Studies on the biology of three species of sea urchin (Echinodermata : Echinoidea), on the South African east coast.

by

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" On all these shores there are echoes of past and future; of the flow of time, obliterating yet containing all that has gone before; of the sea's eternal rythms - the tides, the beat of surf, the pressing rivers of the currents - shaping, changing, dominating; of the stream of life, flowing as inexorably as any ocean current, from past to unknown future."

Rachel Carson - The Edge of the Sea -

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This thesis represents original work by the author and has not been submitted in any form to another University. Where use was made of the work of others it has been duly acknowledged in the text.

ABSTRACT.

Ten species of shallow water echinoid are found on the subtropical east coast of South Africa. Although their distributions are patchy, the most common species, *Echinometra mathaei*, *Stomopneustes variolaris* and *Diadema savignyi*, are nontheless conspicuous components of intertidal communities on this coast. As little was known about these three species, the overall intention of this study was to provide some fundemental information on their biology and ecology. For the purposes of achieving this aim a life history approach was adopted, where the relative investments by each species in growth, maintenance and reproduction were investigated and compared. These patterns of investment were then related to the habitat occupied by each species, in an attempt to identify the selective forces which may have been implicated in shaping their life histories.

It was apparent from the results of investigations conducted between January 1991 and June 1993 that there were distinct differences in the patterns of investment in growth, maintenance and reproduction between the three species. The life history of *S. variolaris*, which occupied exposed habitats in the lower intertidal, was characterised by a large investment in maintenance, lower reproductive output, slower growth and a longer lifespan, relative to the other two species. In contrast, *D. savignyi*, which inhabited less exposed mid-shore pools, had a relatively higher reproductive output, more rapid growth, a smaller investment in maintenance and a shorter lifespan. While selection in *S. variolaris* and *D. savignyi* appears to favour survival and reproduction respectively, the life history of *E. mathaei*, a

species which also occupies mid-shore pools, was balanced between these two extremes, allocating sufficient resources to maintenance to permit tolerance of harsh physical conditions while still making a moderate investment in reproduction over a lifespan of intermediate duration.

The predictions generated by the r-K selection and "bet hedging" theories of life history evolution, were applied in the process of speculating on the selective forces which may have shaped these life histories. However, it was found that neither set of predictions and associated selective forces could adequately explain the observed life histories. Rather, it seemed that the life histories of the three species represented evolved responses to the direct and indirect effects of exposure to wave action and sand movements which dominate the intertidal environment on the South African east coast. In the exposed lower intertidal, unpredictable recruitment, drag and impact forces associated with wave action, which impose limits to body size and necessitate a large investment in maintenance to ensure survival, select for slow growth, low reproductive output and high longevity. In contrast reproduction and growth of species occupying the more sheltered mid-shore pool habitats would be less effected by the demands of maintenance investment or limits to body size. In addition predictable recruitment in the mid-shore, would obviate the need for long life in order to ensure a contribution to future generations.

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CONTENTS.

Page

LIST OF TABLES.

LIST OF FIGURES.

Page

LIST OF PLATES.

Chapter 1. Introduction.

Southern Africa has been endowed with a rich echinoderm fauna, with over 400 species currently known from southern African waters. The class Echinoidea is represented by 59 species, 31 of which have Indo-Pacific distributions, while 23 are endemic to the southern African region (Thandar 1989). Ten species of regular sea urchins have been found inhabiting the rocky intertidal of the east coast, of which *Echinometra mathaei*, *Stomopneustes variolaris* and *Diadema savignyi* are the most common. Yet, prior to 1990, all that was known of east coast intertidal echinoids was derived by inference from studies of the same or closely related species in other parts of their Indo-Pacific range.

Although there are no formal sea urchin fisheries on the South African east coast, sea urchins are heavily exploited in places for the curio trade, for food and by practitioners of traditional medicine. With the combined influence of increasing development for tourism and growing rural subsistence populations, it is inevitable that the intertidal region of the east coast will be subject to increased exploitation and habitat degradation in the future. The overall aim of this study was therefore, to acquire the fundamental information necessary should the need for management of these sea urchins arise in the future.

The east, or Natal coast, of southern Africa (hatched area, Fig. 1.1), between Maputo and East London, experiences subtropical conditions where mean annual sea temperatures vary from 19°C to 25°C. The subtropical nature of this coast is the result of the

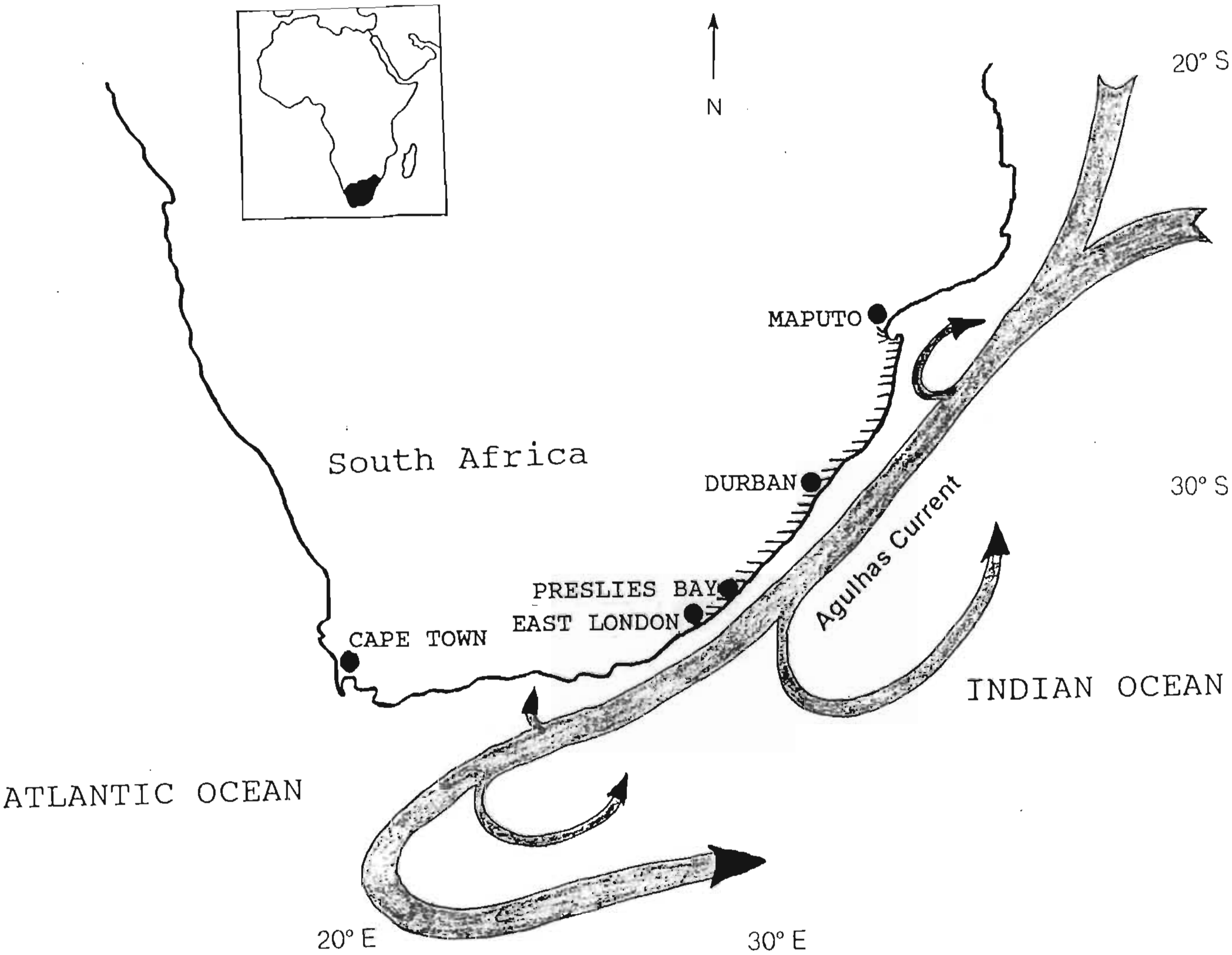


Figure 1.1 Southern Africa, and the location of the warm Agulhas current in relation to the subtropical east coast.

Agulhas current, a western boundary current which originates from the warm tropical equatorial drift, and flows south along the edge of the continental shelf. As the continental shelf broadens in the south, near East London, and the Agulhas current moves further offshore, intrusions of cooler counter-currents (Harris 1961) gain dominance. The consequent change in sea temperatures is marked by a change in the nature of the shore fauna, with Indo-Pacific forms giving way to warm temperate and endemic South African species (Stephenson 1939).

Most of the east coast consists of sandy beaches interspersed by stretches of rocky platforms or shelves and prominent rock outcrops. The east coast of South Africa is extremely exposed as no large offshore islands or substantial reefs are present to moderate the force of ocean swells. The prevailing swell is from the south and has a breaking interval of 10-12 seconds (Harris 1961), so the inshore is subject to a continuous surf. It has been reported (Duncan 1975) that 50% of the swells experienced off Durban are approximately 3.5m in height, consequently tidal range is frequently influenced by swell height. On the east coast there is a semi-diurnal tidal cycle with an average height of 1.31m and a 0.3-2.1m range (Berry 1978). The high swells and vigorous wave action are responsible for the considerable sand movements observed on this coast. The deposition and removal of sand results in marked changes in beach profiles, and the sanding up of reefs and intertidal pools. Furthermore, this essentially unpredictable sand movement has the effect of scouring organisms off the intertidal rocks or subjecting them to periods of burial.

On the Natal coast, particularly the region south of Durban (Fig. 1.1), S. variolaris, E. mathaei and D. savignyi are close to the southern limits of their Indo-Pacific distributional ranges. This fact combined with exposure to heavy wave action and the unpredictable effects of sand movements, creates a set of potentially stressful circumstances for these intertidal sea urchins. It was therefore of interest, as a secondary and complementary aim, to investigate the variation in life histories which had evolved among the three species of sea urchin on this exposed coast.

An organism's life history is "a set of coadapted traits designed, by natural selection, to solve particular ecological problems" (Stearns 1976). Key life history traits are considered to be: brood size, size of young, age distribution of reproductive effort, the interaction of reproductive effort with adult mortality (Stearns 1976), and patterns of growth and development (Begon, Harper & Townsend 1990). A general theoretical problem which has preoccupied plant and animal ecologists with considerable persistence, has been the attempt to predict which combinations of traits will evolve in organisms occupying particular environments. In seeking to formulate a predictive classification, or as Southwood (1977) describes it, "an ecological periodic table", a number of predictive theories have been postulated e.g. those of, Greenslade (1972), Grime (1977), Southwood (1977), Sibly & Calow (1985), and Hildrew & Townsend (1987). However, the two theories of life history evolution which appear to have had the widest acceptance and thus, perhaps, possess greatest explanatory powers are: the deterministic, r-K selection theory (MacArthur & Wilson

1967) and the stochastic or bet-hedging concept (Murphy 1968, Schaffer 1974, Stearns 1976).

As originally defined r-K theory was proposed as a density-dependent model of natural selection, used to explain intraspecific variation in life histories (MacArthur & Wilson 1967). However, Pianka (1970) suggested that it could explain differences between species, and presented a table of correlates of r and K-selection which has been widely used, and misused (Boyce 1984). r-K theory emphasizes the importance of biotic interactions with associated density-dependent effects and environmental stability in favouring selection for longevity. On the other arm of this dichotomy, density-independent effects arising from abiotic forces in unpredictable environments, favour selection for fecundity. However, it is indisputable that all environments experience fluctuations and random mortality affects every population. Murphy (1968) and Schaffer (1974) focused on this, and Stearns (1976), in describing the "bet hedging" concept, predicted that variation in life history traits arose from fluctuations in prereproductive survival relative to that of adults. This concept suggested that environments which conferred predictable juvenile survival, would favour adults which are fast growing, have high fecundity and are short lived, while environments where juvenile survival was less predictable would favour slower growth, lower fecundity but longer lifespan.

Despite its historical position as the bastion of life history theory, there is considerable debate over the utility of the r-K theory, particularly because its basic assumptions and predictions are essentially untestable (Stearns 1976, Ebert 1982). In contrast, general opinion in recent years appears to have favoured the "bet hedging" concept, as the inherent predictions can be tested. However, regardless of the selective forces evoked to account for observed life history characteristics, it is accepted that selection is linked to energy budgets (Cody 1966, Gadgil & Bossert 1970, Ebert 1982). In other words, organisms have limited resources which they have to allocate between the competing demands of growth, reproduction and maintenance - Gadgil and Bossert's (1970) allocation model.

Ebert (1975) showed that sea urchins with rapid growth also had high mortality rates, and proposed that this relationship was the result of the way in which particular species allocate resources. Species which grow rapidly, allocate a large proportion of resources to growth and reproduction; fewer resources are thus available for maintenance and the promotion of survival mechanisms, consequently, mortality rates are high. Ebert (1982) took this idea further and in a very neat study, showed that annual survival rates in 17 species of sea urchin were related to the relative allocation of resources to maintenance (body wall) and the degree of exposure to the surf.

Gadgil & Bossert's (1970) allocation model placed the traits on which selection can act into three categories, those of growth, maintenance and reproduction. For the purposes of achieving the aims of this study, I adopted these three categories and investigated aspects of each. While complete energy budgets were not constructed, the relative allocation by the three species to each category, were compared, using indices which I felt adequately reflected a species investment in a trait.

The approach in this study was, therefore, to determine whether the three species showed differences in their relative investments in growth, maintenance and reproduction, and then, by relating these patterns of investment to the habitat occupied by each species, speculate on the selective forces which might have been implicated in shaping their life histories.

Chapter 2. Species and study sites.

2.1 Species.

Stomopneustes variolaris, Echinometra mathaei and Diadema savignyi are the most common of the ten species of intertidal echinoid found on the South African east coast. However, the distribution of their populations along this coast is patchy, populations are small and densities highly variable. These three species were chosen as the focus of this study for two reasons. Firstly, although ten species of sea urchin were found in the intertidal on this coast, populations of all other species were either too small for a study of this nature, or they were ephemeral as in Tripneustes gratilla and Toxopneustes pileolus. Secondly, while these three species have been studied (E. mathaei extensively) in other parts of their range, with the exception of a study of the reproduction and habitat requirements of S. variolaris (Drummond 1991a, 1991b, 1993), little is known about their biology and ecology on this coast.

2.1.1 Stomopneustes variolaris (Lamarck, 1816).

S. variolaris is the only member of the family Stomechinidae, which along with seven other families of regular echinoids form the superorder Echinacea (Durham 1966). Alternatively, Smith (1984) divides the cohort Echinacea into the superorders Stirodonta and Camarodonta, and places the family Stomechinidae into the superorder Stirodonta. S. variolaris is characterised by the absence of a complete bridge across the V-shaped space at the upper end of the pyramids of the Aristotle's lantern, and by doubly compound ambulacral plates (Clarke & Rowe 1971). It is a long spined sea urchin, purple-black in colour, and may reach test diameters of 140mm. S. variolaris has a wide Indo-Pacific distribution, and on the South African coast is commonly found inhabiting the lower intertidal of rocky shores between Maputo and Preslies Bay (Fig. 1.1) (Marshall, Hodgson & Pretorius 1992).

2.1.2 Echinometra mathaei (de Blainville, 1825).

E. mathaei is a member of the family Echinometridae which is placed in the superorder Echinacea by Durham (1966), but Smith (1984), puts the family Echinometridae into the superorder Camarodonta, cohort Echinacea. This species has short, slender spines which are circular in cross section. The test is oval in shape with the long axis passing through ambulacrum 1 and interambulacrum 3 (Clarke & Rowe 1971). Test and spine colour is very variable, ranging from black to grey, but can be purple, brown or green (Kelso 1971). Uehara & Shingaki (1985) distinguished four distinct types based on morphological, embryological and karyotype studies, and Nishihira, Sato, Arakaki & Tsuchiya (1991) showed that these four types had different habitat preferences on Okinawan coral reefs. On the South African east coast, most E. mathaei were Type C - variable in colour, but generally dark brown to purple-black, no white tip to the spines but the rings at the base of the spines were white. Although occasional individuals of Types A, B and D were present there was no evidence for different habitat preferences as all four types were restricted to the mid-shore. Like S. variolaris, E. mathaei has a broad Indo-Pacific distribution, and on the South African coast is restricted to the mid-shore of the rocky intertidal between Maputo and Morgan Bay, near East London (Fig. 1.1) (Marshall, Hodgson & Pretorius 1992).

2.1.3 Diadema savignyi (Michelin 1845).

D. savignyi is a member of the large family Diadematidae which Durham (1966) placed in the superorder Diadematacea. Smith (1984) removed the echinothuroids from this group and raised the Diadematacea to cohort level. Considerable confusion has surrounded the identification and thus the distribution records of the Indo-Pacific Diadema species, setosum and savignyi. Much of the debate has focused on Diadema in the Gulf of Suez and is summarized by Clark & Owen (1965), Clark (1966) and Pearse (1970). In the Gulf of Suez, as in other parts of its range, the main characters used to distinguish the two species are the shape of the tridentate pedicellariae and the colour patterns, particularly the presence of five white spots on the interambulacrals. However, neither of these characters appears to be consistent between populations (Pearse 1970). Mortenson (1940) has suggested that the two forms may hybridize, therefore accounting for the lack of distinct identifying features. In southern Africa, Clark & Courtman-Stock (1976) identify D. savignyi by the blue ring around the apical system and the presence of blue lines along the interambulacrals, but white spots are absent or inconspicuous. There is no ring on the anal cone and the tridentate pedicellariae have broad valves, (length:median breadth ca. 4.5:1). D. setosum in contrast, has an orange ring on the anal cone, conspicuous white spots on the interambulacrals and the blue lines are broken up into spots. The tridentate pedicellariae have narrow valves, (length:median breadth ca. 15-20:1). I assessed populations of Diadema sp. at three sites on the lower east coast. When the colour patterns of individuals in the three populations were examined using the criteria of Clark & Courtman-Stock (1976), some variation from the expected patterns was observed (Table 2.1).

Table 2.1 The colour patterns observed in three populations of *Diadema* sp. on the east coast of South Africa. n = 171

1) Blue ring around apical system and double blue lines along interambulacrals	153
2) Dotted blue lines, orange ring on anal cone, white spots on interambulacrals	1
3) Blue ring around apical system and blue lines along interambulacrals and five conspicuous white spots on interambulacrals	5
4) No blue lines, but five conspicuous white spots on interambulacrals	7
5) Blue ring around apical system and blue lines along interambulacrals; orange ring on anal cone	5

Furthermore, no tridentate pedicellariae with narrow valves (Clark & Courtman-Stock 1976, Fig. 246) were observed in any individuals examined. All tridentate pedicellariae observed had rounded club shaped valves where the length to median breadth ratio never exceeded 6:1 ($\bar{x}$ = 3.2:1 SE$\pm$ 0.19 n=35). Based on the observations reported in Table 2.1, I regarded individuals which had a distinct blue ring around the apical system and solid blue lines along the interambulacrals as *D. savignyi*, those with orange rings on their anal cones and dotted blue lines, as *D. setosum* and the others as hybrids or mixed forms. McClanahan (1988) had no difficulty in distinguishing between *D. savignyi* and *D. setosum* in East Africa using similar criteria, but observed that hybrid forms only rarely occurred. In contrast, of the three populations examined on the Natal coast ca 10% were mixed forms.

D. savignyi is distributed throughout the Indo-Pacific and on the South African coast is found in sheltered subtidal habitats in the north, Kosi bay and Sodwana bay (Fig. 2.1). However, over the remainder of the east coast to Preslies bay (Fig. 1.1) (Marshall, Hodgson & Pretorius 1992), it appears to be restricted to mid-shore pools in the rocky intertidal.

2.2 Study sites.

The study sites chosen were those which it was felt best reflected the typical habitat of each species on the east coast. In addition, the abundance of each species population had to be able to support two and a half years of monthly sampling and the sites close enough to visit without excessive travelling.

Samples for dissection and reproductive studies were collected as follows: S. variolaris from Oslo beach, E. mathaei from Ramsgate and D. savignyi from Isipingo (Fig. 2.1). Translocations, sampling for food and feeding investigations, experiments on movement and attachment site preferences and other observations were made on other populations of the same species at these sites. In addition, occasional observations were made at Sheffield beach, Hibberdene, Treasure beach and Chaka's Rock (Fig. 2.1).

The zonation patterns, climatic conditions, fauna and flora, topography and geology of the rocky intertidal of the subtropical east coast, has been comprehensively described in Eyre & Stephenson (1938), Macnae (1962), Jackson (1975) and Branch & Branch (1981). The study sites of the present study are described with respect to their location on the east coast, general topography and human

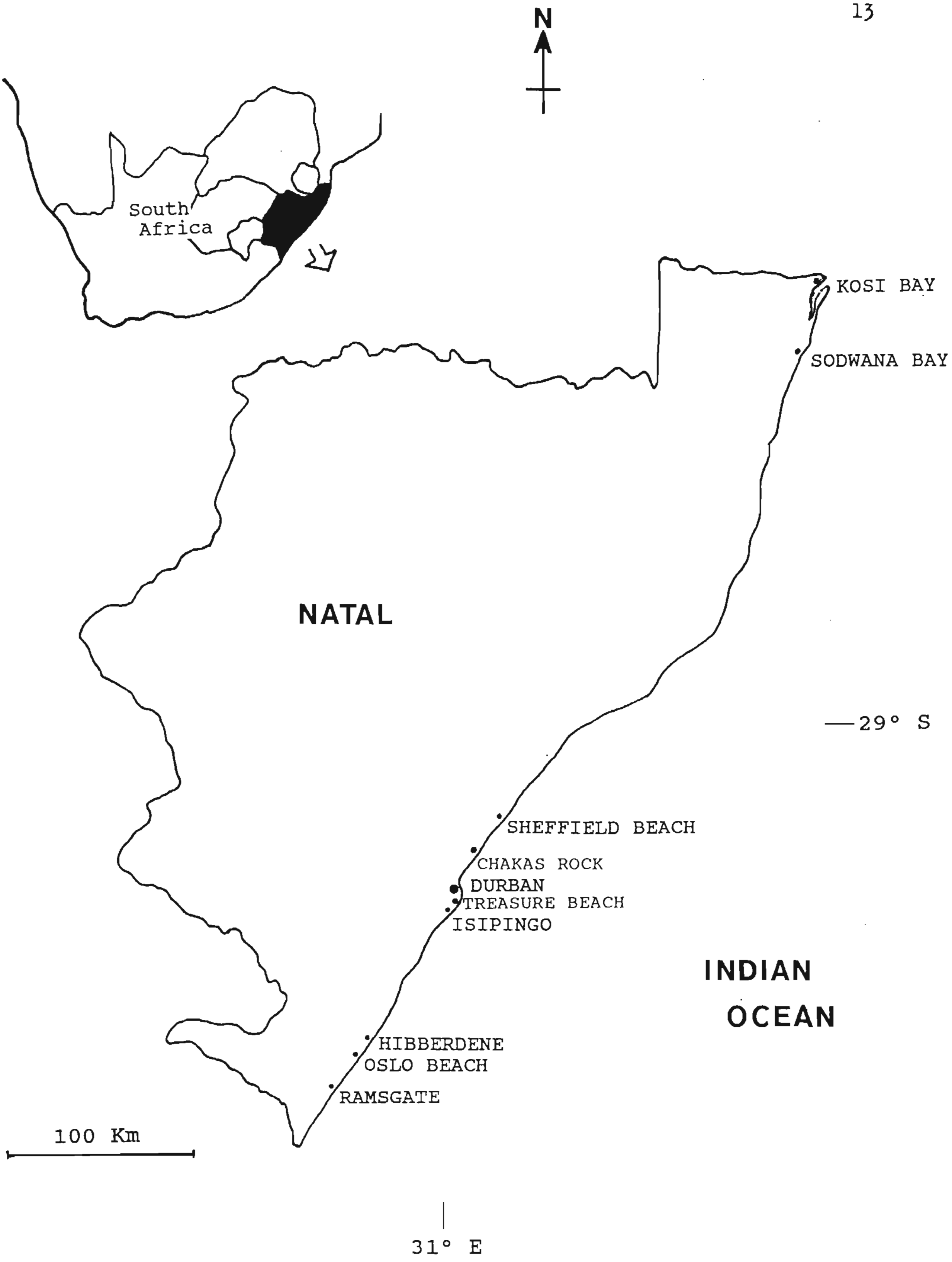


Figure 2.1 The South African east coast showing the sites at which experiments, sampling and observations were carried out during this study.

impact. The algal communities of each site are described in Chapter 5 and the degree of exposure to wave action is quantified in Chapter 4.

2.2.1 Oslo beach. (30°46.5'S, 30°27'E)

This site is located midway between the Mbango and Boboyi river mouths, 115kms south of Durban (Fig. 2.1). It was chosen because tourist facilities were absent and, as only scattered private residences adjoined the beach, recreational use was not excessive. With the exception of occasional anglers and bait collectors, the site remained essentially undisturbed for the duration of the study.

The population of S. variolaris was large and distributed over ca 280m^2 of a rocky platform which dominated the intertidal at this site. Most of the S. variolaris occupied shallow hollows and cracks in the rock of the lower reaches of the shore. A few large pools are located in the mid-shore, and the upper portion of the shore is composed of small boulders and ledges which give way to a coarse grained sandy beach. This beach was subject to marked variations in profile as a result of the deposition and removal of sand.

The intertidal fauna and flora at this site is distributed in typical east coast zones (Stephenson 1943, Branch & Branch 1981) where a well developed oyster belt (Saccostrea cucullata) separates the Littorina zone from the barnacle zone. S. variolaris was found among the Zoanthidea, brown mussels (Perna perna) and corralline algae which characterise the lower Balanoid zone. Occasional S.

variolaris individuals inhabited rock crevices in the algal dominated infratidal zone.

2.2.2 Ramsgate (30°50'S, 30°30'E)

This site is located 200m south of the Mvutshini river mouth, 135kms south of Durban (Fig. 2.1). Although the site initially appeared to be infrequently visited, I realised near the end of the study that aquarists and casual harvesters were active in this area. While their targets were generally the fish in the rock pools and mussels, sea urchins were also taken for consumption.

The intertidal region at this site is narrow and consists of numerous shallow pools (<50cm deep) in the upper shore, while in the mid-shore there are deeper (100-200cm) pools among large sandstone outcrops. These outcrops dominate the lower intertidal and thus significantly reduce the effect of wave action on the mid and upper shore. The rocky shore merges directly with the coastal dune vegetation. Because of the absence of a sandy beach above the rocky shore, I had initially thought that the intertidal would remain relatively sand-free. However, it became apparent that longshore movement of sand resulted in considerable deposition of sand at this site.

S. variolaris, E. mathaei and D. savignyi were all present at this site, as well as Tripneustes gratilla, Diadema setosum and mixed forms of Diadema spp. The occasional Salmacis bicolor and Echinothrix calamaris were also observed. S. variolaris inhabited the high energy lower shore, while all other species were restricted to the deep mid-shore pools. The intertidal fauna and flora was represented by typical east coast species, though the distributional zones were somewhat compacted because of the narrowness of the intertidal region. The oyster belt in particular was not as clearly defined as at Oslo beach or Isipingo.

2.2.3 Isipingo (30°0'S, 30°57'E)

This site is situated 500m south of the Umlaas and Isipingo river mouths, 18kms south of Durban (Fig. 2.1). Isipingo beach was heavily used by anglers and the rocky intertidal exploited by bait collectors, aquarists, casual harvesters and practitioners of traditional medicine. However, this was the only population of *D. savignyi* on the south coast which was large enough, to support the monthly sampling required by the study. Fortunately, *D. savignyi* appeared not to be the focus of any of the users of this beach.

The intertidal region at Isipingo was divided into three distinct shelves or platforms. The lower shelf was extremely exposed and the community present was dominated by a dense turf of coralline algae and *Hypnea spicifera*. The middle platform was highly eroded, with numerous deep pools, some very large (>20m^2). The *D. savignyi* population studied inhabited the largest of these pools. Also present in this pool were large numbers of *Tripneustes gratilla*, numerous *E. mathaei* occupying burrows, *Toxopneustes pileolus*, *Echinothrix calmaris* and *D. setosum* and hybrid forms of *Diadema* spp. A large population of *Echinostrephus molaris* occupied burrows in the unconsolidated sandstone of the lowest regions of the middle platform. The upper platform merged with the coastal dune vegetation. Sand deposition and removal was considerable and unpredictable.

Chapter 3. Reproduction.

Introduction.

The relationship between an organism's reproductive strategy and its habitat is perhaps central to understanding how life history functions to allow persistence in the present environment. As the fitness of an organism is determined by its contribution to the future of the species population, reproduction could therefore be viewed as the expression of the merit of an organism's life history.

Reproduction in sea urchins has been extensively studied since the beginning of this century (Orton 1914, Fox 1924, Stott 1931), but with greatest intensity over the last 20-30 years. A consequence of this quite considerable research effort is that many sound generalizations can be made about reproduction in echinoids, particularly with respect to gametogenic cycles. The gametogenic cycles and spawning periodicity of shallow water echinoids has been studied on the coasts of all the worlds major oceans. Some of the more important of these studies include: Stott (1931), Moore (1934), Yoshida (1952), Fuji (1960), Giese (1961), Holland (1967), Chatlynne (1969), Pearse (1969), Gonor (1972), Gonor (1973a, 1973b) and Cameron (1986). These particular studies illustrate some of the central features of the evolution in approach and methodology which has occurred in the study of echinoid reproduction. Early studies investigated reproductive cycles by monitoring the increases and decreases in gonad size (Moore 1934), or recorded the presence or absence of mature gametes by microscopic examination (Harvey 1956, Wilson

1940 in Boolootian 1966). Yoshida (1952), recognized the presence of progressive stages in the gametogenic cycle and constructed the first scheme categorizing these stages. This nine stage scheme was later refined by Fuji (1960) into five stages which described the cellular processes of most, if not all, echinoid gametogenic cycles. Fertilization tests with ripe gametes allowed the spawning period to be more closely predicted (Giese 1961). The oocyte/ova size frequency method (Pearse 1969), and the grouping of oocytes (Gonor 1973a, 1973b), and testes (O'Connor, Riley, Lefebvre & Bloom 1978) into progressive developmental stages, introduced a quantitative approach to the study of echinoid reproduction. Gonor (1972) examined the assumptions of the gonad index method and cautioned the use of this method without first examining the effects of body size (mass) on gonad size. In recent years the research focus appears to have moved away from single species or single population studies (Giese, Krishnaswamy, Vasu & Lawrence 1964, Pillay 1971), towards comparative investigations (Lessios 1981, Laegdsgaard, Byrne & Anderson 1991). A further trend which appears to have gained momentum in the last 10 years is that of ultrastructural investigations; for example, studies by Nicotra & Serafino (1988) and Mita & Nakamura (1992) on spermatozoan structure and spermiogenesis, have added a different dimension to the knowledge of echinoid reproduction.

Interest in the influence of environmental factors on reproductive cycles was stimulated by Ortons' (1920) proposal that seasonal changes in sea temperature might control the timing of reproductive cycles in marine animals. Numerous studies have attempted to show that the reproductive cycles of echinoids at various localities are entrained to seasonal changes in sea temperature (reviewed by Giese & Pearse 1974, and Pearse & Cameron 1991). However, many of the conclusions rely heavily on correlational evidence, so essentially the role of sea temperature in controlling reproductive cycles remains enigmatic. Giese (1959) suggested that seasonal changes in photoperiod might serve to synchronize reproductive events in sea urchins. Pearse, Pearse and Davis (1986) confirmed this suggestion by showing experimentally that gametogenesis in Strongylocentrotus purpuratus is either enhanced by short days or inhibited by long days. However, the influence of this factor is clearly not universal among sea urchins, as Sakairi, Yamamoto, Ohtsu and Yoshida (1989) showed that gametogenesis in two Japanese species was not under photoperiodic control. Entrainment of gametogenic cycles to lunar rhythms has also been investigated (reviewed by Pearse 1975), but the results are largely inconclusive.

While there is no clear evidence for the control of gametogenic cycles by prevailing or changing food conditions, it has been suggested by Pearse (1969) that gametogenesis is not initiated until sufficient nutrient stores have accumulated. In addition, Chatlynne (1969) used histochemical techniques to show that termination of gametogenesis coincided with the depletion of lipid and glycogen stores in the accessory cells. However, regardless of a possible role in the regulation of gametogenic cycles, the quality and quantity of food available has been shown to affect gonad size and output (Lawrence 1975, Larson, Vadas, & Keser 1980, Nichols, Bishop & Sime 1985).

Members of the genus Echinometra are probably the most frequently studied Indo-Pacific echinoids. Reproduction in E. mathaei has been investigated in populations at Rottnest island, W.

Australia, (Pearse & Phillips 1968), Hawaii (Kelso 1971), the Gulf of Suez and the Red Sea (Pearse 1969), and Japan (Onada 1936, Yoshida 1952, Kobayashi 1969).
In the Australian, Hawaiian and Red Sea populations there was little gametogenic synchrony between individuals, and gonads containing numerous mature gametes could be found in all months of the year. This indicates that spawning in these populations was not a synchronized periodic event, but probably occurred continuously throughout the year. *E. mathaei* at Rottnest island is at, or close to, the southern limits of the range of this species, and continuous reproduction in this population may therefore be regarded as unusual. As Rottnest island lies at approximately the same latitude as the South African east coast it was of considerable interest to investigate the reproductive periodicity of a South African population of *E. mathaei*.

Although reproduction in the genus *Diadema* has been well documented (*D. setosum* Yoshida 1952, Pearse 1970, *D. mexicanum* Lessios 1981, *D. antillarum* Iliffe & Pearse 1982), there appears to be no information on reproduction in *D. savignyi*. From reports on the occurrence of *D. savignyi* it appears that this species is seldom found in abundant single species populations, occurring mostly as individuals or in small groups within populations of *D. setosum* (Pearse & Arch 1969). The apparent limited abundance, and perhaps the confusion regarding the distinctness of the two species (Clark & Owen 1965), might account for the lack of information on reproduction in *D. savignyi*. However, there have been numerous studies on reproduction of other members of this genus. For example, a Singapore population of *D. setosum* (Hori, Phang & Lam 1987), breeds throughout the year while spawning in Japanese and

Australian populations is restricted to the boreal and austral summers respectively (Stephenson 1934, Yoshida 1952). D. antillarum appears to fit the same pattern, with populations in the Virgin Islands and on the coast of Panama breeding continuously (Randall, Schroeder & Stark 1964, Lessios 1981), while reproduction in a south Florida population is restricted to the late autumn months, October-December (Bauer 1976). It was therefore predicted that D. savignyi on the South African coast would possess a distinct annual reproductive cycle with spawning occurring during the summer.

