantly larger individuals at this site. The larger size attained by *A. placenta* at Mission Beach (fig. 3.4; table 3.1) may, on the other hand be related to the warmer sea water temperatures encountered at this site (see fig. 4.1, chapter 4). Increased exposure to waves and currents due to the lack of protective sand bars however probably account for limited population numbers at Mission Beach.

There was a significant correlation between the size of individuals and distance from the upper shore throughout the year at Pallarenda Beach (fig. 3.7, 3.8). Comparable patterns observed for the sand dollar *Dendraster excentricus* in North West America suggest a similar downshore distribution (Parks 1973). Buchanan (1966) reports that offshore sediment is finer and richer in organic material, and intertidal sands by comparison have the lowest organic content (Harrold and Telford 1982). This may explain the occurrence of larger *A. placenta* individuals (≥27mm) towards the lower section of the beach terrace at Pallarenda Beach, as an increased food supply would result in increased growth. Larger individuals may be more capable of handling smaller grain sizes than smaller individuals explaining such a pattern of distribution, although there is no evidence of this from previous studies. Larger individuals of the sand dollar *Encope grandis* in Mexico were also more abundant in the lower intertidal zone, whereas small individuals were distributed throughout the intertidal zone (Ebert and Dexter 1975). On the contrary, Cabanac and Himmelman (1996) observed the presence of larger indivduals of the sand dollar *Echinarachnius parma* (40-60mm test diameter) predominating shallow water and smaller ones (≥ 4mm) occurring at greater depths.

Recruitment studies suggest that newly settled recruits settle across the middle to the lower stretches of the shoreline with no apparent preference for situation on the beach terrace (see Chapter 5). However, at a size of approximately 11mm, individuals are found most commonly on the upper beach terrace and exist there until a size of 20mm is attained (fig. 3.7, 3.8). Individuals at reaching 11mm in size may start actively migrating to the upper section of the shore. At a smaller size recruits most likely have no control over their location on the beach due to wave action and currents and are hence distributed across the beach terrace randomly until they reach a size where they are capable of maintaining a position on the shore. On the contrary, juveniles of the subtidal sand dollar *Echinarachnius parma* slowly migrate into exposed beach areas as they mature (Harrold and Telford 1982), however this species inhabits subtidal shores and is most likely to exhibit differences in size distribution.

The length of time sand dollars are exposed to the air during low tide is an important population-limiting factor. Exposure to air can cause desiccation due to sharp temperature fluctuations particularly if individuals are left stranded on a sand bar. Smaller sand dollar in particular, because of their high surface to volume ratios, are more liable to desiccation than large ones (Harrold and Telford 1982). However, the existence of smaller juveniles on the upper shore at Pallarenda Beach does not support such a limitation, as these individuals are subjected to the greatest risk of dehydration at low tide in comparison to those on the lower beach terrace. The line of salt water drainage springs at the junction of the upper and the beach terrace at Pallarenda Beach however provides a constant flow of seawater over the sediment to prevent the desiccation of individuals at this point on the shore. Observations by Harrold and Telford (1982) show that juveniles of the sand dollar *Echinarachnius parma*, like *Arachnoides placenta*, also aggregate in runoff channels and generally avoid exposure to dehydration at low tide. Individuals from a size of around 11mm also remain covered with 2mm of sand, similar to *E. parma* at low tide (Harrold and Telford 1982), which is not observed in smaller individuals of *A. placenta*.

3.4.4. Growth

Growth of *A. placenta* suggests an S-shaped Richard's growth curve, (also known as an asymptotic growth curve) (Richards 1959) because growth is non-linear in the initial and last phases of growth, with a fast lineal growth rate from a size of 10mm (or smaller) to 27mm test diameter. The growth of the European sea urchin *Echinus esculentus* also follows a sigmoidal growth curve (Nichols et *al*. 1985). Growth of *A. placenta* either reaches 4 or 5-6mm in the first year (according to two estimated growth rates, fig. 3.6) and appears to be the slower phase of growth of the species lifespan. Two growth rates are suggested due to low numbers of recruits within the size frequency histograms of August and September 2001. This suggests the presence of individuals from the major recruitment of other years. Juveniles of the size 5 –6mm and 6 –7mm respectively, although discrete, appear to be present, indicating the presence of recruits that settled in 2000. Smaller recruitments that do occur during the major recruitment period, can also be highly variable in intensity and can also be easily overlooked resulting in an apparently unimodal pattern. Likewise, whenever recruitments are significantly strong, they can lead to reports in bi-modal or poly-modal recruitment dynamics (Ebert 1983). If the suggested cohort of *A. placenta* recruits is present and is small, as a result of a poor year of recruitment or sampling error, newly settled recruits would be estimated to reach a size of 10mm test diameter in 32 months (growth estimate 2, fig. 3.9). If this is not a separate cohort of recruits and is more an uneven size distribution of the same year group of recruits created by differential growth and survival rates, a size of 10mm will be attained in 16 months (growth estimate 1, fig 3.9).

Based on this assumption, individuals should reach a size of 27mm test diameter in three or four years after settlement. Both assumptions should be considered with caution however, due to inconsistencies associated with the sampling of individuals of such small sizes. By comparison, the temperate sand dollar *Dendraster excentricus* is reported to reach 10mm in the first year and 20mm in the second year Birkeland and Chia 1971). *Lovenia elongata*, a spatangoid (but both a temperate and tropical species), grows even faster in France, reaching 10mm in only 10weeks (Ferber and Lawrence 1976).

From a size of about 10mm, it is apparent that growth of *A. placenta* assumes a linear growth phase. There is however a noticeable decrease in growth between January and April of the second year (growth estimate 1, fig 3.9) or third year (growth estimate 2, fig. 3.9) of growth at a size of approximately 20mm. This is the size at which *A. placenta* is reported to reach gonadal maturity (Hines and Kenny 1967), and in which energy is invested in gonadal growth, possibly accounting for significantly decreased somatic growth. Raymond and Scheibling (1987) document a similar decrease in the growth rate of the sea urchin *Strongylocentrotus droebachiensis* in Canada in which growth also slows at 20mm test diameter for the same reason. Growth after this period however maintains a sharp increase, suggesting that *A. placenta* develops mature gonads in a short period of time and maintains a fast rate of growth subsequent to reaching maturity. There may be an abundant supply of food within the sediment at Pallarenda Beach, allowing for the allocation of resources to both gonadal and somatic growth, however the slope at this stage suggest food limitation to some extent. Another reason for this short period of decreased growth may well be related to reduced salinities during the summer rain season, which occur during the months of January through to May, cause the flow of small freshwater streams over the shore, which are often only active during that time of year. The sea urchin *Lytechinus variegatus* undergoes substantial mortality every year in the summer wet season due to reduced salinities (Lawrence 1973).

Contradictory to *A. placenta* at Lucinda, (Hines and Kenny 1969), newly settled recruits at Pallarenda Beach assume a very different rate of growth. Growth rates are only similar to that predicted by Hines and Kenny (1967) in the first year for individuals (growth estimate 1, fig. 3.9), attaining 6mm. For this predicated rate of growth in the second year, individuals are estimated to grow a further 16mm, reaching a size of 23mm test diameter which is more than four times faster than that estimated by Hines and

Kenny (1967). However, a number of temperate and tropical echinoids exhibit growth rates similar to the first growth estimate of *A. placenta*, (growth estimate 1, fig. 3.9). For example, juveniles of the sea urchin *Strongylocentrotus droebachiensis* in Canada grew to 6-8mm in one year and to 19mm in the second year like that estimated for *A. placenta*. Chiu (1990) documents similar growth patterns for the tropical sea urchin *Anthocidaris crassispina* as the species displays a linear growth phase in which growth rates are highest in the first four years, after which there is a decline. Moore (1934a, b) and Buchanan (1966) also suggest that growth of the heart urchin *Echinocardium cordatum* in Northumberland and the Isle of Man is linear for the first four years of life after which it decreases. *E. cordatum* however grows considerably faster, reaching 15 – 20mm in the first year and 30 – 35mm in the second year. The species also grows to a much larger size of 60mm, and is presumably long-lived. No relationship between density and growth rate occurs in *E. cordatum* populations, as evident also amongst populations of *A. placenta* (Table 3.1). The temperate sand dollars *Encope grandis* and *Mellita grantii* attained 95% of their maximum size in 6years (74mm) and 5 years (38mm) respectively (Ebert and Dexter 1975). The growth rate and size achieved by the temperate spatangoid *Lovenia elongata* is like that attained by *A. placenta* at Pallarenda Beach, growing 8-12mm a year and attains a similar size at maturity of 23-25mm and a maximum size of 40-45mm (Ferber and Lawrence 1976). On the contrary, test growth in the tropical sea urchin *Lytechinus variegatus* (Moore et *al*. 1963) decreases rapidly with an increase in size, slowing at a considerably larger size of 70-75mm test diameter, at an age of approximately 3 years. The tropical sea urchin *Tripneustes ventricosus* also only has a documented life span of 2 – 3 years (Moore 1966). It seems apparent a number of tropical urchins and sand dollars grow faster and have a shorter life span than some temperate ones.

Differences in growth achieved by the same year groups of some echinoids may be accounted for by direct variation in the available food supply in a year or annual sea water temperatures. Growth of the sea urchin *Echinus esculentus* for example, in the United Kingdom is limited to only three months in the spring, when sea water temperatures are warmer (Moore 1934a). However, in other species such as the spatangoid *Echinocardium cordatum* in the Isle of Man, growth seems to be constant throughout the year except for the months of February and March when sea water temperatures were at a minimum. The effect of reduced sea water temperatures within the colder months of the year are not assumed to significantly reduce the growth rate of

A. placenta as temperatures remain relatively warm throughout the year, but nonetheless could require further investigation. Further investigation is also required to determine the accurate growth rates of newly settled recruits at Pallarenda Beach, with particular emphasis on larger collections of recruits of all sizes (e.g. >500 individuals / month).

In conclusion, despite observed patchiness in the distribution of *A. placenta* on the beach at Pallarenda, a significant decrease in density downshore was observed along 11 / 17 transects laid at Pallarenda Beach. Significant differences in density were observed between all sites and even over distances of metres. There was also clear temporal and spatial variation in the size-frequency of the population at Pallarenda Beach and significant differences in test diameter between sites. At Pallarenda Beach test diameter increased with distance downshore along 13 / 17 transects. Test diameter at Bucasia Beach, Mackay on the contrary decreased with distance downshore. No relationship between test diameter and population was observed. Significant differences in population density and size-frequency data even over scales of just metres suggest that discrete differences in abiotic or biotic factors, particularly sediment grain size, moisture and protection from wave action, between sites are enough to produce significant variations between populations. Growth of *A. placenta* from settlement demonstrates an s-shaped growth curve that is typical of a number of echinoid species (Ebert 1967, 1968a,b, 1975) . From a size of approximately 10mm growth assumes a linear growth phase which slows at a size of 25mm, at which size individuals are estimated to be 3 or 4 years old.

Chapter 4: Reproductive Biology of *Arachnoides placenta*

4.1. Introduction

An extensive literature describes the seasonality of the reproductive cycle of echinoids in which gamete production characteristically shows annual periodicity (e.g. Lares and McClintock 1991; Pearse and Cameron 1991: review; Guillou and Lumingas 1993; Vernon et al. 1993; Spirlet et al. 1998; Alsaffar and Lone 2000; Kelly 2000). The synchronicity in the reproductive cycles observed for separate populations of the same species has led to the conclusion that such entrainment is controlled by exogenous factors such as photoperiod (Giese 1959; Bay-Schmith and Pearse 1987; Byrne et al. 1998) and sea water temperature (Cocanour and Allen 1967, King et al. 1994; Spirlet et al 1998, Kelly 2000) Interannual variation in reproductive cycles has been linked with nutrient availability and nutrient status of adults (Lawrence and Lane 1982) and population distribution and abundance (Beddingfield and McClintock 1998).

A number of echinoid species are documented to spawn in association with rising or falling sea water temperature cycles. Studies by Cocanour and Allen (1967) at Lamoine, Maine show that in captivity, the sand dollar *Echinarachinus parma* has a distinct annual cycle related to temperature with a spawning period from November to December. Sea water temperatures were highest in Lamoine during August and lowest during January-March indicating the onset of gametogenesis in *E. parma* is inversely related to sea water temperature. Previously Brewin et al. (2000) observed that the sea urchin *Evechinus chloroticus* displayed spatial and temporal variability in spawning in New Zealand, occurring near the time of highest sea-surface temperatures (~15 ^{o}C). Similarly the tropical echinoid *Diadema antillarum* spawned in relation to sea-surface temperature during the early summer in Barbados (Lewis 1966).

Initiation of gametogenesis in the sea urchin *Centrostephanus rodgersii* along the coast of New South Wales is most likely triggered by decreasing day length. Gametogenesis occurs in April when days become shorter than nights and there appears to be little or no influence by temperature (Byrne et *al.*1998). Field studies by Gonor (1973) and Bay-Schmith and Pearse (1987) indicate that the reproductive cycle of the sea urchin *Strongylocentrotus purpuratus* is also dictated by seasonally changing photoperiod, with only a slight or no effect by temperature. Gametogenesis and spawning in the subtidal sand dollar *Clypeaster ravenelli* were highly synchronised with increasing day length during the winter in the northern Gulf of Mexico but not significantly correlated with changes in sea water temperature (Vernon et al. 1993). In the spatangoid *Lovenia elongata*, fluctuations in photoperiod, salinity and sea temperature do not appear to be directly related to the synchronisation of reproduction, but more so to the accumulation of nutrients, which may perhaps are influenced by photoperiod and sea temperature cycles (Pearse 1969).

Although numerous studies have examined aspects of echinoid reproduction (reviewed by Lawrence and Lane 1982; Emlet et al. 1987; Pearse and Cameron 1991) only a comparatively small number have focused on irregular echinoids (Chesher 1969; Ebert and Dexter 1975; Lane and Lawrence 1979; Emlet 1986; Pearse and McClintock 1990). Likewise to date, there is no published documentation on the reproductive cycle of *Arachnoides placenta*. It is also important to note that *A. placenta* is unique in being an intertidal tropical irregular echinoid. Of the few that have been studied, most clypeasteroids are temperate species, which inhabit shallow subtidal waters.