Reproduction in S. variolaris has been studied at Madras harbour on the S.E. coast of India (Giese et. al. 1964), the S.W. coast of India (Pillay 1971) and on the S.E. coast of South Africa (Drummond 1991b). The presence of ripe individuals throughout the year in the Madras harbour population suggests that S. variolaris breeds continuously at this locality. However higher gonad index values in March and April suggest a peak in reproductive activity in these months (Giese et al. 1964). The population on the south west coast of India has an annual cycle with an extended spawning period from September to April (Pillay 1971). Pearse (1968) predicted that S. variolaris would have more discrete periods of reproduction where it occurred further from the equator. The presence of a distinct annual cycle with a restricted spawning period (December - February) in a South African population of S. variolaris (Drummond 1991b) confirmed this prediction. Interannual comparisons achieved by the continued monitoring of the reproductive cycle in S. variolaris would serve to enhance the original data, in addition to permitting comparison with the other two species over the same time period.

My aims in conducting this comparative study of reproduction in S. variolaris, E. mathaei and D. savignyi were broad and had the following intentions:

1) to provide fundamental information on the reproductive biology of these species for use in management or conservation strategies,

2) to assess the relative investment in reproduction by the three species on the east coast of South Africa,

3) to compare reproductive periodicity in the three species across their Indo-Pacific ranges, and

4) to assess whether the results shed any further light on the influence of environmental factors on the periodicity of the reproductive cycles observed in the three species.

In this chapter the reproductive cycles of S. variolaris, E. mathaei and D. savignyi are investigated by the gonad index method and by histological analysis, and estimates of the annual reproductive output by the species are compared.

Materials and methods.

3.1 Analysis of the reproductive cycles.

3.1.1 Sampling.

Diadema savignyi

Reproduction in a population of D. savignyi at Isipingo Beach was studied from February 1991 to June 1993. Details of the study site are given in Chapter 2. Samples of D. savignyi were collected at or soon after the new moon in each month, with the exception of August 1991 and March 1992 when high swells and excessively turbid water prevented collection. In January and December 1992 and January and March 1993 samples were collected at new moon and full moon. Each monthly sample was limited to between 6 and 10 urchins, as initially the population was small, and although it increased in abundance during the study, the numbers of individuals of suitable size were often limited. The sample size was also occasionally limited by high swells which caused the urchins to retreat into cryptic positions from which I could not extract them. A total of 163 urchins were collected during the study. All were of a sexually mature size, ranging in test diameter from 30 to 72mm, with a mean diameter of 47.60mm SE 0.07. The size range was wide as I wanted to acquire morphological data from the same samples to avoid further depleting the already limited population by sacrificing more animals than necessary. The wide size range meant that there was a significant difference in the monthly mean size in 6 of 30 samples.

Echinometra mathaei

Reproduction in this species was investigated from samples of urchins collected from Ramsgate between January 1991 and June

1993. A detailed description of the study site is given in Chapter 2. Monthly samples were collected at or close to full moon. No sample was collected in October 1992. As with D. savignyi limited abundance necessitated a small sample size of 4-8 urchins. A total of 179 urchins were collected during the study. All were of a sexually mature size, ranging in test length from 27 to 66mm with a mean length of 46.24mm SE 0.06. As a result of this wide size range there was a significant difference in monthly mean size in 5 of 28 samples.

Stomopneustes variolaris

A comprehensive study of reproduction in this species was performed at Oslo Beach during 1990 (Drummond 1991b). In order to confirm and enhance the data acquired during 1990 sampling of the Oslo Beach population continued until June 1993. Samples were collected at or close to full moon each month, no samples were collected in March and October 1992. A total of 192 urchins were collected between January 1991 and June 1993. During 1991 each sample consisted of 8 animals (Feb and May n=6) and in 1992 and 1993 the sample ranged from 5-10 animals. All urchins collected were of a sexually mature size and ranged in test diameter from 31 to 70mm with a mean diameter of 48.38mm SE 0.06.

3.1.2 Determination of the gonad index.

The gonad index is a frequently used method for monitoring the reproductive cycles of marine invertebrates; it was first used on sea urchins by Moore (1934) and extensively since then, (Fricke 1979, Chang-Po & Kun-Hsiuing 1981, Dotan 1990 among others). This method rests on the assumption that in individuals that are large enough to be mature, a spent gonad is small

Table 3.1 Correlation of gonad weight to body weight in ripe and spent samples of *S. variolaris*, *E. mathaei* and *D. savignyi* .

		n	r^2	P
S. variolaris:	Ripe	21	0.93	< 0.001
	Spent	17	0.74	< 0.01
E. mathaei:	Ripe	24	0.86	< 0.001
	Spent	18	0.88	< 0.001
D. savignyi:	Ripe	10	0.91	< 0.001
	Spent	13	0.94	< 0.001

whereas a ripe gonad is large (Gonor 1972). Furthermore, this method assumes that at a given time in a given population, animals of different body size have the same ratio of gonad size to body size. Gonor (1972) and Dix (1970) showed that this assumption is not always valid. Ripe and spent gonads of _E. mathaei_, _S. variolaris_ and _D. savignyi_ in the present study showed significant linear correlations between gonad weight and total body weight (Table 3.1). Therefore I assumed that there was no change in proportional gonad weight with body size for individuals in these populations. The gonad index used in this study was calculated as the ratio of gonad wet weight to total body wet weight and expressed as a percentage.

The urchins were processed soon after collection, excess fluid on the urchins was allowed to drain and algal and shell fragments among the spines were removed before the total wet weight of each urchin was determined to the nearest mg. The test was opened on the adoral surface and the whole gonad removed and weighed to the nearest mg.

3.1.3 Histological analysis.

Although the gonad index is a useful means of recording the increase and decrease in gonad size associated with gametogenesis, it provides little information on the reproductive condition of individual urchins. Through histological analysis of sections of testes and ovaries, the timing and duration of sequential cellular events which occur during gametogenesis can be monitored.

Gametogenesis is in synchrony in all five lobes of the echinoid gonad (Pearse 1969), therefore a single piece of one gonad lobe is representative of the whole gonad. Small pieces of gonad from each urchin were fixed for 18-24 hours in Bouins fixative. The tissue was dehydrated and embedded in paraffin wax before being sectioned at 6μm. The sections were then stained with a routine Ehrlichs' Haematoxylin and Eosin stain.

The gonad sections from each monthly sample were examined with a view to ascertaining:

- when gametogenesis in both sexes was initiated,
- the length of time required for gametes to reach maturity,
- the probable time of year when spawning occurred, and
- the degree of synchrony within and between sexes.

This histological analysis, combined with the gonad index data, was used to assess the pattern of reproductive cycles shown by the three species populations, i.e. whether the populations had a restricted annual cycle, reproduced continuously throughout the year or showed a pattern somewhere between these two extremes.

The cellular events which occur during sea urchin gametogenesis are grouped into characteristic stages. For the purposes of this investigation I have used the scheme from Fuji (1960) who splits the reproductive cycle into five stages.

1) Recovering Spent - characterized by a few small primary oocytes along the wall of the ovary, and in the testes by small nests of spermatocytes.

2) Growing - where larger oocytes line the ovary walls and the spermatogenic layer in the testes is thick and continuous and columns of spermatocytes extend into the lumen.

3) Premature - where there are large oocytes along the tubule walls and a few mature ova in the lumen. In the testes there is some accumulation of spermatozoa in the central lumen.

4) Ripe - where many mature ova or spermatozoa are present in the

central lumen.

5) Spent - where empty spaces are present in the lumens and phagocytosis of remaining gametes is occurring.

Testes.

The process of spermatogenesis was investigated by monitoring the change in proportion of tubule lumen occupied by mature spermatozoa. The percentage of an individual tubule lumen occupied by mature spermatozoa was calculated by comparing the diameter of the central mass of spermatozoa with the total diameter of the tubule. Most of the tubules were elliptical in shape, therefore nominal mean diameters were calculated by adding the lengths of longest and shortest axes and dividing by two. Measurements were made on 10 randomly selected tubules in each section and a mean calculated for each monthly sample.

In addition each testis section was placed in one of the five developmental stages.

Ovaries.

The process of gametogenesis was monitored by a size frequency polygon method adapted from Pearse (1969). The frequency of different sizes of oocytes and ova in the sectioned ovaries was estimated by measuring the first 50 oocytes or ova encountered in transects across the section. Only those oocytes with visible nucleoli and ova with nuclei were measured. Obviously relict, misshapen or degenerating ova or oocytes were not included in the analysis. Nominal mean diameters were calculated for the elliptical oocytes and ova and a frequency polygon with size classes of 10μm was constructed for the pooled numbers in each monthly sample.

Each ovary was classified according to developmental stage and the presence or absence of mature or relict ova was noted. As a detailed histological analysis of gametogenesis in S. variolaris was performed during 1990 (Drummond 1991a), gonad sections were only examined histologically in selected months over the spawning, recovering and growing periods of the reproductive cycle in 1991-1993.

3.2 Environmental factors.

Monthly mean sea temperatures and swell heights were calculated from daily data supplied by the Natal Sharks Board.

3.3 Estimated annual reproductive output.

Estimates of annual reproductive output were used as a direct means of comparing the investment in reproduction by each species. Lawrence (1985) maintained that reproductive output was not a measure of fecundity nor necessarily of the amount of energy allocated to reproduction because of the differences in energy value of the gonads of different sexes. Although the energy value of the spawned gametes would obviously constitute only part of the total amount of energy allocated to reproduction, I believe that the amount of gametes spawned must logically be a reflection of a sea urchin's investment in reproduction.

The gonad mass of standard urchins (of masses 30g, 61g and 90g) were determined from regressions of gonad weight on body weight for a pooled sample of males and females representing the ripe and the spent population of each species. The 30 and 90g standard animals represented those in their first breeding season and the larger size classes respectively, while 61g was the mean body mass of all urchins dissected during the study.

As only two D. savignyi could be classified as ripe, my "ripe" sample for this species was composed of the individuals containing the greatest number of mature gametes and a high gonad index. The difference between the ripe and spent masses for all three species was assumed to be the mass of gametes produced by an average urchin. The calorific value of pooled male and female gonad tissue for each species was determined by bomb calorimetry; this figure was then multiplied by the mass of gametes produced to give the estimated annual reproductive output for an average urchin in each species.

Results.

Stomopneustes variolaris

3.1.2 Gonad index.

The gonad index for the Oslo Beach population of S. variolaris showed clear annual cycles of increase and decrease over the study period (Fig. 3.1). These results for the 1991-1993 reproductive cycles support the conclusion of the 1990 study that there is a well defined annual cycle of gonad growth in the Oslo beach S. variolaris population (Drummond 1991b). Aspects of the annual gonad index cycle showed considerable interannual consistency: during each year the gonad index peaked in January and was followed by a significant decrease indicative of spawning. This decrease was most marked in January-February 1991 where the gonad index decreased by 47% compared with 21% and 36% for the same period in 1992 and 1993 respectively. The decrease in gonad index in 1992 and 1993 was somewhat extended (Fig. 3.1), suggesting a less synchronized spawning event than that of 1991. The lowest point in the gonad index cycle was reached in May of each year; then in June (1990 & 1991) or July (1992) a significant increase in gonad index reflected the accumulation of nutrients and growth associated with initiation of the new gametogenic cycle.

3.1.3 Histological analysis.

The intention of the histological analysis was to extract data which pertained to the life history of this species, not to describe the process of gametogenesis. The process of gametogenesis has been documented in detail for this population (Drummond 1991a, 1991b). The histological analysis performed on sections of both sexes during 1991-1993 confirmed the findings

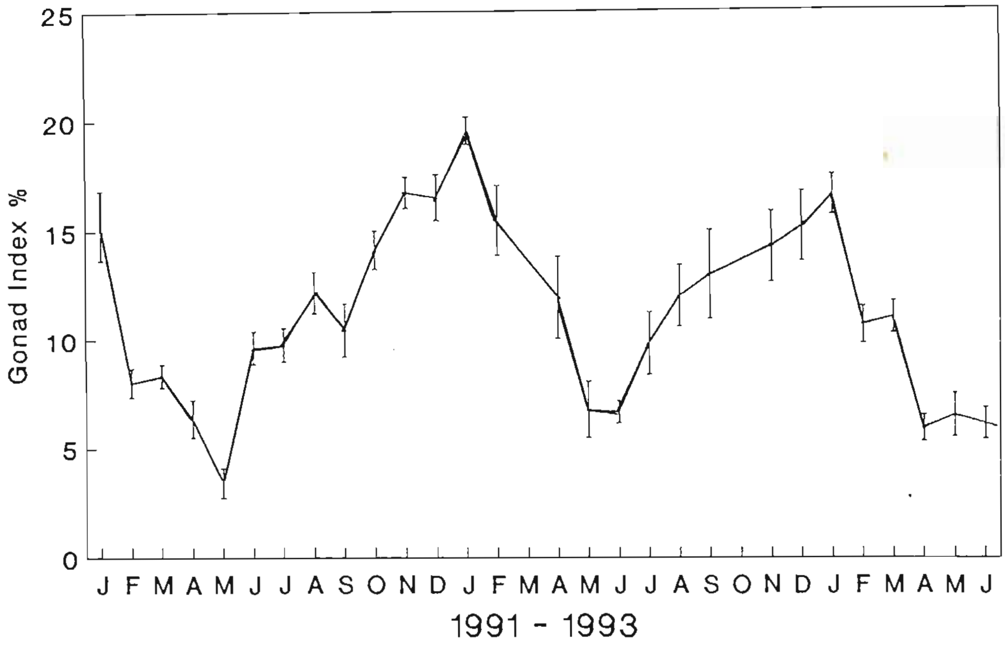


Figure 3.1 The mean monthly gonad indices (and Standard Error bars) for Stomopeustes variolaris from Oslo beach between January 1991 and June 1993.

of the 1990 study. This species has a distinct annual cycle of gametogenesis with spawning occurring between mid-December and mid-February with greatest intensity in January. Following spawn out, the percentage of spermatozoa in the testes decreases to a minimum in June (Fig. 3.2). This decrease in the percentage of an individual tubule lumen occupied by mature spermatozoa was accompanied by an increase in the thickness of the nutritive phagocyte tissue. As the testes in this species appear to exhibit a period of inactivity following spawn out (Drummond 1991b), the increase in gonad index observed during May-July of each cycle is probably largely the result of the accumulation of nutrients by the nutritive phagocytes. In 1990 the testes were in the recovering stage by September, and in 1991 testes of the July sample had numerous nests of spermatogonia lining the tubule walls. Unfortunately the September 1992 sample did not contain any males. However, by October all testes sectioned had dense spermatogenic layers and varying amounts of mature spermatozoa had accumulated in the central lumens (Fig. 3.2). Therefore spermatogenesis in _S. variolaris_ probably takes 3-4 months from initiation to the premature stage, and accumulation of spermatozoa continues for a further 2-3 months before ripe males are present in the December or January samples. Synchronisation of gametogenesis between males within each monthly sample appeared to vary over the course of the reproductive cycle. During the post-spawning and recovering months synchrony was poorest among individual males (Fig. 3.3 A), but as the cycle progressed synchrony became closer and in the November-February samples the males were in fairly close synchrony.

The decrease in size and numbers of mature ova in the February 1992 and 1993 samples (Fig. 3.4) combined with the reappearance

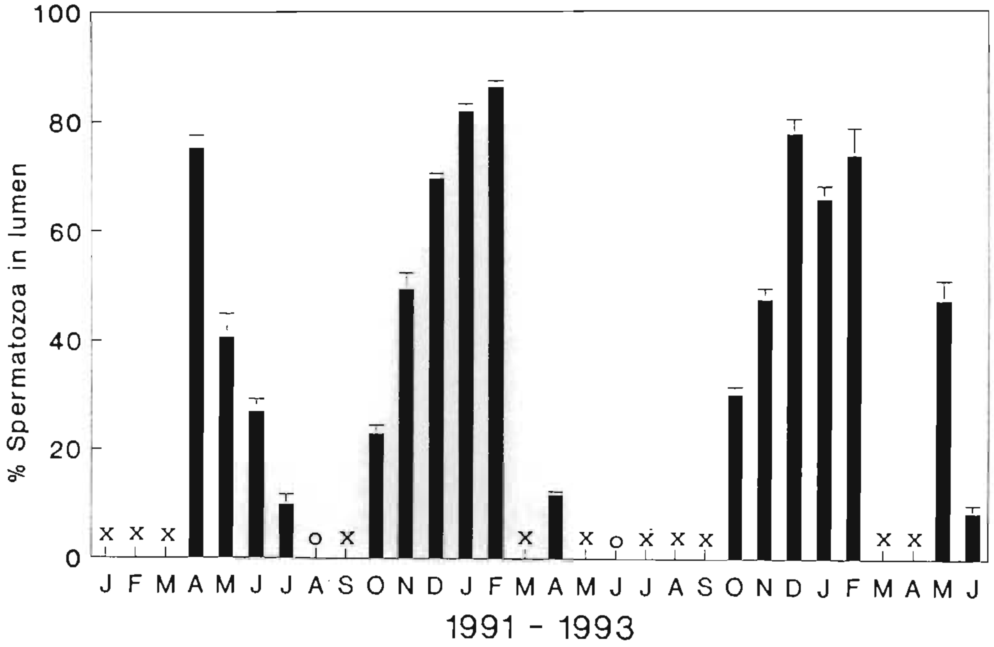
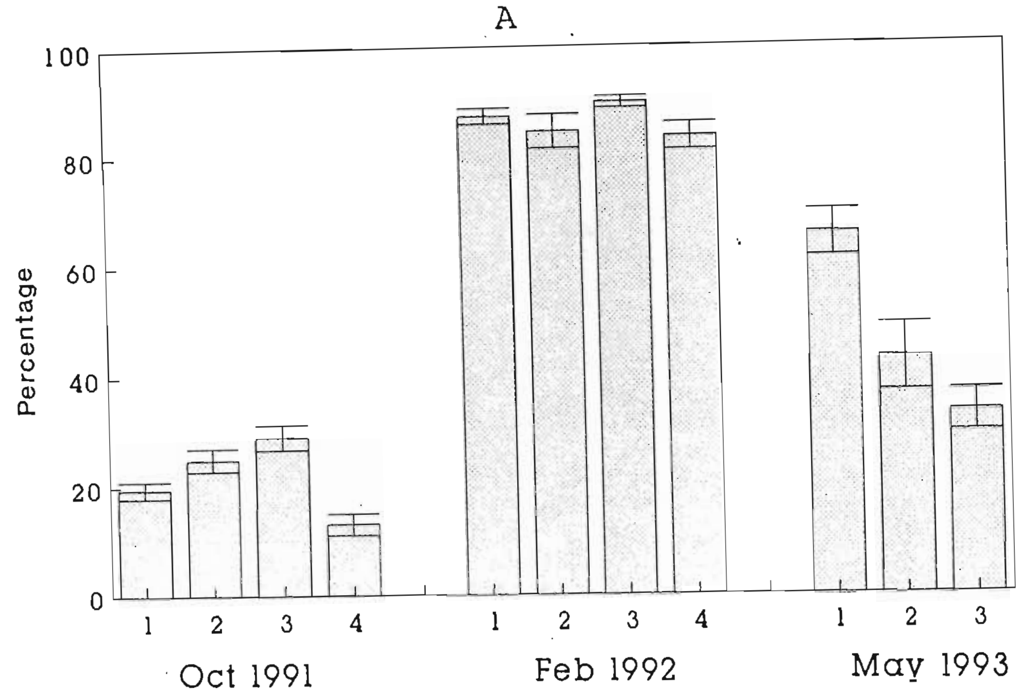


Figure 3.2 The mean percentage of tubule lumen occupied by mature spermatozoa (and Standard Error bars) in <u>Stomopneustes</u> <u>variolaris</u> in selected months during 1991-1993.

o = 0%

x = no sample



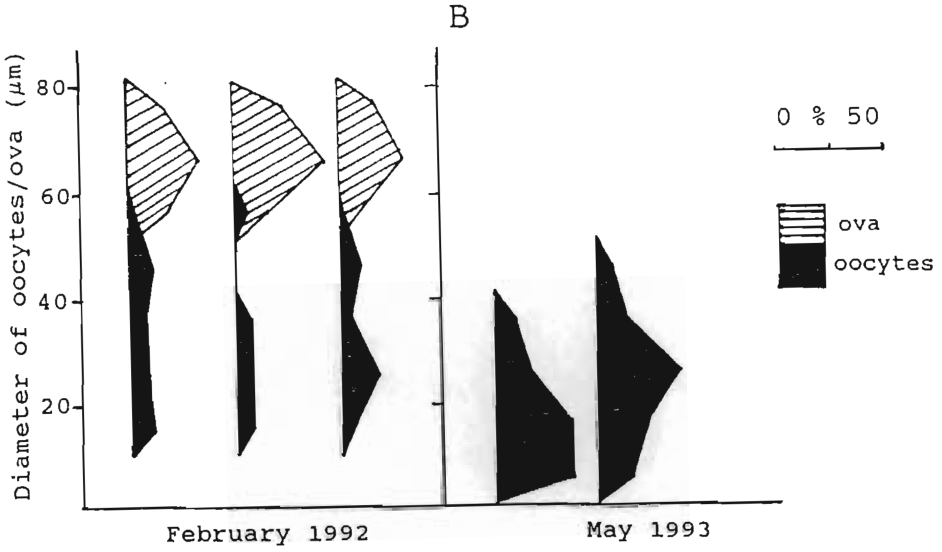


Figure 3.3 The size frequency distribution of oocytes and ova and percent spermatozoa of individuals within selected monthly samples of <u>Stomopneustes variolaris</u>.

A) Males B) Females

of oocytes in the smallest size class (<10μm) supports the conclusion that the major spawning event in S. variolaris occurs in January. Relict ova and large oocytes persisted in the ovaries for varying lengths of time in the cycles studied, but in all years ovaries of the June samples were dominated by growing oocytes (5-30μm). By October large vitellogenic oocytes (>55μm) were present and in November, mature ova (70-90μm) had begun accumulating in the lumens. Large oocytes continued maturing and ova accumulated through December. In contrast to the 1990 cycle, where small oocytes (<10μm) were present all year, the smallest oocytes disappeared from the November-January samples in 1992 and 1993. This could imply that all or most of the small oocytes were able to develop toward maturity in the latter cycles. The reappearance of small oocytes in February indicates that oogenesis is initiated soon after spawn out without the inactive or resting phase observed in the males. Therefore gamete growth and maturation takes 6-8 months in the ovaries of this species. Although monthly samples occasionally contained gonads in more than one developmental stage, synchrony between individual females of each monthly sample was fairly close (Fig. 3.3 B). Synchrony between the sexes was good, though mature spermatozoa were present in the post spawning samples for longer than mature ova, perhaps a means whereby maximum fertilization success could be achieved.

The smallest individual containing active gonads was a male with test diameter of 28mm and a total body mass of 12.4g. The growth rate data in Chapter 6. indicate that this urchin was probably 20-24 months old.

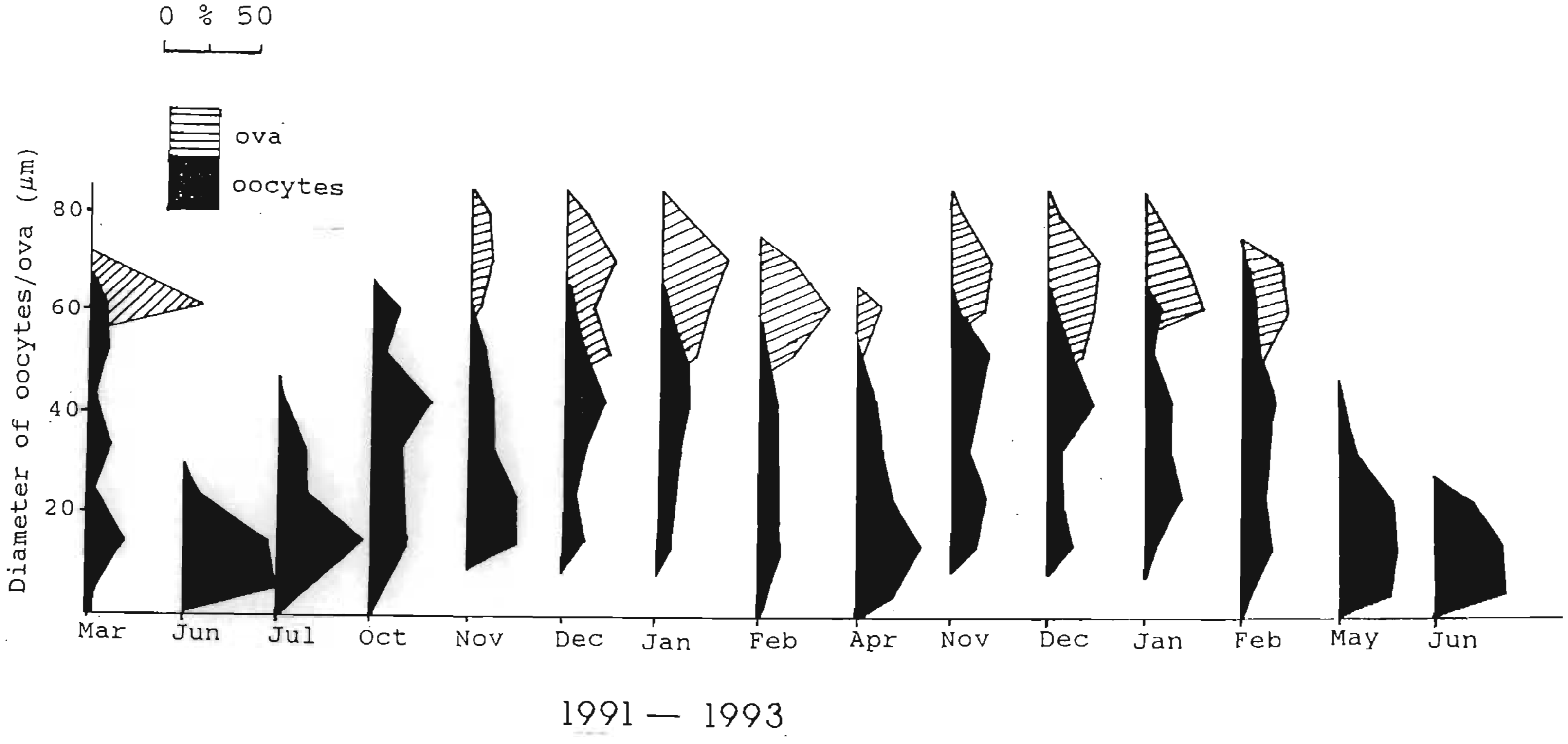


Figure 3.4 The size frequency distribution of oocytes and ova in monthly samples of <u>Stomopneustes variolaris</u> from Oslo beach during 1991-1993.

Diadema savignyi.

3.1.2 Gonad index.

In each of the three cycles monitored, the increases and decreases in gonad size followed a clear seasonal pattern (Fig. 3.5). From the lowest point in February-March, the gonads increased in size gradually over the autumn and winter months. Gonad growth during the early part of this increase was the result of growth of the nutritive phagocycte tissue, which by July was heavily globulated and completely filled all gonad lumens. Between October and December gonad growth was more rapid and by December the gonad index had reached its highest point in the cycle. A 40% decrease in gonad size between December 1991 and January 1992, and a 56% decrease between December 1992 and January 1993 indicates that spawning probably occurred during this time. The continued sharp decline through to February suggested that the spawning period extended from late December to late February.

The possibility that D. savignyi might show repeated spawning with a monthly rhythm was investigated by examining samples collected at new moon and full moon in January and December 1992, January and March 1993. At the December full moon (Fig. 3.5 D1) the gonad index was at the highest point in the cycle (Fig. 3.5), this was followed by a 60% decrease in gonad mass between full moon and new moon (D2) in December. Although the gonad index increased between December new moon and January full moon (J1), this increase was not statistically significant ($t=1.35$, $p > 0.05$). However this increase was followed by a 56% decrease as the urchins spawned between January full moon and January new moon (J2). A similar pattern was observed in March but the magnitude of the decrease in gonad mass was considerably smaller.

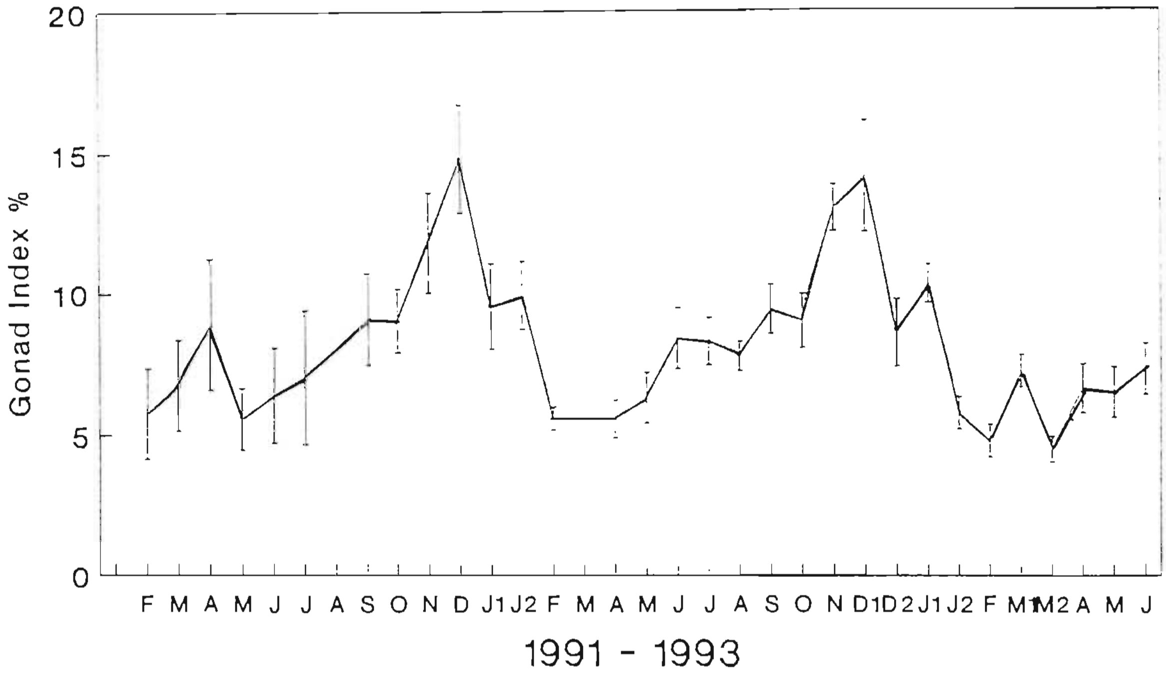


Figure 3.5 The mean monthly gonad indices (and Standard Error bars) for Diadema savignyi from Isipingo between February 1991 and June 1993.

3.1.3 Histological analysis.

The smallest individual possessing sexually mature gonads had a test diameter of 24mm and body mass of 8.0g. The growth rate data (Chpt. 6) suggested that this animal was 6-8 months old. The timing of gametogenic events in D. savignyi was remarkably consistent between the cycles monitored over the course of this study. As suggested by the gonad index, the urchins had spawned out by February-March. The February and March samples in all years were dominated by spent gonads in both sexes (Fig. 3.6), with small numbers of relict spermatozoa and disintegrating oocytes and ova still present. By April both ovaries and testes were in recovering or growing stages. In the testes this was characterized by a continuous deeply basophillic spermatogenic layer (Plate 1), and in the ovaries by the presence of previtellogenic and early vitellogenic oocytes in the 10-30μm size classes (Plate 2). Also present in these ovarian sections was a component of larger vitellogenic oocytes (30-50μm) (Fig. 3.7). The presence of these medium sized early vitellogenic oocytes in many post spawning recovering ovaries suggests that not all relict oocytes are phagocytized by nutritive phagocytes immediately after spawning and may be retained and resume growth during the next gametogenic cycle.