This present study determines and compares the reproductive cycle and pattern of gonad growth of *A. placenta* at specific north Queensland sites, documents the process of gametogenesis by histological examination of gonads and aims to evaluate the impact of sea water temperature and photoperiod as a cause for the initiation of gametogenesis.

4.2. Materials and Methods

4.2.1. Sample collection and processing

In 2001 all data collections were made at Pallarenda Beach, however in 2002, four new sites were introduced, which introduced the utilisation of a different data collection protocol

Monthly samples of *Arachnoides placenta* were collected at Pallarenda Beach every month from May to December 2001 and three further data collections were made in 2002 (January, April and July 2002). Data was collected twice in the year from Mission Beach (May and August 2002) and from Cape Hillsborough and Bucasia Beach (March and September 2002). Bucasia Beach creek end site was also sampled in June 2001. All samples were fixed in jars of 10% sea water and formalin for laboratory analysis.

As *A. placenta* shows no obvious external dimorphism between sexes, the first 30 sand dollars encountered with a test diameter of ≥20mm were collected to ensure that each sample contained close to 10 males and 10 females. This size is reported to be greater than the minimum size at sexual maturity, which has been shown to range from 15mm to 20mm in test diameter, depending on location (Hines and Kenny 1967). Sand dollars were randomly collected from upper, middle and lower sections of the intertidal shore at low tide. Test diameter was measured to the nearest millimetre with vernier callipers across the aboral surface.

4.2.2. Histology

Gonadal tissue from sand dollars at all sites was removed by breaking open the test and removing tissue with forceps. Tissue was then removed to processing cassettes, dehydrated in ethanol and embedded in paraffin wax for histological examination. Samples from twenty individuals were sectioned (5µm thick) medially, and mounted and stained with haemotoxylin and eosin. Oogenesis in *A. placenta* was divided into six stages of ovarian growth based on the amount of nutritive material present, the size of oocytes and affinity for stains. Spermatogenesis in *A. placenta* was divided into five stages, distinguished primarily on thickness of the germinal epithelium. As with the observations made for the ovaries, abundance of nutritive material and affinity for stains were also noted. Maturity stages in both male and female gonads were based on modified morphological criteria characterised for the sea urchin *Evechinus chloroticus* by Brewin et al. (2000). Oocyte size-frequency distributions were determined by measuring the cross-sectional area of the first 50 oocytes encountered, sectioned through the nucleolus.

4.2.3. Environmental parameters

Sea surface temperatures and air temperatures for Cleveland Bay, Townsville from January 2001 to December 2002 were obtained from the Australian Institute of Marine Science, Queensland (fig. 4.1a). Sea surface temperatures were recorded every half hour daily using two temperature sensors, and air temperature was recorded with one sensor every half hour every day. Inshore sea surface temperatures collected by Walker (1981) and Kenny (1974) from Cleveland Bay, off Townsville, displayed similar patterns to surface sea water temperatures for 2001/2002 and were also used to

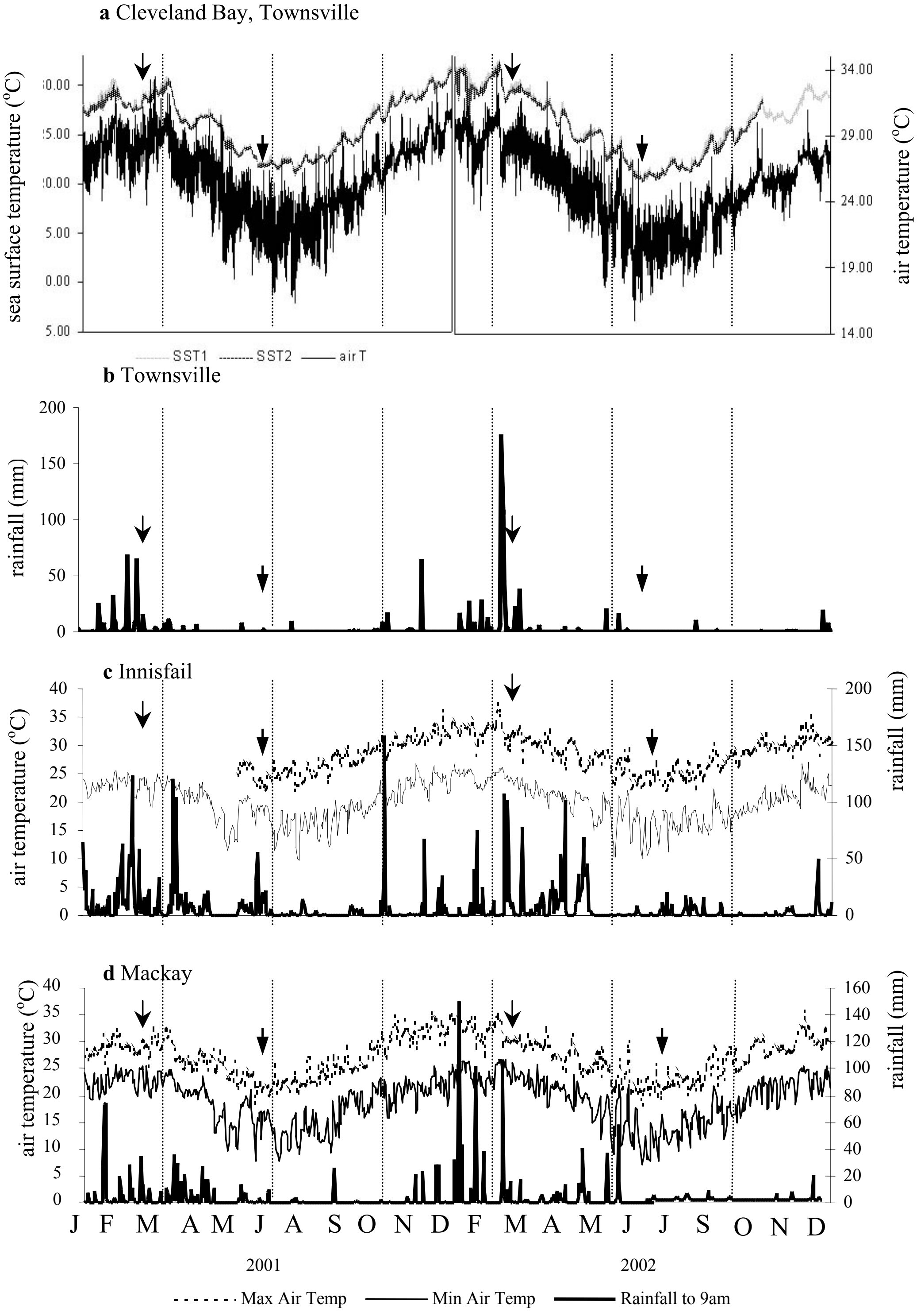


Figure 4.1 **a** Cleveland Bay, Townsville sea surface temperature and air temperature January 2001 to December 2002, (Australian Institute of Marine Science), **b** Townsville rainfall January 2001 to December 2002 (Queensland Bureau of Meteorology), **c** Innisfail minimum and maximum air temperatures and rainfall January 2001 to December 2002 (Queensland Bureau of Meteorology), **d** Mackay minimum and maximum air temperatures and rainfall January 2001 to December 2002 (Queensland Bureau of Meteorology). ↓ indicates the start of the major spawning period, ⬇ indicates the end of the major spawning period.

assess the gametogenic pattern of *A. placenta* with respect to sea surface temperatures at Pallarenda Beach.

Rainfall data for Townsville from January 2001 to December 2002 were obtained from the Queensland Bureau of Meteorology (fig. 4.1b). Daily minimum and maximum air temperatures and rainfall for Innisfail (closest data collection to Mission Beach) (fig. 4.1c) and Mackay (fig. 4.1d) from January 2001 to December 2002 were obtained from the Queensland Bureau of Meteorology. To determine the role of photoperiod in the gametogenic cycle of *A. placenta*, annual day length recordings for all sites were calculated from The Nautical Almanac (1999).

4.3. Results

4.3.1. Histology of the gonads

4.3.1.1. *Arachnoides placenta* ovaries

Oogenesis in *Arachnoides placenta* was divided into six stages of ovarian growth based on the amount of nutritive material present and the size of oocytes (fig. 4.2).

Stage 1: recovering

Groups of dark purple stained previtellogenic oocytes (≤20μm) line the germinal epithelium (fig. 4.2a). Such dark staining indicates that oocytes at this stage are basophilic. The lumen comprises a paler meshwork of nutritive phagocytes with randomly dispersed darker globules from the phagocytosis of relict ova. Some spaces also exist centrally within the lumen.

Stage 2: early vitellogenesis

The same previtellogenic oocytes are now clustered along the wall of the germinal epithelium. Early vitellogenic oocytes (30 – 40μm), stained light purple (indicative of becoming less basophilic) (fig. 4.2b), are also present, indicating the onset of vitellogenesis. Nutritive phagocytes are still dispersed centrally in the lumen, although the globules of nutritive material are decreasingly less dense in comparison to those in Stage 1.

Stage 3: late vitellogenesis

Nutritive phagocytes and nutritive material are noticeably reduced, and are accompanied with a considerable increase in vitellogenic oocytes (>40µm) (fig. 4.2c). A number of different stages of oocyte development are evident and oocytes are continually being produced and maturing. In the centre of the lumen some ova exist, typified by a lack of a distinct nucleus.

Stage 4: mature

Large irregular shaped ova (60 - 80µm) that have completed maturation division densely pack the lumen centrally, pushing nutritive material against the germinal epithelium (fig. 4.2d). Very small primary oocytes line the germinal epithelium in clusters. The medium sized oocytes at this stage in many females no longer occur leaving only mature eggs and very small oocytes.

Stage 5: partly spawned

A large number of ova (80 – 110µm) fill the ovary with a few spaces formed between them (fig. 4.2e). Nutritive phagocytes are rare, seen only on the outer wall although nutritive material is present around germinal epithelium in increasing thickness compared to the previous stage. Few developing oocytes are present.

Stage 6: spent

After spawning, remaining oocytes detach from the germinal epithelium and are actively resorbed (fig. 4.2f). In some, all sizes of remaining oocytes disintegrate, in others only large oocytes and relict ova are absorbed. Very small primary oocytes are present at the periphery of the thin germinal epithelium. Nutritive phagocytes have increased in density, comprising most of the lumen space and appear to play a role in the lysis of large oocytes, replacing spaces left by released ova and leaving nutritive material behind. Some non-phagocytised oocytes may be found until the beginning of the next active growing season.

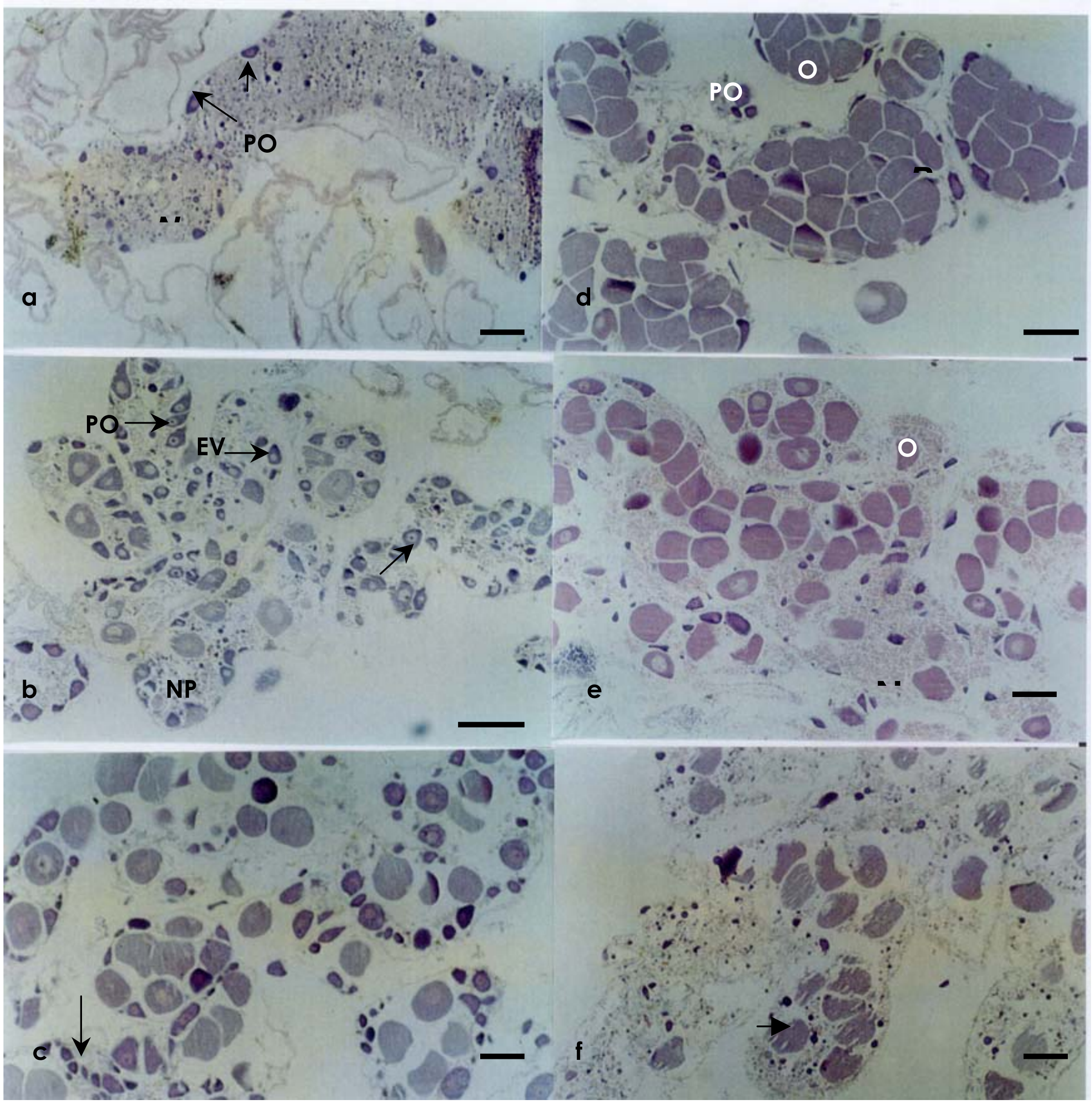


Figure 4.2 *Arachnoides placenta*. Histological sections of ovaries. **a** Stage 1: recovering ovary, note abundant nutritive phagocyte meshwork (*NP*) throughout section; some previtellogenic oocytes (*PO*) are present around germinal epithelium wall. **b** Stage 2: ovary in growing stage,with previtellogenic oocytes now tightly packed around germinal epithelium wall; larger early vitellogenic oocytes (*EV*) are abundant, with distinct nucleoli (*NC*) darkly stained inside nucleus. Vitellogenic oocytes exist towards lumen (VO) although nutritive phagocyte (*NP*) meshwork still predominates in section. **c** Stage 3: premature ovary; vitellogenic oocytes (*VO*) distributed along germinal epithelium wall and in lumen; some ripe ova (*O*) also present in the lumen, characterised by lack of distinct nuclei; nutritive phagocytes reduced in area compared to previous stage. **d** Stage 4: mature ovary; packed with ripe ova (*O*) in lumen; clusters of previtellogenic (*PO*) oocytes present around germinal epithelium wall, with some nutritive material in between. **e** Stage 5: partially spawned ovary; at this stage lumen still contains many mature oocytes (*O*) separated by large spaces; few developing oocytes are present around ovary wall; nutritive material is present around wall in increasing thickness compared to previous stage. **f** Stage 6: ovary in spent stage. Germinal epithelium wall very thin, with very few previtellogenic oocytes and no developing oocytes; number of mature ova in lumen is reduced and they are considered relict oocytes (*R*) at this stage; some lysis of relict ova may be visible (*L*); area of nutritive phagocytes (*NP*) has greatly increased. Scale bars = 100 μm

4.3.1.2. *Arachnoides placenta* testes

Spermatogenesis in *A. placenta* was divided into five stages, distinguished primarily on thickness of the germinal epithelium (fig. 4.3). As with the observations made for the ovaries, abundance of nutritive material and affinity for stains were also noted.