The growth and maturation of gametes is initially slow, as all gonads in the April to September samples were in the recovering or growing stages (Fig. 3.6). In the testes, lines of spermatocytes fill the lumens and in the ovaries only a small percentage of oocytes were in size classes larger than 40μm. As suggested by the gonad index, the period of most rapid growth was between October and December. This rapid growth is reflected in a change in the oocytes/ova size frequencies (Fig. 3.7). From

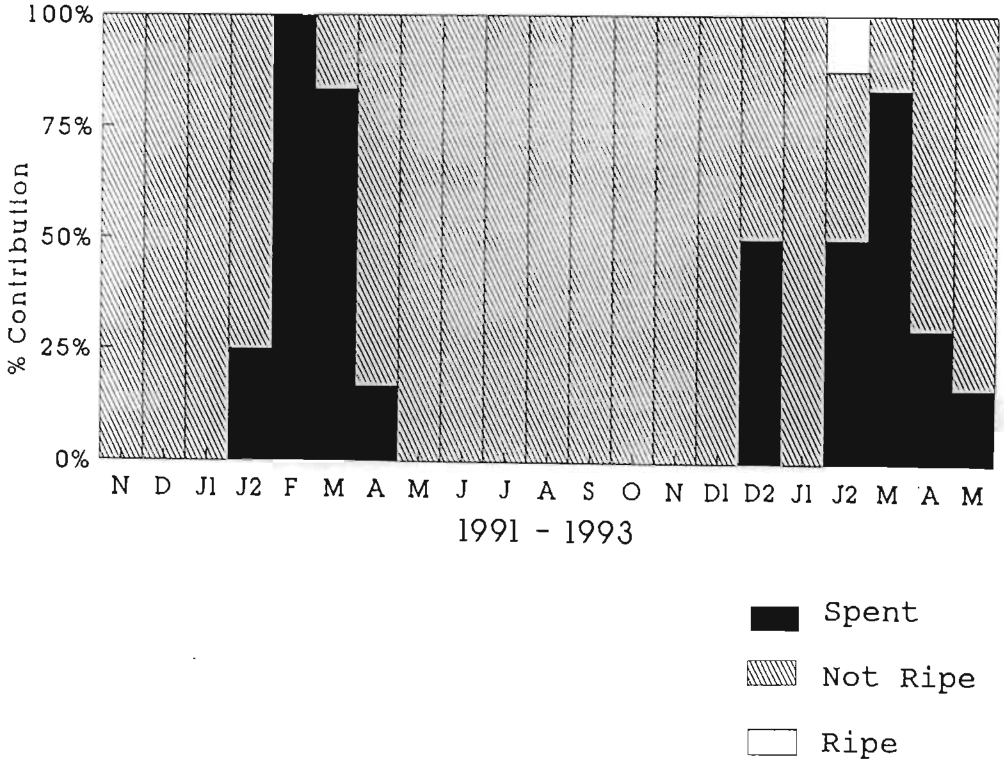
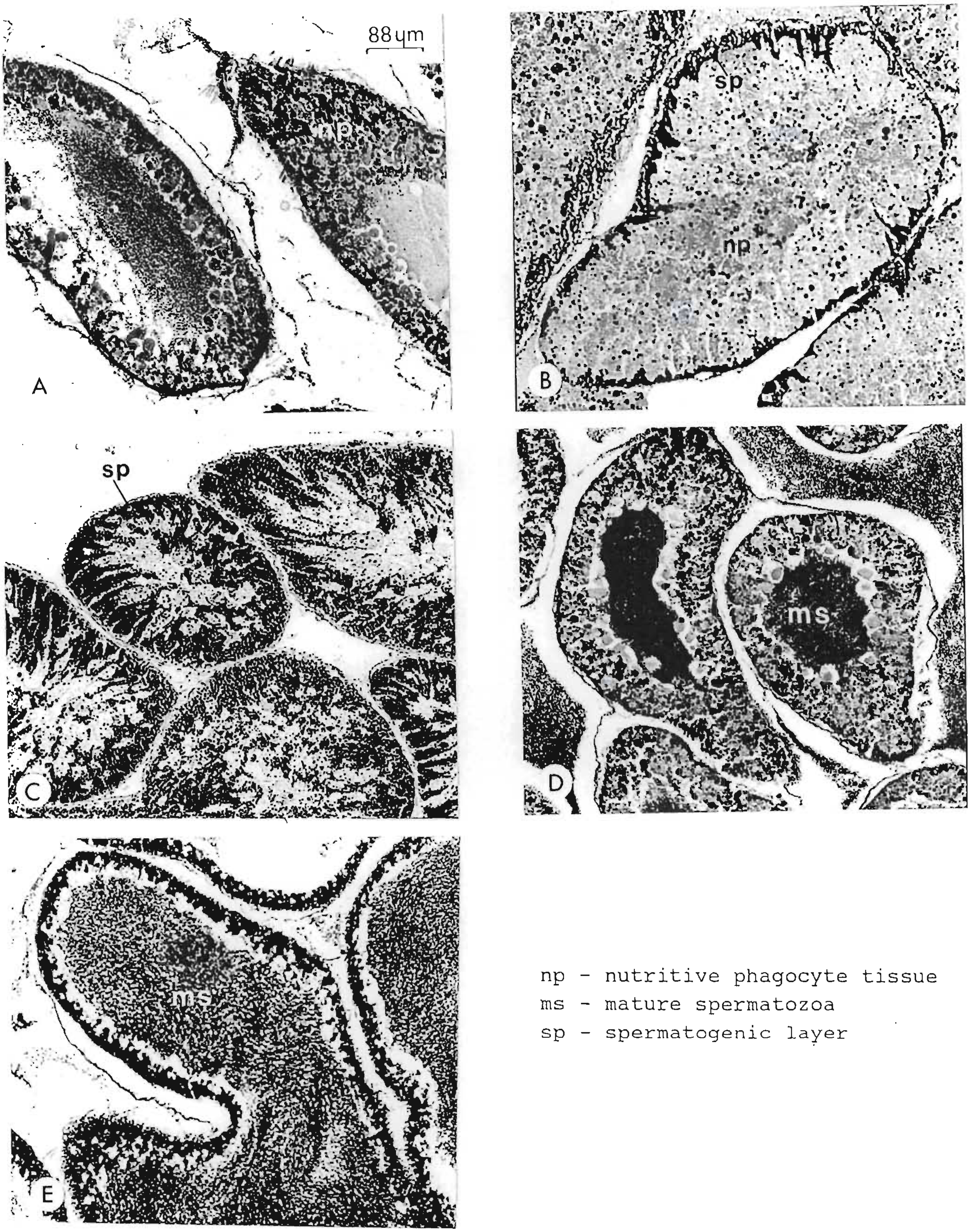


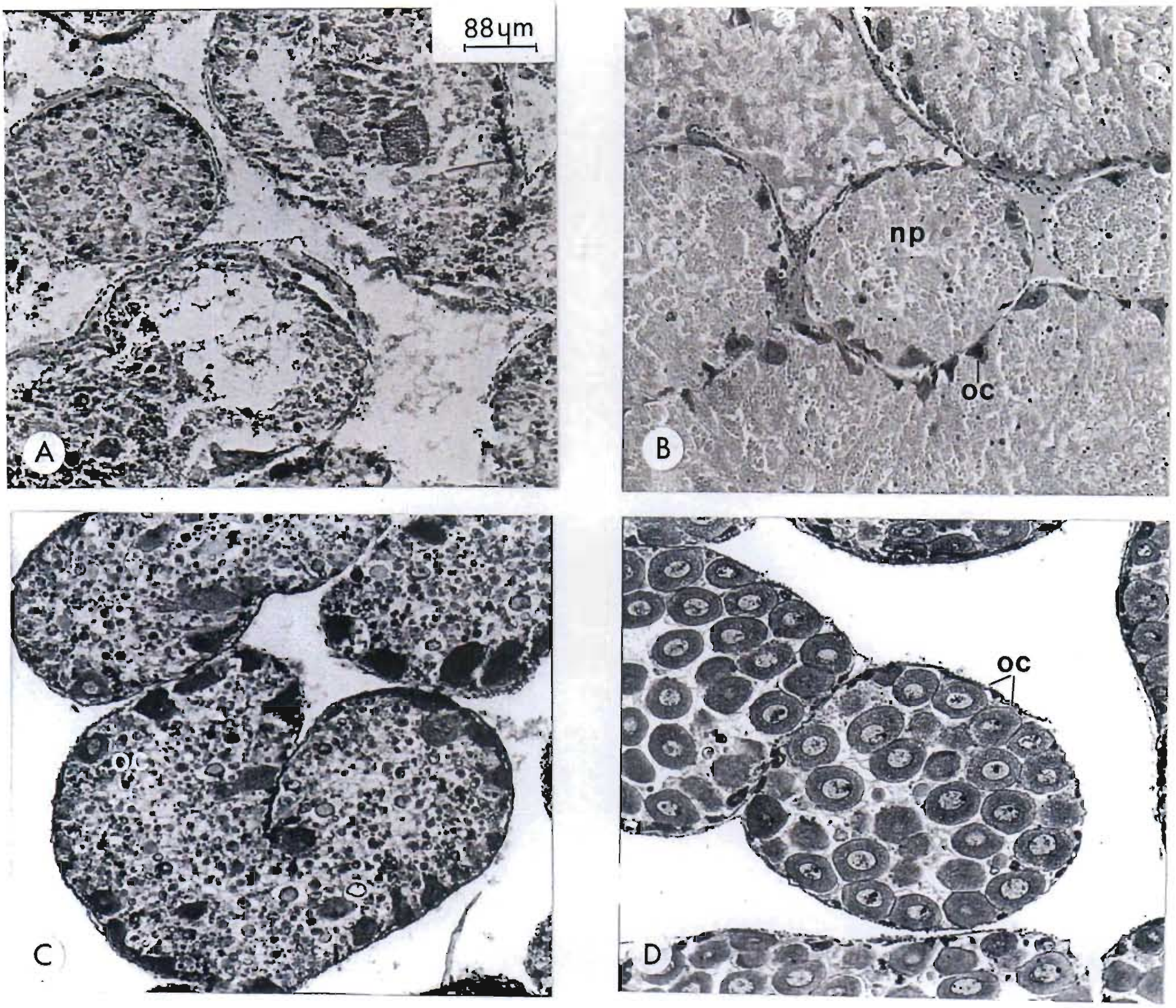
Figure 3.6 The percent contribution of gonad developmental stages in monthly samples of Diadema savignyi from Isipingo between November 1991 and May 1993.



np - nutritive phagocyte tissue
ms - mature spermatozoa
sp - spermatogenic layer

Plate 1. The characteristic developmental stages during spermatogenesis in *Diadema savignyi*.

A) Spent
B) Recovering
C) Growing
D) Premature



oc - oocyte
np - nutritive phagocyte tissue

Plate 2. The characteristic developmental stages during oogenesis in Diadema savignyi.

A) Spent
B) Recovering
C) Growing
D) Premature

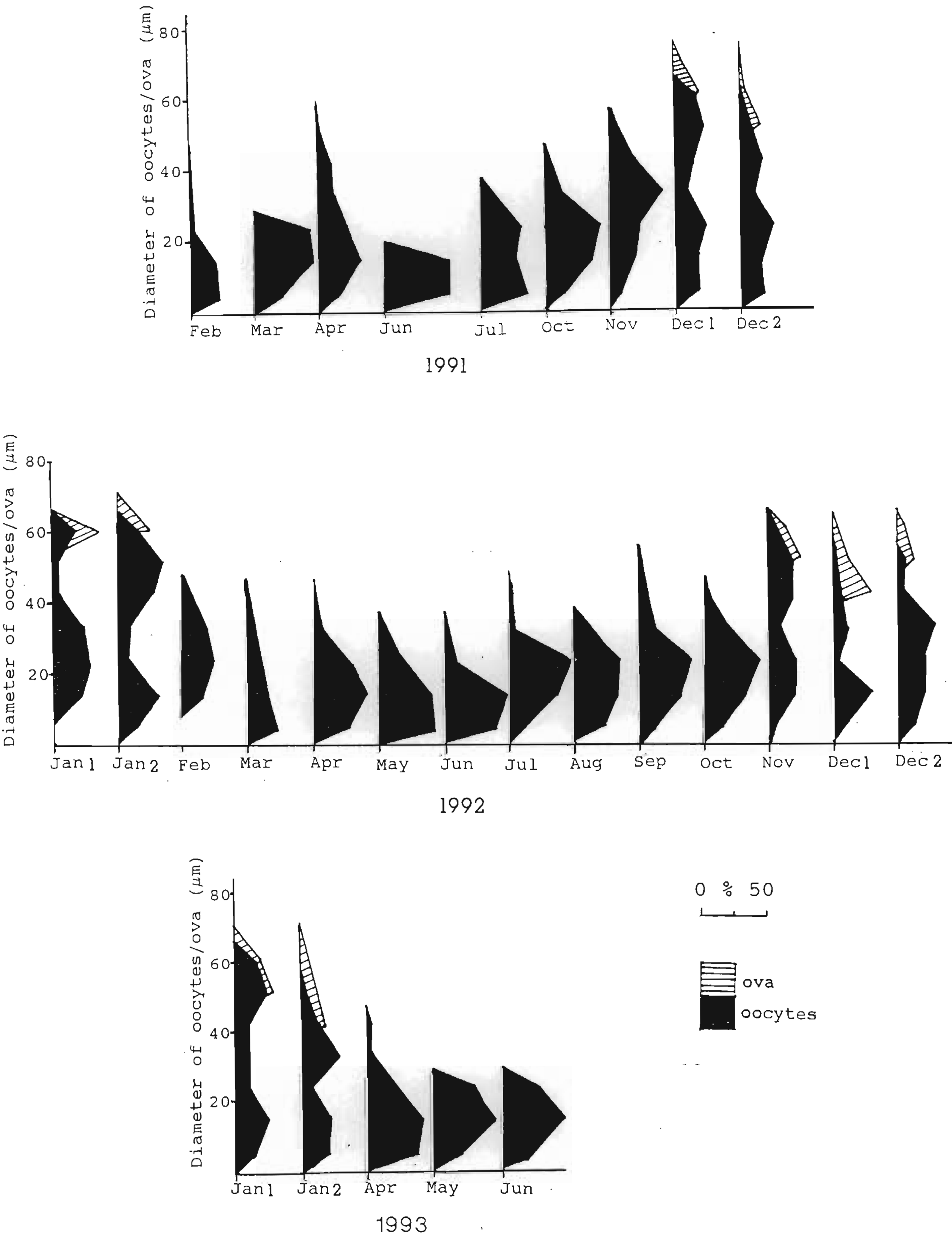


Figure 3.7 The size frequency distribution of oocytes and ova in the monthly samples of *Diadema savignyi* from

a persistent unimodal distribution of oocytes dominated by the size classes 20-40μm, rapid growth of larger oocytes and the differentiation of oogonia and subsequent rapid growth, resulted in a distinctly bimodal distribution. This bimodal distribution of oocytes was present in all samples over the spawning period. The first mature gametes of each cycle appeared in the December 1991 and November and December 1992 samples (Figs 3.7 & 3.8). Although small accumulations (15%, Dec. 1991 and 30%, Nov. 1992) of mature spermatozoa and scattered mature ova were present, none of the gonads could be classified as ripe. Of the 60 urchins of this species examined histologically over the 1992 and 1993 spawning periods, only two individuals (male) were classified as ripe. Growth and maturation of gametes in both sexes therefore probably takes 7-9 months at this locality.

Synchrony within the females was remarkably close, with oocytes/ova size frequencies being essentially similar in all individuals in a sample (Fig. 3.9 A). A similar degree of synchrony was observed among the males (Fig. 3.9 B). Synchrony between the sexes was close, as suggested by the sharp increase and decrease on either side of the high point in the gonad index cycle. Furthermore males and females in most samples were in the same developmental stage.

Echinometra mathaei.

3.1.2 Gonad index.

The gonad index data showed distinct cycles of increase and decrease in gonad size (Fig. 3.10). Although the rate of increase and decrease appeared to differ between cycles, the timing of these changes was similar. Sharp decreases in gonad index between January and February 1991, February and April 1992

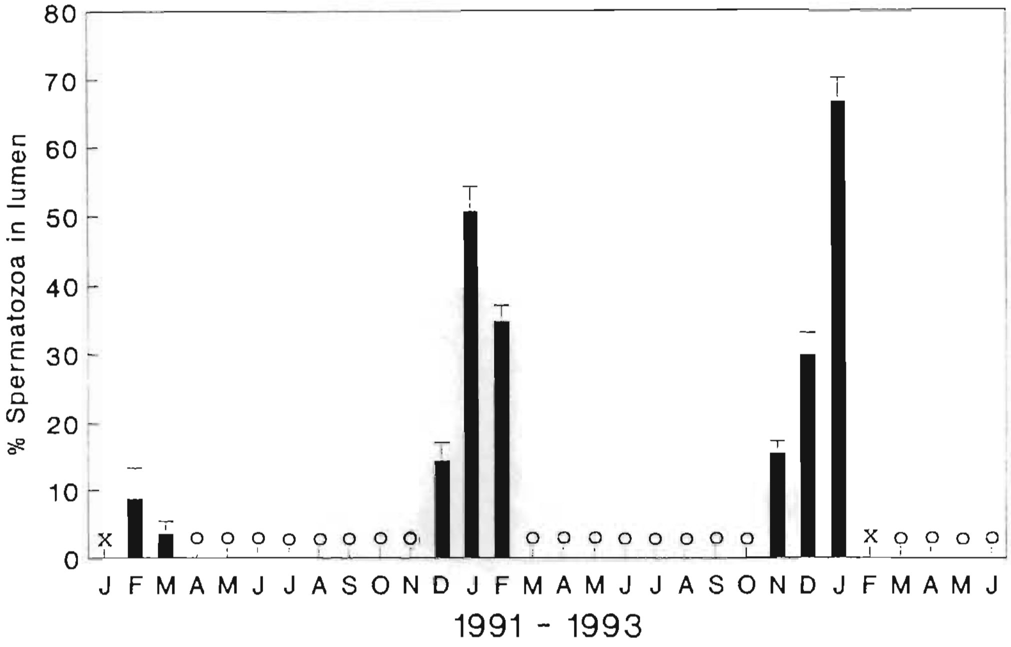


Figure 3.8 The mean percentage of tubule lumen occupied by mature spermatozoa (and Standard Error bars) in Diadema savignyi between February 1991 and May 1993.

o = 0%

x = no sample

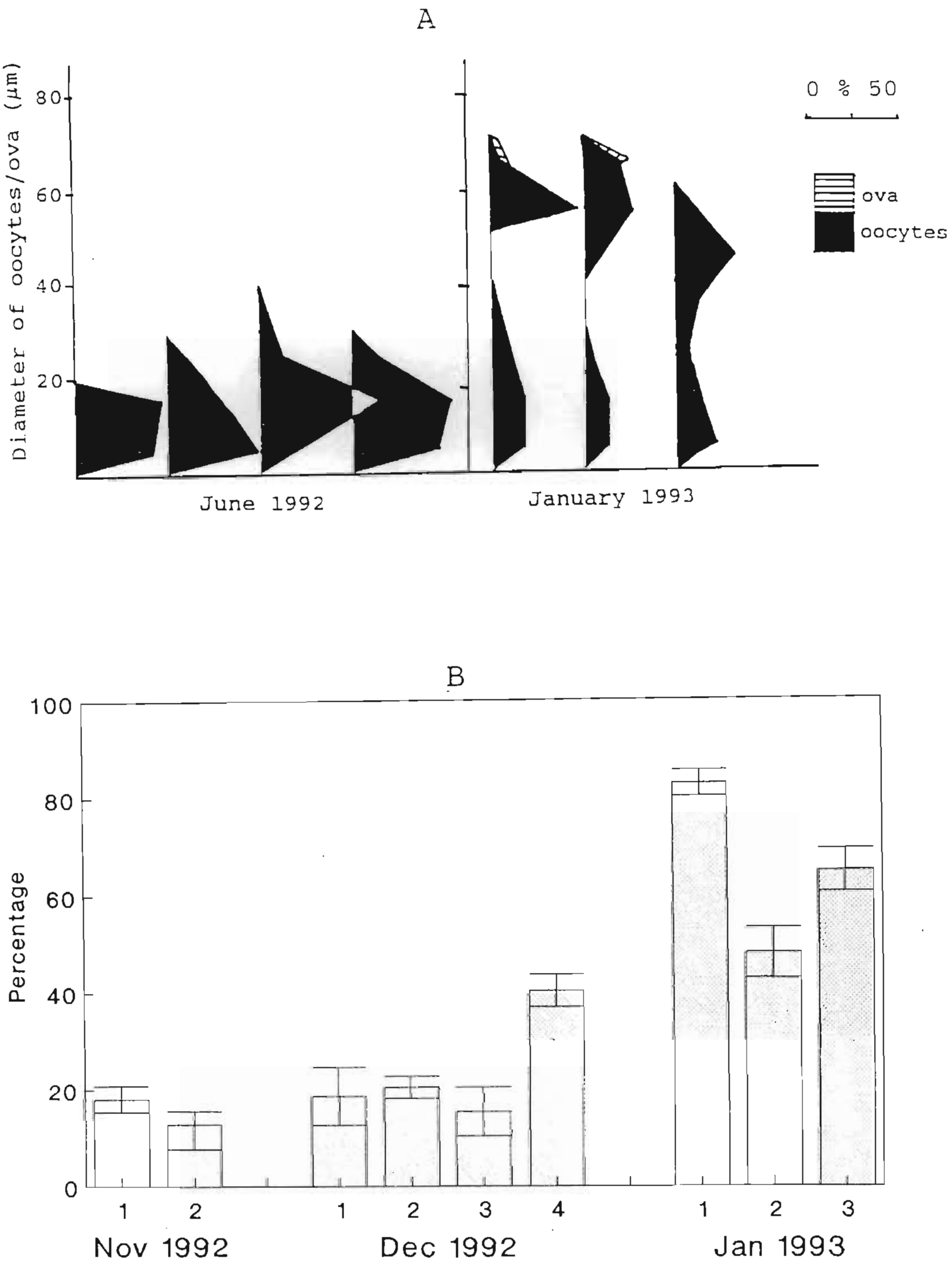


Figure 3.9 The size frequency distribution of oocytes and ova and percent spermatozoa of individuals within selected monthly samples of <u>Diadema</u> <u>savignyi</u>.

A) Females B) Males

and January and February 1993 suggest that spawning occurs between January and March/April. The nature of the spawning event appeared to vary between cycles. In 1991 the high gonad index (23.35 SE 1.33), and the 58% decrease in gonad size over a single month, suggested close synchrony among individuals over this spawning event. In 1992 the decrease in gonad size occurred over two months (Feb-Apr) suggesting poorer synchrony within the population. During the 1992/1993 spawning period the gonad index was highest in November 1992, and the decrease in gonad size associated with spawning occurred in a series of steps until April. The most marked of these were between January and February, and March and April. In all years the gonad index decreased to a low point in May and then increased throughout the winter and spring; thus it would appear that E. mathaei, at this locality, has an annual reproductive cycle with an extended period of spawning over the summer months.

3.1.3 Histological analysis.

The smallest sexually mature E. mathaei dissected had a test diameter of 25mm and a body mass of 8.6g and was ca. one year old.

The distribution of gonadal developmental stages (Fig. 3.11) indicates that in the samples from July to September, most of the gonads were in the recovering and growing stages, while over the remainder of the year most gonads were ripe or spent. Ovarian sections in June-September samples were dominated by small to medium sized oocytes (5-30μm) with a small component of vitellogenic oocytes in larger size classes (Fig. 3.12). Ovary sections for the rest of the year showed a range of oocytes of all size classes and a significant component of mature ova.

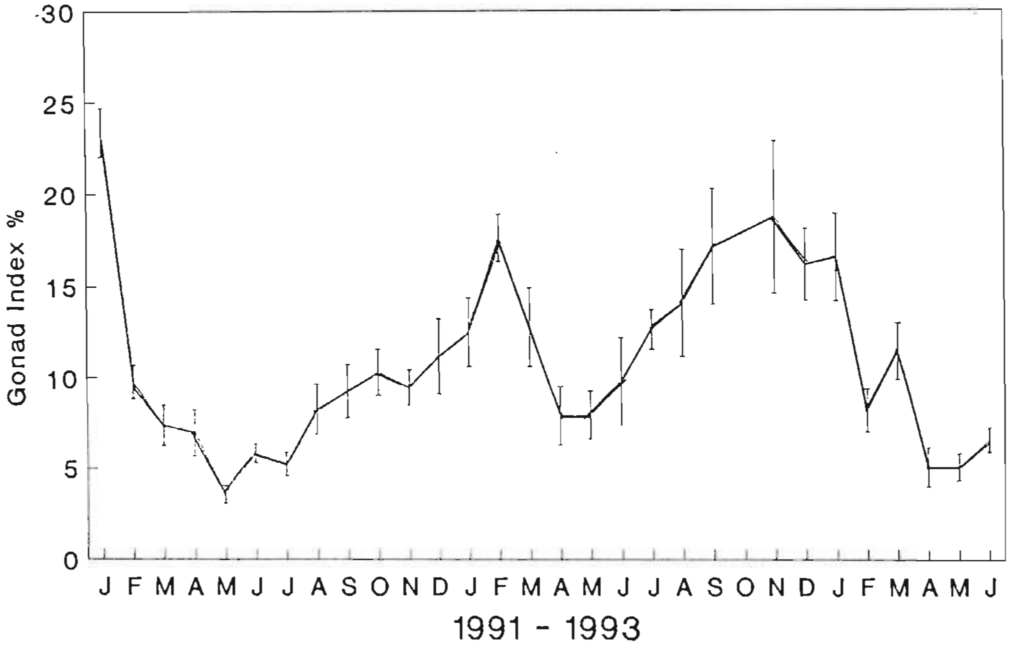


Figure 3.10 The mean monthly gonad indices (and Standard Error bars) for Echinometra mathaei from Ramsgate between January 1991 and June 1993.

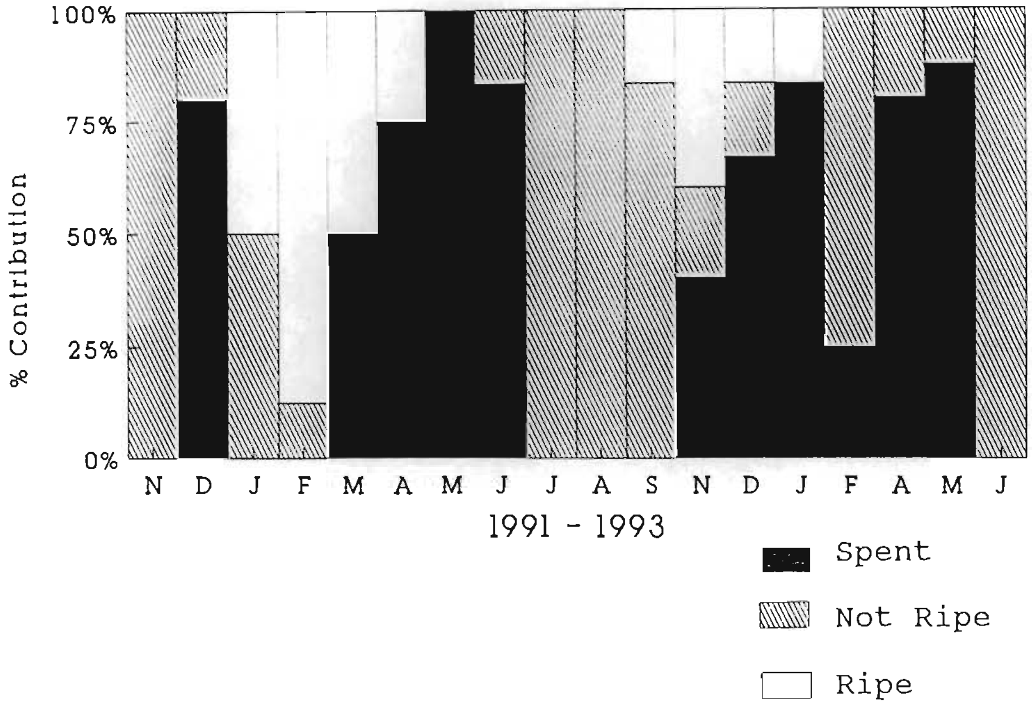


Figure 3.11 The percent contribution of gonad developmental stages in monthly samples of Echinometra mathaei from Ramsgate between November 1991 and June 1993.

However, no sequence of oocyte growth could be discerned from the oocytes/ova size frequencies over the course of the study. Synchrony among the females was close during the spawning period (Feb 1992, Fig. 3.13 A), though less so in the recovering/growing phase (Sept 1992).

With exception of May to July 1991 and June 1993, spermatozoa were present in every monthly sample of the study (Fig. 3.14). While this could suggest that spermatogenesis and spawning occurred continuously throughout the year, the absence of ripe or spent gonads in July, August and September discounts this possibility. Synchrony among the males is only evident during the spawning period (Feb 1992, Fig. 3.13 B). The asynchrony over the remainder of the year probably accounts for the continuous presence of spermatozoa in the monthly samples. Synchrony between the sexes was only relatively close during the latter part of the spawning period.

The predominance of gonads in the recovering stage in both sexes in June in all three years, suggests that gametogenesis is initiated at about this time. Although occasional mature ova and small numbers of spermatozoa were present from July, ripe gonads only appeared three months later. Gamete growth therefore takes 4-6 months, though gametogenic asynchrony during the growing phase lends some doubt to the accuracy of this prediction.

3.2 Environmental factors.

Changes in sea temperatures along the South African east coast show a distinct seasonality, with the highest temperatures recorded in January and February (24°C & 25°C) and lowest in July and August (19°C). Figure 3.15 shows the 25 year mean monthly

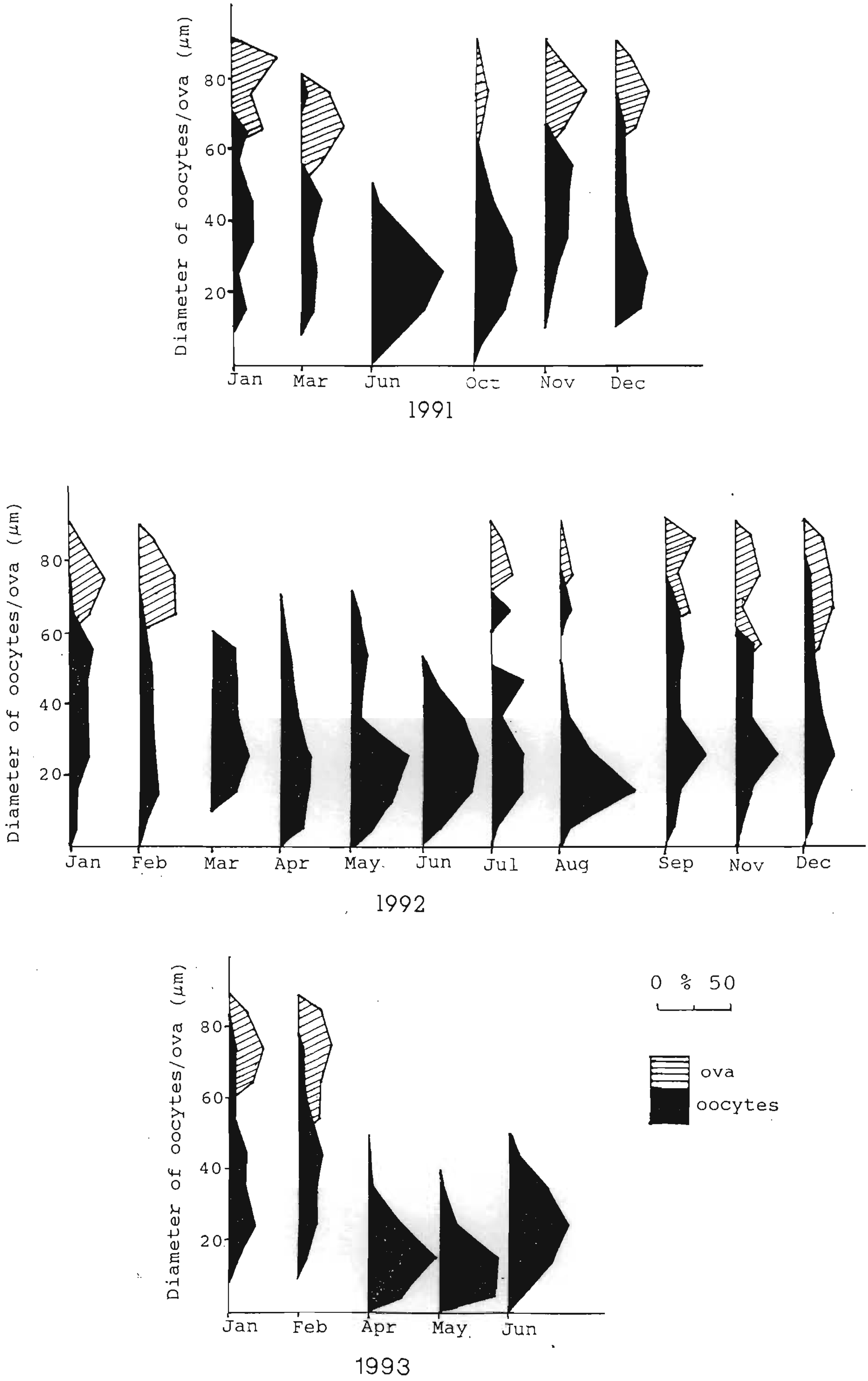


Figure 3.12 The size frequency distribution of oocytes and ova in the monthly samples of <u>Echinometra mathaei</u>

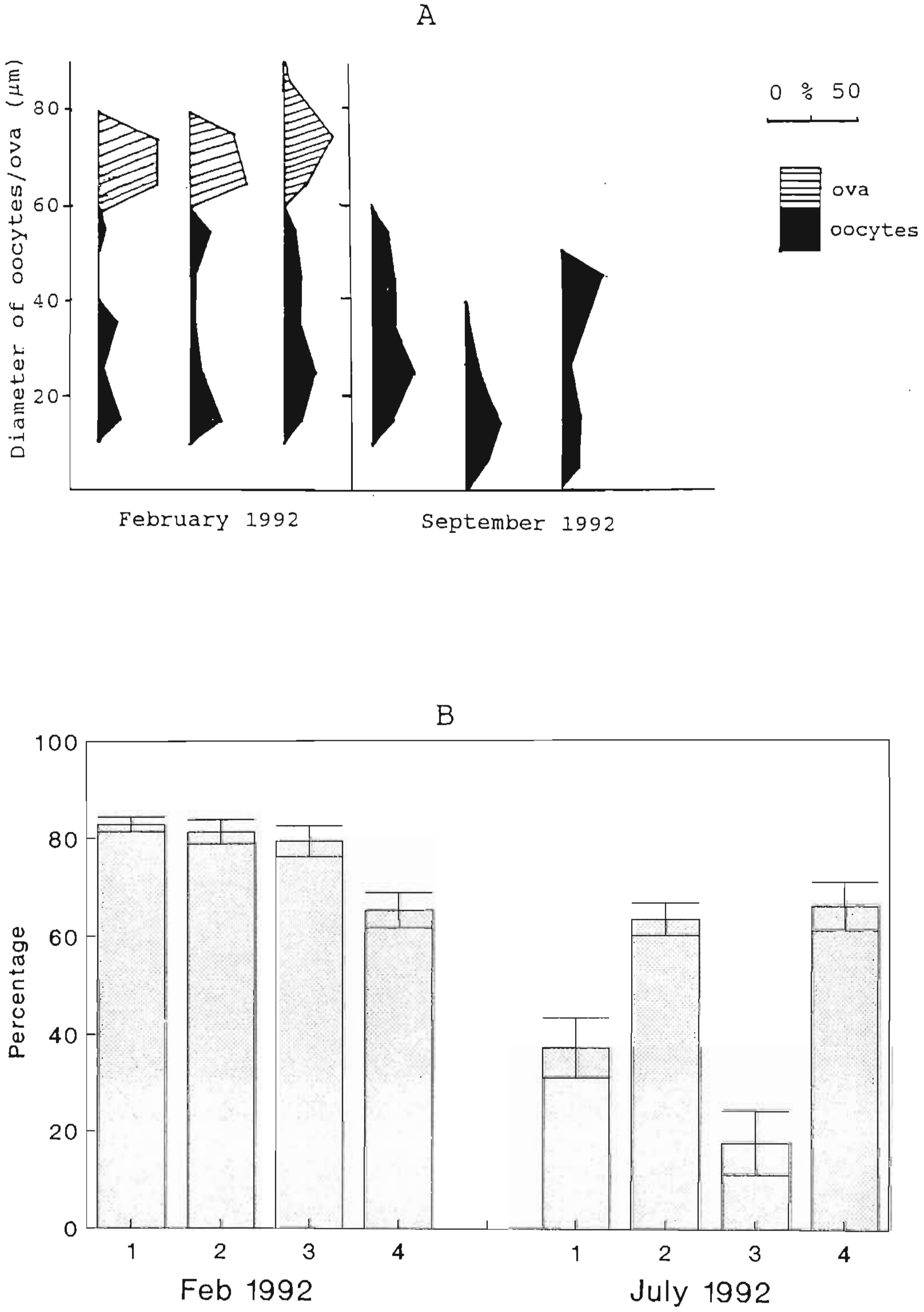


Figure 3.13 The size frequency distribution of oocytes and ova and the percent spermatozoa of individuals comprising selected monthly samples of <u>Echinometra mathaei</u>

A) Females B) Males

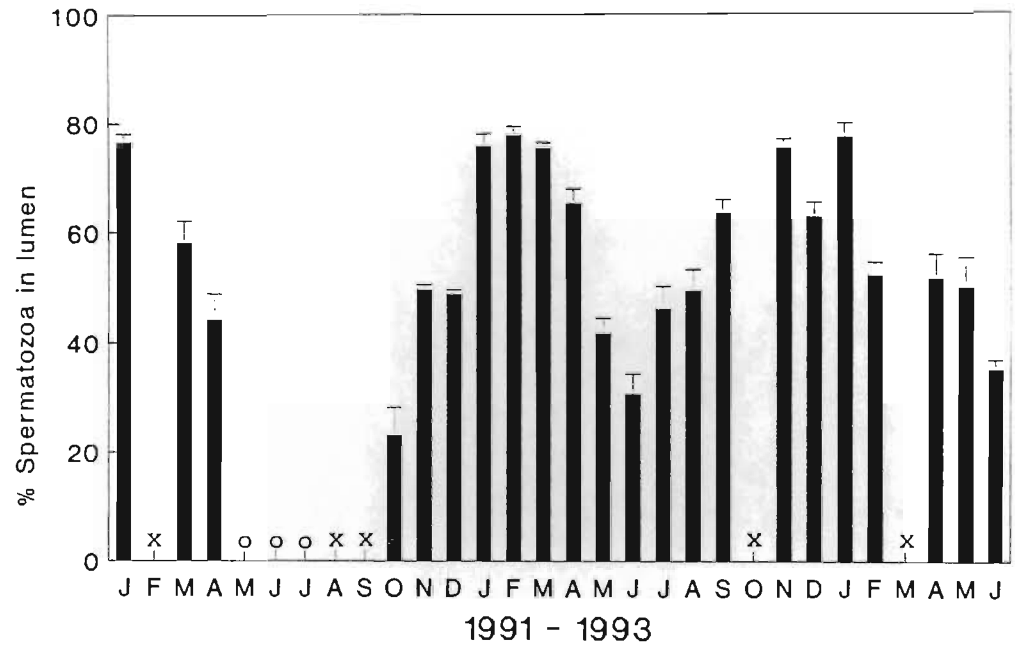


Figure 3.14 The mean percentage of tubule lumen occupied by mature spermatozoa (and Standard Error bars) in _Echinometra_ _mathaei_ from January 1991 to June 1993.

o = 0%

x = no sample

temperatures for the east coast and the mean monthly temperatures for Oslo Beach, Ramsgate and Isipingo over the study period. When the gonad index cycles were considered in the light of the seasonal fluctuations in sea temperatures, some points of interest were revealed. Firstly, growth of the gonads in all years coincided with increasing sea temperatures and secondly, the spawning period of each reproductive cycle occurred only during the time when sea temperatures exceeded 23°C. In *D. savignyi* the end of the spawning period coincided with the highest temperatures for the year.