Stage 1: recovering

Darkly stained (basophilic) spermatogonia and primary spermatocytes form a thin layer (15-20 μm) around the germinal epithelium (fig. 4.3a). A nutritive phagocyte meshwork partly or completely occludes most of the lumen with droplets of nutritive material present in varying amounts. Relict sperm may be present in some lumen and primary spermatozoa may be present as dark spots along the germinal epithelium wall.

Stage 2: growing

In stage 2 testes, columns of spermatocytes form a dark (basophilic) layer lining the germinal epithelium, which project towards the lumen (fig. 4.3b). Nutritive phagocytes form a conspicuous layer within the lumen, which in some sections is seen to be pushed to the wall of the testes by accumulating spermatozoa in the lumen.

Stage 3: pre-mature

The germinal epithelium at Stage 3 is lined with spermatocyte columns that have increased in depth (fig. 4.3c). Active recruitment of spermatozoa to the lumen is apparent, and the lumen is darkly stained (basophilic) as a result of the accumulation of spermatozoa. The nutritive phagocytes form a decreasing layer around the germinal epithelium, as more spermatozoa build up in the lumen.

Stage 4: Mature

Stage 4 testes contain large amounts of densely packed spermatozoa (fig. 4.3d). The testis wall is thin and the nutritive phagocytes are compacted to a thin layer at the walls and are no longer eosinophilic.

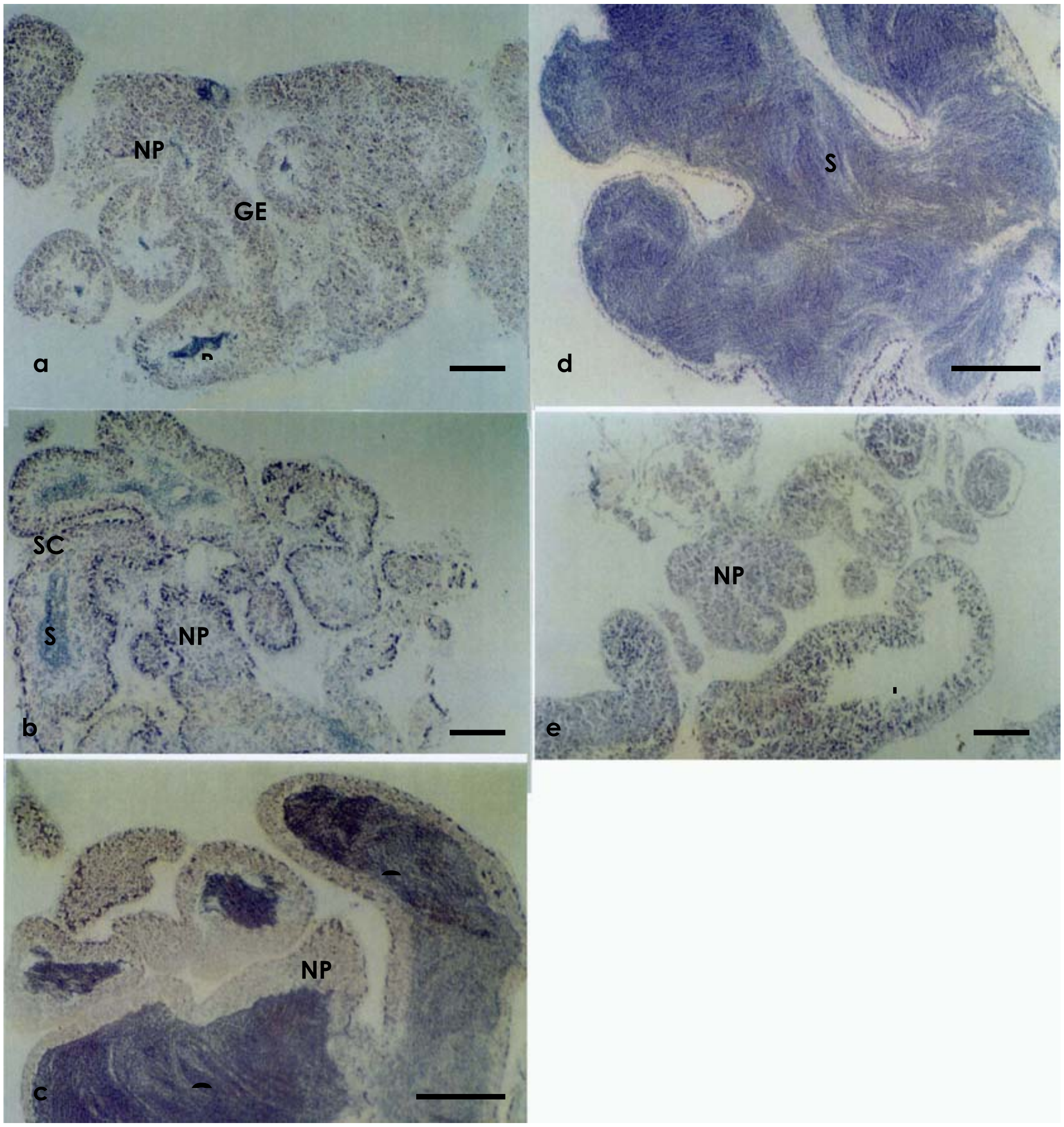


Figure 4.3. *Arachnoides placenta*. Histological sections of testes. **a** Stage 1: testes in recovering stage; nutritive phagocytes meshwork (*NP*) fills majority of testis; darkly stained germinal epithelium (*GE*) is present, made up of primary spermatocytes (*PS*); some relict spermatozoa may be present in lumen. **b** Stage 2: growing testis; germinal epithelium increasing in thickness; spermatogenic columns (*SC*) project towards lumen; mature sperm (*S*) present in lumen; nutritive phagocytes (*NP*) are still plentiful. **c** Stage 3: premature testis; dark stained germinal epithelium wall present; nutritive phagocytes (*NP*) starting to become compressed against germinal epithelium. Large amounts of spermatozoa (*S*) accumulating in lumen **d** Stage 4: mature testis; lumen densely packed with spermatozoa (*S*) germinal epithelium wall thin. **e** Stage 5: spent testis; testis made up mostly of nutritive phagocytes (*NP*) or empty lumen (*L)*. Scale bars = 100µm

Stage 5: spent

Spent testes have thin germinal epithelium walls and the lumen is empty (fig. 4.3e). Nutritive phagocytes form a thin pale meshwork around the periphery and scattered relict spermatozoa may be present.

4.3.2. Environmental parameters

Sea surface temperatures and air temperatures at all sites follow a very similar annual cycle (fig 4.1). Sea surface temperatures in Cleveland Bay, Townsville (Kenny 1974, Walker 1981, Australian Institute of Marine Science 2001 – 2002) (fig 4a), strictly follow the cycle of air temperature in Townsville. As sea water temperatures for the sites of Innisfail and Mackay, were not recorded I will assume they closely reflect air temperatures. In all regions there is a period of high seasonal rainfall in which normally about 50% of the annual total rainfall occurs (fig 4.1b, c, d). In Townsville the rain season occurs from November to the end of March, in Mackay from November to May and in Mission Beach from October to May. Approximately 100 - 180 mm of rainfall falls daily during this period, while for the rest of the year daily rainfall varies from 0 to 25 mm. Due to a shorter rain season Townsville is categorised as being in the dry tropics. Innisfail and Mackay have considerable rainfall throughout the year, and are considered to be in the wet tropics.

A maximum variation of two and a half hours in day length occurred between winter and summer months at each site, in comparison to temperate zones which, at a latitude of 50^{o}S, exhibit a variation of six hours of daylight over the year (The Nautical Almanac 1999). Such minimal variation in annual day length is assumed unlikely to influence the gametogenic cycle of *A. placenta* and upon observation appears to show no correlation at all with the start of the major spawning period.

4.3.3. Gametogenic cycle

Seasonal patterns in the gametogenesis in *Arachnoides placenta* were similar at the five locations (fig. 4.4, 4.5). *A. placenta* showed an annual reproductive cycle at Pallarenda Beach from 2001-2002, with gametogenesis beginning in December and January when sea surface temperatures are at an annual maximum of 27 – 29^{o}C (fig. 4.4a). Spawning was recorded in individuals at Pallarenda Beach in May of both years, but most probably commenced in March. In 2001 partial spawning was also prolonged in some Pallarenda Beach individuals to June/July and in some, to September. All individuals at Bucasia Beach (creek end site) and a percentage of individuals at Casuarina Beach were spawning in March 2002 (fig. 4.4b, d).

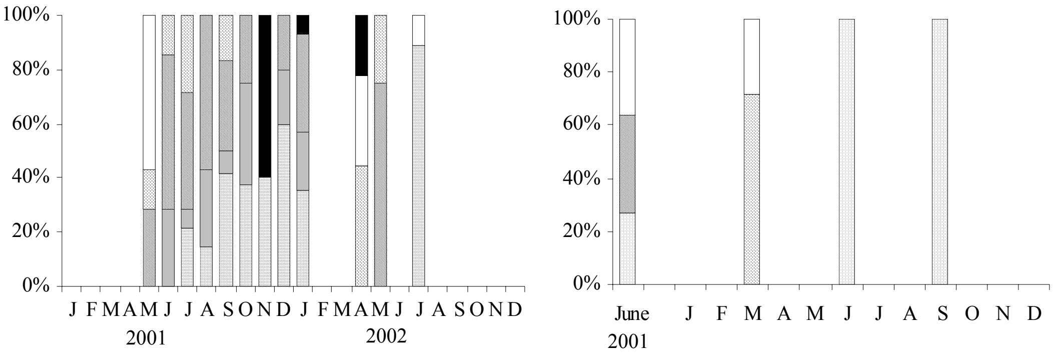
The start of the breeding season of *A. placenta* at Pallarenda Beach appears to coincide with the start of the decline of local sea water temperatures in March when temperatures are approximately 26 – 28^{o}C (fig. 4.1a). The major spawning period continues with a decline in sea surface temperature and ceases shortly before annual temperatures are at the lowest of the year in June (22-24^{o}C) or are just starting to rise again, in August. Throughout the year, a maximum difference in air temperature of only ±8^{o}C between each site could be the main reason minimal or no effect of site on gametogenesis was observed. Gametogenesis is also only synchronous among individuals of *A. placenta* during months of the major spawning period, i.e. March 2002 Bucasia Beach creek end site, and May 2001 Pallarenda Beach (fig. 4.4a, b; 4.5.a, b).

In females, gonads returned to the recovering condition within a month or less of spawning at Pallarenda Beach. However, from July to November no spawning occurred in females and a very slow rate of gametogenesis was observed (fig. 4.4.a). As a result, the spent stage was rarely found in *A. placenta* females. A significant decrease in gonad size was also observed in females at Pallarenda Beach in the months of October and November 2002. This decrease in amount of gonad in this period is probably the result of gonad resorption rather than spawning, as no ripe eggs were evident in histological sections from these months.

In males, 30-100% of individuals at all populations were in a stage of late gametogenic growth or spawning throughout both years except in June 2002 at Bucasia Beach (swimming enclosure site) and September 2002 at Casuarina Beach and Bucasia Beach (both sites) (fig. 4.5). Ripe spermatids in the lumen also usually preceded and persisted beyond the appearance of ripe eggs.

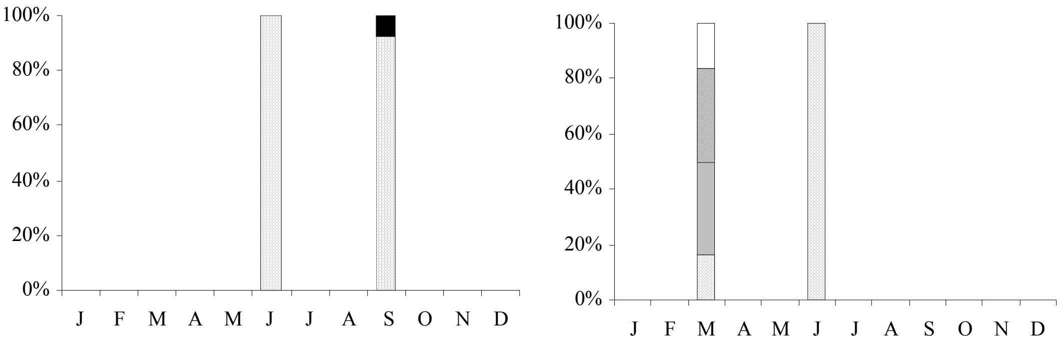
a Pallarenda Beach

b Bucasia Beach, Creek end



c Bucasia Beach, Swimming enclosure

d Casuarina Beach, Cape Hillsborough



e Mission Beach

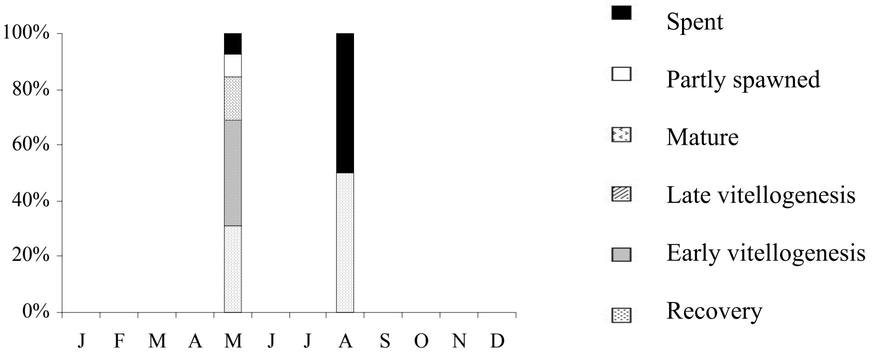


Figure 4.4. *Arachnoides placenta*. Progression of gametogenic stages in females from **a** Pallarenda Beach (May 2001 to July 2002), **b** Bucasia Beach, creek end (June 2001, March, July September 2002) **c** Bucasia Beach, swimming enclosure (June and September 2002) **d** Casuarina Beach (March, and June 2002) and **e** Mission Beach (May to August 2002)

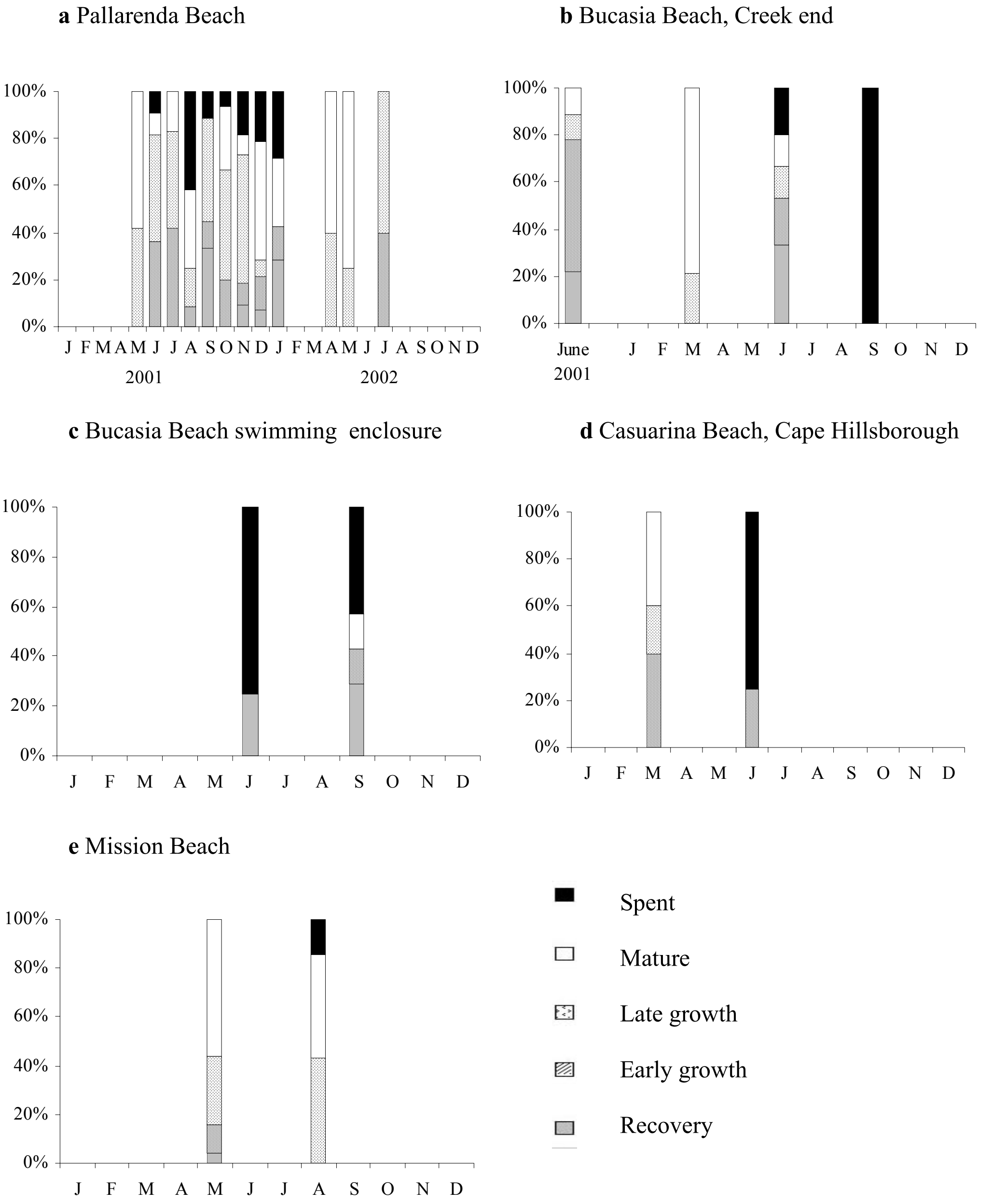


Fig. 4.5. *Arachnoides placenta*. Progression of gametogenic stages in males from (**a**) Pallarenda Beach (May 2001 to July 2002), **b** Bucasia Beach, creek end (June 2001, March, July September 2002) **c** Bucasia Beach, swimming enclosure (June and September 2002) **d** Casuarina Beach (March, and June 2002) and **e** Mission Beach (May to August 2002)

4.3.4. Oocyte/ova size-frequencies

The variation in oocyte and ova size-frequency distributions for Arachnoides placenta at Pallarenda Beach from May 2001 to July 2002 substantiate the presence of an annual gametogenic cycle, and are particularly consistent with histological data (fig. 4.6).

At Pallarenda Beach, it is clear to see the onset of oogenesis during December 2001 and January 2002, as evident in the appearance of a small mode of oocytes/ova, 50 - 80µm. In April 2002 and May of both years, a distinct bimodal frequency of small vitellogenic oocytes 10 – 40µm and larger mature ova 50 - 80µm, indicate a period of major spawning. In accordance with Pallarenda Beach in April 2002, histological and oocyte size-frequency data from Bucasia Beach creek end site in March 2002, suggest most females were in the mature or premature stages, therefore most ova had yet to be released. Oocytes were therefore probably still in a stage of development.

During the months of May 2002 and June 2001 at Pallarenda Beach, smaller oocytes (10-40µm diam) are more abundant than larger ova (50-80 µm diam). It is likely that the process of oocyte maturation had ceased at these sites during those months, particularly as histological results show 80% of female gonads by this time were in the recovery stage. This is also evident during the month of May 2002 at Mission Beach.

From June through to August at Pallarenda Beach there are smaller peaks of larger ova indicating extended but significantly reduced spawning, or a slower oocyte resorption time. However, histological data suggests most individuals in this month (fig. 4.2.a) had spawned and were in the recovery stage.

From August through to November the presence of only very small oocytes (0 - 50µm), and the absence of no maturing oocytes within ovaries, indicate no spawning is taking place at Pallarenda Beach. In particular in November 2001 there was insubstantial or no gonadal tissue available within all females collected indicating that gametogenesis had completely declined. It must be noted that sea surface temperatures are at their lowest during August (22- 24^{o}C), from which they increase to a maximum at the start of December (26 –28^{o}C), when gametogenesis again begins.

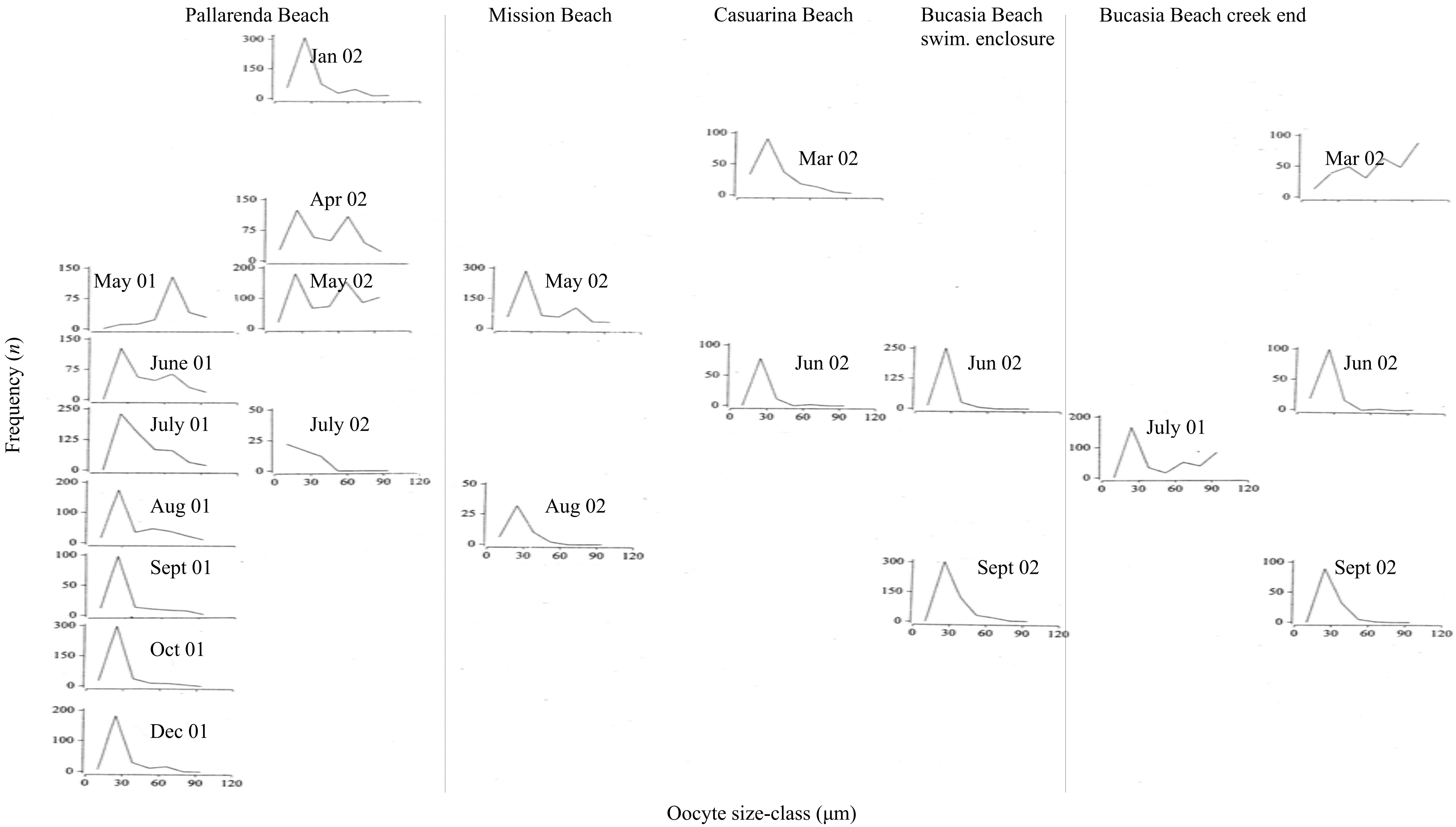


Figure 4.6. *Arachnoides placenta*. Oocyte size-frequency distributions for females, Pallarenda Beach (*n* = 5 to 10^{-mo}) (May 2001 to July 2002), Bucasia Beach creek end (*n* = 2 to 5^{-mo}) (June 2001, March, July September 2002), Bucasia Beach swimming enclosure (*n* =1 to 12^{-mo}) (June and September 2002), Casuarina Beach (*n* = 1 to 4^{-mo}) (March, and June 2002) and Mission Beach (*n* =1 to 5^{-mo}) (May to August 2002)

4.4. Discussion

Characteristics of gametogenesis in the clypeasteroid *A. placenta* are similar to general sequential changes in most echinoids as described by Pearse and Cameron (1991), and others for example, in the sea urchins, *Centrostephanus rodgersii* (Byrne et al 1998), *Evechinus chloroticus* (Brewin et al. 2000), *Heliocidaris erythrogramma* (Laegdsgaard et al. 1991), *Strongylocentrotus droebachiensis* (Boolootian 1966, Himmelman 1978, Meidel and Scheibling 1988, Garrido and Barber 2001) and *S. purpuratus* (Chatlynne 1969, Gonor 1973, Cochran and Engelmann 1975, Pearse 1981), and the irregular echinoids *Clypeaster ravenelii* (Vernon et al 1993), *Echinarachnius parma* (Cocanour and Allen 1967), *Mellita quinquiesperforata* (Lane and Lawrence 1979).

Although the gametogenic condition varied to some degree between local populations, *A. placenta* exhibited an overall seasonal cycle with a period of gamete growth and accumulation from December to February culminating in a March to May main spawning period at Pallarenda Beach (figs. 4.2; 4.4; 4.6). The continuation of partial spawning of females in June, July and August 2001 at Pallarenda Beach is consistent with the decline of sea water temperatures which during these months reaches a minimum (fig 4.1a). The optimal temperature range for spawning in *A. placenta* appears to be between 28 – 24 ^{o}C but the species is capable of spawning until temperatures reach a minimum of 22 ^{o}C. Despite variations in the annual temperature ranges that occur between each site, spawning in *A. placenta* appears to coincide with the start of a decrease of local sea water temperature specific to each latitude, and not in response to a particular temperature. During months of major spawning, (March – May 2001, 2002) there was also a noticeable synchronisation of ripe male and female gonads that was not observed in other months of the year. Gonads were coordinated only during this time mainly because the majority of females were ripe only during the months of March to June, and a percentage of male gonads were consistently in the mature phase for nine or more months of a year (fig. 4.4a; 4.5a).