The mean monthly swell heights recorded off Port Shepstone do not show a marked seasonal pattern (Fig. 3.16). However, there does appear to be some seasonal variation in the number of days per month when the swell height exceeds the monthly mean value. From December to April the mean swell height is exceeded on 4-11 days/month (mean = 7d), while in the remaining months the mean swell height is exceeded on 14-17 days/month (mean = 15d).

3.3 Estimated annual reproductive output.

The values used in estimating annual reproductive output for the three species are presented in Table 3.2. In terms of the 61g standard animal, *E. mathaei* had a slightly higher reproductive output than the other two species, though where small (30g) animals were compared *S. variolaris* had a marginally higher output. However, neither of these differences are significant, so in effect *S. variolaris* and *E. mathaei* have a similar reproductive output in the small and medium size classes. In contrast to the marginal differences between species in the small and medium size classes, when larger 90g animals were compared, *D. savignyi* had a considerably higher reproductive output than

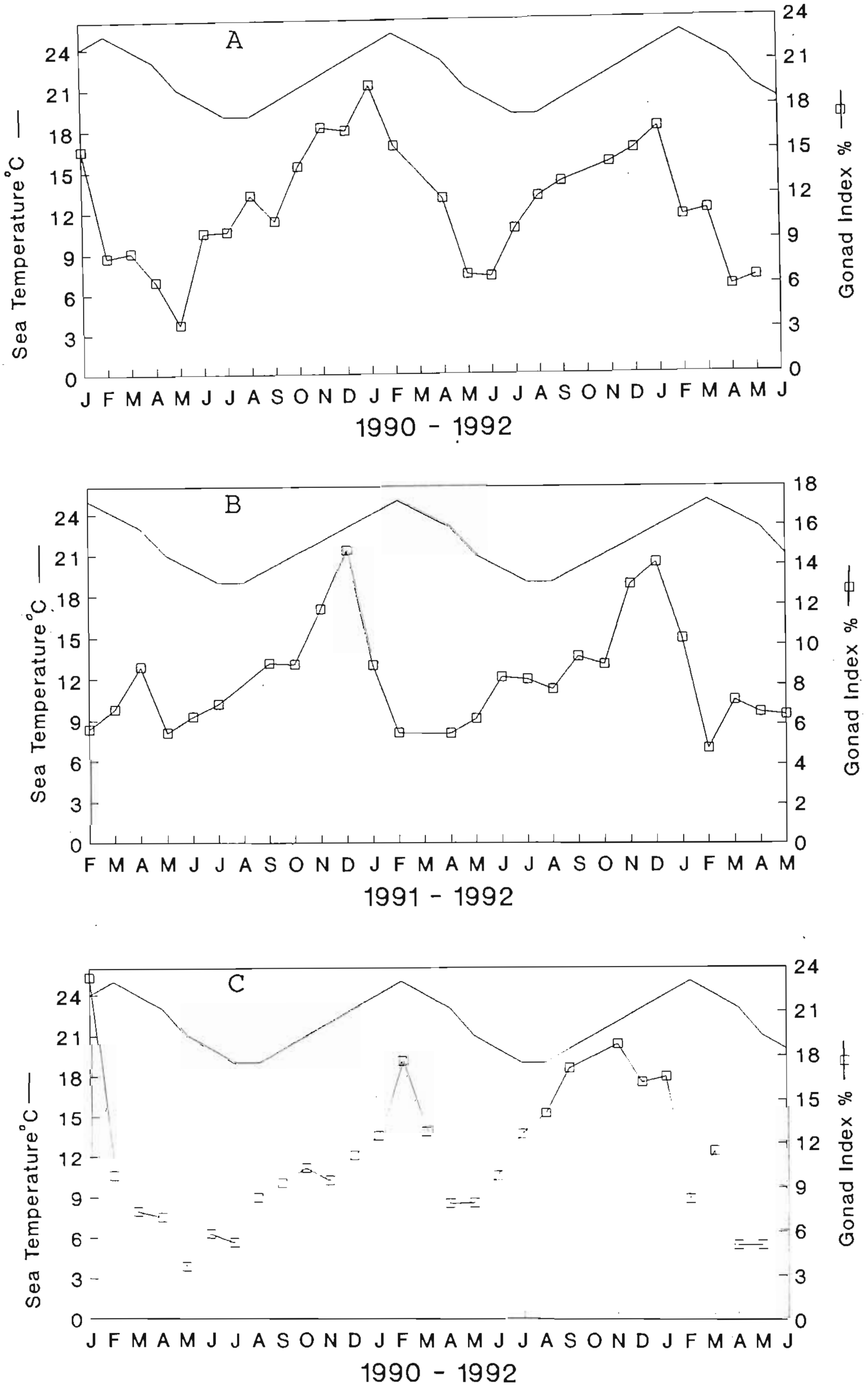


Figure 3.15 The 25 year mean monthly sea temperatures* for the Natal coast and the gonad index cycles for, A) S. variolaris at Oslo beach, B) D. savignyi at Isipingo, C) E. mathaei at Ramsgate.

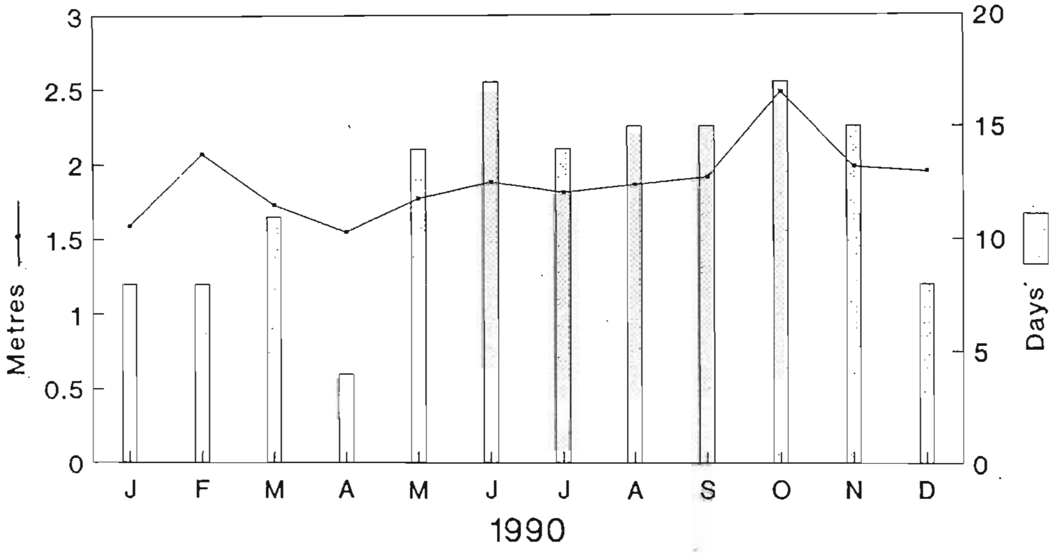


Figure 3.16 The mean monthly swell heights and the number of days in the month when swell heights exceeded the average, recorded off Port Shepstone in 1991.
* Swell height data from Natal Sharks Board.

the other two species, and *E. mathaei* a higher reproductive output than *S. variolaris*.

Table 3.2 The values used in estimating the annual reproductive output of *S. variolaris*, *E. mathaei* and *D. savignyi*.

Species	*S. variolaris*	*E. mathaei*	*D. savignyi*
Calorific value of gonad tissue	19.68	18.55	20.13
Mass of standard urchin	30.0g...............		40.0g
Reproductive output Kj yr^{-1}	78.72	77.35	69.78
Mass of standard urchin	61.0g............................		
Reproductive output Kj yr^{-1}	143.52	149.23	147.04
Mass of standard urchin	90.0g............................		
Reproductive output Kj yr^{-1}	203.88	217.66	253.68

Discussion.

Reproduction of the Oslo Beach population of S. variolaris has proved to be remarkably predictable and consistent over the course of this study. In contrast to the indistinct cycle in the Madras harbour population (Giese et al. 1964) and the extended spawning period in the S.W. Indian population (Pillay 1971), the Oslo beach population has a well defined annual cycle with a restricted spawning period. Ripe gonads were only present between December and February each year; although gametes did persist in small quantities until April these were obviously relict and degenerating.

The population of D. savignyi at Isipingo showed an annual reproductive cycle where synchrony within and between the sexes was close. This close synchrony among individuals of the same population was also observed in D. setosum by Pearse (1968). Spawning in the Isipingo population occurred between late December and late February. Changes in the gonad index suggested that repeated spawning with a monthly rhythm may have occurred, and the histological analysis provided some evidence in support of such a rhythm. Firstly, both the December and January new moon samples were dominated by spent gonads while the full moon samples contained only growing and premature gonads. Secondly, the persistence of a bimodal distribution of oocytes over the spawning months suggests that as the group of larger oocytes matures and are spawned they are replaced by growth of smaller oocytes. These two observations together with close gametogenic synchrony shown by this population suggest that repeated spawning may have occurred. More frequent sampling over the spawning period might have provided more conclusive evidence.

At no stage in the gametogenic cycle of D. savignyi were ripe ovaries present and only two ripe testes were observed. Figure 3.8 shows that significant accumulations of spermatozoa were only found in the testes over the spawning period. During the growing stage from April to November spermatocytes accumulated in the lumens and only in December\January did spermatozoa begin replacing the spermatocytes. Over the spawning period the ovaries contained numerous large oocytes but only occasional ripe ova were present (Plate 1B). This apparent absence of the extended phase of accumulation of mature gametes, which is characteristic of echinoid gametogenic cycles, is curious, yet I cannot offer any adequate explanation. However it is perhaps of value to compare the present observation with work done by Holland (1967), who reported that in the cidaroid Stylocidaris affinis, primary oocytes undergo maturation divisions only a short while before spawning, and so the ovaries did not contain a mass of stored ova for an extended time before spawning. This maturation of ova immediately prior to spawning or during spawning has also been reported for non-echinoid echinoderms, eg. crinoids (Dan 1952) and holothurians (Courtney 1927, Smiley 1984), and after spawning as in asteroids (Walker 1982).
If this apparent absence of accumulation and storage of mature ova in D. savignyi is a real characteristic of gametogenesis in this species, it raises the question of what possible significance might be attached to the extended storage of ova.

The gonad index cycle for E. mathaei at Ramsgate reflects an annual reproductive cycle. However, a few points revealed by the histological analysis suggest that this annual cycle is not as distinct as those of S. variolaris and D. savignyi on the South African coast. Firstly, with the exception of June 1991 and May, June and August 1992 all the oocytes/ova frequency polygons are similar, with oocytes of all sizes present. Furthermore, no sequence of oocyte growth could be followed through the frequency polygons over the years. In 1992 ripe gonads were present in samples from eight months of the year and 60% of all urchins sampled over the study were either ripe or spent. However, the predominance of recovering and growing stages in samples from June to September, plus the high gonad index peak in January or February each year provides evidence for the presence of an annual reproductive cycle in this species. The relative asynchrony among individuals suggests that gametogenesis was initiated at different times between April and September, and when spawning occurred ca six months later it was over an extended period as different individuals matured. There was some synchronisation over the spawning period and possibly a large proportion of the population spawned between January and February while spawning at a lower intensity occurred between November and April. Reproduction in a population of E. mathaei in the Gulf of Suez (Pearse 1968) showed similar features, in that there was poor gametogenic synchrony yet the population displayed a relatively distinct annual cycle.

Correlations between sea temperature seasonality and reproductive cycles have been demonstrated for sea urchins (Pearse & Cameron 1991) and other marine invertebrates (Korringa 1947). However correlation alone is scant evidence for a causal relationship. I believe that it is unlikely that a single seasonal environmental factor could act to regulate as complex a process as reproduction, and indeed there is little if any conclusive evidence that this actually occurs (Pearse 1981). It is more conceivable that regulation of gametogenic cycles arises from the interaction of a number of biotic and abiotic factors which are capable of influencing gametogenesis and other aspects of reproduction. Although perhaps not strictly part of the reproductive cycle, the planktonic larval stage, metamorphosis and settlement, with their associated requirements for success, must be capable of exerting pressure selecting for optimal gametogenic periodicity. Views which emphasize the combined influence of a number of factors on the reproductive cycle have been expressed by Lessios (1981), Cameron (1986), Guillou & Michel (1993), and Hendler (1991).

From a review of the timing and patterns of reproduction in marine invertebrates by Giese and Pearse (1974) it is apparent that where species have broad latitudinal ranges their breeding seasons vary, generally being most limited where the environment is highly seasonal and most extended in the essentially aseasonal tropics. Yet, there are significant exceptions where species possess annual cycles in environments where there is no temperature seasonality, for example, the deep sea echinoid Echinus affinis in the Rockall Trough (Tyler & Gage 1984). While an environment on a geographic scale may be considered aseasonal or seasonal, is it not possible that factors prevailing on the habitat or microhabitat scale may not show the same characteristics? And could these factors not be significant enough to override the influence of more obvious seasonal or aseasonal conditions? Furthermore, within a geographical area, or even within a habitat, these factors may have species specific effects resulting in different species showing restricted and continuous reproduction under apparently similar aseasonal or seasonal conditions. This might perhaps explain, for example, the situation in the N.W Red Sea, where D. setosum has a restricted annual cycle (Pearse 1970) and *E. mathaei* is reproductively active all year (Pearse 1969).

The geographical gradation in the reproductive periodicity of *S. variolaris* fits the general correlation between environmental seasonality and reproductive periodicity. It is however interesting to note that the two factors with the most predictable seasonal fluctuations, photoperiod and sea temperature, appear not to influence reproductive periodicity in *S. variolaris* (Drummond 1991b). If these factors were implicated, it could be expected that populations in opposite hemispheres would breed in the same season but at different times of the year. This is not so, as the Oslo Beach and S.W.Indian populations reproduce at the same time of the year, peaking in December-January. It has been suggested that ecological factors such as fluctuations in occurrence of food for adults or larvae, presence or absence of larval predators or factors affecting settlement of larvae, may play a role in the timing of reproduction in *S. variolaris* on the South African coast (Drummond 1991b).

Although there are no data for reproduction of tropical populations of *D. savignyi*, the closely related *D. setosum* shows a geographical gradation in reproductive periodicity similar to that of *S. variolaris*. Populations near the equator (Philippines and Singapore) are reproductively active all year (Tuason & Gomez 1979, Hori *et al.* 1987), while in northern (Japan) and southern (Australia) populations where the environment is more seasonal, reproduction is restricted to the summer months (Stephenson 1934, Yoshida 1952). Therefore I suspect that populations of *D. savignyi* closer to the equator could also be reproductively active for all or most of the year.

Reproduction in E. mathaei is an exception to the correlation between environmental seasonality and reproductive periodicity. In the Gulf of Suez and off Japan, populations of E. mathaei spawn during the summer months (Onada 1936, Pearse 1969), but over most of the rest of its range, including Rottnest Island (S.W. Australia), reproduction is continuous and asynchronous (Pearse 1968, 1969, Pearse & Phillips 1968). Pearse and Phillips (1968) suggest that winter sea temperatures at Rottnest Island are probably high enough to maintain reproductive activity and this accounts for the continuous reproduction observed in this population. Sea temperatures at Rottnest I. remain between 18° and 22°C throughout the year (Hodgkin, Marsh & Smith 1959), while on the South African coast where E. mathaei has an annual reproductive cycle with spawning in the summer, the sea temperatures range between 19° and 25°C over the year. This evidence supports the contention that sea temperatures probably do not play a role in regulating reproduction in sea urchins.

The east coast of South Africa is very exposed, as there are no large offshore islands to limit the force of ocean swells. This is reflected in a statement by Duncan (1975) that 50% of the swells off Durban are ca 3.5m in height. The prevailing swell is from the south, and Harris (1961) reports that the swell has a breaking interval of 10-12 seconds, so the inshore is subject to a continuous surf. Swell heights, and thus inshore wave action, vary seasonally on the east coast as shown in Figure 3.16. Associated with the greater frequency of high swells during May-November, is an increased amount of drift algae present in the intertidal (personal observation), and a greater incidence of sand deposition and removal (J. Heeg, pers. comm.). Excessive wave action, increased availability of food and sand movements have well documented consequences for adult and juvenile sea urchins. Firstly, excessive wave action increases the risk of displacement (McPherson 1968, Lawrence & Sammarco 1982) and reduces fertilization success by rapid dilution of gametes (Pennington 1985). Increased amounts of drift algae, torn from subtidal beds by high seas, are present over the time when the sea urchins are accumulating nutrients to support gametogenesis. Sand movements appear enhance the risk of displacement in S. variolaris (Drummond 1991a), and by burying sedentary sea urchins, interferes with respiration and feeding (de Ridder & Lawrence 1982), and probably extrusion of gametes.

I suggest that reproduction in the three species studied, could be timed to exploit the advantageous and limit the effect of disadvantageous consequences of swell height seasonality. By spawning over the months when inshore wave action is at its lowest, fertilization success is likely to be highest, as Pennington (1985) has shown that dilution of sea urchin sperm by high current velocity significantly reduces fertilization success. Recruitment of juveniles in all three species occurs during the period of increased swell heights. Although the higher swells and associated local currents probably assist the inshore transport of larvae (Coe 1956, Cameron & Rumrill 1982), mortality at settlement and during early growth in the high energy environment is likely to be high. The juveniles of the three study echinoids show distinct attachment site preferences or behaviour which possibly serve to limit mortality arising from water and sand movements and possibly predation. S. variolaris recruits are almost always found under the canopy of adult spines; 18 out of 20 juveniles observed at Sheffield Beach 1991 were within 20mm of the test of an adult. All juvenile E. mathaei with test diameter less than 25mm were cryptic, under boulders or in rock or coral crevices, but never closely associated with adults. D. savignyi recruits at Ramsgate in 1991 and 1992 were observed to remain in distinct, tight aggregations as they grew from a test diameter of <5 to 30mm, a period of ca. 5 months. This behaviour probably served an anti-predation role rather than protection against excessive wave action. The mobility of this species would enable it to move into cryptic positions as water movement increased with the incoming tide.

When assessing the relative investment in reproduction, two points of interest are noteworthy. Firstly, when standard animals of 90g are compared, D. savignyi had a greater reproductive output than either S. variolaris or E. mathaei. Yet when smaller size classes were compared there were only marginal differences between the species, suggesting that for the first 12-18 months after settlement D. savignyi allocates resources to growth at the expense of reproduction. Secondly, although the estimated reproductive output for E. mathaei was higher than that of S. variolaris, the difference was not great. This is curious because S. variolaris occupies a higher energy habitat than E. mathaei, and exposure to wave action is known to lower gonadal production (Gonor 1973a). So I would have expected gonadal production in S. variolaris to have been much lower than that of E. mathaei.

In summary.

The tropical echinoids S. variolaris, E. mathaei and D. savignyi all show annual reproductive cycles on the South African coast. Spawning occurs in the summer, from mid-December to February and March in S. variolaris and D. savignyi respectively. Relatively poor gametogenic synchrony in E. mathaei results in an extended spawning period, December to late April.

D. savignyi become reproductively active after ca. 6 months of growth, in contrast to the other two species which only reach sexual maturity after 12-24 months of growth.

Differences in annual reproductive output are most apparent in the larger size classes. Large (90g) D. savignyi produced 15-20% more gametes than E. mathaei and S. variolaris respectively. This suggests that D. savignyi makes a greater relative investment in reproduction than the other two species on this coast.

Chapter 4 Maintenance.

Introduction.

Investment in maintenance encompasses the allocation of resources to those morphological, physiological and behavioral features which enhance the probability of an organism reaching the age of first reproduction, and then surviving to reproduce during future breeding periods (Gadgil & Bossert 1970, Ebert 1982).

The physical conditions operating in the intertidal region of the South African east coast are dominated by a continuous surf; the sedentary organisms occupying these waveswept intertidal habitats are therefore subject to considerable drag and impact forces (Denny, Daniel & Koehl 1985). Maintenance must therefore function to provide resistance to, or protection from, these forces. In addition, maintenance allocation must serve to offer defence against predation.

For the purposes of comparing the relative allocation to maintenance by the three sea urchin species, morphological features were selected which were considered to be associated with the avoidance of damage or death. Measurements of these morphological features relative to body size (mass or diameter) were regarded as reflections of the species' investment in maintenance.

As sedentary organisms the sea urchins' prime mode of defence is their test and spines. Therefore the proportion of total body mass contributed by test and spines is a means whereby the relative allocation by the three species to maintenance could be compared. That the relative contribution to test and spines is a valid reflection of allocation to maintenance, is supported by the results of a study by Ebert (1982). In this study it was shown that survivorship in 38 populations of 17 echinoid species was positively related to the relative thickness of the body wall and the degree of protection from the surf. This positive relationship supported Eberts' (1982) hypothesis that survival of echinoids is related to the investment of resources in maintenance.

Two other features of the sea urchin body have implications for maintenance. The peristome with its uncalcified membrane represents the weak point in the sea urchin's defence, as predators e.g. fish, crustaceans and shore birds, gain access to the soft parts through this opening (Lawrence 1975, personal observation). Perhaps of greater significance, however, is that the size of the peristome relative to body size affects the area of the adoral test surface available for the accommodation of tube foot pore pairs. This would have an effect on the sea urchins' ability to attach to the substratum, as strength of attachment is determined by tube foot strength and the total number of tube feet (Smith 1978). Displacement by water and sand movements is a significant cause of mortality for sea urchins on this high energy coast (personal observation) and elsewhere (Ebert 1982), therefore the ability to resist displacement would have considerable survival value. The number and arrangement of tube feet pore pairs was assumed to reflect the ability of each species to resist displacement (Smith 1978). Quantifying the force with which each species adhered to the substratum would support the conclusions of the pore pair analysis.

The first part of this chapter assesses the relative allocation to maintenance by each species. This was then correlated with exposure indices for their habitats in order to test the hypothesis that the species occupying higher energy habitats would show a relatively greater allocation to maintenance.

In addition to measurable morphological features which are associated with maintenance there are behavioral mechanisms which have significance for protection and defence. For example, the covering response observed in numerous species (Yoshida 1966, Lawrence 1976), has been suggested to provide protection against high light intensity, extreme temperatures, desiccation, predation and to provide resistance to wave action (de Ridder & Lawrence 1982). Aggregation, as observed in Diadema species, is considered to have a protective function (Pearse & Arch 1969). Goss-Custard, Jones, Kitching & Norton (1979) and Lawrence and Sammarco (1982) list a number of species which assume sedentary, cryptic or burrowing lifestyles in response to heavy predation or excessive wave action. On the South African east coast S. variolaris appears to have responded to the high energy environment by adopting a sedentary, often cryptic and occasionally burrowing lifestyle (Drummond 1991a). Subjective observations suggest that E. mathaei on this coast is also sedentary, cryptic and may excavate burrows. In contrast, D. savignyi, as with other members of the genus Diadema, probably relies on its mobility to seek appropriate shelter from water and sand movements. The final part of this chapter documents the degree of movement of, and the positions occupied by D. savignyi and E. mathaei on the Natal coast.

Materials and Methods.

4.1 Proportional contribution by the body wall to total mass.

Sampling frequency, study sites and the size ranges of the samples are described in Chapter 3. Body wall data was acquired from 130 E. mathaei, 119 S. variolaris and 76 D. savignyi. Excess water was allowed to drain away and algal fragments removed from between the spines before the total wet mass of each individual was determined. Each animal was dissected and the following component parts separated and their masses determined: gonad, Aristotle's lantern, gut and contents, perivisceral fluid and body wall. The body wall component included the test, spines, pedicellaria, tube feet and ampullae. Linear regression techniques (Draper and Smith 1981) were used to compare the rates of change in the relationship between mass of body wall and total body mass. A common regression coefficient was fitted to the data, the analysis was then extended to compare the regression coefficients calculated for each species separately.

4.2 Relative size of the peristome, pore pair analysis and force of attachment.

4.2.1 Relative size of the peristome.

The maximum test diameter was measured from ambulacrum to opposite interambulacrum with outside calipers. The diameter of the peristomial opening was measured along this same axis. In E. mathaei, where the test is elliptical, close correlations between test length and test width, test length and wet mass ($r^2 = 0.94$, $r^2 = 0.90$), justified the use of test length as a measure of size.

The relationship between peristome diameter and test diameter was analysed in the manner described in section 4.1 above.

4.2.2 Pore pair analysis.

Ten individuals of each species were sun dried and the spines removed by soaking in 5% sodium hypochlorite overnight. The total number of pore pairs in 3 ambulacra of each urchin were counted, and a mean per ambulacrum calculated for each individual. The arrangement of the pore pairs was also noted. Regression equations were calculated from the relationship between number of pore pairs and test diameter for each species and the regression coefficients compared.

4.2.3 Force of attachment.

The tenacity with which each species adhered to the substratum was quantified in a manner similar to that of Dotan (1991). However, the loop of cord used by Dotan (1991) was replaced by a small three pronged aluminium grapple (Fig. 4.1), which was attached to a 10Kg or 30Kg spring balance. A rubber O-ring held the arms of the grapple securely around the sea urchin, and a plastic "tell-tale" on the spring balance registered the kilogram measurement at detachment. Kilogram-force so determined was converted to Newtons by multiplying by 9.8 (S.A. Bureau of Standards, 1972). Test diameters and the force of attachment of 20 specimens of S. variolaris and E. mathaei were measured. It was not possible to acquire measurements from D. savignyi as this species responded to placement of the grapple by attempting to move away. As urchins occupying crevices use spines as well as tube feet to resist displacement, only those urchins attached on exposed rock surfaces

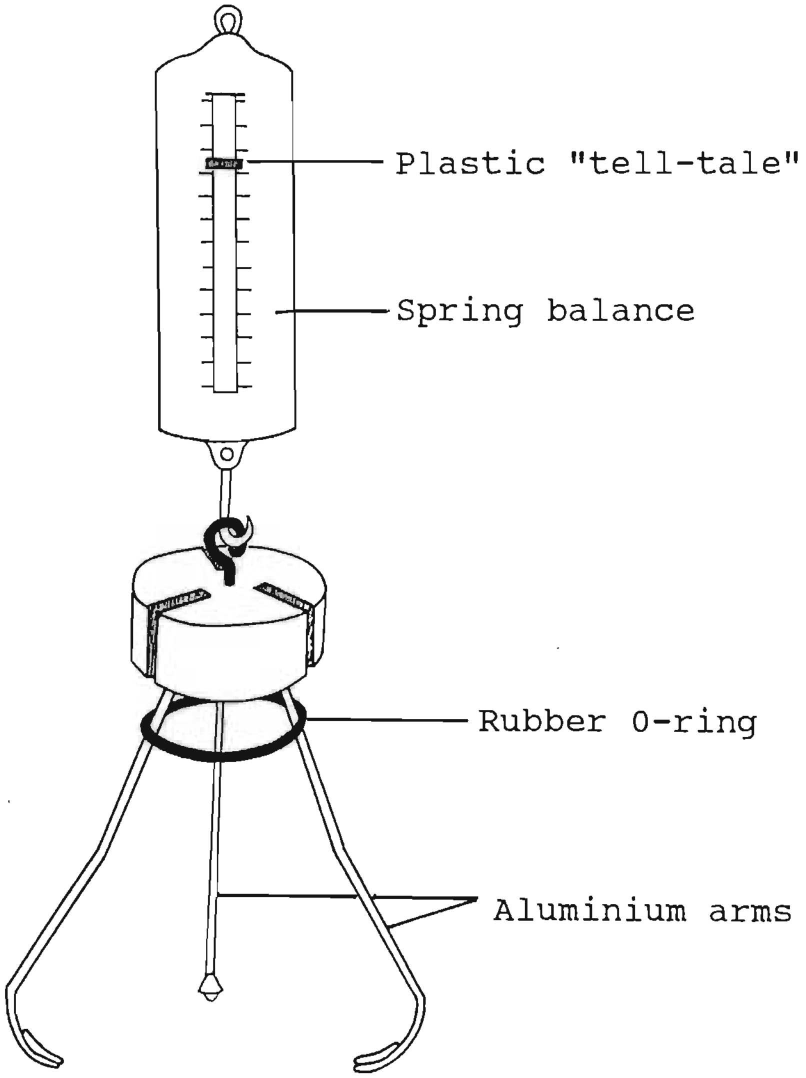


Figure 4.1 The apparatus which was used to determine the tenacity with which S. variolaris and E. mathaei adhered to the substratum.

were tested.

4.3 Relative water movement.

Relative water movement as an index of exposure in each habitat was determined using the clod card technique pioneered by Doty (1971) and used subsequently by Russo (1977) and Lissner (1978, 1983). This method is based on the knowledge that the melting of calcium sulphate in water is diffusion controlled, therefore the weight loss of each clod is directly related to water movement (Doty 1971). Calcium sulphate clods were prepared by mixing 55g of calcium sulphate with 40ml of water in paper cups. The clods were dried for two days at room temperature and humidity and then attached to plastic cards with Epidermix contact cement, numbered and weighed. The mean mass of the clod and card was 92.8g (SE 0.4g n=16). Clod cards were taped onto concrete blocks and wedged into channels in the intertidal shelf at the Oslo Beach (n = 4, n = sample size) and placed on the bottom of pools at Isipingo (n = 4) and Ramsgate (n = 6). The clod cards were retrieved 24 hours later, allowed to dry for two days at room temperature and humidity and then weighed. The exposure index was calculated by dividing the weight lost by each clod card placed in the field by the weight lost by control cards kept in still water in the laboratory.

4.4 Translocation experiments.

The ability to survive under different regimes of water movement, was tested by translocating ten individuals of each species to positions where they were subject to greater or lesser turbulence than in their original positions.

S. variolaris from an exposed intertidal shelf habitat were placed in a deep (1-1.5m) mid-shore pool; E. mathaei and D. savignyi from a sheltered mid-shore pool were translocated into the more exposed lower intertidal.

4.5 Movement and attachment site preferences.

It is known from a previous study (Drummond 1991a) that S. variolaris is sedentary and often cryptic on the Natal coast. Sand free cracks, crevices and hollows as well as vertical rock walls are the preferred attachment sites. Therefore movement and attachment site preference were only investigated for E. mathaei and D. savignyi.

4.5.1. Movement.

The timing and degree of movement by E. mathaei and D. savignyi were investigated by monitoring a group of each species in large mid-shore pools at Ramsgate between 3rd January 1992 and 6th April 1992. An area of ca $2m^2$ was selected for each species, and the positions of all D. savignyi and E. mathaei present were recorded. Although sea urchins were not individually labelled the test diameter of each urchin present was measured as a means of keeping track of individuals. The pools were visited that night at low tide and again during low tide the following morning, and then at monthly intervals for a further three months. At each visit the positions of all urchins in the demarcated area were recorded.

4.5.2 Attachment site preferences.

The nature of attachment sites occupied by E. mathaei and D. savignyi was recorded along line transects placed through the pools at Ramsgate and Isipingo.

Results.

4.1 Proportional contribution by body wall to total mass.

A significant positive linear relationship between body mass and body wall was evident in all three species (Fig. 4.2). The regression coefficients of the three equations were found to be significantly different from each other (Table 4.1).

Table 4.1 Comparison of the regression coefficients calculated for the relationship between mass of body wall and total body mass for; 1) *S. variolaris*, 2) *E. mathaei*, 3) *D. savignyi*.

Species	Difference between slopes	SE	t	p
1 vs 2	(0.584 - 0.482)	0.011	9.29	<0.001
1 vs 3	(0.584 - 0.444)	0.010	13.66	<0.001
2 vs 3	(0.482 - 0.444)	0.012	3.12	<0.01

S. variolaris n = 119
E. mathaei n = 130
D. savignyi n = 76

This shows that, for the same size urchin, the body wall in *S. variolaris* accounted for a relatively greater proportion of the total body mass than in the other two species. Furthermore, the observed difference in the regression coefficients of *E. mathaei* and *D. savignyi* was significant (Fig. 4.2, Table 4.1). Therefore in terms of the maintenance function ascribed to the body wall, *S. variolaris* shows a relatively greater investment in

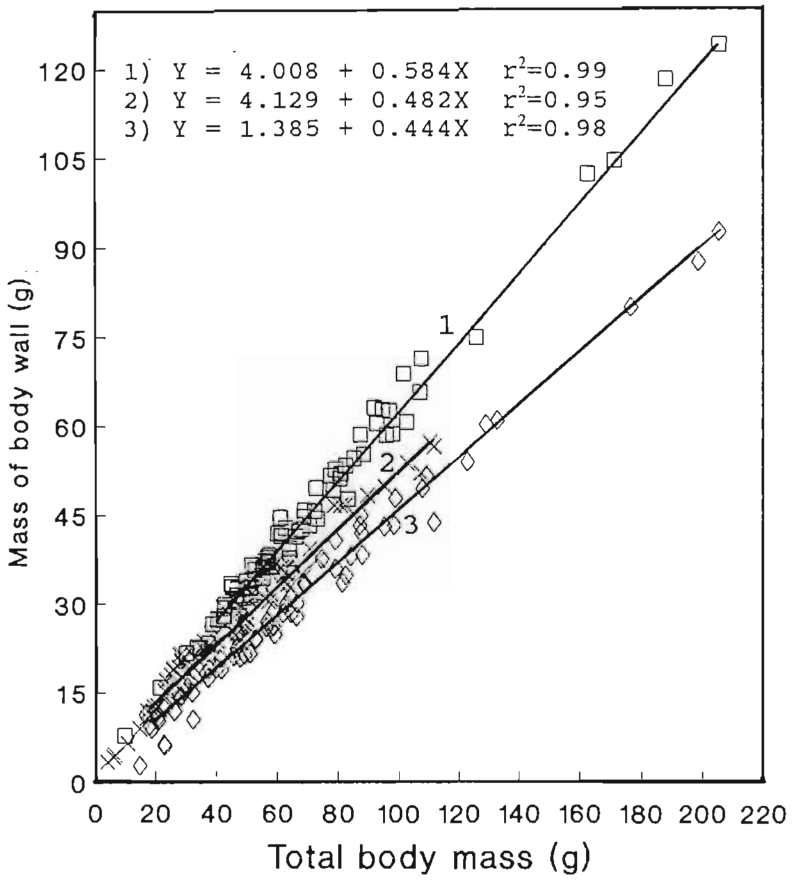


Figure 4.2 The linear regressions and regression equations for the relationship between mass of the body wall and total body mass for; 1) S. variolaris, 2) E. mathaei, 3) D. savignyi.

maintenance than E. mathaei or D. savignyi, and E. mathaei a greater relative investment than D. savignyi.

4.2 Relative size of the peristome, pore pair analysis and force of attachment to substratum.

4.2.1 Relative size of the peristome.

In all three species the size of the peristome increased linearly with increase in test diameter (Fig. 4.3). The coefficient for the regression line for S. variolaris was significantly smaller than that of E. mathaei and D. savignyi (Table 4.2). There was a significant difference between the regression coefficients of E. mathaei and D. savignyi (Table 4.2), however, this difference was perhaps only valid for larger individuals. S. variolaris therefore has a smaller peristomial opening than the other two species, and thus a potentially larger area available to accommodate tube feet pore pairs.

Table 4.2 Comparison of the regression coefficients calculated for the relationship between peristome diameter and test diameter for; 1) S. variolaris, 2) E. mathaei, 3) D. savignyi.

Species	Difference between slopes	SE	t	p
1 vs 2	(2.059 - 3.073)	0.188	5.40	<0.001
1 vs 3	(2.059 - 4.182)	0.209	10.17	<0.001
2 vs 3	(3.073 - 4.182)	0.198	5.59	<0.001

S. variolaris n = 119
E. mathaei n = 130
D. savignyi n = 76

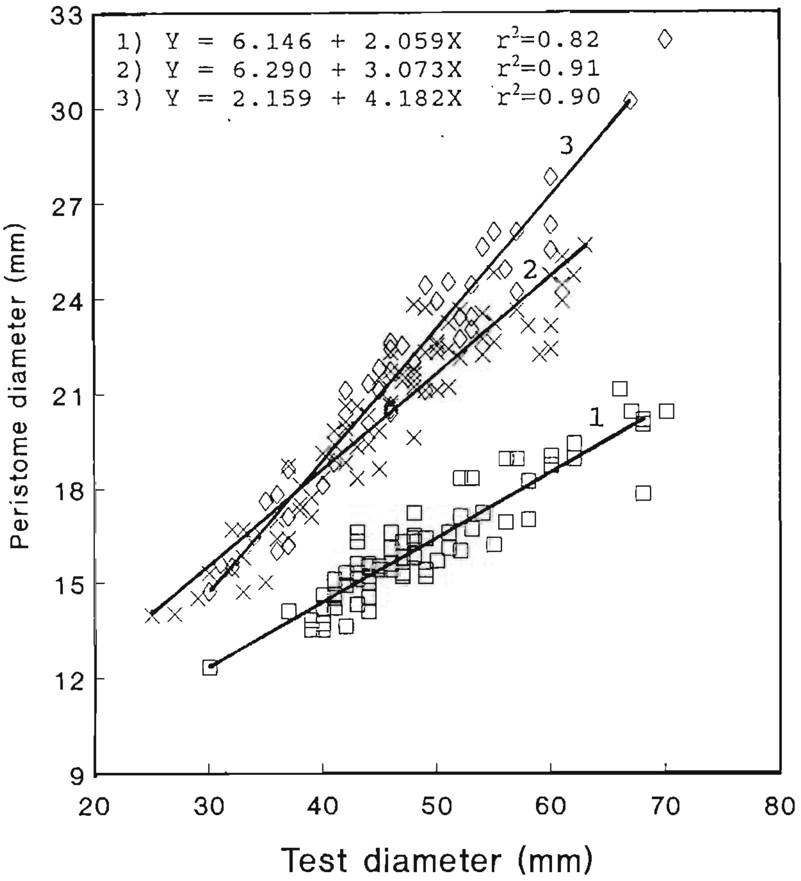


Figure 4.3 The linear regressions and regression equations for the relationship between peristome diameter and test diameter for; 1) S. variolaris, 2) E. mathaei, 3) D. savignyi.

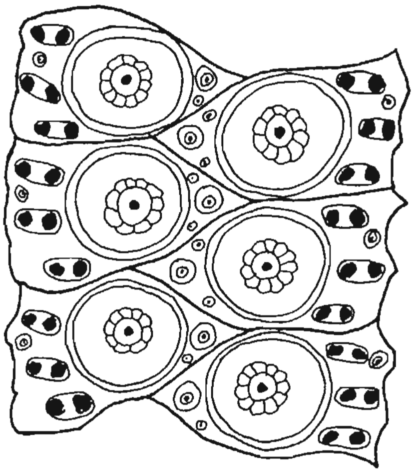
4.2.2 Pore pair analysis.

In each of the three species the pore pairs were grouped in two columns per ambulacrum; however the distribution of pore pairs within each column differed markedly (Fig. 4.4). In E. mathaei and D. savignyi the pore pairs on the oral surface were in four and three pair arcs respectively. In S. variolaris the pore pairs were in three regularly defined rows within each column, these rows were expanded into broad phyllodes on the oral surface of the test and more tightly packed in the remainder of the ambulacrum.

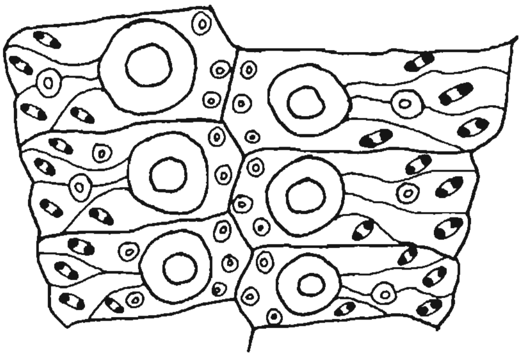
There was a close linear correlation between test diameter and number of pore pairs for all three species (Fig. 4.5). The elevation of the regression line for S. variolaris is significantly higher than that of E. mathaei and D. savignyi ($t=4.92$ and $t=16.47$ $p<0.001$) and the difference between E. mathaei and D. savignyi is significant ($t=7.04$ $p<0.001$). These results indicate that for the same size urchin S. variolaris and E. mathaei have more pore pairs than D. savignyi, and therefore a potentially greater ability to resist displacement by water movements.

4.2.3 Force of attachment.

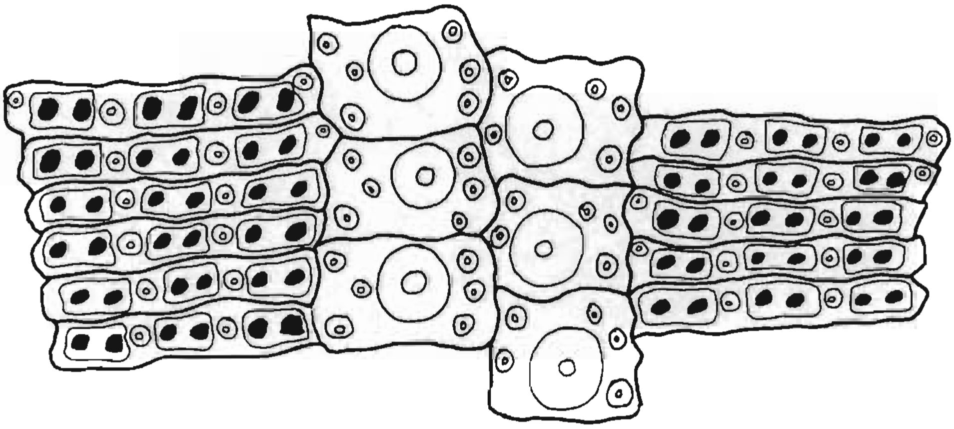
Statistically significant correlation coefficients for S. variolaris and E. mathaei respectively ($r^2=0.53$, $r^2=0.69$, $p<0.01$ $n=20$), indicate that larger urchins of both species, were capable of attaching to the substratum with greater tenacity than smaller individuals (Fig. 4.6). The regression coefficient for S. variolaris was significantly larger than that of E. mathaei ($t=2.4$, $p<0.05$, Df 38). Therefore, where individuals of the same size were



Diadema savignyi

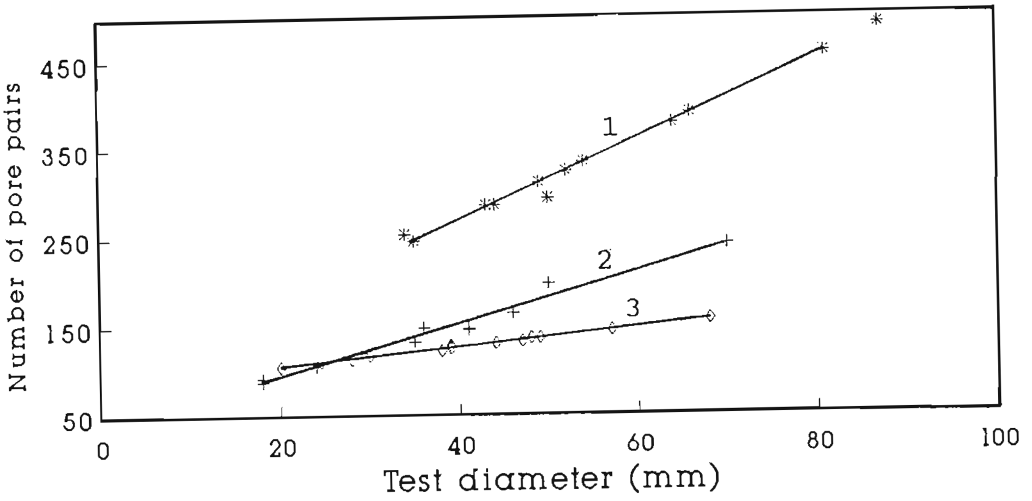


Echinometra mathaei



Stomopneustes variolaris

Figure 4.4 The arrangement of pore pairs in the ambulacra on the oral surface of S. variolaris, E. mathaei and D. savignyi.



1) $Y = 86.106 + 45.542X$ $r^2 = 0.98$

2) $Y = 34.592 + 29.363X$ $r^2 = 0.94$

3) $Y = 83.696 + 10.621X$ $r^2 = 0.97$

Figure 4.5 The regression lines and regression equations for the relationship between test diameter and number of pore pairs in 1) S. variolaris 2) E. mathaei 3) D. savignyi.

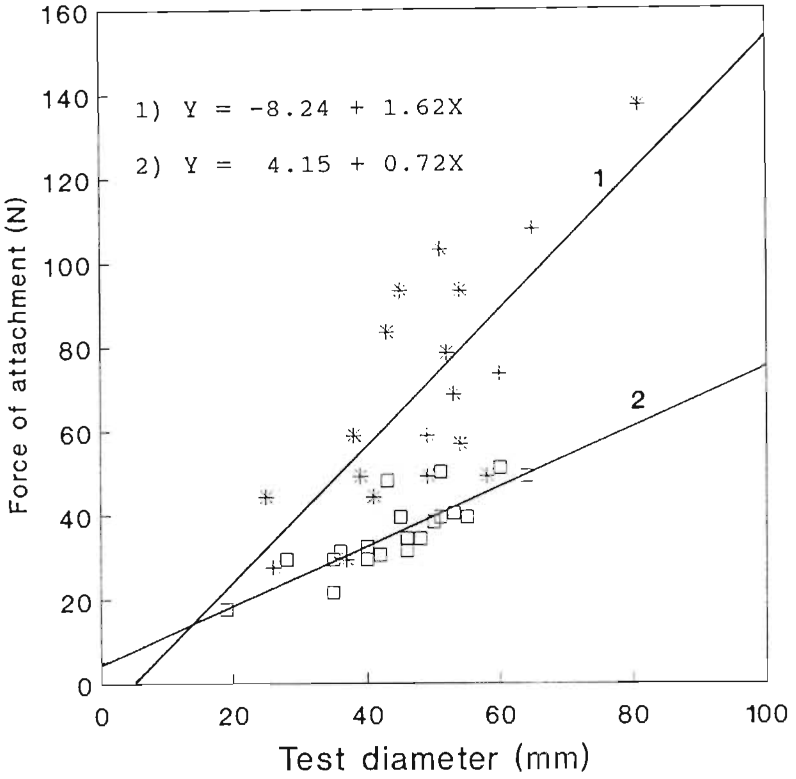


Figure 4.6 The regression lines and equations for the relationship between test diameter and force of attachment for 1) S. variolaris, 2) E. mathaei.

compared, S. variolaris was capable of attaching to the substratum with greater tenacity than E. mathaei.

4.3. Relative water movement.

The differences in water flow index (Table 4.3) between Oslo Beach and Ramsgate and Oslo Beach and Isipingo were highly significant ($t=10.55$, $t=27.34$ $p< 0.001$). No significant difference was found between the water flow index for the mid-shore pools at Isipingo and Ramsgate.

Exposure to wave action at Oslo Beach is therefore greater than at the other two study sites. The predominance at Oslo Beach of algal species adapted to high energy environments, e.g. Hypnea spicifera and the articulated calcareous red algae, provides supporting field evidence for exposure to wave action.

Table 4.3 Exposure to wave action expressed in terms of a water flow index for Oslo Beach, Ramsgate and Isipingo.

	Mean	Range	n
Oslo Beach	5.16	4.36-6.04	4
Ramsgate	1.36	1.15-1.46	6
Isipingo	1.12	1.08-1.20	4

4.4 Translocation experiments.

Survival of S. variolaris in the sheltered mid-shore pool was low, with three individuals missing after 24 hours and none present after a week (Table 4.4). Only one of the ten D. savignyi translocated into a more exposed habitat on the lower intertidal shelf had survived after 24 hours and none remained after one week. In contrast, E. mathaei translocated onto the lower intertidal shelf appeared able to tolerate the increased exposure to wave action, as only one individual was missing after 24 hours and five remained after a week. As no control animals were monitored these results have limited value, however they do infer that the three species have different levels of tolerance of water movement.

Table 4.4 Percent survival of sea urchins translocated to other habitats. (n = 10)

Species and new habitat	after 24hrs	after 7days
S. variolaris: mid-shore pool	70%	0
E. mathaei: lower intertidal	90%	50%
D. savignyi: lower intertidal	10%	0

4.5 Movement and attachment site preferences.

4.5.1 Movement.

On 3rd January 1992, nine D. savignyi individuals were recorded in the area chosen for observation. These individuals were either attached to the rock sides of the pool or just under boulders. No individuals were moving, exposed to direct sunlight or positioned on sand. During that evenings' low tide no individuals were observed in the initial positions, four urchins were actively moving across the sandy floor of the pool and one was on top of a submerged boulder. There had been so much movement it was not possible to determine which individuals had been present 12 hours previously. When the site was visited during low-tide the next morning, five urchins were present, none were active, and all were occupying sheltered positions against the pool wall or in the lee of boulders. With the exception of one individual, which had a few grey spines and was not observed previously, it was impossible to say whether these individuals had been in the area on previous visits. A month later (2nd February 1992) there were four D. savignyi present, these were not individuals I had observed earlier, as they were smaller (2-3cm); all four were under boulders. For three days prior to the March visit there had been a persistent on-shore wind, and the associated high swells had scoured all the sand out of the pool. No urchins were seen during this visit. However, when a large boulder was levered over, three urchins were seen wedged deeply into crevices between the boulder and the pool wall. By the next month some sand had accumulated in the pool and by filling the deep crevices, had forced the urchins into more visible positions.

Therefore it seems that D. savignyi at this site showed a nocturnal activity pattern, being active during the hours of darkness and occupying sheltered positions during the day. While this conclusion was based on only a single night of formal observation, nocturnal activity was noted on numerous previous occasions (personal observation), and has been reported by other workers (Pearse & Arch 1969). The potential for shelter is probably affected by the transportation of sand in and out of the pool by water movements.

On 3rd January 1992 ten E. mathaei were present in the area chosen;

of these four were juveniles with test diameters ca 2cm, the others larger adults (test diam. 3-5.5cm). The two largest individuals were attached in exposed positions on the sides of boulders, while the others were all lodged in cracks and crevices. That evening a large urchin was ca 10cm away from its earlier position, two of the smaller individuals had also moved, but only a few centimetres. At the morning lowtide the urchins were in the same positions as they had been in the night before, although for three of them their orientation within the crack was different. A month later (2nd February) one large urchin was missing, and all the small ones had moved into wider portions of their cracks. The next visit was after the wind induced swells in March, and on this occasion all the urchins were cryptic. At the next visit one small urchin was missing, the other small individuals had moved into a parallel crack and the remaining large urchins were in new positions 5-10cms from their positions as observed on the first visit.

_E_. _mathaei_ therefore appears to be essentially sedentary; although they do move short distances they remain in the same general area with some persistence. It seems likely that their movement is in response to sand accumulation and an attempt to find a better protected attachment site. However, it is possible that their movement is associated with the acquisition of food.

4.5.2 Attachment site preferences.

Subjective observations and the results reported in Table 4.5 A, suggest that the avoidance of high light intensity plays a role in _D_. _savignyi_'s choice of attachment site during the day. In addition to seeking shaded sites this species appeared to prefer

Table 4.5 The attachment sites occupied by _E_. _mathaei_ and _D_. _savignyi_ during the day, along transects at Ramsgate and Isipingo respectively.

A. Isipingo - _Diadema savignyi_ 2nd February 1992.

Type of attachment site	Number of urchins
Sides of boulders	26
Crack\crevice in shade	10
Crack\crevice in sun	3
Pool sides in shade	32
Flat rock in shade	3
Flat rock in sun	1

B. Ramsgate - _Echinometra mathaei_ 4th January 1992

Type of attachment site	Number of urchins
Cracks	12
* Burrow	4
Exposed surface	4
Among coral heads	3
Under rocks	15

* Burrows which appeared to have been excavated at least in part by the sea urchin.

attaching to vertical rather than horizontal surfaces. This may be to facilitate capture of drift material or simply because horizontal surfaces were often covered with sand to some degree. That the majority of individuals were in exposed as against cryptic positions indicates that this species probably depends on its mobility to seek shelter when necessary.

In contrast, E. mathaei appeared most often to be cryptic at Ramsgate (Table 4.5 B), and at other sites on the Natal coast where it was present (personal observation). However, larger individuals were observed in exposed positions, which could suggest that mortality due to predation or wave action is size dependent, or that no large cryptic attachment sites were available. A further preference evident in their choice of attachment site was for sand free rock surfaces. The smallest individuals <20mm were most frequently found under rocks and coral rubble on the floor of pools.

In summary then, D. savignyi shows a nocturnal pattern of activity, avoids high light intensity and is not normally cryptic, but readily seeks shelter when high seas prevail. E. mathaei, in contrast, consistently occupies cryptic positions, from which it may move short distances. Burrowing by this species was uncommon at Ramsgate and other sites where it was observed.

Discussion.

Intertidal echinoids have evolved three solutions to the problem of exposure to wave action. Species either tolerate the turbulence by occupying burrows (Goss-Custard et al. 1979), resist it by virtue of thick tests, stout spines and numerous suckered podia (Smith 1978, Ebert 1982) or are limited to sheltered habitats in the mid or upper shore (Ebert 1982).

These three solutions are reflected in a considerable body of literature which indicates that the distribution of shallow water echinoids is governed by water movement (Herring 1972, Ebert 1982, Lissner 1983, Dotan 1991). The results of the present study certainly confirm this contention. Of the three species studied, S. variolaris was found to make a significantly greater allocation of energy and resources to the test and spines. This investment in maintenance correlates with an ability to survive in the lower intertidal, despite the almost constant turbulence experienced in this region. Poor survival of this species in aquaria and in sheltered habitats suggests it may have a lower limit to its tolerance of water movement. D. savignyi and E. mathaei both show a lesser allocation to the body wall, and on the Natal coast are restricted to sheltered mid-shore pools. However, D. savignyi is found subtidally in sheltered sections of coral reefs off the northern Natal coast (Chpt. 2, Fig. 2.1). Although the test of E. mathaei is not as thick, nor are its' spines as stout as those of S. variolaris, it does occupy high energy habitats in other parts of its range, eg. the seaward edges of coral reefs off the coast of Kenya (Khamala 1971) and Gulf of Eilat (Dotan 1991). E. mathaei has been able to occupy these habitats by inhabiting burrows which they or other urchins have excavated in the substratum.

As most accounts of burrowing by E. mathaei have involved coral rock, sandstone or other loosely cemented sedimentary rock (Otter 1932, Russo 1980), the exclusion of E. mathaei from the lower intertidal on this coast may be due in part to the prevalence of dolerite and other rock types which may be resistant to abrasion by sea urchin jaws and spines. However, there are two alternative reasons which may explain the observed distribution of E. mathaei on the Natal coast. Firstly, wave action on this coast may be greater than that which E. mathaei can tolerate. The higher average wave heights and water flow indices for the South African coast when compared with data from Lissner (1983) suggests that wave action here could be more intense than on most other tropical or subtropical coasts. A second possible explanation is that in high energy habitats, S. variolaris is able to exploit drift algae more effectively than E. mathaei. Differences in podial morphology provide some evidence in support of this suggestion. Firstly, a larger number of pore pairs and the presence of broad phyllodes on the oral surface of the test in S. variolaris impart a greater potential to resist displacement while feeding, and secondly, while the oral podia in both species are of the P3 type (Smith 1978) with terminal sucker discs, the aboral podia differ. S. variolaris has P2 type, which have terminal sucker discs and the stem contains moderately well developed connective tissue and muscle layers. In contrast the aboral podia in E. mathaei are of the P1 type which are characterized by the absence of a sucker disc and the stem has only a single layer of connective tissue and sparse muscle fibres.

The significance of the difference in their aboral podia is that, S. variolaris would probably be able to grasp and manipulate drift algae more effectively in turbulent water than E. mathaei. A study by Contreras and Castilla (1987) provides some support for this suggestion. The aboral podia of Tetrapygus niger are of the C1 type which do not have a sucking disc but only a sensory pad, and the connective tissue and muscle layers are thin. This species obtains food mostly by grazing, while a sympatric species, Loxechinus albus, which is a drift feeder has aboral podia of the P2 type. Furthermore, S. variolaris is frequently observed holding algal fragments or pebbles on its aboral surface, but this behaviour has not been observed in E. mathaei on the Natal coast (personal observation). In addition to differences in podial morphology which might affect feeding, the spines of E. mathaei are relatively shorter and more closely spaced than those of S. variolaris. Most accounts of feeding by E. mathaei (including the present study) maintain that this species is wholely or partly a drift feeder. However, I suggest that while this species undoubtedly feeds on drift material, they are less likely to use their aboral podia and spines to capture drift algae and are more likely to ingest algal fragments which are washed into their burrows or encountered while foraging.

Ebert (1982) compared allocation to the body wall among species by means of α-values, which are the intercepts of regression equations where a common functional slope of 0.976 was assumed. Where B, the body wall wet mass, and T, the total wet mass of the sea urchin, the allometric equation for any species would therefore be,

$B = \alpha\ T^{0.976}$ (Ebert 1982).

When values of B and T for the three study species were inserted into this allometric equation and the resulting α-values compared with results from Ebert (1982), some interesting points emerged. Ebert (1982) correlated α-values with subjective exposure indices and survival probabilities and showed that survival of echinoids in exposed habitats was related to the investment of resources in maintenance. The greater allocation to maintenance in exposed habitats applied between species as well as within species. *E. mathaei*, for example, at Enewetak Atoll with an exposure index of 5, had a higher α-value (Table 4.6) than at the less exposed (6) site at Eilat (Table 4.6). An α-value of 0.607 for the Ramsgate population of *E. mathaei* suggests that the degree of exposure at Eilat and Ramsgate are similar. In contrast, *D. savignyi* from Isipingo had a higher α-value than *D. setosum* at Eilat. The α-value of the Oslo Beach *S. variolaris* population (Table 4.6) was higher than that of the Madras Harbour population. This was to be expected as the degree of exposure at Oslo Beach was undoubtedly higher than that of the deep water harbour habitat of the Indian population. While the regime of wave action experienced by a sea urchin is unlikely to undergo long term changes, this apparent relationship between α-value and degree of exposure to wave action within species is further evidence of the capacity of shallow water echinoids for adaptive morphological plasticity. The inverse relationship between relative size of the Aristotle's lantern and food availability (Ebert 1980) is another instance.

Table 4.6 The α-values for South African populations of _S_. _variolaris_, _D_. _savignyi_ and _E_. _mathaei_ compared with other localities.

	South Africa	Enewetak Atoll *	Eilat *	Madras Harbour *
_S_. _variolaris_	0.718			0.647
_D_. _savignyi_	0.516		0.422 [1]	
_E_. _mathaei_	0.607	0.672	0.604	

* Ebert (1982), [1] _D_. _setosum_

In addition to offering resistance to wave action, maintenance allocation must also function to provide defence against predation. Little is known about predation on echinoids on the South African east coast. However, Van der Elst (1993) lists a number of Indian ocean reef fish of families Labridae and Balistidae that consume sea urchins, and Kilburn and Rippey (1982) list a number of species of the molluscan families Cassidae and Cymatiidae that prey on sea urchins on the South African coast. In addition, the parasitic gastropods _Vexilla_ _vexillum_ (Fam. Muricidae) and _Vitreobalcis_ sp. (Fam. Eulimidae) have been observed on the tests of _E_. _mathaei_ at Ramsgate (personal observations). On three occasions the gastropod _Charonia_ _lampus_ _pustulata_ was observed feeding on _E_. _mathaei_ (personal observations).

Of the three study species, _S_. _variolaris_ with its' thick test and stout spines, combined with a small peristomial opening and ability to resist displacement is probably the least vulnerable to predation. Furthermore, there is refuge in the turbulence prevalent in the lower intertidal habitat of this species. The thin test and fragile spines of D. savignyi exclude it from exposed habitats, and with a large peristomial opening and poor attachment ability renders this species vulnerable to predation. However, as suggested for D. setosum (Lawrence 1987), their many long spines serve to increase the effective size of individuals, which, combined with the venomous nature of the spines and a habit of aggregation, probably provide a measure of protection against predators. E. mathaei is possibly the most vulnerable to predation, as it has short spines, large peristomial opening and only moderate attachment ability. Furthermore it occupies mid-shore habitats where there is little or no refuge in turbulence. This species' habit of burrowing or occupying cryptic positions is probably its' prime means of defence against predation, a view also held by McClanahan (1988).

In summary: S. variolaris on the Natal coast allocated relatively more energy and resources to the body wall than did E. mathaei and D. savignyi. S. variolaris had the smallest peristome, greatest number of pore pairs and therefore a superior ability to attach to the substratum. The relatively greater investment in maintenance by this species correlates with its occupation of the high energy lower intertidal habitat. Relative to S. variolaris, E. mathaei makes a lesser investment and D. savignyi the least; as a consequence these two species are restricted to more sheltered habitats on the Natal coast.

Chapter 5. Diet and Food harvesting.

Introduction.

A number of studies have reported that body size, growth rate and gonadal development correlate with quality and or quantity of food (Moore 1935, Ebert 1968, Gonor 1972, Guillou & Michel 1993). Furthermore, the feeding activities of regular echinoids have been shown to influence distribution and abundance of, and diversity within, algal communities (Leighton 1968, Kitching & Ebling 1961, Paine & Vadas 1969, Pearse & Hines 1979). The creation, of what Pearse _et_ _al_. (1970) term "barren grounds" is an extreme expression of this influence.

The diet and feeding behaviour of echinoids have been well documented and much of this literature has been reviewed by Reese (1966), Lawrence (1975, 1987) and De Ridder and Lawrence (1982). Analysis of gut contents and direct observations of feeding have revealed that a wide range of food items is exploited by regular echinoids. In addition, the diets of several species have been shown to differ with habitat (Dix 1970a, Herring 1972) and over time (Gonor 1973b). These two points support the conclusion that the diet of regular echinoids generally reflects the composition of food available at the place and time of feeding (Lawrence 1975).

Although regular echinoids appear to be generalists, as defined by Emlen (1973), Larsen, Vadas & Keser (1980) showed that _Strongylocentrotus_ _droebachiensis_ exhibited a high degree of preference. As somatic and gonadal growth was maximized on a diet of preferred algal food, and strong non-random feeding occurred in the presence of preferred foods, Larsen *et al*. (1980) suggested that *S. droebachiensis* was a facultative specialist. Both specialist and generalist feeding modes have adaptive significance for the life history of a sea urchin: the specialist, through selective feeding on high quality foods could maximize reproduction and the potential contribution to future generations, while the varied feeding of generalists would allow persistence in habitats which are food limited.

Lawrence (1987) suggests that the acquisition of food rather than digestion or absorption is the limiting factor. That the relative size of the gut of *E. mathaei* does not vary with food availability (Black *et al*. 1984) provides support for this suggestion. Acquisition of food involves the tube feet, spines, Aristotle's lantern and associated peristomial membrane. Algae torn from intertidal and subtidal beds and transported by tidal movements and currents become available to sea urchins as drift material. Although there has been no accurate assessment of the extent to which drift material is exploited by sea urchins, it undoubtedly forms part of the food of many regular echinoids. Burrowing species such as *Echinometra mathaei*, *Heterocentrotus mammillatus* and *Echinostrephus molaris* appear to feed exclusively on drift-algae (De Ridder & Lawrence 1982), while exploitation of drift-algae by more active echinoids probably depends on the availability of other food and the abundance of drift-algae. Sea urchins therefore have two methods of acquiring food, active grazing on attached macro-algae and the capture of drift-algae (Lawrence 1987). However, the food harvesting method used appears to vary with habitat; *Stomopneustes variolaris*, for example, was classified as a grazer on the Zanzibar coast (Herring 1972), and on South Africa's east coast as a sedentary drift feeder (Drummond 1991a). Similar variation in feeding habits was observed in Evechinus chloroticus (Dix 1970a) and Echinometra mathaei (Russo 1977, Downing & El-Zahr 1987). The amount of drift food available (Harrold & Reed 1985), the degree of exposure to wave action (Goss-Custard, Jones, Kitching & Norton 1979) and predation (Lawrence 1987), seem to be the factors which determine the method of food harvesting employed.

The investigation presented in this chapter was not intended to provide a detailed report on feeding in the three study species. As the acquisition of nutrients has direct implications for maintenance, growth and reproduction, my aim was to assess the diets and method of food harvesting in each species and to attempt to determine if there were differences between the three species in their relative investment in food harvesting.

1) S. variolaris on the South African east coast is a sedentary and often cryptic drift feeder (Drummond 1991a), but it is not known what mode of food harvesting is employed by E. mathaei and D. savignyi at this locality. D. savignyi were sedentary and occupied shaded positions during the day, especially in summer when light intensity was high, but during the night they moved about the bottom and sides of mid-shore pools (Chpt. 4. this study). E. mathaei were frequently cryptic and although they appeared to move short distances, individuals remained in particular areas with considerable persistence. Their movement was possibly in response to accumulation of sand in their pools, though the possibility that it was related to the acquisition of food cannot be excluded.

Therefore my hypothesis was that D. savignyi was an active grazer and E. mathaei a drift feeder. This hypothesis was tested by comparing the composition of their gut contents with the algal species growing in their vicinity. The presence of a "foreign" component in the gut contents would indicate that drift feeding was occurring.

2) S. variolaris is most commonly found in the lower intertidal, occupying cryptic positions on intertidal shelves or in gullies and channels, while D. savignyi and E. mathaei are restricted to mid-shore pools. As quantity and nutritional quality of food available have implications for growth and reproduction, it was of interest to compare the relative availability and type of food on a lower intertidal shelf with that of the mid-shore pools. And secondly, to determine whether there was any difference in the quality of the diets of the three species.

3) While the spines and tube feet are involved in the capture and manipulation of drift algal food, the Aristotle's lantern is the means whereby attached algal food is rasped or torn and ingested. The relative size of the jaws and Aristotle's lantern varies among species (Lawrence 1987) and among populations within species, e.g Diadema setosum, Strongylocentrotus purpuratus (Ebert 1980) and E. mathaei (Black, Johnson & Trendall 1982). In these three species it was shown that this variation correlated with food availability. Ebert (1980) suggested that this reflected adaptive morphological plasticity, whereby sea urchins allocated more resources to the Aristotle's lantern when food was scarce. The size of the jaws and overall mass of the Aristotle's lantern clearly appears to be

important in food gathering, as Black et al. (1984) have shown that individuals with relatively larger lanterns are able to graze larger areas and consume more food than individuals with relatively smaller lanterns. Lawrence (1987) comments that it is perhaps difficult to compare effectiveness in food harvesting with the relative size of the Aristotle's lantern among species, because of the differences in mode of feeding. However, I suggest that the Aristotle's lantern of an active grazer could be relatively larger than that of a sedentary drift feeder, as the biting, tearing and rasping of attached macroalgae is likely to require larger muscles and jaw elements than the more passive manipulation and ingestion of drift algae.

Furthermore, as the principal food harvesting component of sea urchins, the Aristotle's lantern, must require allocation of material and energy, resources are thus diverted away from overall growth and reproduction. This allocation to the Aristotle's lantern can account for a large proportion of the total energy of the sea urchin, e.g. 42% in Echinothrix diadema (Lawrence 1987). But, if this allocation to the Aristotle's lantern enhances fitness by permitting relatively more effective food harvesting, then it is conceivable that larger lanterns might have been selected for by species whose life histories seek to maximize growth or reproduction. The questions raised are: if relative size of Aristotle's lantern, mass of muscle, and jaw length are regarded as reflections of allocation to food harvesting, then is there any difference in the relative investment made in food harvesting by the three species and, is there a relationship between the mode of feeding and relative size of the Aristotle's lantern among the three study species?

Materials and methods.

5.1 Feeding mode employed by Diadema savignyi and Echinometra mathaei.

5.1.1 Assessment of algal communities.

The algal communities at the Isipingo and Ramsgate study sites were assessed in order to determine what species could be expected in the gut contents of grazing sea urchins at these sites.

The algal communities were assessed in terms of relative frequency of occurrence and percentage cover of species in the three algal Divisions. The presence or absence of species was recorded in 15 x 100cm^2 quadrats distributed randomly across the pools. Percentage cover of algae was estimated from 10 x 100cm^2 quadrats.

5.1.2 Gut content analysis.

The mode of feeding in S. variolaris was investigated in a previous study (Drummond 1991a); however I chose to examine the gut contents in the present study in order to permit comparison with the other two species over the same time period.

The gut contents of 6 D. savignyi, 7 E. mathaei and 5 S. variolaris from each of four monthly samples were examined, in order to determine:

a) the dominant constituents, and

b) whether algal species which were not part of the local algal community, i.e. the "foreign" component had been consumed, which would indicate that drift feeding had occurred.

Ten microscope fields (10x mag.) of the dispersed contents were examined for each gut sample. In each field the percentage cover of each of the three algal Divisions, bottom material and animal and terrestrial plant material was estimated. Although the gut contents were fragmented, attempts were made to identify the most frequently occurring algal species.