A critical range of temperatures are necessary for the development of gametes in a number of echinoids (Pearse 1970) including the tropical sea urchin *Eucidaris tribuloides* (Lares and McClintock 1991). At an ambient temperature of 27 ^{o}C individuals produce mature gonads. However, when exposed to 30 °C for two months, males lacked mature spermatozoa and individuals held at lower than ambient temperatures for a similar time delayed gametogenic development, as indicted by small gonads which lacked definitive gametes. However, although sea-surface temperatures appear to be essential for maximal oocyte growth and maturation (Boolootian 1966, pers. obs.), sea water temperature at the time of spawning can be adjusted to some degree before gametogenesis is significantly prevented or delayed (Cochran and Engelmann 1975). In this investigation, the ±8 °C difference in sea surface temperatures between sites probably explains the only slight spatial variation in the timing of spawning observed for *A. placenta*. Significant differences in the timing of gametogenesis and persistence of ripe gonads will most likely be observed between *A. placenta* populations at the northern and southern distribution of the species, for example between Amoy, South China and Gladstone, Queensland, Australia. Persistence of gametogenesis in captivity to variable temperatures is probably indicative of the temperatures at the extreme northern and southern latitudes inhabited by a particular species (Lares and McClintock 1991). However in certain years for the sea urchin *Paracentrotus lividus*, sea surface temperatures are documented to not always reach critical values for mass spawning to be triggered, which in turn may cause population changes, ultimately through the lack of recruitment (Barnes et *al*. 2001).

The reproductive cycle of *A. placenta* is inversely related to annual water temperature patterns, so gonads are ripe when water temperatures are lowest and gonads are spent when water temperature is highest. This has also been reported for other echinoids (Cocanour and Allen 1967; Chatlynne 1969, Cochran and Engelmann 1975). A positive correlation between temperature and size of nutritive phagocytes in the gonads of *A. placenta* was also observed, which is consistent with the findings of Garrido and Barber (2001) for *Strongylocentrotus droebachiensis* and Chatlynne 1969 for *S. purpuratus*. Cooler temperatures also appear more favourable for the development of greater numbers of oocytes in the sand dollar *Echinarachnius parma* (Cocanour and Allen 1967), the sea urchins *Eucidaris tribuloides* (Lares and McClintock 1991) and *S. droebachiensis* (Garrido and Barber 2001).

There may also be some correlation of the gametogenic cycle with salinity at Pallarenda Beach as spawning commences at the end of the rain season that typically occurs from January to March in Townsville (fig. 4.1b). *A. placenta* may respond to the salinity of seawater within the sediment, and spawn when the salinity increases at the end of the rain season. There does not appear to be such a correlation with individuals at Mission Beach (Innisfail) and Mackay sites as rainfall is relatively continuous throughout the year with a longer rain season (fig. 4.1c, d). Spawning in individuals at both Mackay sites and Mission Beach appears to commence also in March indicating that variable rainfall is not responsible for causing variable gametogenesis between sites. Prolonged reduced salinities caused by rainfall may affect gametogenesis in individuals however (Moore 1934b). Further investigation would be required to determine whether reduced salinities play a significant role in the reproductive cycle of *A. placenta.*

In the first stage of gametogenesis in *Arachnoides placenta* at Pallarenda Beach, oogonial proliferation, accompanied with nutrient accumulation, commenced in December/January, four to five months after the completion of spawning and resorption of relict gametes. The nutrients necessary to sustain vitellogenesis are most likely obtained from carbohydrate stores, as shown by droplets in the nutritive phagocytes. Following nutritive build-up, gametogenic cells begin to grow and mature along the ovarian wall (King et al. 1994). In *A. placenta* development of oocytes and sperm culminates in mature gametes occupying the entire lumen of the gonad with little or no nutritive material remaining. This marked inverse relationship between the development of the nutritive phagocytes and gametes in the gonads of *A. placenta*, is characteristic of a number of echinoids (King et al 1994, Brewin et al 2000). Mature oocytes in *A. placenta* at Pallarenda Beach (2001) were first observed in March and were present until the end of May. After spawning occurred the remaining gametes were either resorbed or did not grow until the start of the next reproductive period in which nutritive material again accumulates. From June to December 2001 the persistence of small primary oocytes (0 – 40 µm diam) without the development of new ova, indicated a quiescent phase in gametogenesis of approximately four to five months. Similarly, in the sand dollar *Mellita quinquiesperforata*, the presence of small primary oocytes does not always indicate the beginning of oocyte growth since in some years, small oocytes from the previous gametogenic cycle also remain quiescent for four to five months (Lane and Lawrence 1979). In particular in November 2001 at Pallarenda Beach, there was insubstantial or no gonadal tissue present within all females collected, indicating that no gametogenesis was taking place. Gonads had considerably shrunk and/or gonadal tissue dissected from individuals was of a dark brown to black soft tissue inconsistent with the firm orange or ochre shades of gonadal tissue sampled in other months. The majority of sectioned gonads lacked distinct evidence of male or female gametes at any stage. Higher sea-surface temperatures during this period may have had the same effect on gametogenic development as reduced temperatures for the tropical sea urchin *Eucidaris tribuloides*, in which gonads shrink and lack definitive gametes in either males or females (Lares and McClintock 1991).

Initiation of oocyte growth in *Arachnoides placenta* in December appears to be abrupt and noticeable (figs. 4.3, 4.6), similar to the onset of gametogenesis in the sand dollar *M. quinquiesperforata* (Lane and Lawrence 1979). Ripe spermatids in the lumen of *A. placenta* usually preceded and extended beyond the appearance of ripe eggs indicating male gonads are in the mature condition for a longer time than female gonads (figs. 4.4, 4.5). This trend is common amongst echinoid populations, including the sea urchins *Paracentrotus lividus* (Byrne 1990), *Heliocidaris erythrogramma* (Laegdsgaard et al. 1991) and *Centrostephanus rodgersii* (King et al. 1994) and the sand dollar *Mellita quinquiesperforata* (Lane and Lawrence 1979). Only females were observed to show significant synchronisation with annual sea surface temperature changes. Males were observed to spawn throughout the majority of the year without corresponding to a decline in sea water temperatures. It is most probable therefore that females, unlike males, do not have the resources to spawn all year round.

In conclusion *A. placenta* exhibits an overall seasonal cycle with a period of gamete growth and accumulation from December to February culminating in a March to May main spawning period. The breeding season appears to coincides with the start of a decline in sea water temperatures that occurs from March and reaches a minimum over the months of June – August. Over the range studied, *A. placenta* experienced similar annual air/sea water cycles and relatively comparable rainfall cycles. possibly accounting for minimal differences in gametogenesis between sites. Spawning was only synchronous between males and females during months of the major spawning period (March to July). From July to November, female gonads were spent or in a phase of recovery accompanied by a slow rate of gametogenesis. 30-100% of males in all populations had ripe gonads throughout both years except for June and September 2002 at Mackay.

Chapter 5: Recruitment Biology of *Arachnoides placenta*

5.1. Introduction

Although the processes of gametogenesis and development in echinoids are well understood, the ways in which they contribute to recruitment in the field remain little studied (Walker 1984). Echinoid recruitment can be broadly divided into three components: 1) pre settlement processes comprising larval production and larval development, mortality and transport; 2) settlement and metamorphosis; and 3) post-settlement growth and mortality of juveniles, all of which consecutively determine the demography, distribution and abundance of echinoid populations (Boolootian 1966, Ebert 1975, Ebert 1983, Keough and Downes 1984, Emlet 1986, Pedrotti 1993). The passage from the larval stage to the adult stage involves not only a gradual fall from the water column to a permanent residence on the substratum, but also a series of morphological changes that give the settled larvae the features required for adult life (Rodriguez et *al*. 1993).

A number of studies document large spatial and temporal variability (over tens of metres to thousands of kilometres and from months to years) in both settlement and recruitment rates of echinoids, which are derived from a number of variables that are difficult to isolate (Starr et *al.* 1993, Hunt and Scheibling 1997, Lopez et *al.* 1998, Balch and Scheibling 2000a,b, Lamare and Barker 2001). These variables can act individually or in cooperation at the pre-settlement, settlement and / or post-settlement levels (Gosselin and Qian 1997, Hunt and Scheibling 1997). At the pre-settlement stage, the supply of planktonic larvae to benthic echinoid populations is regulated by a poorly understood complex interaction of biotic and abiotic factors such as near-shore currents, sea temperature, salinity, food availability, predation and starvation (Highsmith 1982, Butman 1987, Miller and Emlet 1997, Balch and Scheibling 2001). Metamorphosis is an important factor that influences the supply of settling larvae to populations particularly as a considerable reorganisation of the body occurs during this time, which is subject to developmental complications (Walker 1984, Gosselin and Qian 1997). Temperature extremes or ultraviolet rays during metamorphosis may produce dysfunctional juveniles (Gosselin and Qian 1997). Larval life spans in a variety of sea urchin species from temperate waters can vary from 2 to 8 months if a suitable substrate for settlement is not available (Hinegardner 1969, Strathmann 1974). Predation is also another factor documented to affect the larval supply in echinoids, the risk of which is enhanced with a longer planktonic period (Ebert 1983, Rumrill et al. 1985).

Extreme variations in temperature may alter the metabolic rate of echinoid larvae to the extent that rates of nutrient and oxygen accumulation are insufficient to support basic requirements, resulting in death by starvation and asphyxiation (Pechenik 1987). In a more narrow range, higher or lower than ambient temperatures may cause development rates of echinoid larvae to vary (Miller and Emlet 1999). The effect of near shore hydrodynamics on larval supply and settlement is also fundamental to understanding the variability in recruitment to local populations of sea urchins (Miller and Emlet 1999).

A variety of post-settlement processes, including predation, migration, disease and starvation, also play an important role in population structure through the regulation of recruitment rates and patterns in sea urchins (Rumrill et *al*. 1985). Early survival of juvenile sea urchins following settlement is poorly understood, but it seems reasonable that tiny predators must consume many small echinoids (Ebert 1983). Interannual variation in settlement and/or recruitment is also often high in echinoids, and several years may elapse between successful recruitment events (Ebert 1983, Pearse and Hines 1987, Balch and Scheibling 2001).

In spite of the ecological importance of *Arachnoides placenta* to north Australian sandy shores, its population dynamics are still poorly known, particularly for its recruitment. The larval development and metamorphosis of *A. placenta* already comprise a number of studies (Feliciano 1933; Chen and Chen 1992; Chen and Run 1989; Chen and Huang 1990). Hines and Kenny (1967) state that metamorphosis of *Arachnoides placenta* at Lucinda, north Queensland, occurs during September when Queensland winter sea temperatures are between 20^{o}C and 22^{o}C. Koizumi (1997 unpublished) however suggests *A. placenta r*ecruits first appear within the sediment in mid-August at Rowes Bay and Pallarenda Beach, Townsville, and suggests they may be present from mid-April through to August.

The purpose of this investigation is to determine how recruitment amongst populations of *A. placenta* differs spatially and temporally at separate locations on the north Queensland coast and how variation in abiotic and biotic factors might alter recruitment. In this study, recruitment is defined as the appearance of small individuals of less than 10mm test diameter. It must be noted that assessment of settlement is often problematic due to the small, cryptic and transient nature of very new recruits (Lamare and Barker 2001). Rapid mortality prior to observation, can also lead to underestimation, and may result in populations being sampled disproportionately to their true abundance (Harrold et *al*. 1991, Pearse and Cameron 1992, Ebert et *al.* 1993). It is also possible that variability in interannual variation may be attributed to measurement inaccuracies (Balch and Scheibling 2000).

5.2. Materials and methods

5.2.1. Sampling recruit size structure and density

Monthly samples of *A. placenta* recruits and individuals that could not be easily seen by the naked eye (<10mm) were collected and recorded at low tide between April 2001 and January 2002 at Pallarenda Beach, which provided long-term data with which other sites could be compared. Between February and September 2002, newly settled recruits and juveniles (<10mm) from Townsville, Mission Beach, and the Mackay region were sampled sequentially each month. The greatest length of time between any two sampling dates of the same site never exceeded three months. For recruit settlement analysis, two to three transects, were placed approximately 150m apart, perpendicular to the shore from the high water mark. Two 0.3 x 0.3 m square quadrats were placed either side of each transect at three-metre interval sections downshore (fig. 5.1).

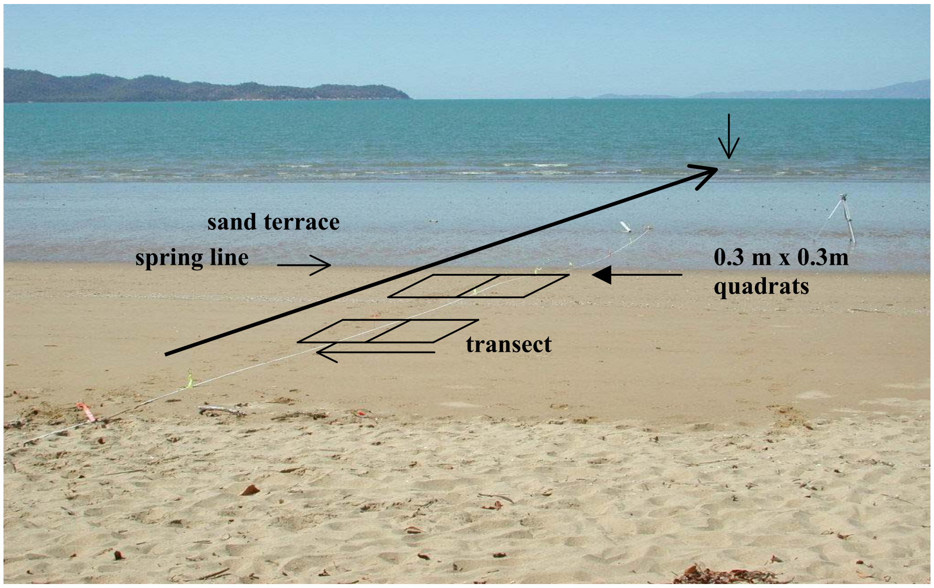


Fig. 5.1. Sampling method used for the recording and collection of the size frequency structure and density of *A. placenta* recruits (<10mm) downshore

Within each quadrat, the top centimetre of sand was removed with a small spade and sieved through 0.5mm mesh using sea water. This size mesh was small enough so as to trap the smallest of recruits which in a pilot study were found to be no smaller than 0.5mm in diameter. The residual sediment was collected in containers and labelled according to the position collected on shore and taken back to the laboratory. In the laboratory individuals were removed and counted out of the sediment and placed in labelled containers of formalin. The test diameter (TD) of recruits were measured to the nearest 0.1mm in the laboratory using a light compound microscope with a graduated ocular micrometer.

5.2.2. Statistical analysis

Minitab (version 13.32) was used to carry out one-way ANOVAs and linear regression analyses on the effect of distance from the high water mark on 1) individual density m^{-2} and 2) size frequencies of populations at Pallarenda Beach and Bucasia Beach in 2001.