5.2 Comparison of diets and food availability.

5.2.1 Food availability.

Food availability at each site was compared in terms of percentage cover of attached macroalgae and the mass and composition of drift algae present on selected occasions. Data acquired in section 5.1.1 (this Chpt.) were used to compare algal percentage cover at the three study sites. Drift algae were collected from 10 x 50cm^2 quadrats distributed randomly in the Ramsgate pool and on the rocky shelf at Oslo Beach on 15th May 1992, 14th June 1992 and 16th June 1993. Obviously this method of comparing drift algal abundance only considered macroscopic algal drift. Nevertheless, it was felt that it would provide a valid indication of the relative differences in availability of drift algae. Because of the distance between Isipingo and the other two sites it was not possible to sample all three sites during the same low tide. Therefore the amount of drift-algae present on the lower intertidal shelf and in the mid-shore pool at Isipingo was compared subjectively on three other occasions.

5.2.2 Quality of diets.

The quality of the diets of the three species was compared by analysing the gross energy (MJ/Kg), protein content (%) and relative contribution of organic and inorganic material. Gut contents were extracted from the oesophagus and initial portions of the foregut of the urchins, rinsed in sea water and dried at 60°C for 12 hrs before milling to a fine powder. Gut contents were collected over four months from a total of 30 urchins of each species, and pooled. Protein analysis was by the Kjeldahl method and gross energy was determined by bomb calorimetry. Samples were ashed at 480°C for six hours to acquire an estimate of the percentage of organic and inorganic material in the urchin's diets. All analyses were performed in triplicate.

5.3 Relative size of the Aristotle's lantern and length of jaws, and mass of muscle associated with the Aristotle's lantern.

5.3.1 Aristotle's lantern and jaw length.

Aristotle's lanterns were extracted from 83 _S_. _variolaris_, 113 _E_. _mathaei_ and 72 _D_. _savignyi_; the total wet weight of each urchin and the wet weight of the Aristotle's lantern was determined. The lantern wet weight included the skeletal elements and all the associated muscles. The lanterns were placed in 5% sodium hypochlorite for 24 to 48 hrs to remove the organic material. The jaw elements were separated and the length of 5 half pyramids per urchin were measured to 0.01mm with vernier calipers. Jaw measurements were taken from the oral tip to the epiphysis junction at the aboral end, as described by Ebert (1980). Linear regression techniques (Draper & Smith 1981) were used to compare the regression coefficients for the relationships between size (mass) of Aristotle's lantern and total body mass, the length of jaws and test diameter.

5.3.2 Mass of muscle associated with the Aristotle's lantern.

The total body mass of 50 individuals of each species was determined, and their Aristotle's lanterns and attached muscles dissected out. The portion of the oesophagus within the lantern was removed before the wet weight of the lantern and muscles were determined to the nearest 0.01g. The muscle was removed by standing the lanterns in 5% sodium hypochlorite for 24 hours. The lanterns were placed in a desiccator to dry to a constant weight before their mass was determined. The difference between the initial wet weight and the tissue free weight was taken to represent the mass of muscle associated with the Aristotle's lantern. Regression equations were fitted to the data and the regression coefficients compared.

5.4 Amount of food in the gut of the three species.

The gut contents of 60 urchins of each species were extracted and the wet weights determined to the nearest 0.01g. The samples for each species were collected over eight months (Jan-Aug 1992), so any seasonal variation was accommodated, but could not dominate the results. Regression equations were fitted to the data and the regression coefficients compared.

Results.

5.1 Feeding mode employed by *Diadema savignyi* and *Echinometra mathaei*.

5.1.1 Assessment of algal communities.

In both Ramsgate and Isipingo mid-shore pools, the encrusting *Lithothamnion* sp. dominated in terms of percentage cover and frequency of occurrence (Fig. 5.1 & Fig. 5.2). A further encrusting species, *Ralfsia expansa*, was present at both sites. The absence of significant amounts of macroalgae in the Isipingo and Ramsgate pools was possibly accounted for by the high density of herbivores (molluscs, fish and other echinoid species) in the pools. The only macroalgal species present were small patches of *Dictyota* sp. and *Padina commersonii* in the shallowest areas of the Ramsgate pool and high on the sides of the Isipingo pool. In both pools a well grazed "turf" of stunted *Jania* sp. and a mossy filamentous green alga, which I was unable to identify with confidence (possibly *Bryopsis* sp.), was present on the pool sides and upper surfaces of boulders. In the Isipingo pool the algal turf and rock surfaces were covered by a fine organic film which I suspect was composed largely of bacteria.

5.1.2 Gut content analysis.

The dissections performed during this study showed that food pellets were always present in all loops of the intestines in the three species, and only rarely was food not present in the oesophagus and initial (stomach) portion of the gut.

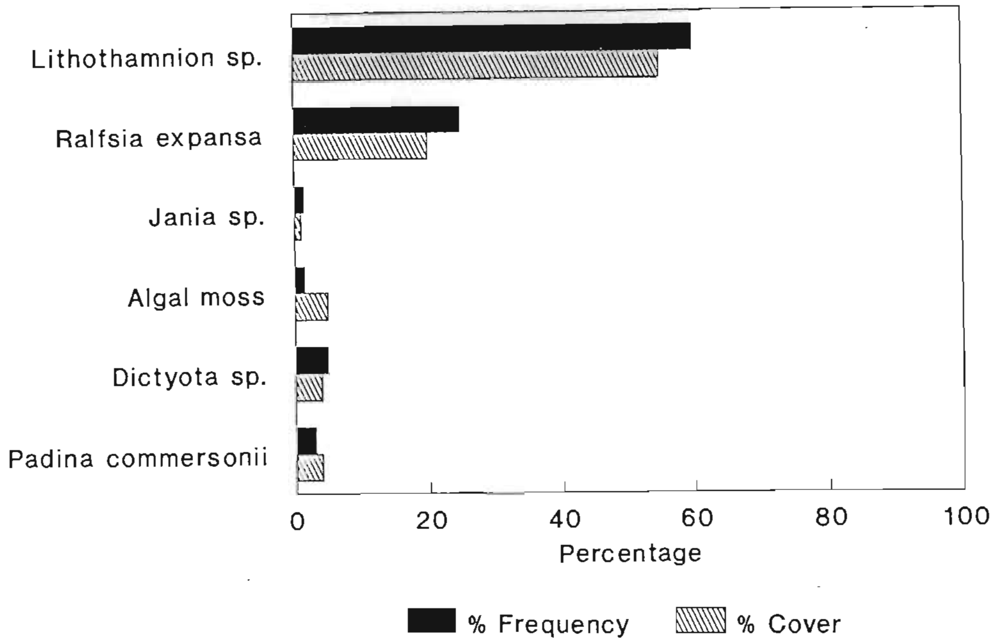


Figure 5.1 The percent frequency of occurrence and percentage cover of algal species at Ramsgate.

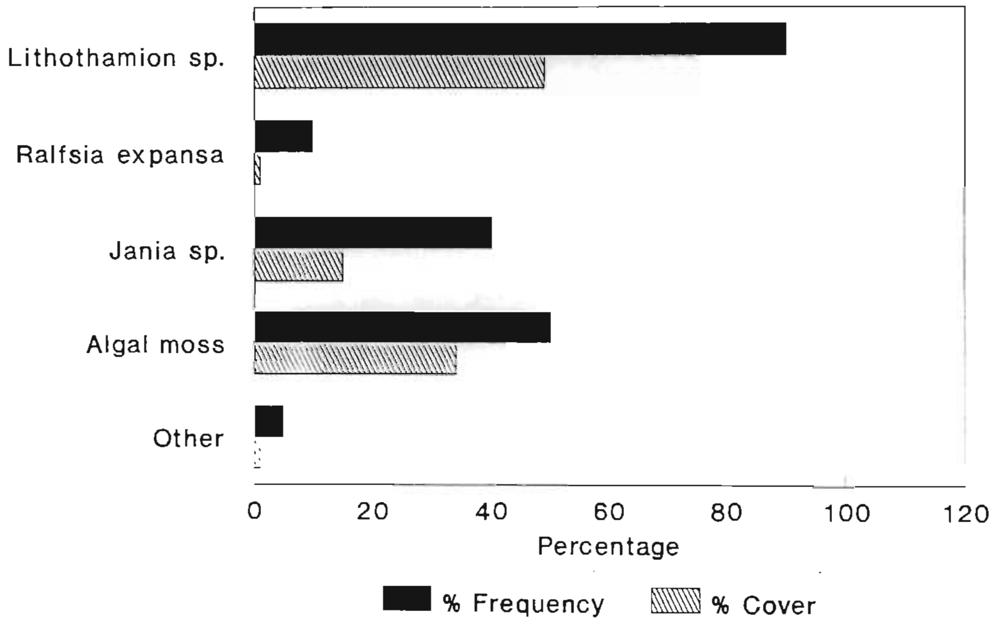


Figure 5.2 The percent frequency of occurrence and percentage cover of algal species at Isipingo.

A previous study suggested that S. variolaris at Oslo beach was a sedentary drift feeder (Drummond 1991a). In the present study, dominance by calcareous red algae (Fig. 5.3) and the presence in the gut contents of a number of species found in the drift material confirmed the earlier results. The gut contents of D. savignyi (Fig. 5.4) contained a wider range of food items than either S. variolaris (Fig. 5.3) or E. mathaei (Fig. 5.5). The presence of a considerable amount of sediment, mollusc shell, coral fragments, filamentous green algae and fragments of Jania sp. suggested that D. savignyi acquired a proportion of its food by rasping the substratum, and grazing the Jania sp. present in the pool at Isipingo. Comparing the list of species present in the gut contents (Table 5.1), with those constituting the available drift material (Table 5.2) and growing (Fig. 5.2) in the Isipingo pool, indicated that drift material also contributed to the diet of this species. The presence of animal material, mostly crustacean fragments, in all four samples suggested that D. savignyi had a more omnivorous diet than either S. variolaris or E. mathaei, possibly as a result of its greater mobility. The presence of sediment, coral fragments and pieces of Lithothamnion sp. in the gut contents of E. mathaei (Fig. 5.5) suggested that this species acquired part of its nutrients by grazing or rasping the substratum. That many of the species present in the gut contents of E. mathaei (Table 5.3) were not present in their habitat (Fig. 5.5), but were present in the drift material (Table 5.2), indicated that drift algae formed part of the diet of this species. Although the proportion of drift algae versus grazed algae could not be determined quantitatively, a subjective assessment suggested that drift algae formed a larger proportion of the diet of E. mathaei

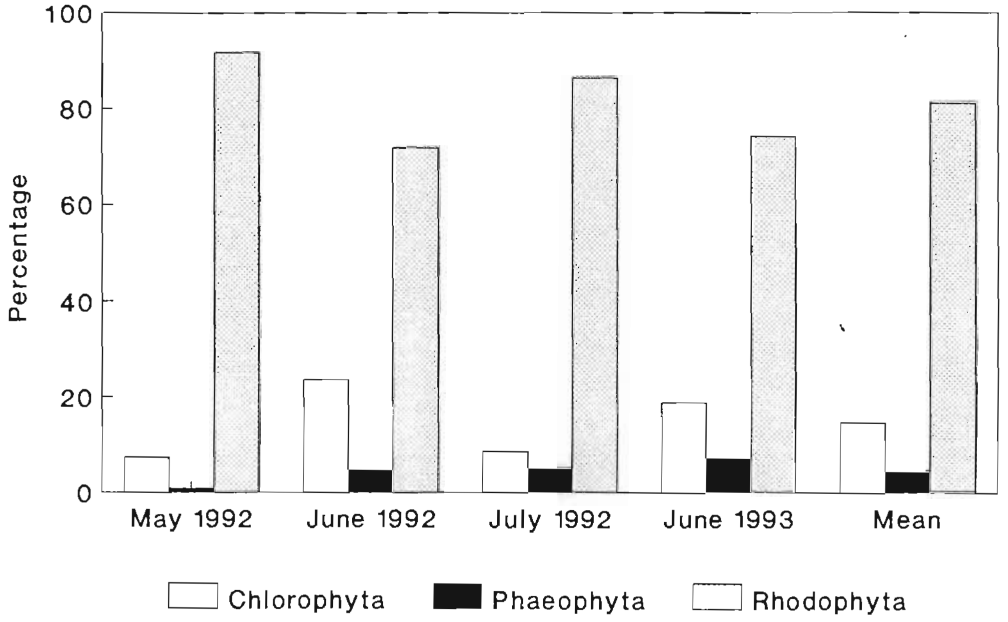


Figure 5.3 The percent composition of the algal Divisions present in the gut contents of _Stomopneustes variolaris_ from Oslo Beach.

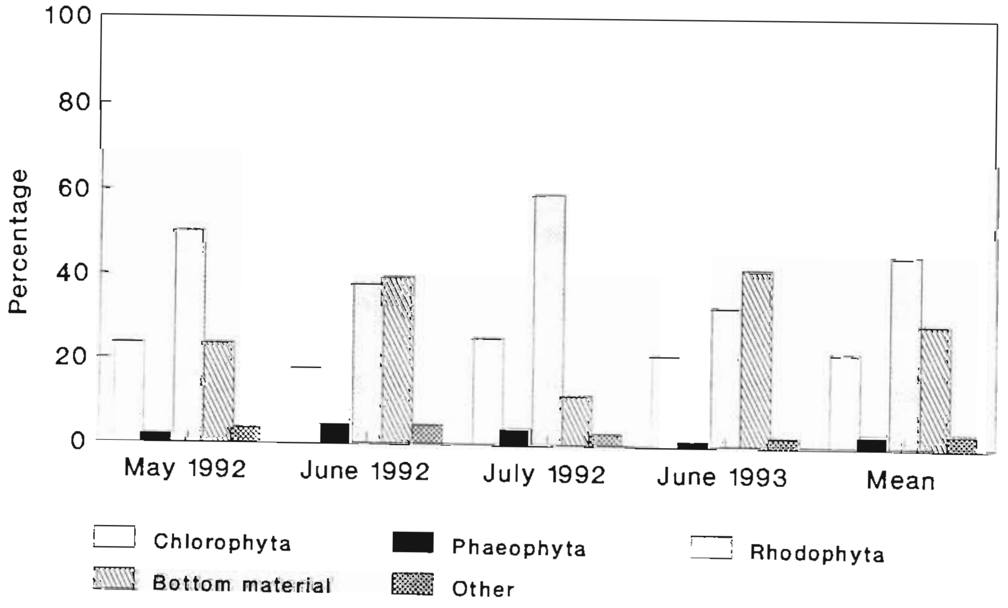


Figure 5.4 The percent composition of the algal Divisions present in the gut contents of _Diadema savignyi_ from Isipingo.

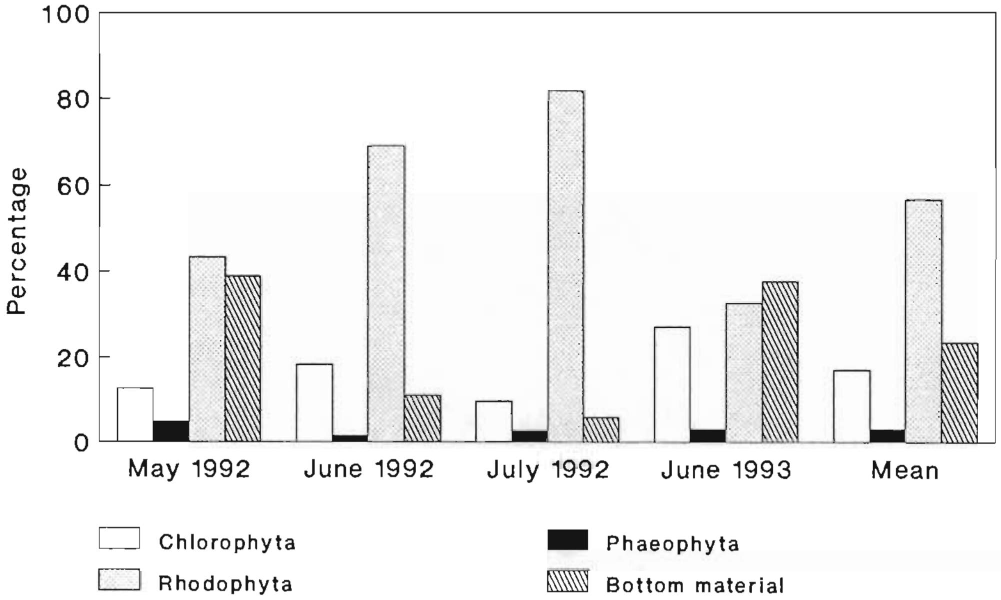


Figure 5.5 The percent composition of the algal Divisions present in the gut contents of <u>Echinometra</u> <u>mathaei</u> from Ramsgate.

Table 5.1 The species of algae identified in the gut contents of *D. savignyi*

Rhodophyta	**Chlorophyta**	**Phaeophyta**
Champia compressa	*Codium duthiae*	*Sargassum heterophyllum*
Cheilosporum sagittatum	*Ulva* sp.	
Jania sp.	*Bryopsis* sp.	
Hypnea spicifera	*Halimeda cuneata*	
Corallina sp.		

Table 5.2 Algal species present in the drift material collected at Oslo beach, Ramsgate and Ispingo in May, June 1992 and June 1993

Oslo beach

Rhodophyta	**Chlorophyta**	
Corallina sp.	*Caulerpa filiformis*	
Arthrocardia sp.		
Jania sp.		
Cheilosporum sagittatum		
Amphiroa sp.		

Ramsgate

Rhodophyta	**Chlorophyta**	**Phaeophyta**
Laurencia flexiosa	*Caulerpa filiformis*	*Sargassum heterophyllum*
Ballia beckerii	*Halimeda cuneata*	*Dictyota dichotoma*
Polyzonia elegans		
Plocamium corallorhiza		
Gelidium pristoides		
Jania sp.		
Cheilosporum cultratum		
Rhodymenia natalensis		
Hypnea spicifera		
Cheilosporum sagittatum		

Isipingo

Rhodophyta	**Chlorophyta**	**Phaeophyta**
Cheilosporum sagittatum	*Caulerpa filiformis*	*Sargassum heterophyllum*
Gelidium sp.	*Halimeda cuneata*	
Corallina sp.	*Ulva* sp.	
Hypnea spicifera		
Rhodymenia natalensis		

Table 5.3: The species of algae identified in the gut contents of *E. mathaei*

Rhodophyta	**Chlorophyta**	**Phaeophyta**
Corallina sp.	*Ulva* sp.	*Padina commersonii*
Ballia beckerii	*Caulerpa filiformis*	*Dictyota dichotoma*
Polyzonia elegans	*Bryopsis* sp.	*Sargassum heterophyllum*
Cheilosporum sagittatum		
Jania sp.		
Gigartina sp.		
Champia compressa		
Hypnea spicifera		
Rhodymenia natalensis		
Plocamium corallorhiza		

than in D. savignyi. While the proportions of the various components of their diets appeared to differ with time, the diets of the three species reflected what was available in terms of drift algae and in situ species at the time of the investigation.

5.2 Comparison of diets and food availability.

5.2.1 Food availability.

The total percentage cover of macroalgae was highest at Oslo Beach, ca 87% (Drummond 1991a), compared with <50% and <20% at Isipingo and Ramsgate respectively (Figs 5.1 & 5.2). In addition the macroalgae at the latter two sites consisted almost entirely of stunted Jania sp. and a fine green algal moss. In contrast a greater mass of drift algae were present in the pool at Ramsgate than on the intertidal shelf at Oslo Beach on all three sampling occasions (Fig. 5.6). In addition, subjective observations at Isipingo showed that relatively more drift-algae were present in the pool than on the rocks of the lower intertidal. On two of the three sampling occasions, the drift-algae at Oslo Beach consisted almost exclusively of calcareous red algal species (Fig. 5.7 & Table 5.2), and subjective observations over four years of visiting this site revealed little variation in the composition of the drift material. On the three sampling occasions, the drift material at Ramsgate consisted of non-calcareous red algal species with smaller proportions of calcareous Rhodophyta, Chlorophyta and Phaeophyta (Fig. 5.7 & Table 5.2). The drift material observed at Isipingo contained species from all three algal Divisions (Table 5.2), and although the various components were not quantified, the drift material appeared to be dominated by non-calcareous species.

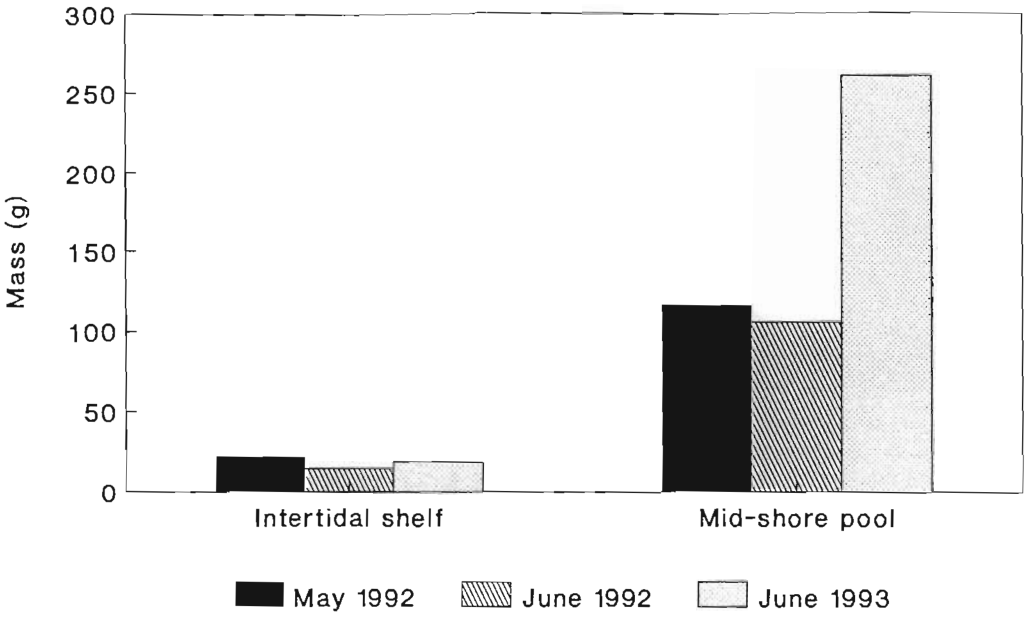


Figure 5.6 The mass of drift algae collected on three occasions from 10 x 50cm^2 quadrats, distributed randomly on the intertidal shelf and in a mid-shore pool.

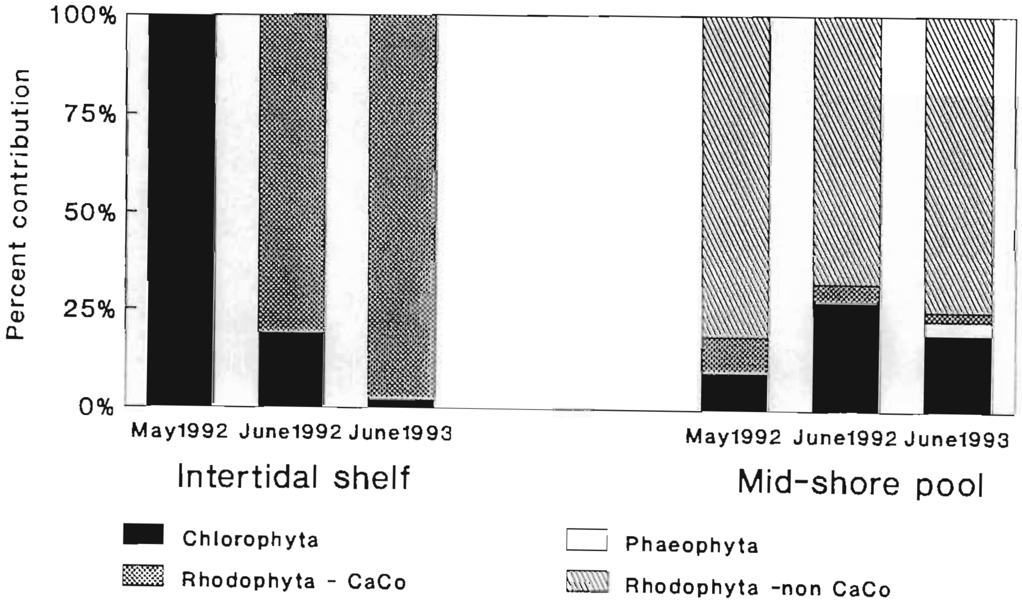


Figure 5.7 The composition, by algal Division, of the drift algae collected on three occasions from the intertidal shelf

5.2.2 Quality of diets.

Table 5.4 The nutritional values used to compare the quality of the diets of the three study species.
Values are means and ranges
Sample size, n = 3 for all values.

	Ash %	Protein %	Gross Energy MJ/Kg
S. variolaris	70.48 70.07 - 70.88	8.04 7.65 - 8.28	4.10 3.95 - 4.28
E. mathaei	66.71 64.44 - 70.18	11.30 10.18 - 12.28	5.69 5.62 - 5.78
D. savignyi	88.74 80.84 - 93.26	6.52 6.07 - 7.15	3.79 3.03 - 4.58

Although the diet of E. mathaei had the highest inorganic fraction, higher protein and gross energy values (Table 5.4) suggest that its diet was possibly of higher quality than those of S. variolaris and D. savignyi. However, sample sizes preclude statistical comparison. Furthermore, as the assimilation efficiency of the three species for their diets was not ascertained, my comparison of the quality of their diets can only indicate that E. mathaei has perhaps the potentially higher quality diet.

5.3 Relative size of the Aristotle's lantern, length of jaws and mass of lantern muscles.

5.3.1 Relative size of the Aristotle's lantern and length of jaws.

When the size of Aristotle's lantern relative to body size was compared (Fig. 5.8), it was found that the regression coefficients of the equations for *E. mathaei* and *D. savignyi* were significantly greater than that of *S. variolaris* (Table 5.5). These results indicate that *E. mathaei* and *D. savignyi* have larger lanterns than *S. variolaris*, and *E. mathaei* has a larger lantern than *D. savignyi*. When jaw length is compared (Fig. 5.9), the difference between *E. mathaei* and *D. savignyi* is not significant (Table 5.6) but both have significantly longer jaws than *S. variolaris*.

Table 5.5 Comparison of the regression coefficients calculated for the relationship between size of Aristotle's lantern and body mass in the three study species. 1) *S. variolaris*, 2) *E. mathaei*, 3) *D. savignyi*.

Species	Difference between slopes	SE	t	p
1 vs 2	(0.017 - 0.050)	0.002	16.22	<0.001
1 vs 3	(0.017 - 0.038)	0.002	11.98	<0.001
2 vs 3	(0.050 - 0.038)	0.002	5.90	<0.001

S. variolaris n = 83
E. mathaei n = 113
D. savignyi n = 72

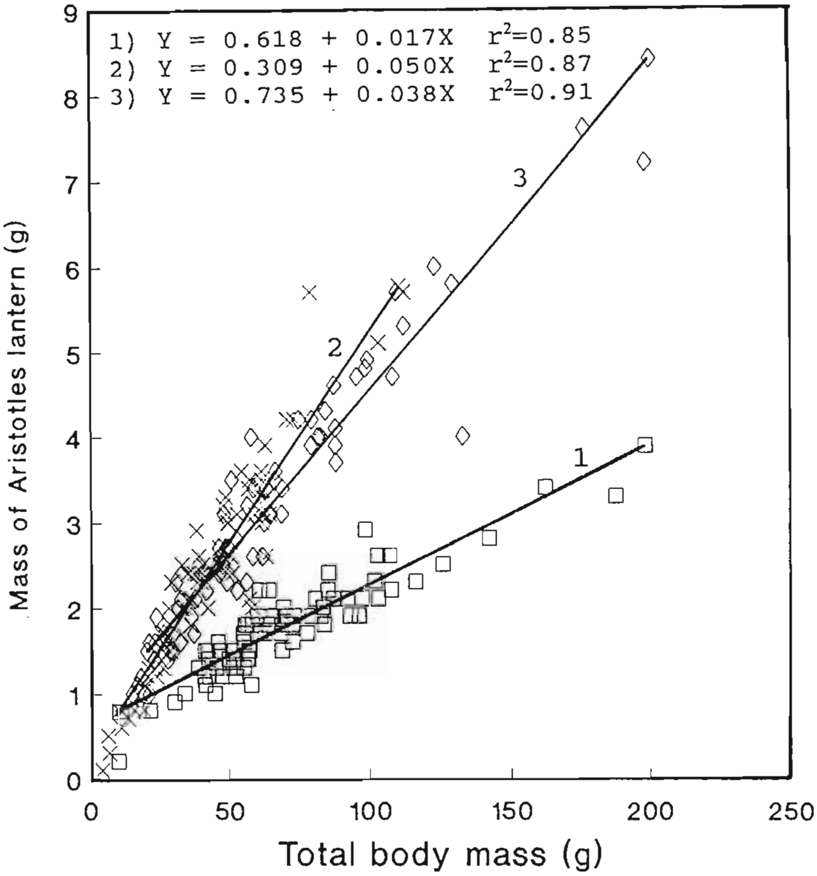


Figure 5.8 The linear regressions and regression equations for the relationship between size of Aristotles lantern and total body mass for; 1) S. variolaris, 2) E. mathaei, 3) D. savignyi.

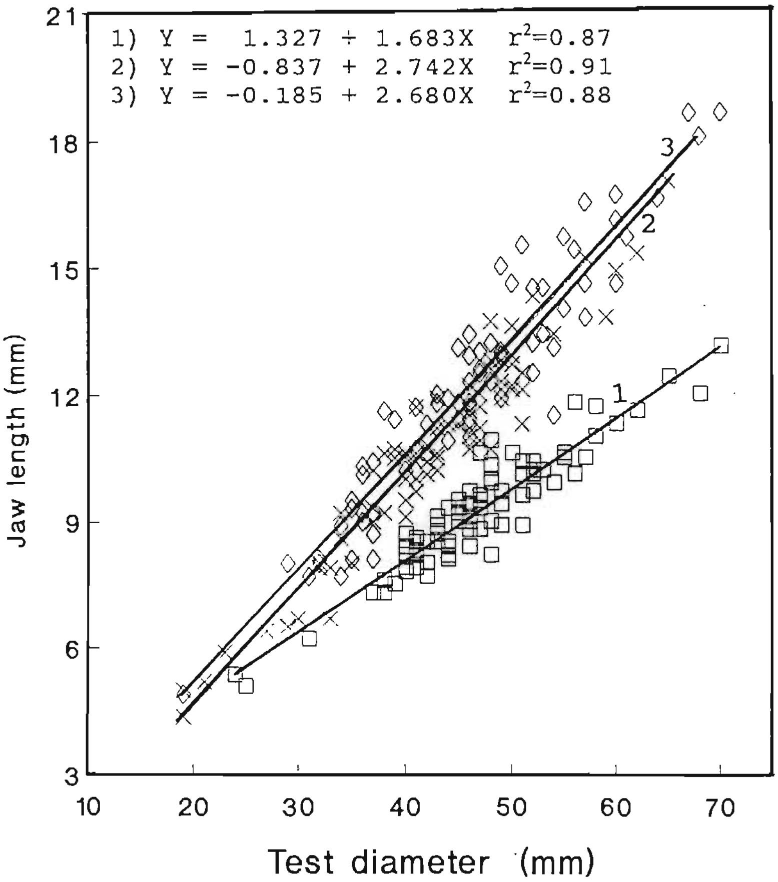


Figure 5.9 The linear regressions and regression equations for the relationship between jaw length and test diameter for; 1) S. variolaris, 2) E. mathaei, 3) D. savignyi.

Table 5.6 Comparison of the regression coefficients calculated for the relationship between jaw length and test diameter in the three study species.

1) S. variolaris, 2) E. mathaei, 3) D. savignyi.

Species	Difference between slopes	SE	t	p
1 vs 2	(1.683 - 2.742)	0.182	5.83	<0.001
1 vs 3	(1.683 - 2.680)	0.193	5.17	<0.001
2 vs 3	(2.742 - 2.680)	0.162	0.38	ns

S. variolaris n = 83
E. mathaei n = 113
D. savignyi n = 72

5.3.2 Mass of muscle associated with the Aristotle's lantern.

A significant linear correlation between total body mass and mass of lantern muscle was evident in all three species (Fig. 5.10 & Table 5.7). The regression coefficients of the equations for E. mathaei and D. savignyi are significantly different from that of S. variolaris (t=8.93, t=7.35 p<0.001). In other words for urchins of the same size, the lanterns of S. variolaris have a smaller mass of associated muscle than the lanterns of E. mathaei and D. savignyi.

5.4 Amount of food in guts.

As expected larger urchins consume more food than smaller individuals in all three species (Fig. 5.11). However the greater elevation of the regression line (Table 5.8) for D. savignyi indicates that this species had more food in its gut than the other

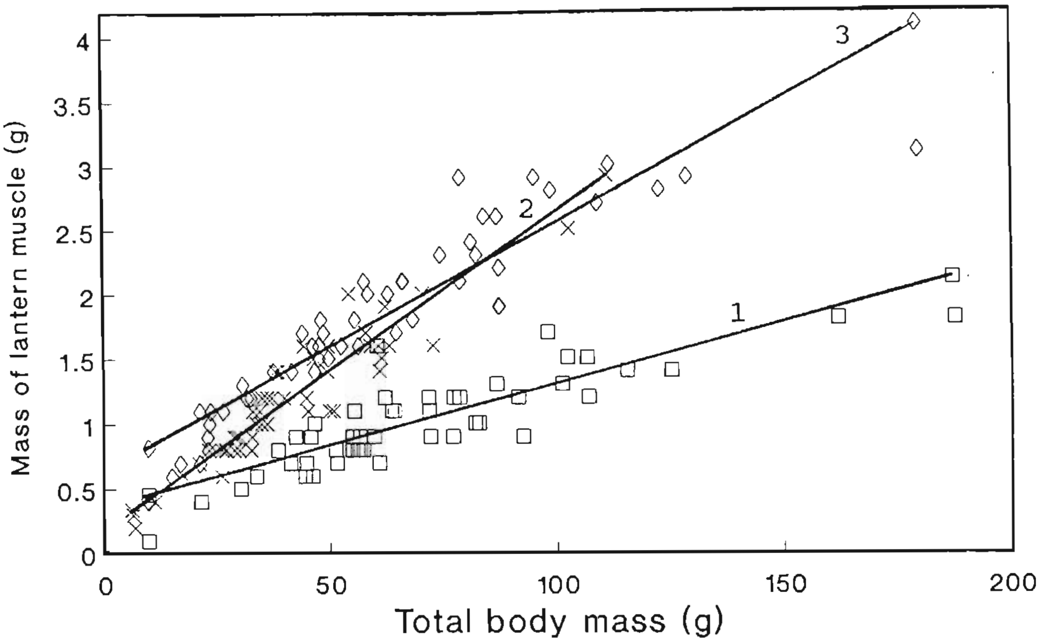


Figure 5.10 The linear regression lines for the relationship between total body mass and mass of lantern muscles for 1) S. variolaris 2) E. mathaei, 3) D. savignyi.