5.3. Results

5.3.1. Size range of individual settlers

The average test diameter of newly settled recruits at all sites ranged from 0.5 – 0.8 mm. Individuals of this size (fig. 5.2) were extremely cryptic, and had a test the same colour as the sand grains from which they were sampled. Each recruit was covered with a large number of long spines in relation to its diameter, and possessed long tube feet, which Feliciano (1933) suggested were used to attach to and feed off sand grains. *A. placenta* recruits were found very shallowly buried (less than 4 mm) below the surface of the substratum and smaller individuals tended to become resuspended in the surface water when the surface of the sediment was disturbed with a flat hand moved from side to side. From 0.5 - 10mm in size, newly settled recruits progressively change from a paler sand colour to a darker brown colour, from which the colour remains the same to adulthood.

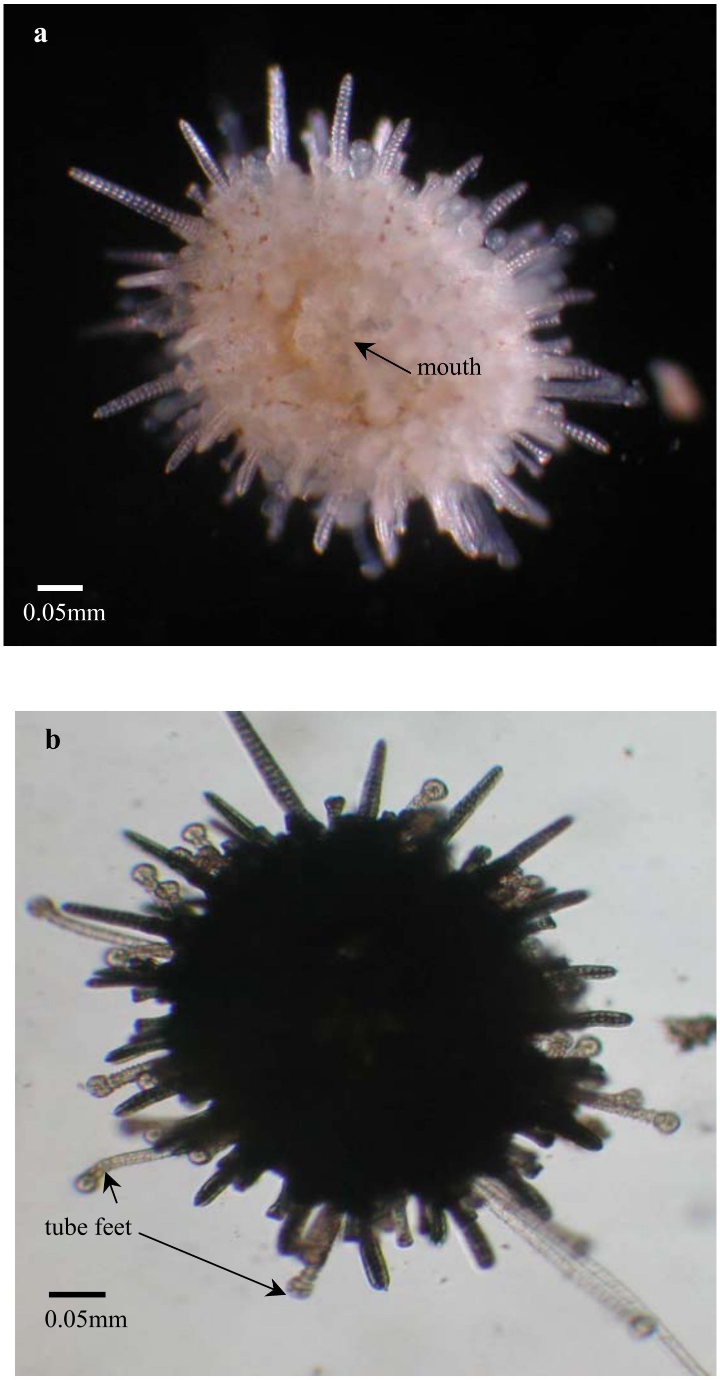


Figure 5.2. *Arachnoides placenta* **a** Oral view of post-larval recruit, showing mouth centrally located, numerous long spines covering test and tube feet between spines **b** Silhouette of aboral view of post-larval recruit, showing long tube feet

5.3.2. Recruitment

Recruits 0.5 – 1 mm TD were found within the sediment throughout 2001 at Pallarenda Beach, however there were months of significant heavy recruitment from May until July 2001,which are clearly reflected in the size structure of juveniles for these months (fig 5.3). High numbers of recruits in May suggests that the major recruitment period commences in April. During the major recruitment period, individuals 0.5 – 4 mm in diameter, dominated the size frequency structure of the population. An observed two- to three fold decrease in the abundance of recruits > 2mm occurred from August through to October 2001. There was also noticeable interannual variation in recruitment between 2001 and 2002 at Pallarenda Beach, for example in May and July 2001 there were 35 and 32 newly settled recruits m^{-2} sampled respectively, but in the same months in 2002 there were no newly settled recruits or individuals smaller than 3mm test diameter found within the sediment.

In the Mackay region, the major months of recruitment corresponded with that of Pallarenda Beach (fig. 5.4). No newly settled recruits were observed at Bucasia Beach in March indicating possibly that major recruitment had yet to commence. A mode of juveniles approximately 6mm in size was however present, suggesting these individuals were the recruits that settled in the months of April to June in 2001. At Cape Hillsborough newly settled recruits were common within the sediment somewhat earlier than that observed for other sites, occurring at the end of March. This indicates that spawning at this site was occurring at the start of March and possibly earlier. Newly settled juveniles were also common at Cape Hillsborough in June but in reduced numbers indicating the close of the major period of recruitment. At Bucasia Beach creek end site in June 2001 a peak of individuals 1.8mm in size points to a late March to early June recruitment period. Likewise at the swimming enclosure site in June 2002, a 2mm mode of individuals also suggests that recruitment occurs in the same months.

At Mission Beach in the months of May and August 2002, the sediment comprised recruits of only 5 – 10 mm test diameter (fig. 5.5).

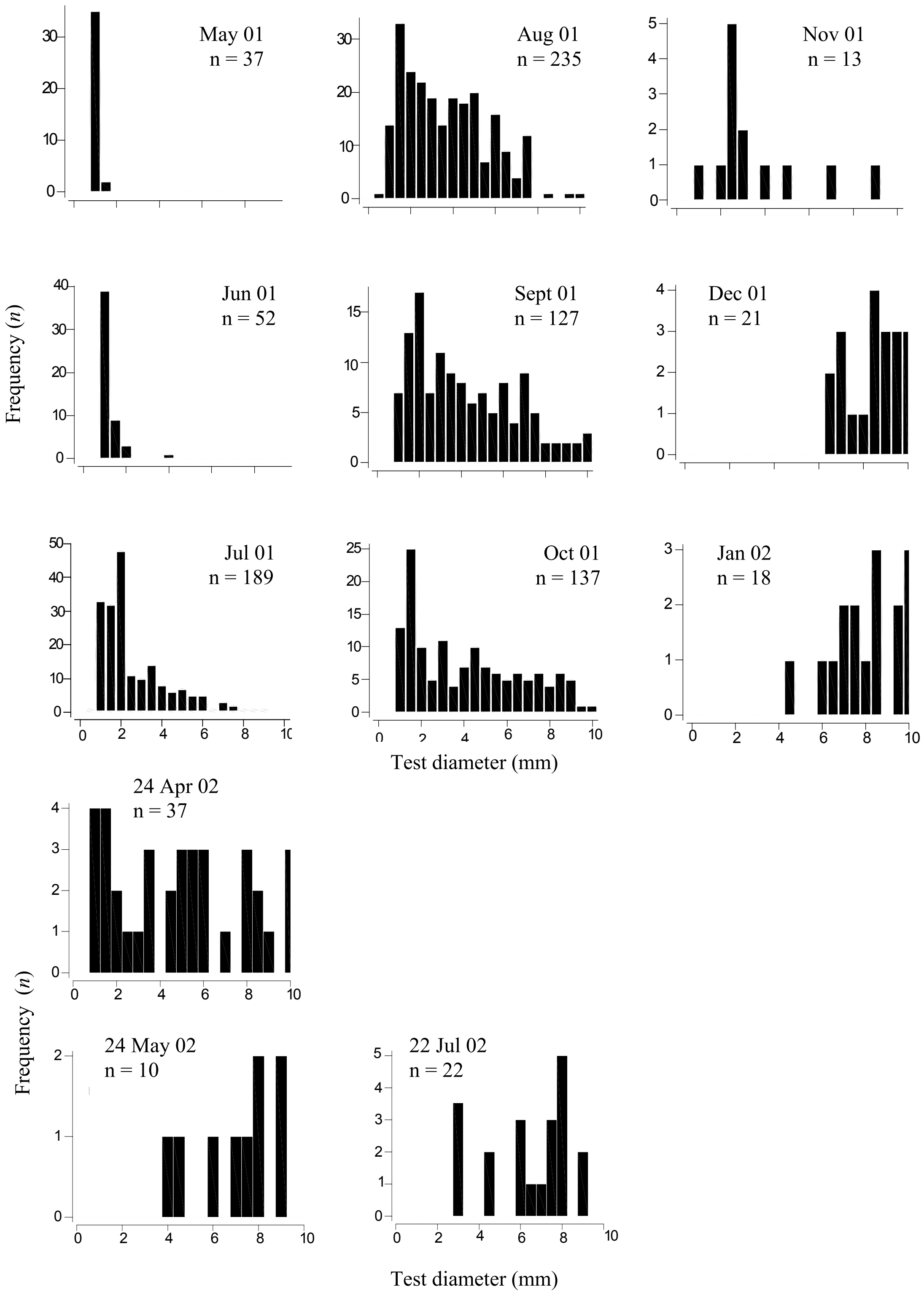


Figure 5.3. *Arachnoides placenta.* Size-frequency histograms of recruits and juveniles (≤10mm) from sieved sand Pallarenda Beach, May 2001- Jan 2002, and April - July 2002.

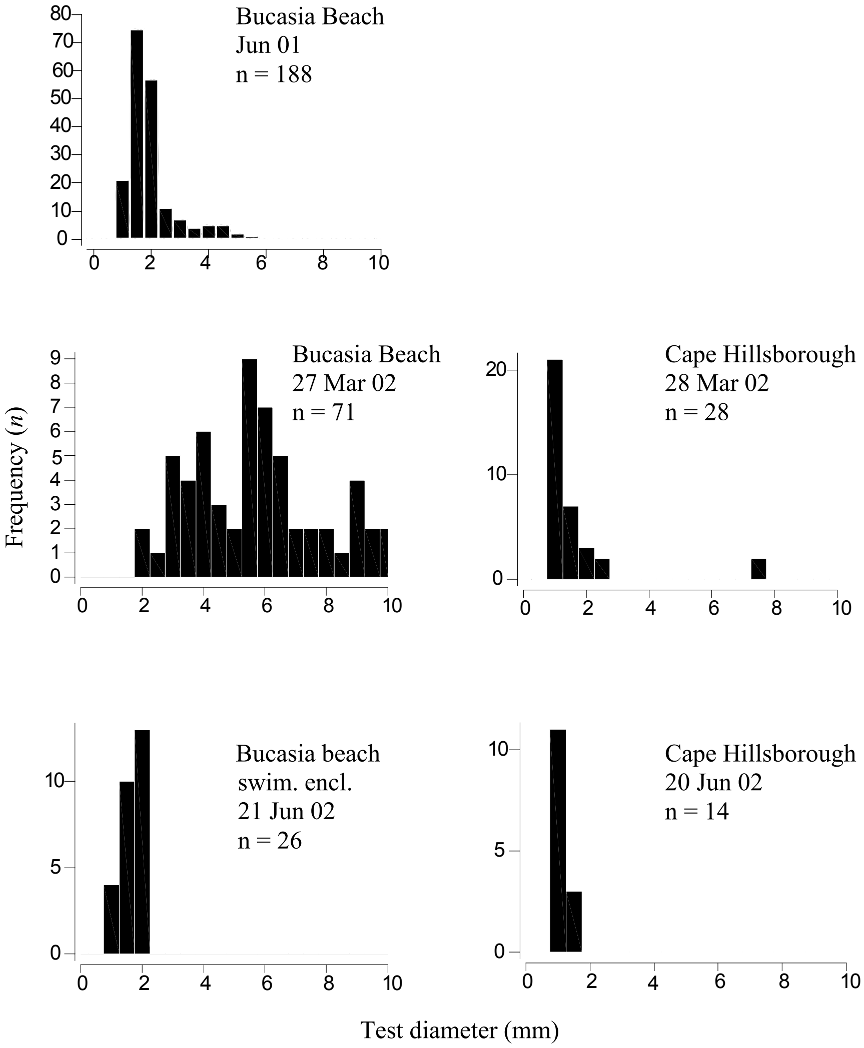


Figure 5.4. *Arachnoides placenta*. Size-frequency histograms of recruits and juveniles (≤10mm) from sieved sand, Bucasia Beach and Cape Hillsborough NP June 2001/2002 and March 2002

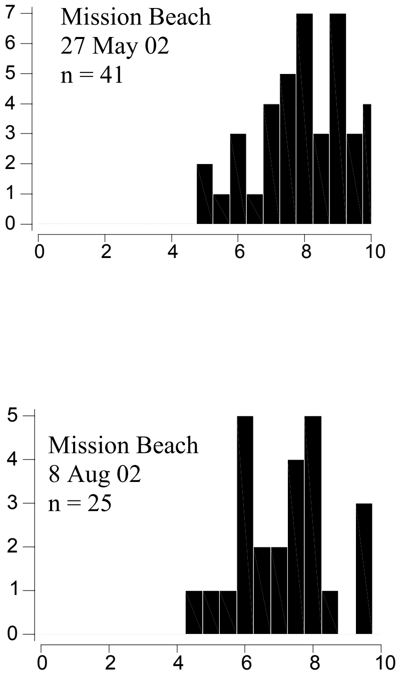


Figure 5.5. *Arachnoides placenta.* Size-frequency histograms of recruits (≤10mm) from sieved sand, Mission Beach, May and August 2002

5.3.3. Recruit density and shoreline distribution

A significant decrease in density of *Arachnoides placenta* recruits and premature individuals (<10mm) m^{-2} downshore was observed in the months of July, August and October 2001 (fig. 5.6) however there was no effect on distance downshore on density for the remaining three months sampling was undertaken. In all six months there was noticeable patchy distribution of recruits and juveniles downshore and individuals were present on the middle to lower shore, with few present towards the upper shore. At Bucasia Beach creek end site, recruits were also common on the mid to lower shore (fig. 5.7). Contrary to the downshore distribution of Pallarenda Beach, a significant increase in density m^{-2} of recruits from the middle shore to the lower shore was observed ($p = 0.01$). The density of individuals <10mm sampled from the same transect as individuals >10mm followed a similar density pattern downshore. The result from Bucasia Beach however should be treated with caution as only one transect was laid.

5.3.4. Recruit size and shoreline distribution

There was no consistent relationship between the size of recruits and distance downshore over a period of six months at Pallarenda Beach. In May and October 2001 individuals exhibited a significant decrease in size downshore ($p = 0.000, 0.012$) (fig. 5.8, 5.9), however in July 2001 individuals significantly increased in size downshore ($p = 0.001$). In the remaining months there was no relationship between distance downshore and size of recruits. At Bucasia Beach in June 2001 only one transect was laid, along which there was no significant effect of distance downshore on the size of recruits ($p = 0.993$) (fig. 5.10). At both sites newly settled recruits 0.5 –1mm, occurred on the middle to upper shore, and were continually absent from the upper shore.

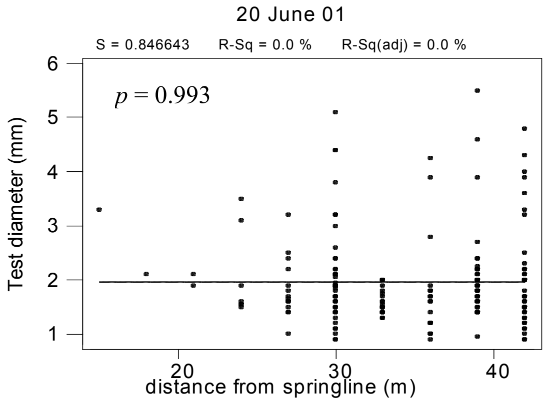


Fig. 5.10. *Arachnoides placenta*. Recruit and juvenile (<10mm) size versus distance downshore, Bucasia Beach creek end, June 2001. *P*-value displays effect of distance from upper shore on size

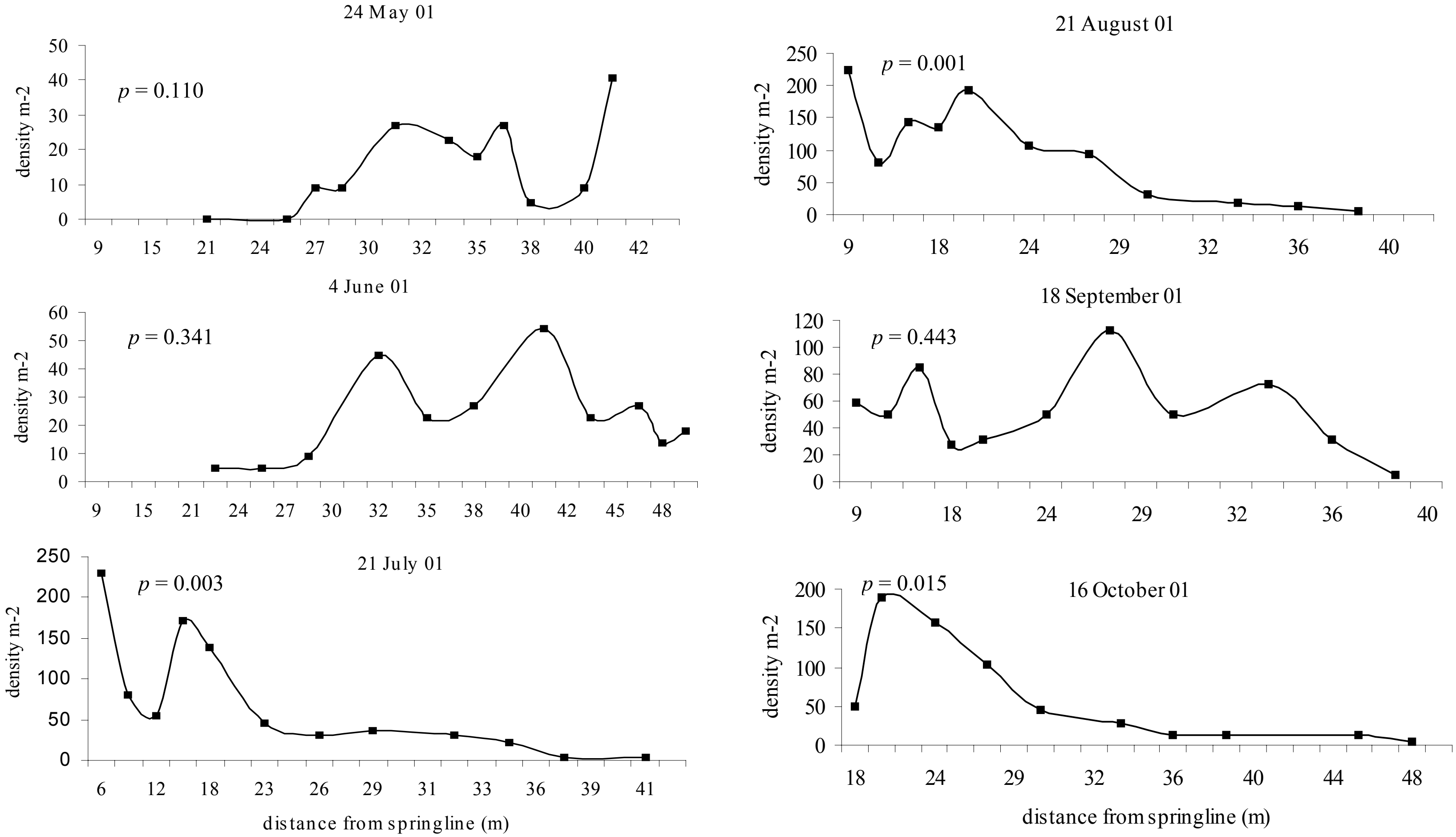


Figure 5.6. *Arachnoides placenta*. Mean density m^{-2} of recruits and juveniles (<10mm), from the upper shore Pallarenda Beach, May to July 2001. *P*-values display effect of distance from springline on density m^{-2}

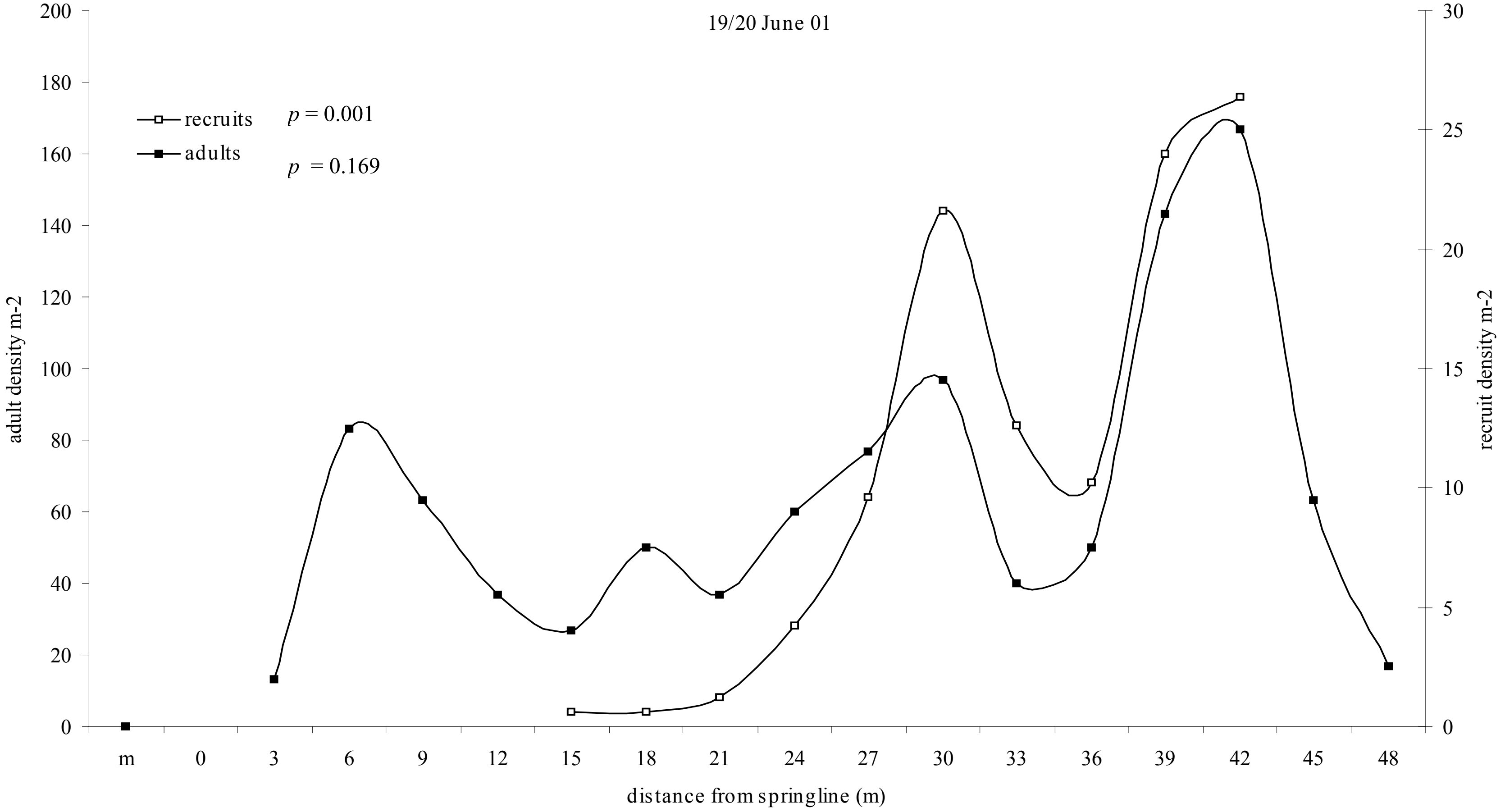


Figure 5.7. *Arachnoides placenta*. Mean density m^{-2} of recruits and juveniles (<10mm), from the upper shore Bucasia Beach creek end, June 2001. P-values display effect of distance from springline on adult and recruit density m^{-2}

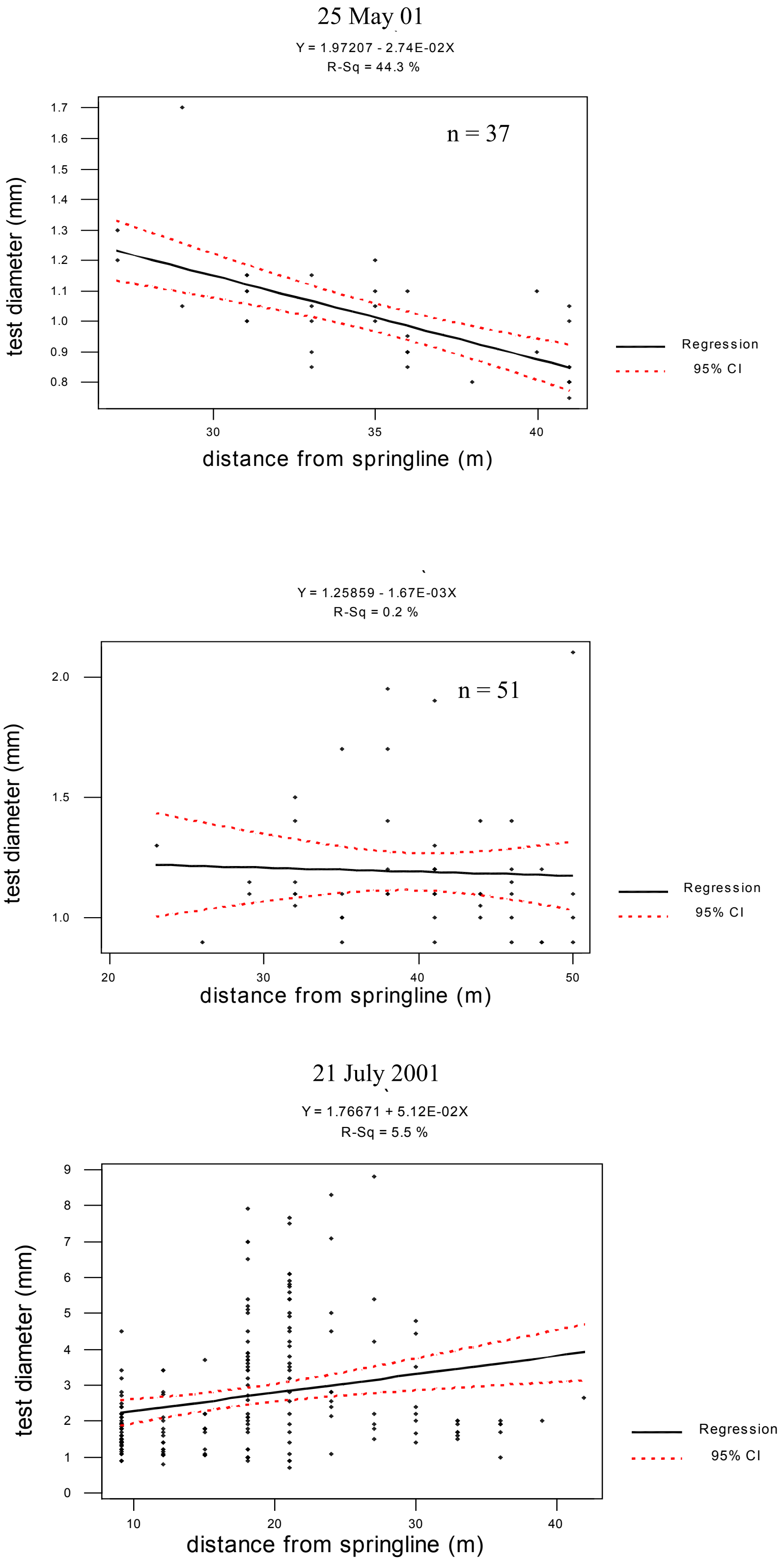


Figure 5.8. *Arachnoides placenta*. Regression plots of recruit and juvenile test diameter versus distance downshore, Pallarenda Beach, May – July 2001. *P*-values display effect of distance from upper shore on density m^{-2}