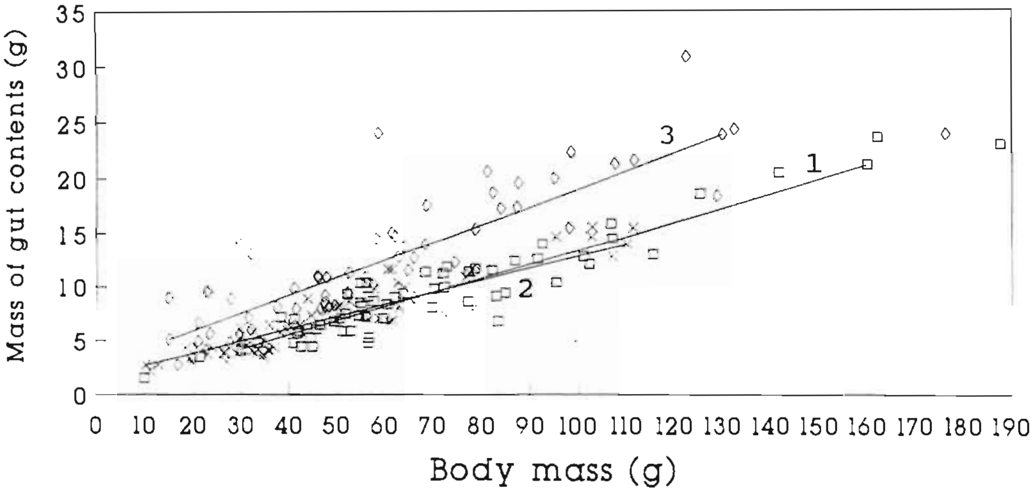


Figure 5.11 The linear regression lines for the relationship between body mass and mass of gut contents for 1) S. variolaris, 2) E. mathaei, 3) D. savignyi.

two species. The difference between the regression coefficients of _D. savignyi_, and _E. mathaei_ and _D. savignyi_ and _S. variolaris_ were significant (t= 3.22, t= 2.62, $p<0.01$). The difference between _S. variolaris_ and _E. mathaei_ was not significant.

Table 5.7 The regression statistics for the relationship between total body mass and mass of lantern muscles for the three study species.

	Regression equations	r^2	SE of slope
S. variolaris	$Y = 0.364 + 0.009X$	0.71	0.0008
E. mathaei	$Y = 0.191 + 0.024X$	0.84	0.0015
D. savignyi	$Y = 0.632 + 0.019X$	0.85	0.0011

n = 50 for all species

Table 5.8 The regression statistics for linear regression lines presented in Figure 5.11 for the relationship between gut contents and body mass in the three study species.

	Regression equation	SE of slope	r^2
S. variolaris	$Y = 0.307 + 0.130X$	0.006	0.939
E. mathaei	$Y = 1.597 + 0.112X$	0.011	0.802
D. savignyi	$Y = 2.641 + 0.163X$	0.011	0.882

n = 60 for all species

Discussion.

The results presented indicate that the diets of the three species reflected what was available in terms of in situ algae and drift material. This agrees with the findings of most other studies on echinoid feeding as reviewed by Lawrence (1975) and supports the generally accepted contention that echinoids are essentially opportunistic and generalist in their feeding (De Ridder & Lawrence 1982). However, despite the generalist nature of their diets, differences were apparent among the three species with respect to the types of items eaten and the proportions of these items. In addition, there were differences in the mode of food acquisition among the three species. The observed differences in their diets were most probably accounted for by the differences in feeding mode and habitat.

S. variolaris at Oslo beach is sedentary and does not emerge from its' cryptic positions to forage (Drummond 1991a). It has been suggested that the adoption of this sedentary and cryptic lifestyle has been in response to the high energy environment (Drummond 1991a). However, until more is known about the predators of this species, predation cannot be ruled out as a factor associated with the sedentary cryptic lifestyle shown by S. variolaris at this locality. The gut contents of S. variolaris examined in this study, and in the 1990 study, were all dominated by calcareous red algae. As bottom material or animal material was not observed in the gut contents it would seem that this species seldom grazes or rasps the substratum for food. This suggests that S. variolaris at this locality probably depends almost entirely on drift algae.

However, the epithelial absorption of dissolved organic matter (Bamford 1982) cannot be eliminated as a potentially significant source of nutrition for this (and other) species. Despite the fact that feeding in *S. variolaris*, does not appear to involve extensive rasping of the substratum, the hollows and crevices occupied by *S. variolaris* were devoid of foliose algae, and lined by the encrusting *Lithothamnion* sp. In a zone where competition for space among algal species is high (Branch & Branch 1981), the presence of the slow growing, poorly competitive *Lithothamnion* sp. has probably been dependent on *S. variolaris* to remove colonizing algal sporelings and diatoms. The maintenance of these *Lithothamnion* "gardens" could possibly have resulted from jaw and spine abrasion during the feeding activities or adjustment of position by the urchin. Despite the apparent absence of grazing by the sea urchin, this situation is reminiscent of the *Ralfsia* sp. gardens maintained by patellid limpets (Branch 1976, Robson 1986). Furthermore, this apparent relationship between *S. variolaris* and *Lithothamnion* sp. is probably mutualistic as it has been observed that juvenile *S. variolaris* show a preference for attaching in close proximity to adults (Chpt. 3 this study). The absence of foliose algae around adults would facilitate this. In addition there is evidence that the larvae of echinoids settle and metamorphose in response to the presence of coralline red algae such as *Lithothamnion* and *Phymatolithon* sp. (Pearce & Scheibling 1990).

The lower intertidal on the South African east coast is an algal dominated zone (Eyre & Stephenson 1938, Branch & Branch 1981), as macro-herbivores are effectively excluded from this habitat by the almost continuous turbulence resulting from wave action. However, by virtue of its numerous suckered podia and a predilection for hollows and crevices, S. variolaris has been able to occupy a niche in this habitat. The key to the occupation of this niche by S. variolaris has probably been its ability to trap and consume drift algae. The combination of a burrowing habit and drift feeding has enabled Echinostrephus molaris to exploit a comparable situation on coral reefs in the central Red Sea (Campbell, Dart, Head & Ormond 1973).

On the basis of differences in lifestyle displayed by E. mathaei and D. savignyi I hypothesized that the nocturnally active D. savignyi would acquire its food by grazing foliose algae, and that the more sedentary E. mathaei would trap and ingest drift algae. The gut contents of both E. mathaei and D. savignyi contained sediment/bottom material and, in the case of D. savignyi, animal material, mostly crustacean fragments and the occasional sipunculid worm. In addition, both species had obviously consumed drift algae, as evidenced by the presence of algal species not present in the pools occupied by the urchins. That the mobile D. savignyi had consumed drift algae could suggest that drift algae are more abundant than attached foliose algae in its habitat, which certainly appears to be so. It also suggests that the exploitation of drift algae by non-burrowing echinoids is probably of greater significance than generally acknowledged.

In terms of optimal foraging theory the sea urchins should adopt a feeding mode which would yield the best return in food energy for the lowest costs. The costs associated with feeding by echinoids are the risk of displacement by turbulence and increased vulnerability to predation. The sedentary drift feeding mode would seem to reduce these costs, but drift algae is only available to sedentary urchins during times of turbulence. Through the combination of drift feeding and rasping the substratum, *D. savignyi* and *E. mathaei* are probably able to maximize their intake, despite occupying habitats where food availability is limited by high herbivore densities. Because drift algae is available at high tide and grazing or rasping the substratum can occur at low tide, the duration of feeding is thus potentially longer for *D. savignyi* and *E. mathaei* than for *S. variolaris*. This, combined with the indications that more drift algae was available to sea urchins in mid-shore pools than on the lower intertidal shelves, suggests that *E. mathaei* and *D. savignyi* might be able to acquire more food than *S. variolaris*. That *D. savignyi* did have a greater mass of gut contents than the other two species lends some support to this suggestion. However, different rates of passage of food through the gut among the three species may have influenced this result. Alternatively, *D. savignyi* may have a larger gut and thus be able to ingest greater quantities of food. If this is so, it implies that *D. savignyi* makes a relatively greater investment in food harvesting than the other two species. Whatever the reason for the difference in quantity of food in the guts, *D. savignyi* appears to have the lowest quality diet with respect to gross energy and protein; so if this species does eat more, the difference in quality of diet may be offset by the greater quantity consumed.

Where individuals of the same size are compared, *D. savignyi* and *E. mathaei* have larger lanterns, more muscle associated with the lantern and longer jaws than *S. variolaris*. And as *S. variolaris* is clearly a sedentary drift feeder while E. mathaei and D. savignyi rasp the substratum, it seems possible that a relationship may exist between the relative size of the feeding apparatus and mode of feeding. Regis (1978) observed that Arbacia lixula, which feeds by rasping, had a relatively larger Aristotle's lantern than Paracentrotus lividus, which inhabits cavities and feeds on drift algae. Furthermore, Contreras and Castilla (1987) showed that on the coast of central Chile, Tetrapygus niger, which is a grazer, had a larger Aristotle's lantern than Loxechinus albus, which captures and consumes drift algae. These three sets of comparisons indicate that the demands of a grazing or rasping mode of feeding might require a larger Aristotle's lantern with more muscles and longer jaws. Ebert (1980) interpreted the negative correlation between relative size of the Aristotle's lantern and the supply of food as adaptive morphological plasticity; sea urchins responded to food scarcity by increasing their investment in the feeding apparatus. Black et al. (1984) showed that larger lanterns did indeed increase the effectiveness of grazing. While there is no reason to dispute these findings or the concept of adaptive plastic responses, I think that the extent to which the drift feeding or grazing/rasping mode is employed will have implications for the plastic response of the Aristotle's lantern to food scarcity. For example, if a sea urchin's benthic algal food became scarce and drift algae offered an adequate alternative, then there would be no reason for the lantern to increase in size to enhance grazing or rasping effectiveness as the lantern would mainly serve to ingest food particles rather than rasping and tearing. This assumes that the sea urchin will switch to consuming drift algae rather than intensifying grazing efforts.

When the jaw lengths of individuals of D. savignyi with a test diameter of 50mm (this study) and those of D. setosum of the same size (Ebert 1980) are compared, D. setosum from both a "high" (water intake) and "low" (turtle tank) food availability population had longer jaw elements than D. savignyi on the Natal coast. This implies that these populations have a lower food availability compared with the Isipingo D. savignyi population. Yet, from the information provided in Ebert (1980), I do not think that the habitat of D. savignyi (Isipingo), has more food available than his water intake site. Obviously, the sizes of the Aristotle's lanterns could merely reflect basic differences between the two species. However, I suggest that it could reflect differences in feeding mode. Very little foliose algae (<20% cover) is present in the habitat of D. savignyi on the Natal coast, and in addition to grazing and rasping, their diet contains a considerable proportion of drift algae. In contrast the urchins of Ebert's (1980) "high food" population are considered to graze the Thalassia sp. and other macroalgal species present in their habitat, with no mention of drift feeding. Furthermore, Ebert (1980) reports that the guts of his "low food" population were "packed with chips of paint", indicating that these urchins had rasped the substratum. Therefore, if based only on food availability, it might be expected that the jaw lengths of the Natal D. savignyi population would be smaller than Ebert's (1980) turtle tank population, but larger than those of the water intake population. But, if feeding mode is considered together with food availability, I would expect the population which combines grazing/rasping with drift feeding to have the relatively smaller jaws, which appears to be the case. Of course, it must be considered that perhaps not all echinoids can or do respond to food scarcity by increasing allocation to the food harvesting apparatus. Echinoids have been shown to lower their metabolism (Farmanfarmaian 1966, Lilly 1977), reduce growth (Levitan 1988) or show negative growth (Ebert 1967) and reduce their gonadal output (Keats, Steele & South 1984) in response to a lowered food supply. Species with more conservative, low risk life histories may accommodate a lowered food supply by adopting a "reduce expenditure approach" as an alternative to increasing allocation to the feeding apparatus.

While it remains debatable whether the size of Aristotle's lanterns could be related to the demands of rasping and grazing, larger lanterns are a reflection of greater allocation of resources to the acquisition of food (Lawrence 1975, Black et al. 1984). In the present study, the larger Aristotle's lantern, greater mass of lantern muscles and longer jaws of D. savignyi and E. mathaei indicate that these two species make a relatively greater investment in food harvesting than does S. variolaris. And in terms of overall size of the Aristotle's lantern, D. savignyi allocates more energy and resources to feeding than does E. mathaei.

In summary:

On the Natal coast S. variolaris is a sedentary drift feeder, while D. savignyi and E. mathaei graze or rasp the substratum. However drift algae did contribute significantly to the diets of the latter species.

While the diet of D. savignyi had the lowest inorganic fraction, the diet of E. mathaei had a higher calorific and protein content than either D. savignyi or S. variolaris.

Size for size, D. savignyi and E. mathaei have larger Aristotle's lanterns, a greater mass of lantern muscle and longer jaws than S. variolaris. Therefore on the Natal coast D. savignyi and E. mathaei appear to make a relatively greater investment in food harvesting than does S. variolaris.

Chapter 6. Growth, recruitment and mortality.

Introduction.

The sea urchin endoskeleton or test is composed of numerous calcium carbonate plates or ossicles. Increase in the size of the test occurs by addition of plates in the apical region and by growth of individual plates by accretion of calcium carbonate around the edges (Pearse & Pearse 1975).

It is apparent that the rates of growth, size at sexual maturity and maximum size of sea urchins, and other marine invertebrates (Paine 1976, Sebens 1982), often depends on characteristics of the habitat they occupy. The amount of food available (Swan 1958, 1961, Ebert 1967, Dix 1970a), sea temperature and sea water quality (Nichols, Sime & Bishop 1985), population density (Levitan 1989) and wave action and spine breakage (McPherson 1968, Ebert 1968), have all been shown to influence growth rates in sea urchins. Furthermore, work by Ebert (1968) on Strongylocentrotus purpuratus suggests that sedentary sea urchins grow to the capacity of their attachment sites, and Denny, Daniel and Koehl (1985) argue that the water movements experienced by sedentary intertidal organisms effectively place mechanical limits to the potential size of these animals. The rate of growth and ultimate body size of sea urchins is thus not predictable but, in the sense of Sebens (1982), indeterminate. Sebens (1982) defined indeterminate growth as "the ability to increase and decrease size over a wide range as conditions vary". This indeterminate growth is epitomized by the size plasticity displayed by the sea urchins Diadema antillarum and Strongylocentrotus purpuratus, where body size is regulated by growth and negative growth in response to changes in resource availability (Ebert 1967, Sebens 1987).

Growth of sea urchins has been estimated by a number of methods, including: mark and recapture techniques where individuals are tagged either with nylon filament (Ebert 1968) or by injection with tetracycline (Kobayashi & Taki 1969), cohort analysis where change in modal size is monitored over time (Raymond & Scheibling 1987, Guillou & Michel 1993), size frequency analysis (Swan 1958, 1961, Ebert 1973), the use of annual rings on test plates to assess the age of sampled individuals (Sumich & McCauley 1973, Nichols, Sime & Bishop 1985), and monitoring the change in size of urchins maintained in field enclosures (Larson, Vadas & Keser 1980) or aquaria (Raymond & Scheibling 1987). A comprehensive background to the mathematical computation of growth, mortality and survivorship in animals has been provided by Ricker (1958). The nature of the growth profile and the rates of growth of sea urchins have been described using the Brody-von Bertalanffy growth equation (Ebert 1973, Sumich & McCauley 1973, Ebert 1975), the Richards function (Ebert 1980), and the "single logistic" model (Nichols, Sime & Bishop 1985).

Growth and maximum body size, as components of a sea urchin's life history, have considerable significance arising from the relationship between growth and reproduction. The sea urchin gonad occupies most of the internal volume of the test, therefore it cannot become larger unless the test increases in size. Thus an increase in reproductive output is dependent upon an increase in body size. Furthermore, a positive correlation between growth rate and mortality rate in sea urchins (Ebert 1975), indicates that the greater relative allocation of resources to growth and reproduction is at the expense of investment in maintenance.

One of the concepts which ecologists have evoked to explain life history variation is the "bet hedging" theory as discussed by Murphy (1968), Schaffer (1974) and Stearns (1976). This theory links lifespan and growth rate to recruitment success, and suggests that where recruitment success is predictable, selection will be for rapid growth to maturity, early reproduction and short lifespan, while in environments where survival of recruits is unpredictable, selection will favour longer life span, slower growth and greater investment in maintenance. The evolutionary processes which have led to the adoption of a particular set of growth related traits cannot be separated from those processes which have influenced the reproduction and maintenance components of an animal's life history. Therefore an investigation into the patterns of growth in S. variolaris, E. mathaei and D. savignyi was essential to the understanding and interpretation of the life histories of these sea urchins. Furthermore, knowledge of a specie's growth curve, rate of growth, recruitment and mortality characteristics, is central to any conservation management strategy, as this information forms the basis for estimations of standing stock and production as well as providing an index of an organism's well-being (Moore 1958).

The intentions of the investigation described in this chapter were, therefore, to assess the patterns of growth in the three sea urchin species, and acquire a measure of their recruitment predictability and mortality rates.

Materials and Methods.

6.1 Growth.

Initially it was hoped that the determination of monthly size frequency distributions would enable me to acquire growth data from the changes in modal size of cohorts. However, by June 1992 it was apparent that this would not be possible. Firstly, the growth of S. variolaris, was too slow for cohort analysis to provide a realistic estimate of growth rate, and secondly, it was brought to my attention that casual harvesters had been removing the larger E. mathaei from the population that I was monitoring. It was also evident that the usefulness of the size frequency data collected for D. savignyi was limited, as the number of individuals that I was able to measure each month fluctuated considerably. This was largely the result of variation in the numbers of individuals occupying cryptic positions where they could not be seen or from which they could not be extracted. Although population size frequency data were collected for the three species, the problems outlined above invalidated them as a reliable source of growth data. Therefore it became necessary to acquire growth data by monitoring designated groups and recognizable individuals.

D. savignyi.

The test diameters of two groups of ten and six individuals respectively, occupying a pool in the mid shore at Ramsgate, were measured each month between February and May 1992. Measurements were discontinued after May 1992 as individuals were missing from each group. As recently recruited juveniles of this species formed aggregations, which remained in a particular area of the pool for a number of months (personal observations), groups of smaller individuals could be monitored. Three such groups with initial mean sizes of between 11 and 25mm, were monitored between September 1992 and April 1993, before mortality and/or dispersion reduced their numbers. As it was impossible to recognise individuals within these groups, individual measurements were pooled, and growth increments calculated from the difference between initial and final mean sizes.

S. variolaris.

As this species was sedentary, it was easier to monitor individuals. Ten individuals ranging in size between 20 and 45mm were chosen and their sizes recorded each month between August 1992 and April 1993. In addition, 20 large individuals with test diameters ranging between 50 and 61mm, were monitored over the same time period. In the case of the latter group individual measurements were pooled as explained for *D. savignyi* above.

E. mathaei.

A group of five juveniles with test diameters between 8 and 10mm, and four individuals (8mm, 9mm, 10mm, 21mm) were monitored between October 1992 and February 1993. A group of 24 large urchins with test diameters ranging from 51 to 64mm, were monitored between February 1993 and June 1993. As I could not be completely sure of recognizing individuals within the groups, the individual measurements were pooled and growth increments calculated from initial and final mean sizes.

The von Bertalanffy growth equation has frequently been used in studies of sea urchin growth (Ebert 1973, 1975, 1977, Sumich & McCauley 1973), therefore it was assumed that the von Bertalanffy curve would adequately describe the growth of the three species in this study.

6.2 Recruitment.

The frequency and predictability of recruitment in each species was assessed from population size frequency distributions and field observations. Recruitment was considered as the appearance of sea urchins of a size visible to the naked eye, thus differentiating from settlement, which would have occurred at some earlier time.

As size frequency distributions could not be determined from the same populations that I had sampled for reproductive and morphological data, these data were collected from another population of each species, (see Appendix 1, pg 185) These populations were, however, very similar in size structure, population density and habitat as the original populations. The size structures of the three populations were assessed by regular measurements of as large a proportion of the population as possible. Test diameters were measured using outside calipers and size frequency histograms, with size classes of 10.0mm, were constructed for each set of measurements.

It was only possible to measure _S_. _variolaris_ at Sheffield Beach at the lowest low tides, and consequently reliable data were acquired on only seven occasions between April 1991 and September 1992. Although, casual harvesters had removed a number of the larger individuals from the _E_. _mathaei_ population at Ramsgate

North, data collected between February 1991 and June 1992 were used to provide information on recruitment. As rates of natural mortality could not be calculated from these data, the numbers in a further population were monitored for twelve months. Size frequency data for the population of D.savignyi at Ramsgate were acquired on 23 occasions between February 1991 and March 1993.

6.3 Mortality.

Mortality was assumed to be constant, and was calculated from the following relationship:

$$\mathrm{Log}_e(N_t/N_0) = M \qquad (1)$$

Where: N_t = the number of individuals at time t,

N_0 = the initial number of individuals,

M = the instantaneous rate of natural mortality.

Results.

6.1 Growth.

The von Bertalanffy growth equation was used in the following form:

$$S_t = S_\infty(1-e^{-Kt}) \qquad (2)$$

Where: S_t is linear size at time t,

S_∞ is the asymptotic size,

K is an estimate of the rate at which the sea urchin approaches asymptotic size.

The growth increments acquired from monitoring individuals and groups of sea urchins of each species are presented in Table 6.1.

Table 6.1 The growth increments acquired from monitoring individuals and groups of the three species.

Species	Size t_1 (mm)	Size t_2 (mm)	n	t_2-t_1 (months)
<u>S</u>. <u>variolaris</u>	52.9	59.0	20	8
	30.0	35.0	1	8
	32.0	37.0	1	8
	26.0	33.0	1	8
	30.0	38.5	1	8
	27.0	31.5	1	8
	20.0	27.0	1	8
<u>E</u>. <u>mathaei</u>	10.0	16.0	1	4
	8.0	16.0	1	4
	9.0	18.0	1	4
	57.9	60.6	22	4
	21.0	29.0	1	4
<u>D</u>. <u>savignyi</u>	12.0	27.5	9	3
	25.0	39.0	7	3
	35.5	50.0	6	3
	61.4	65.5	10	3

From the linear regression of the Walford plot (St_1 vs St_2), the parameters S_∞ and K were calculated, using the following relationships:

$$Y \text{ intercept} = S_\infty \, (1\text{-slope}) \qquad (3)$$

$$\text{Slope} = e^{-K/x} \qquad (x = t_2 - t_1) \qquad (4)$$

Asymptotic sizes obtained from equation 3 were:

S. variolaris	145.4mm
E. mathaei	86.8mm
D. savignyi	84.9mm.

The values of K yielded by equation 4 were:

S. variolaris	0.007
E. mathaei	0.43
D. savignyi	0.79

This K value for *E. mathaei* approximated the value reported by Ebert (1975), for *E. mathaei* in Hawaii. However, using $K = 0.43$ in the von Bertalanffy equation produced a growth curve which implied growth rates far in excess of what was observed in the field. K was recalculated using non-linear regression techniques (Draper & Smith 1981) and a more realistic value of 0.32 was obtained. The calculated K value for *S. variolaris* resulted in a poor fit of the von Bertalanffy curve to the field data. This K value was recalculated using a method from Ricker (1958), where the slope of the linear relationship between $\log_e(S_\infty - S_t)$ and t is equal to K. This method produced a value of 0.09 which was adjusted to 0.11 to produce a better fit between the von Bertalanffy growth curve and the growth increments measured in the field.

The problems associated with the calculation of K were probably the result of the limited data used in the Walford plot. The data set (Table 6.1) possibly provided insufficient contrast; K would probably have been more precisely estimated from equation 4 if the growth data had spanned a larger portion of the size/age range of the urchins, particularly for S. variolaris and E. mathaei.

Growth curves for the three species (Fig. 6.1) were drawn using the following von Bertalanffy equations:

S. variolaris $S_t = 145.4(1-e^{-0.11t})$

E. mathaei $S_t = 86.8(1-e^{-0.32t})$

D. savignyi $S_t = 84.9(1-e^{-0.79t})$

As the actual ages of the urchins monitored in the field were not known, fit could only be assessed by comparing the slope of the curve at a particular size, with the increments measured in the field. Despite the inadequacies of the data set, the fit between the von Bertalanffy curve and the growth increments was good (Fig. 6.2), and therefore the theoretical growth profiles probably provide a realistic description of growth in the three species.

D. savignyi and E. mathaei and to a lesser extent S. variolaris showed an initial period where growth was more rapid, differences in the rate of growth and the point at which growth rate began declining resulted in characteristic growth profiles for each species (Fig. 6.1). D. savignyi displayed the most rapid growth of the three species, with urchins achieving a test diameter of ca 46mm in their first year of growth compared with ca 15mm and 23mm for S. variolaris and E. mathaei respectively. The growth rate in

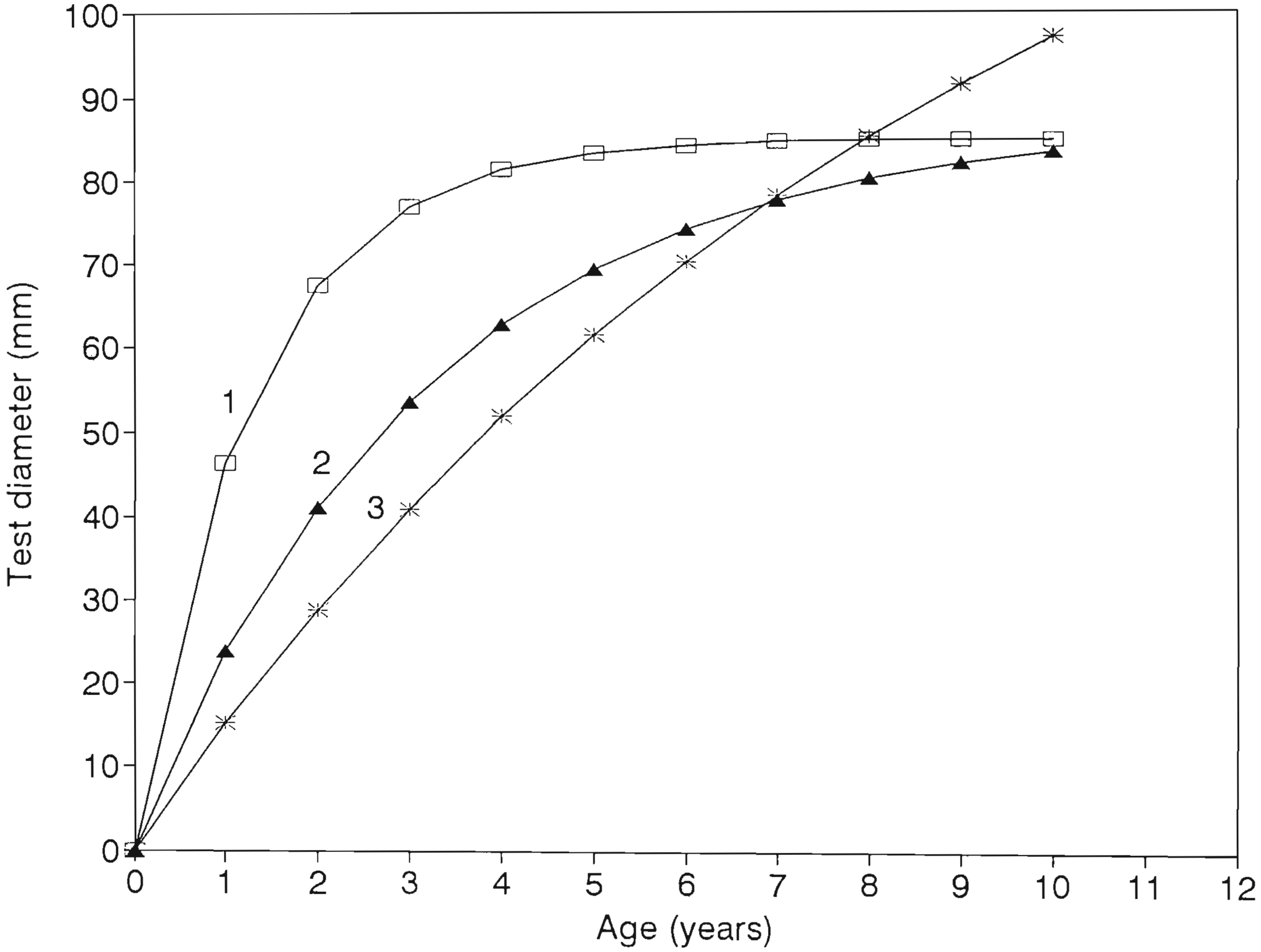


Figure 6.1 The theoretical von Bertalanffy growth curves for 1) D. savignyi, 2) E. mathaei, 3) S. variolaris.

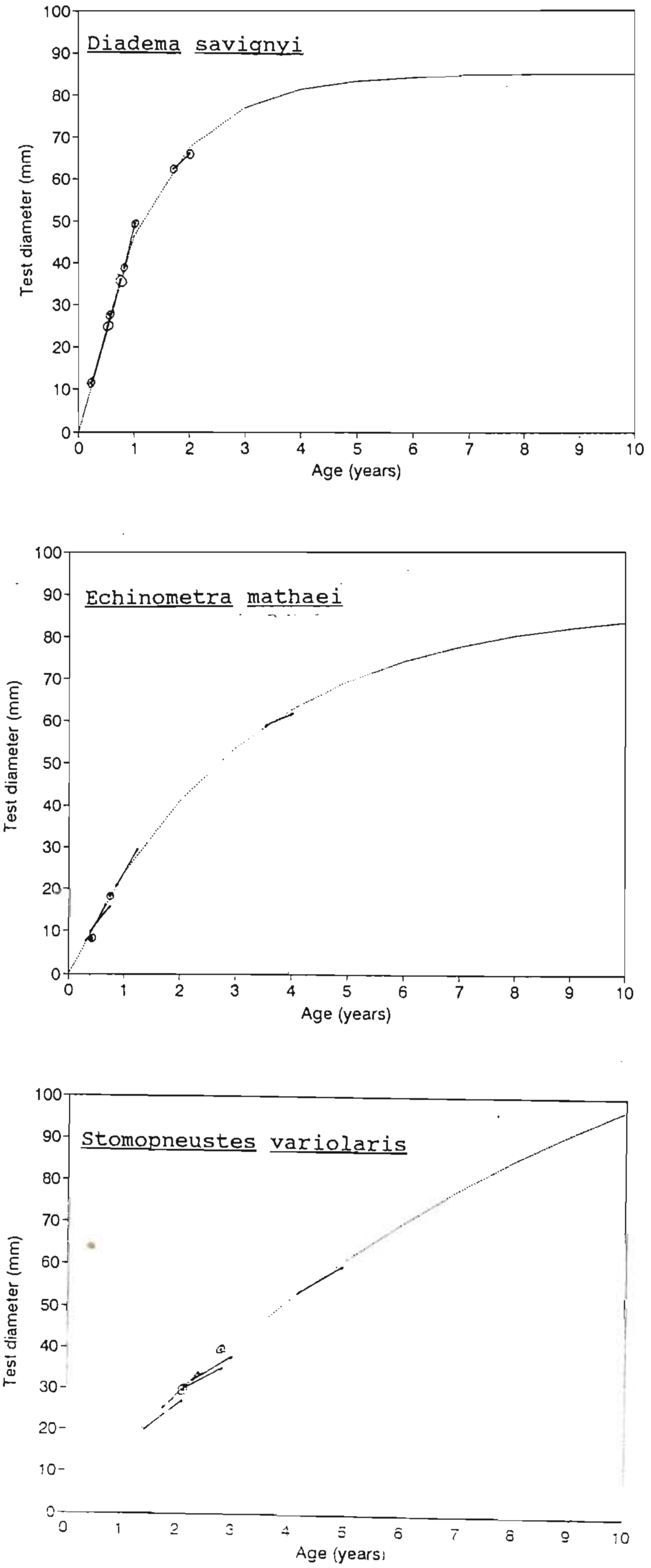


Figure 6.2 The theoretical von Bertalanffy growth curves with actual growth increments superimposed to show fit.

D. savignyi decreased by almost 50% in the second year reaching an inflection point at the end of that year, from where growth to asymptotic size was considerably slower. Growth rates were slower and the point of inflection was less marked in E. mathaei, which nonetheless showed a decline in growth rate with increasing age. S. variolaris displayed the lowest growth rates and there was no distinct point at which a decrease in growth rate occurred.

6.2 Recruitment.

The appearance of individuals in the 0-10mm size class was regarded as indicative of a recruitment event. Table 6.2 summarises the recruitment events for each species during 1991 and 1992, and Appendix 1 contains the complete set of size frequency histograms for the three species populations.

Although the population size distribution data were unsuitable for determining growth rates I am confident that the timing of recruitment of juveniles into the respective populations was reliably represented. In addition, subjective observations of recruitment in other populations supported the size distribution results.

From the results presented in Table 6.2 it appears that recruitment of juveniles into D. savignyi populations occurred predominantly during the latter parts of 1991 and 1992 (winter to spring months). In contrast, recruitment into the E. mathaei and Ramsgate S. variolaris populations occurred during the spring and summer months of 1991 and 1992. That recruitment into the monitored population at Sheffield beach apparently failed in both 1991 and 1992 suggests

Table 6.2 The months in which new recruits (<9.9mm) were observed in (A) the monitored populations, and (B) other populations.

(A)

Ds - D. savignyi - Ramsgate
Sv - S. variolaris - Sheffield beach
Em - E. mathaei - Ramsgate North

	1991			1992		
	Ds	Em	Sv	Ds	Em	Sv
J				*		
F		*			*	
M					*	
A						
M	*					
J						
J	*					
A						
S				*		
O	*	*				
N	*	*				
D		*		*	*	

(B)

Ds - D. savignyi - Isipingo
Sv - S. variolaris - Ramsgate
Em - E. mathaei - Isipingo

	1991			1992		
	Ds	Em	Sv	Ds	Em	Sv
J						*
F		*			*	*
M						
A						
M						
J						
J	*					
A				*		
S	*			*		
O					*	
N	*					
D		*				

that recruitment of *S. variolaris* was less predictable than in either *D. savignyi* or *E. mathaei*.

Juvenile *S. variolaris* were almost without exception observed beneath the canopy of spines of adults. Although *E. mathaei* juveniles were occasionally observed in exposed positions they were more frequently found under rocks, in crevices or among coral heads. *D. savignyi* juveniles were observed to form aggregations which remained stable for three to six months, furthermore these juveniles appeared to be far less active than the adults and seldom moved far from the positions in which they were first observed. The smallest recruits observed were 4mm for *E. mathaei* and *S. variolaris* and 3mm for *D. savignyi*. Settlement probably occurred approximately, 5, 8 and 3 weeks earlier for these individuals.

6.3 Mortality.

The instantaneous rates of natural mortality per year (M), the annual survival rates (finite) (S %) and the values used in calculating these values are summarised in Table 6.3.

Table 6.3 The instantaneous rate of natural mortality and annual survival rates (finite) for the three species of sea urchin.