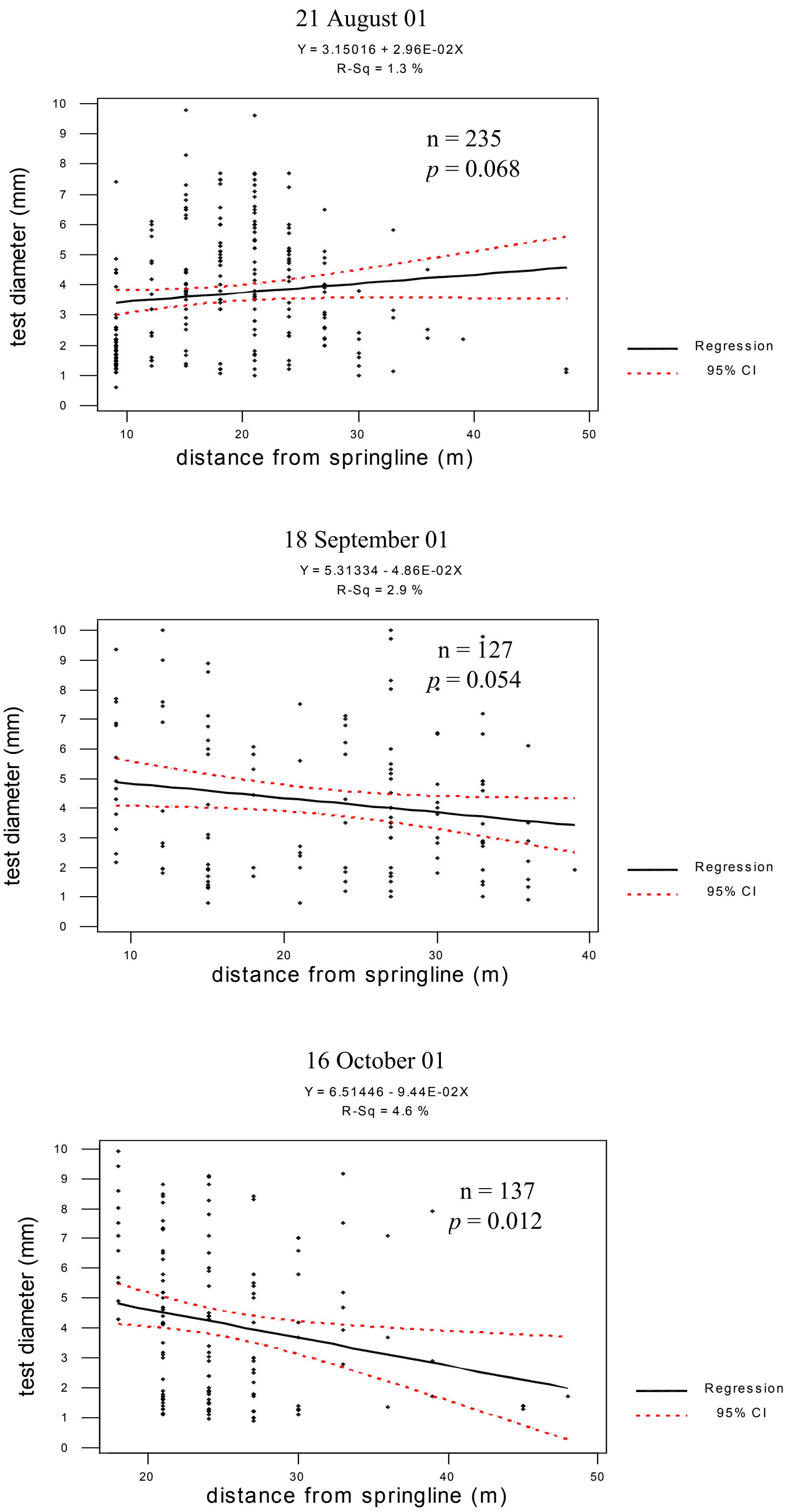


Figure 5.9. *Arachnoides placenta*. Regression plots of recruit and juvenile test diameter versus distance downshore, Pallarenda Beach, August - October 2001. *P*-values display effect of distance from upper shore on density m^{-2}

5.4. Discussion

The results presented indicate that major recruitment of *A. placenta* at Pallarenda Beach appears to occur between April and June-July, although minor recruitment episodes were apparent during the remainder of the year as newly settled recruits were found in other months, often as isolated individuals. The yearly unimodal structure of recruits confirms that only one effective spawning occurs over a short period. Sea surface temperatures at Pallarenda Beach from April to July are either decreasing or at their lowest for the time of year (from approximately 28^{o}C to 22 ^{o}C), indicating that decreasing cooler temperatures as opposed to warmer temperatures provide optimal conditions for *A. placenta* recruitment. By comparison, the appearance of a number of temperate echinoid larvae often coincides with warmer sea water temperatures and/or an end of spring bloom of algae and dinoflagellates which provide an increased source of larval food. These conditions are optimal for the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus* (Miller and Emlet 1997) and *Paracentrotus lividus* (Pedrotti 1993).

The rate of larval development is an adaptation subject to selection. The faster the development the shorter the period of time larvae are at risk to predation. Shorter planktonic life also results in greater number of recruits/g spawn (Ebert 1975). According to Feliciano 1933 and Aung (1975), *A. placenta* larvae spend approximately 14 days in the water column prior to settlement, and a minimum of seven days are required for metamorphosis (Chen and Chen 1992), amounting to a period of approximately 3 weeks from the first occurrence of spawning. Larvae of the sand dollar *Dendraster excentricus* in northeast America also do not occur for longer than 14 days in the plankton (Emlet 1986). In comparison to other echinoids, *A. placenta* and *D. excentricus* larvae spend a relatively short time in the plankton. Larvae of the sea urchin *Strongylocentrotus purpuratus* require at least 45 days in the laboratory to reach competency and larval development of *Strongylocentrotus droebachiensis* (Raymond 1985) and the sea urchin *Evenchinus chloroticus* in New Zealand (Walker 1984) both require a period of 30 - 60 days in the plankton prior to settlement. In culture, larvae of the tropical sea urchin *Tetrapygus niger* has a planktonic interval of 94 – 120 days (Fuentes and Barros 2000). Over this period in their natural habitat, the larvae have the potential to be transported hundreds of kilometres in near shore currents. An extended planktotrophic period may also increase the mortality rate by predation and hence the potential for dispersion (Pedrotti 1993). With a shorter larval phase, *A. placenta* and *D. excentricus* larvae may not be transported as far from their site of origin, particularly as most observed populations exist within bays that are moderately protected from currents and wave action and may be subject to less predation.

At Pallarenda Beach from April to June 2002 onwards, the occurrence of significant numbers of small recruits (0.5 – 0.8mm test diameter), approximately three weeks after the start of the major spawning period from March to May 2002 (fig. 5.3), demonstrates a clear annual recruitment cycle dependant on the timing of gametogenesis. This clear relationship, combined with a relatively shorter larval period, appears also to suggest there is little or no reason to assume that larvae have arrived by sea water currents from other shores along the north Queensland coast that are populated by other *A. placenta* populations. Prior to reaching 10mm, recruits are of a pale straw colour from which they progressively become darker individuals. Smaller individuals most likely acquire darker pigmentation with greater food consumption and the paler colour at the juvenile stage may provide a means of camouflage within the sand grains from predators like the crab *Matuta linaris* which were found buried within wet sediment of the beach terrace. Individuals of the heart urchin *Echinocardium cordatum* are also of a pale colour up to one year of age from which time they become darker (Moore 1934c). The smallest newly settled recruit of the temperate and tropical sand dollar *Lovenia elongata* discovered by Ferber and Lawrence (1976) was 1mm in size.

There was no apparent latitudinal variation in the occurrence of the major recruitment period, as individuals 0.5 – 3 mm test diameter were also at their highest density within the sediment in March and June 2002 at Cape Hillsborough and Bucasia Beach. The absence of recruits <4mm in May at Mission Beach, possibly suggests a year of poor recruitment success, particularly as histological data suggest the species spawns between March and May 2002 (see chapter 4). The occurrence of smaller numbers of newly settled recruits in August through to October 2001 at Pallarenda Beach, beyond the major recruitment period, also correspond with the extended spawning period that occurs through the months of June, July and August 2001. These periods outside of major recruitment are highly variable in intensity. Lopez et *al*. (1998)

states a similar trend for the sea urchin *Paracentrotus lividus* on both geographical and spatial scales.

There was noticeable interannual variation in recruitment density between months of the major recruitment period at both Pallarenda Beach and Bucasia Beach. It is known that echinoids can feature low levels or even absence of recruitment during several year punctuated by episodic highs (Ebert 1983, Pearse and Hines 1987) for example, recruitment in the sea urchin *Strongylocentrotus droebachiensis* is temporally variable, in which there is no evidence of recruitment in some years (Raymond and Scheibling 1987). Small scale (of the order of thousands of metres) variation in recruitment is also documented for echinoids (Ebert 1983, Keesing et *al*. 1993).

The constantly shifting sand bars combined with the possibility of a greater number of storms or rough weather at Pallarenda Beach, may also have produced lower than normal numbers in 2002 through the burial and smothering of recruits by sediment. This would suggest the population of *A. placenta* at Pallarenda Beach is maintained by episodic recruitment events, rather than being dependent on migration of larger-sized forms. The lack of recruitment at Pallarenda Beach in May and July 2002 should be considered with caution however, as individuals of such a small and cryptic nature may well produce inconsistencies within data collected despite using precise sampling methods.

Most species of benthic marine invertebrates have been documented to suffer very high mortality within the first days to months of life after settlement (Gosselin and Qian 1997) and *Arachnoides placenta* appears to be no exception. A two- to three-fold decrease in recruit size classes smaller than 5mm test diameter was observed from August to October 2001 at Pallarenda Beach (fig 5.3). Thorson (1966) and Rumrill (1990) claim a 100-fold reduction in recruits is often possible during this period. Factors attributed to high post-settlement mortality or losses from a population include migration, predation, disease, storms and reduced salinities (Balch and Scheibling 2000). Predation is often assumed to be the single most important cause of early juvenile mortality (Thorson 1966). Known predators of larvae of the temperate sand dollar *Dendraster excentricus* include the mussel *Mytilus edulis* (Cowden et *al*. 1984) which feeds on the planktonic larvae, and the intertidal crustacean *Leptochelia*, which prey upon recently metamorphosed individuals of the same species (Rumrill et *al*.1985).

At Pallarenda Beach the primary predator of *A. placenta* is most probably the crab *Matuta linaris*. In captivity the species was observed to break off edges of the test of adult *A. placenta* with relative ease (pers. obs.) and was observed in high abundance at Pallarenda Beach. Decapod crustacean predators have been recognised as the major source of predation in a number of marine invertebrate species including echinoids (Thorson 1966, Gosselin and Qian 1997). The potentially large impact of decapods results from their general high abundances, broad distributions in both intertidal and subtidal habitats, high motility, their ability to crush protective structures and their need to process large amounts of food (Gosselin and Qian 1997). A reduced number of recruits in the months of November 2001 through to January 2002 at Pallarenda Beach may also be the result of increasing sea water temperatures during this time of year resulting in the mortality of smaller individuals. In these months there was also a considerable decrease in the number of day time low tides, which may have contributed to such a reduction, possibly because the exposure of individuals at low tide plays an important role in the survival through increased feeding that may occur at low tide. This would however require further investigation.

The density of recruits downshore at Pallarenda Beach in 2001 (fig 5.6) demonstrate a clear patchy distribution, however a significant decrease in recruit density downshore was apparent in three out of six months of sampling ($p = < 0.05$). Recruits, like adults, may have a preference for wet areas of medium grain sediment, which account for localised distributions on temporal and spatial scales. The distribution of recruits at Bucasia Beach creek end followed a very similar pattern to that of adults downshore (fig. 5.7), indicating the possibility that larvae have a preference for adult associated sand. Adults of the sand dollar *Dendraster excentricus* produce a chemical cue, (possibly a small peptide) which is sequestered into the sand and remains stable for seven weeks (Highsmith 1982, Burke 1984), which causes larvae to become competent to metamorphose in 4 –6 weeks (Burke 1984). The preferential settlement of *D. excentricus* larvae near adults results in the increased larval and juvenile survival, particularly from predators such as the tube building tanaeid crustacean *Leptochelia dubia* which are excluded from sand dollar beds by the sediment reworking activities of adults (Highsmith 1982). A chemical peptide released into the sand by adult *A. placenta* may account for the similar adult-recruit distribution pattern at Bucasia Beach, however there was no strong evidence at other sites to suggest that larvae are attracted to adult sand dollar beds. Recruits were not always found with adults, and were absent from the upper shore at all sites, unlike adults, which were found across the entire stretch of the intertidal shore, in groups or as isolated individuals. The upper shore at all sites comprised a very abundant number of juveniles of the bivalve *Paphies altenae* (family Mesodesmatidae), commonly known as pippi's, combined with very wet coarse sediment that contained large amounts of shell fragments. This type of substrate may well have not been suitable for the settlement of *A. placenta* larvae due to the grain size of the sediment or the presence of *P. altenae* and requires further investigation. Another reason for the absence of recruits from the upper shore of most beaches is that the coarse sand that exists there may not be suitable for successful larval settlement. The sand dollar *Lovenia elongata* prefers sediments ranging from medium to fine grain size, which are also suitable for larval settlement. Coarse sediment produced unsuccessful larval settlement in *L. elongata* (Ferber and Lawrence 1976).

In conclusion, it appears significant numbers of newly settled recruits occur within the sediment from March – May, which strongly correlates with the timing of the annual gametogenic cycle of adults. The density of recruits downshore at Pallarenda Beach in 2001 demonstrate a clear patchy distribution, however a significant decrease in recruit density downshore was apparent in three out of six months of sampling. Newly settled recruits prefer the middle to lower section of the beach terrace until a size of around 10mm is reached, in which individuals show a preference for the inhabiting the upper –middle section of the beach terrace. Such size-related positions on the beach terrace point to optimal grain-size preference possibly related to feeding and movement. There does not appear to be an adult-larval attraction during settlement.

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