Species	t(yrs)	N_0	N_t	**M**	**S %**
S. variolaris	1	87	70	**-0.22**	**80**
E. mathaei	1	64	40	**-0.47**	**62**
D. savignyi	1	60	31	**-0.66**	**52**

From these results it appears that the Ramsgate population of *D. savignyi* experiences greater mortality than either the Ramsgate North *E. mathaei* or Sheffield Beach *S. variolaris* populations, and mortality rates for *E. mathaei* are higher than *S. variolaris*.

Discussion.

Sebens (1987) placed the major types of animal growth into seven categories, based on the shape of the growth curve, and the degree to which the growth trajectory and maximum size were genetically constrained. Of these seven categories, four are of the determinate type where growth rate and maximum size are primarily under genetic control. Of the remaining three types, two describe the indeterminate growth patterns displayed by sea urchins and other marine invertebrates (Paine 1976, Sebens 1982, Palmer 1983). Indeterminate growth is distinguished from determinate growth by the absence of genetically fixed limits to maximum body size, and by the ability to alter size throughout life, as conditions such as food supply, fluctuate. Indeterminate growth is therefore plastic and habitat dependent and the growth curves can be asymptotic or attenuating (Sebens 1987).

D. savignyi and E. mathaei on the South African coast appear to display asymptotic growth. The asymptotic sizes predicted by the Walford plots for E. mathaei are somewhat higher (Table 6.4), than those reported for E. mathaei from Hawaii, Kenya and Israel (Ebert 1982). Although this could in part, be the result of the limitations of my data set, individuals of sizes approaching the predicted asymptote were observed on the South African coast. And as asymptotic size in sea urchins is determined by habitat factors (Ebert 1968, Dix 1972, Vadas 1977), it was possible that more favourable habitat conditions prevailed on the South African coast which gave rise to the larger asymptotic size. While it is difficult to compare the habitats in question, the low population densities ($3.3/m^{2,}$ range 0-13) of *E. mathaei* on this coast may mean less competition for food; higher food availability would therefore permit growth to larger sizes, as shown for *D. antillarum* by Levitan (1988). In addition, as Moore *et al* (1963) and McPherson (1968) have shown, test growth decreases with increasing sea temperatures. The lower sea temperatures on the South African east coast, compared with more tropical coasts, may result in more rapid growth and larger body size. There appears to be no data on growth and maximum size for *D. savignyi*. However, asymptotic sizes of *D. setosum* on coasts of Zanzibar and Israel (Ebert 1982), are very similar to the value predicted for *D. savignyi* on the South African coast (Table 6.4).

Table 6.4. A comparison of the asymptotic sizes of *D. savignyi* and *E. mathaei* predicted by the Walford plot, for a range of localities.
* from Ebert 1982.

	Asymptotic size $S\infty$ (mm)				
	Natal S. Africa	Zanzibar E. Africa	Eilat Israel	Kapapa Is. Hawaii	Ras Iwatine Kenya
D. savignyi	84.9	91.9* *D. setosum*	83.6* *D. setosum*		
E. mathaei	86.8		44.9*	54.9*	48.9*

In contrast to the asymptotic growth shown by *E. mathaei* and *D. savignyi* on the South African coast, the von Bertalanffy growth equation predicts an attenuating growth pattern for *S. variolaris*.

The theoretical implication of this type of growth is that no asymptote will be reached, although growth decreases with increasing size (Sebens 1987). The subjective observation that this species is slow growing, long-lived and may achieve test diameters of 140mm or more, supports the predicted attenuating growth pattern. However, the maximum size of individuals from populations occupying the more exposed lower intertidal habitats was significantly smaller than the maximum size for individuals in less exposed habitats (Drummond 1993). This suggests that either exposed populations of this species are forced to an asymptote, or that individuals continue to grow, but once they exceed a certain size they are susceptible to dislodgement and death by wave action. As natural mortality of S. variolaris appeared to be low on the Natal coast, it is probable that the growth rate and maximum size attained in the more exposed populations was severely constrained by, for example, the mechanical factors of drag and impact forces arising from wave action (Denny, Daniel & Koehl 1985).

The size plasticity inherent in the indeterminate growth patterns displayed by sea urchins means that, with the exception of the period of initial growth, age and size are not necessarily correlated. Therefore considerable caution needs to be exercised when interpreting size distributions of populations. This applies particularly to long-lived species such as S. variolaris, which may have undergone significant periods of growth and negative growth in response to fluctuations in food availability. Based on the maximum sizes observed on the Natal coast, I suggest that S. variolaris has a potential life span of 15-20 years, D. savignyi, three to five years and E. mathaei, eight to ten years.

Ebert (1975) showed that, for 18 species of tropical and temperate sea urchins, a positive correlation existed between the von Bertalanffy growth constant (K) and the rate of natural mortality (M). D. savignyi with high K (0.79) and M (-0.66 yr^{-1}), S. variolaris with low K (0.11) and M (-0.22 yr^{-1}) and E. mathaei with K (0.32) and M (-0.47 yr^{-1}), all conform to the relationship demonstrated by Ebert (1975). Ebert (1975) speculated that it was the manner in which resources were allocated to growth, maintenance and reproduction that gave rise to this relationship. Furthermore, he maintained that it was the predictability of recruitment success which drove selection for particular patterns of resource allocation. This is the essence of the "Bet hedging" theory (Murphy 1968, Schaffer 1974, Stearns 1976) and will be discussed in greater detail in Chapter 7.

It might be expected that where sea urchins exhibited well synchronised annual reproductive cycles, settlement and recruitment would be confined to discrete periods. However this assumption did not appear to apply to either D. savignyi or S. variolaris, which showed highly synchronised reproductive cycles. Recruitment in D. savignyi occurred in a number of months spanning the latter parts of 1991 and 1992, while in S. variolaris, recruitment was highly unpredictable. That recruitment in S. variolaris on the Natal coast is probably characteristically unpredictable, is supported by the observation that in four years of monitoring the Oslo Beach population, there was not a single successful recruitment. Based on the January 1990 size structure of this population (Drummond 1991a), it is probable that the last successful recruitment into this population occurred in 1989. Successful recruitment appeared to be more predictable in D. savignyi and E. mathaei, as recruitment into the monitored populations occurred in 1991 and 1992. In addition, the size distributions in both populations indicated successful recruitment in the years prior to 1991.

While it is not known how long the larvae of the three study species spend in the plankton prior to settlement, the pattern of recruitment in D. savignyi in 1991 and 1992 gives the impression of it having occurred in pulses. This suggests that the larvae which settle may have been transported from more northerly populations, where the reproductive cycles may differ in timing from that of the populations on the southern Natal coast. Fish larvae are known to be transported southwards by the Agulhas current (Beckley 1992). However, Dye (1992) presents evidence, for three species of barnacle on the Transkei coast of South Africa, which suggests that larval dispersal is limited and recruitment arises predominantly from existing adults. Dye (1992) maintains that the headlands and embayments which characterise this coast, create complex currents and localized eddies which may reduce the offshore transport of larvae, and thus limit their dispersal. However, the settlement of other echinoid species, Tripneustes gratilla, Toxopneustes pileolus and Echinothrix diadema (personal observation) not previously present in particular pools, suggests that the larvae of these species, and by inference other echinoid species, do experience some dispersal before settlement. In the light of the work by Beckley (1992) and Dye (1992), it is certainly worth considering that recruits into echinoid populations may arise from larval populations which have experienced long distance dispersal, as well as from local populations contained by nearshore currents and eddies.

Strathmann (1978) gives the time from fertilization to settlement for the relatively long-lived *Strongylocentrotus purpuratus* as 63-86 days in the north-east Pacific. Based on the probable age of recruits and the timing of spawning in each species, the following developmental times were estimated: *S. variolaris*, 5-7 months, *E. mathaei*, 3-5 months and *D. savignyi*, 2-4 months. These estimates seem somewhat long especially as development is considered to be enhanced in warmer oceans (Kinne 1970). That recruits may have developed from gametes spawned at vastly different times may well render these estimates inaccurate. Alternatively, as productivity in the tropical and subtropical waters of the Indian ocean is generally lower than in the N.E Pacific (Parsons 1979), it may be reasonable to expect that developmental times, for *S. variolaris* in particular, might exceed those given for *S. purpuratus*.

Ebert (1983) reported that the recruitment of *S. purpuratus* varies with intertidal position, as more recruits were observed in the upper intertidal than in the lower stations. On the exposed Natal coast it appears that settlement and recruitment success may be more predictable in the mid-shore than in the lower intertidal regions, as recruitment of *D. savignyi* and *E. mathaei* in mid-shore pools was successful each year, and the only *S. variolaris* recruits observed during 1991 and 1992 were in mid-shore pools at Ramsgate and Sheffield beach. Furthermore, the size structure of mid-shore populations at Sheffield beach (Drummond 1993) suggested that substantial successful recruitments had occurred each year for at least four to five years prior to 1991. In contrast, the last significant recruitment into the population on the lower intertidal shelf probably occurred in late 1988 or early 1989. As exposure to wave action is significantly lower in the mid-shore pools than on the lower intertidal shelves (see Chpt. 4 this study), it is possible that mortality, at or soon after settlement, due to wave action could be a factor accounting for the unpredictable recruitment observed in *S. variolaris*. Thus, settlement and successful recruitment of *S. variolaris* into the lower intertidal may be, at least in part, dependent upon infrequent periods of unusually low swells and wave action.

If Dye's (1992) contention that recruits of sessile invertebrates may arise largely from existing adults has validity, then a point to be considered is that the relatively small numbers of recruits, particularly of *S. variolaris*, may reflect a low level of fertilization success on the Natal coast. Studies by Pennington (1985), and Levitan, Sewell & Chia (1991, 1992), indicate that a high percentage of fertilization success can only be achieved by aggregation and synchronous spawning of echinoids. Certainly in the light of the limited mobility (Gemmill 1900), and inability of sperm to detect the presence of eggs (Rothschild 1956, Chia & Bickell 1983), combined with the implications of the "respiratory dilution effect" (Chia & Bickell 1983), and current velocity (Pennington 1985), this is a reasonable suggestion to make. But, does this condemn sedentary and burrowing echinoids to insignificant fertilization success? The almost continuous movement of water across the lower intertidal shelves suggests that fertilization success in this habitat may well be low, and dependent on the coinciding of extremely low tides with the spawning period. However, as the high energy lower intertidal appears to be the preferred habitat of S. variolaris, additional mechanisms must exist whereby fertilization success can be enhanced. Levitan, Sewell & Chia (1992) demonstrated that where the density of spawning individuals was high, fertilization success was greater. The density of populations of S. variolaris on the Natal coast was variable, ranging from 1 to $15/m^2$. Furthermore, this species is sedentary and therefore density cannot be increased by aggregation of adults. The preference displayed by juveniles for attachment sites under the canopy of adult spines may, in addition to providing protection for the juvenile, have been selected for as a means whereby density could be increased over time. As this species is long-lived the protection of juveniles could be regarded as investment in future fertilization success. Although the predilection of S. variolaris for occupying crevices, hollows or excavating burrows serves to isolate spawning individuals, the currents which deliver drift algae to these urchins could also transport gametes. Therefore spawned gametes could become contained within these burrows or crevices, at concentrations which would result in high fertilization success. Some support for this idea of containment and concentration of gametes, is provided by Denny, Dainki & Distefano (1992). These authors suggested that external fertilization could be enhanced on wave swept rocky shores, by the concentrating of gametes in channels and blindended embayments, where there was little mixing with the mainstream flow. However, this mechanism probably has greater implication for E. mathaei and D. savignyi which occupy such embayments and channels in the mid-shore on the Natal coast.

Clearly the factors influencing the temporal and spatial patterns of recruitment of these three echinoids are many. Yet, I think it is reasonable to suggest that, as with other aspects of the biology and ecology of these three species, wave action is probably the dominant factor affecting settlement and recruitment. However until we have a better understanding of the requirements, interactions and movements of the planktonic larvae, it will be difficult to fully account for the observed recruitment patterns.

In summary:

The results presented in this chapter, indicated that S. variolaris on the Natal coast had relatively slow growth rates, is long-lived, and showed the lowest mortality rates over the study period. Recruitment into lower intertidal shelf populations of this species appeared to be unpredictable. In contrast, D. savignyi showed more rapid growth and a relatively short lifespan and high mortality. Recruitment in the latter species was predictable and occurred during several months over the latter half of 1991 and 1992.
E. mathaei showed growth rates, mortality and lifespan intermediate between S. variolaris and D. savignyi, and recruitment was predictable and confined to the spring and summer months.

Chapter 7. GENERAL DISCUSSION.

Natural selection acts on the variation in the existing adaptations among organisms and on the way these adaptations contribute to the variation in individual fitness. While acknowledging the role played by an organism's phylogenetic history, selection is considered to be related to energy budgets (Cody 1966, Gadgil & Bossert 1970, Calow 1979, Ebert 1982). An organism's life history therefore represents the differential allocation of limited resources to various traits, in an evolved response to the problems in their present environment. It is assumed (Stearns 1976), that the pattern of allocation or combination of traits selected for, represents the optimal solution for the prevailing situation. In reality an optimal life history is probably never achieved, as environments change and populations' perceptions of the environment alter. Thus any investigation into an organism's life history can only provide a small window into what is a continual process of adjustment.

The stated aim of this study was to acquire fundamental information on the biology of the intertidal echinoids, Stomopneustes variolaris, Echinometra mathaei and Diadema savignyi on the South African east coast. Concomitant with the acquisition of this information was the opportunity to investigate the variation in echinoid life histories which have evolved within the wave-swept intertidal region on this coast. The approach in this study was to determine whether the three species showed differences in their relative investments in growth, maintenance and reproduction. By relating these patterns of investment to the habitat occupied by each species, this discussion: a) shows how their life histories function in the present environment, and b) speculates on the selective forces which might have been implicated in shaping the life histories of these three species.

It is apparent from the results of investigations conducted between January 1991 and June 1993 that among the three species populations there are distinct differences in their patterns of investment in growth, maintenance and reproduction. Table 7.1 summarises the characteristics of the life histories of the three species.

Table 7.1 A summary of the life history characteristics shown by D. savignyi, E. mathaei and S. variolaris on the South African east coast.

	D. savignyi	E. mathaei	S. variolaris
REPRODUCTION			
Reproductive output (KJ/Yr)	258	217	203
Age at first reproduction	6 mnths	12mnths	18-24mn
MAINTENANCE			
Contribution to test & spines	Low	Moderate	High
Number of podia/ambulacrum, (urchins 50mm test diameter)	137	181	314
GROWTH			
K (Growth co-efficient)	0.79	0.32	0.11
Lifespan	3-5 yrs	8-10 yrs	15-20 yrs
Recruitment predictability	High	High	Very low
Adult mortality (M)	-0.66	-0.47	-0.22

A sea urchin occupying a habitat on the lower intertidal shelf on the South African east coast has to contend with:

1) unrestricted wave action with the accompanying potential for damage and/or displacement. Furthermore, a high energy habitat imposes restrictions on movement (Lawrence & Sammarco 1982) and feeding (McPherson 1968), as well as limiting body size (Denny, Daniel & Koehl 1985),

2) sand deposition which can hamper feeding and respiration by burying the sea urchins,

3) exposure to air, high temperatures and high light intensity at spring low tides with consequent physiological stresses,

4) limitations to the duration of feeding time as a result of excessive turbulence during high tide (Sammarco 1972 in Lawrence 1975) and the absence of water movement at the lowest tides (McPherson 1968),

5) competition for primary space with zoanthids and the brown mussel, Perna perna, which might affect recruitment success of S. variolaris,

6) fluctuations in food availability, more drift algae being available in times of high seas (personal observations, Russo 1977), and

7) possible limitations to fertilization success as a result of high current velocity (Pennington 1985) and low population density (Levitan 1991a).

The successful and persistent occupation of this high energy habitat by S. variolaris can be attributed to its relatively thick test and stout spines. In addition, relative to other species, S. variolaris has a small peristomial opening and a greater number of podia per ambulacrum, which combined with the adoption of a sedentary and often cryptic lifestyle, allows this species to effectively resist displacement by water movements. The relatively massive test and the practice of "covering" with mollusc shells or algal fragments probably serve to prevent desiccation and reduce the effect of high temperature and light intensities at low tides, as suggested by Orton (1929) and Sharp & Grey (1962). The slow growth shown by S. variolaris is possibly a function of a relatively greater allocation of resources to the body wall, diversion of resources into repair of damaged spines or food limitations. While this slow growth may render these urchins vulnerable to being outcompeted by faster growing organisms such as mussels in the lower intertidal, it is perhaps adaptive within the context of a life history shaped by selection for survival. In addition to a thick test and stout spines, survival of this species in the lower intertidal is enhanced by the occupation of hollows and crevices which provide a measure of protection from the force of wave action (Drummond 1991a). Slow growth and the observation that these sea urchins appear to enlarge their attachment sites to some degree, would mean that individuals are unlikely to outgrow their protected attachment sites.

The small body size which, on this coast, is characteristic of lower intertidal populations of S. variolaris is probably imposed by the drag and impact forces associated with wave action. Support for this suggestion is provided by the experimental work of Denny, Daniel and Koehl (1985) and by the observation that individuals in lower energy habitats were larger; for example, a sample of 319 individuals from a population of S. variolaris from Madras Harbour had a mean body size of 100mm (test diameter) (Giese, Krishnaswamy, Vasu & Lawrence 1964), while the mean body size of the population at the high energy Oslo Beach habitat was only 48mm (test diameter) (this study). Subjective observations and a preliminary study (Drummond 1993) suggest that body size in S variolaris may be further limited by the ability of their habitat to provide adequate protection from water and sand movements. I believe that populations of S. variolaris assume a mean body size in response to the available protection provided by substratum rugosity and the degree of wave action experienced in their particular habitat. This suggestion is not unrealistic, as it has been shown that populations of sea urchins can adjust body size in response to for example, food availability as mediated by population density (Levitan 1988, 1991b). The patchy distribution of S. variolaris on the South African coast could therefore be related to the presence of rock substratum which can provide suitably shaped and sized attachment sites, or is of a type which can be eroded by sea urchin jaws and spines.

The relatively large investment in maintenance shown by S. variolaris, small body size with associated lower metabolic requirements, which would allow this species to cope with fluctuations in food availability, a sedentary lifestyle and predeliction for occupying sheltered crevices and hollows, all suggest selection for a life history which favours efficiency and survival.

Conditions in mid-shore pools contrast with those of the lower intertidal in the following ways:

1) wave action is reduced, as the depth of the pools and distance up shore effectively absorb some of the wave shock,

2) sand deposition and removal is of greater magnitude,

3) there is no exposure to air, and the effects of high temperatures and light intensity are ameliorated by the depth of the pools,

4) there is a higher density of fish, molluscs and crustaceans and consequently predation on sea urchins is likely to be higher,

5) potential feeding time is longer as a result of less turbulence, and the lower energy environment permits mobile grazing by sea urchins,

6) greater food availability, but also probably more competition for food as a result of a higher density of sea urchins and other herbivores, and

7) potential for higher fertilization success.

The thinner tests and long fine spines makes D. savignyi vulnerable to damage or death if exposed to unrestricted wave action. The distribution of this species is thus restricted to suitably deep intertidal pools on the South African east coast and sheltered sites either intertidally or in the shallow subtidal in other parts of its range (Pearce & Arch 1969, Ebert 1982). The mobility of this species enables them to seek shelter in crevices in times of heavy seas, or to avoid burial by sand deposition, a phenomenon which characterises this mixed rocky shore/sandy beach coastline. Rapid growth and predictable recruitment result in rapid replacement of individuals removed by heavy seas. In addition, D. savignyi juveniles are capable of breeding after only six months of growth, while E. mathaei and S. variolaris juveniles breed only after 12 and 18-24 months respectively. However the reproductive output of Diadema at first spawning is lower than that of juveniles of the other two species. This suggests that, during their first year, resources in D. savignyi are allocated preferentially to growth, and it is only in their second year, when this initial rapid growth is curtailed, that the high reproductive output which characterises the species becomes evident. A similar interaction between relative investment in growth and reproduction was reported for the barnacles Elminius modestus (Crisp 1960) and Chthamalus anisopoma (Malusa 1986), which typically display high reproductive outputs. In terms of the relationship between body size and gonad size in sea urchins, an increase in gonad size is only possible if body size increases, as the gonads occupy most of the internal volume of the test. Therefore the priority in terms of resource allocation in D. savignyi would seem to be the rapid achievement of a large body size in order to accomodate the growth of large gonads. In other words the issue is not simply early reproduction, but high reproductive output as soon as possible.

The characteristics of the life history of D. savignyi suggest that selection has been for productivity, rapid growth and high reproductive output.

Differences in phylogeny and design constraints result in more than one solution to a set of environmental problems being possible (Southwood 1988). E. mathaei which occupies the same mid-shore habitat as D. savignyi, shows life history traits in which the relative allocations to growth, reproduction and maintenance are more equitable than in D. savignyi and S. variolaris. Aspects of the pattern of resource allocation in E. mathaei suggest that, relative to D. savignyi, it has evolved a lower risk response to the factors prevailing in the mid-shore. A larger investment in the body wall would enable E. mathaei to tolerate higher energy conditions than D. savignyi, and therefore, a wider range of potential attachment sites within pools are available to it. Although the greater relative investment in maintenance by E. mathaei occurs at the expense of growth and reproduction (Ebert 1975), mortality is reduced, and life span is thus longer. As a consequence, reproductive value (Williams 1966), the proportionate rather than absolute contribution to the future populations, is increased as individuals will survive to reproduce for more years. That the life history of E. mathaei does represent a lower risk solution for the mid-shore is perhaps confirmed by the longer lifespan and lower mortality of E. mathaei relative to D. savignyi. However, this lower risk strategy, particularly its slower growth, predominantly sedentary and drift feeding lifestyle as well as the requirement of shelter for juveniles, could reduce the competitive ability of E. mathaei. The lower, density and abundance of this species in the mid-shore pools compared with D. savignyi was possibly an expression of this.

Exposure to wave action is known to reduce gonadal production in sea urchins (Gonor 1973a); it is therefore curious that the reproductive output of S. variolaris and E. mathaei, occupying the high energy lower intertidal and sheltered mid-shore habitats respectively, appeared to be relatively similar in magnitude (Table 7.1). This anomaly might be explained by examining allocation of resources in terms of the advantages and costs associated with an increase in allocation to a trait. Basically, an increase in resources may result in an increase in reproductive or somatic investment depending on the relative benefits to fitness achieved by increased fecundity or increased survival (Michod 1979). Ebert (1975), focussing on sea urchins, maintained that a positive correlation between growth rate and mortality rates indicated that a greater relative investment in growth and reproduction was at the expense of investment in maintenance. But Calow (1979) predicted that if resources were adequate to meet maintenance requirements, then an increase in reproductive output need not be accompanied by increased costs in terms of reduced survival. In terms of this prediction, the higher than expected reproductive output in S. variolaris could reflect the absence of food limitations. This is contrary to the generally held belief that slow growing species are food limited (Gonor 1972, 1973a, Lawrence 1990). In addition, the absence of S. variolaris with test diameters larger than 54mm, suggested that large body size was selected against in the lower intertidal. Therefore, the lower energy requirements associated with smaller body size could mean that surplus resources were available for investment in reproduction. The benefits to fitness, associated with an increased reproductive output, may be via improved fertilization success as a result of the larger number of gametes spawned; as Pennington (1985) and Levitan, Sewell & Chia (1992) have shown that fertilization success is enhanced by a high concentration of gametes. However, it should also be considered that while E. mathaei might be occupying the less stressful habitat in terms of exposure to wave action, this might represent a sub-optimal habitat for this species. The lower than expected reproductive output in E. mathaei may thus be a reflection of this.

Comparison with work done by MacClanahan (1988) on the Kenyan coast, provides some evidence that limiting factors might be affecting E. mathaei on the South African coast. MacClanahan (1988) reported that E. mathaei, where it co-occurred with D. setosum and D. savignyi, was the top competitor for space and showed the highest densities and abundance of the three species. In contrast, where E. mathaei and Diadema spp. co-occur at the Ramsgate and Isipingo sites, density and abundance of D. savignyi is higher (personal observations). These differences may be related to the fact that on the Kenyan coast E. mathaei occupies burrows (MacClanahan 1988), while at Ramsgate they do not; burrowing is probably precluded by the hardness of the rock, which is dolerite and a mature, well cemented, sandstone. This inability for E. mathaei to burrow may affect feeding and decrease resistance to wave action and/or predation, factors which are likely to be expressed in a lower reproductive output.

The discussion to this point illustrates the adaptive nature of resource allocation in the life histories of the three species studied, while what follows, focuses on the assumptions and predictions of the two major approaches to life history evolution, which are invoked in explaining such adaptations. It is not intended as a test of the general explanatory powers of the two approaches, but rather their applicability in specifically identifying the selective forces which might have shaped the life histories of the three species of sea urchin.

The major theoretical approaches to life history evolution have been soundly reviewed by Stearns (1976), but I will briefly summarize the assumptions and predictions of r-K theory for the sake of clarity. r-K theory emphasizes the importance of biotic interactions with associated density dependent effects and environmental stability in favouring the development of longevity (MacArthur & Wilson 1967). A K- selected population occupies a habitat which is constant or predictable, therefore crowded populations develop, which result in intense competition among adults. Mortality in these populations is density dependent. The predicted characteristics of such a population are: large body size, delayed reproduction, lower reproductive output, slow growth and long lifespans. In contrast r- selected populations occupy harsh and unpredictable habitats where benign periods, which permit rapid population growth, are followed by periods of density independent mortality. The predicted characteristics are: smaller body size, early reproduction, higher reproductive output, rapid growth and short lifespans. When the characteristics shown by the three sea urchin species of the present study are considered, the rapid growth, high adult mortality, high reproductive output and short lifespan of D. savignyi suggests r-selection. The slow growth, lower adult mortality, low reproductive output and long lifespan of S. variolaris suggests K-selection, with E. mathaei somewhere on the continuum between. While these life histories appear to match the predictions of r and K- selection (MacArthur & Wilson 1967), I do not believe that they are the results of density independent or dependent effects operating in harsh and favourable habitats respectively.

Conditions across the intertidal are typically considered to become increasingly more harsh with distance up the shore (Stephenson

1943), and this is certainly true for some species such as intertidal molluscs (Branch & Branch 1981). However, from the point of view of an adult sea urchin, it is not possible to define the lower intertidal as a favourable, predictable K- selecting habitat, or mid-shore pools as harsh, unpredictable r-selecting habitats, as indicated by the respective life histories shown by sea urchins in these habitats. If anything, the reduced wave action, more food and no possibility of exposure to air make mid-shore pools the relatively more stable and predictable habitat. However the high adult mortality of sea urchins occupying this habitat could suggest that r-selecting factors are nonetheless present. It might therefore be more realistic to view the abiotic and biotic environments experienced by sea urchins in both habitats, as a mosaic of r and K- selecting factors, and as such, not a situation capable of shaping the clearly dichotomous life histories shown by <u>S</u>. <u>variolaris</u> and <u>D</u>. <u>savignyi</u>. My second point on which I reject the role of density dependent or independent effects in shaping these life histories, is that density-independent selection can occur at any density (Prout 1980), not only at low densities as assumed for r- selecting habitats. Wave action, although a constant factor, is essentially unpredictable in magnitude, and with the concomitant transport of sand is a density independent source of mortality and as such should exert r-selection on populations in both the mid-shore and lower intertidal.

r-K theory assumes that mortality and fecundity schedules are fixed. However, it is indisputable that fecundity and mortality varies, between populations and between age groups within populations (Murphy 1968, Schaffer 1974, Stearns 1976). This is illustrated by the observed differences in juvenile and adult survival among the three species of the present study. Recruitment of S. variolaris in the lower intertidal of the east coast is unpredictable and adult mortality is low. In contrast, recruitment of E. mathaei and D. savignyi into mid-shore pools is predictable, but adult mortality is high. Recruitment into mid-shore populations is perhaps more predictable because there is a lower risk of displacement by wave action, and more protection is available for juveniles in the form of boulders, crevices and coral heads.

Variation in recruitment predictability between the two habitats may therefore be a force capable of shaping the different life histories. Variation in juvenile survival is the basic tenet of Stearns (1976) "Bet hedging" concept, which suggests that where prereproductive survival is predictable, greater fitness would be had by rapid growth and a large investment in reproduction. As a consequence there would be a low investment in maintenance and thus high mortality and shorter lifespan. This scenario appears to fit the life history shown by D. savignyi on the South African east coast. In contrast, where prereproductive survival was unpredictable, as in S. variolaris, greater fitness would be achieved by investment in maintenance rather than reproduction. As a consequence these sea urchins displayed slow growth, lower adult mortality and longer lifespans. Although recruitment was predictable, E. mathaei appeared not to favour reproduction at the expense of maintenance. Rather, this species "sits on the fence", allocating sufficient resources to enable individuals to tolerate the physical environment, while still making a moderate investment in reproduction over a lifespan of intermediate duration. As a consequence their life histories are balanced between production and survival, a low risk approach which possibly accounts for their widespread distribution and adaptation to a range of habitats.

Despite the neatness with which the "bet hedging" approach appears to explain the three contrasting life histories, I am hesitant to accept variation in juvenile survival as the only selective force implicated in these life histories. Even if recruitment was predictable, survival in the high energy lower intertidal to the age of first reproduction, would still be dependent upon a large investment of resources in maintenance (body wall thickness). Furthermore drag and impact forces (Denny, Daniel & Koehl 1985), and the capacity of the habitat to provide protection would impose limits on the maximum body size of sea urchins in the lower intertidal. So, small body size and a large allocation of resources to maintenance preclude a high reproductive output in S. variolaris. Therefore I suggest that slow growth of S. variolaris is a response to the necessity for a large investment in maintenance, the diversion of resources into repair of damaged test or spines and possible food limitations, while a long lifespan, is a means whereby fitness is enhanced in the face of low reproductive output and unpredictable recruitment.

While not discounting the insights provided by evoking general demographic theories to explain the observed life histories, I maintain that on wave swept shores such as the South African east coast, the specific effects of exposure to wave action generate a greater selective pressure than do forces arising from biotic interactions. This dominance by selective forces arising from the effects of wave action is illustrated in the life history of S. variolaris, where it is only by a massive investment in maintenance that it can survive in its' lower intertidal habitat. As a consequence, other aspects of its life history must be constrained by the considerable allocation of resources to the body wall. Echinostrephus molaris, which occupies burrows in the unconsolidated sandstone of the mid and lower intertidal on this coast, perhaps illustrates the point in a different way. Although this species has a thin test and fine spines, the energy expended in excavation of a 6-10cm burrow represents its investment in maintenance. The energetic considerations of burrow construction and subsequent enlargement would preclude rapid growth and large body size and therefore, this species probably has a low reproductive output. Although the occupation of burrows provides protection from wave action and a unique means of trapping drift algal food, it would also serve to isolate individuals and I would therefore predict that this species would have relatively low fertilization success and unpredictable recruitment, but high longevity would ensure a contribution to future populations.

In the mid-shore pools sea urchin life histories are released from the constraints imposed by the need for a large investment in maintenance. The reduced wave action in the pools permits more active lifestyles, consequently the acquisition of more food is possible; drag and impact forces probably have little or no effect on body size in this habitat. As a consequence more resources are available for growth, and a larger body size permits a higher reproductive output. Predictable recruitment in this habitat would obviate the necessity for long life to ensure a contribution to future populations. The release from the large maintenance requirements means that sea urchin life histories in mid-shore habitats are influenced more eclectically, and as a result a wider range of evolved solutions to environmental conditions can be expressed.

My contention that the effects of exposure to wave action are capable of generating selective pressure, is in part supported by the well documented effects of wave action on echinoid life history traits such as: body size (Denny, Daniel & Koehl 1985), growth rates (MacPherson 1968, Baker 1973), reproductive output (Gonor 1973a), fertilization success (Pennington 1985) and mortality (Ebert 1982). Furthermore, as it is accepted that life histories are related to the energy budget of an organism (Gadgil & Bossert 1970), and since exposure to wave action has an impact on the acquisition and retention of resources by sea urchins, the suite of effects associated with wave action could therefore generate a significant selective pressure. A similar view of echinoderm life histories was expressed by Lawrence (1990, 1991) in his interpretation of Grime's (1974, 1977) triangular model of life history evolution. However, where Lawrence (1991) regards low levels of food acquisition as the significant stress factor, and attributes slow growth and long life to food limitations, I suggest that slow growth and high longevity in sea urchins could be an evolved response to the necessity for a large investment in maintenance, the constraints imposed on maximum body size, and unpredictable recruitment, all of which characterize high energy habitats.

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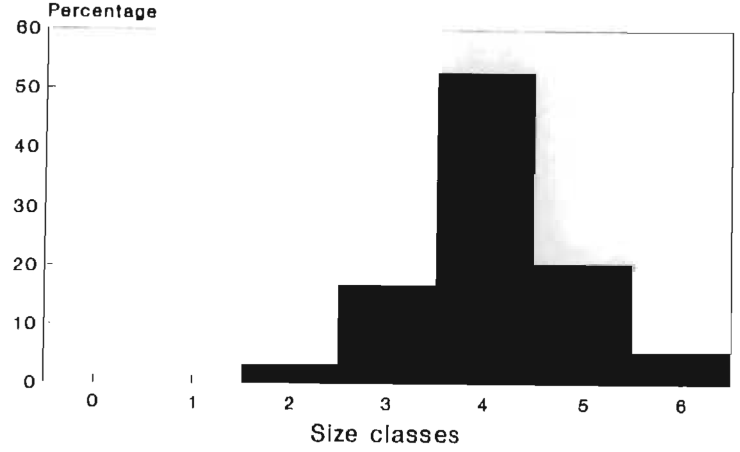
APPENDIX 1.

1.1 Population size distributions for Stomopneustes variolaris at Sheffield beach from April 1991 - September 1992.

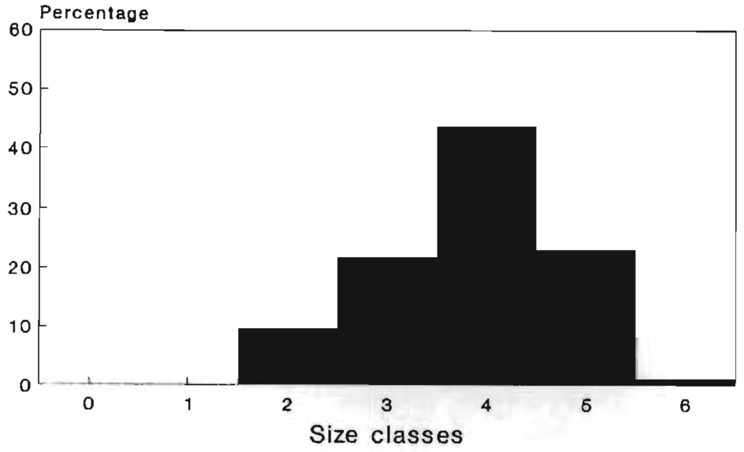
1.2 Population size distributions for Diadema savignyi at Ramsgate from February 1991 - March 1993.

1.3 Population size distributions for Echinometra mathaei at Ramsgate North from February 1991 - December 1992.

APRIL 1991



AUGUST 1991



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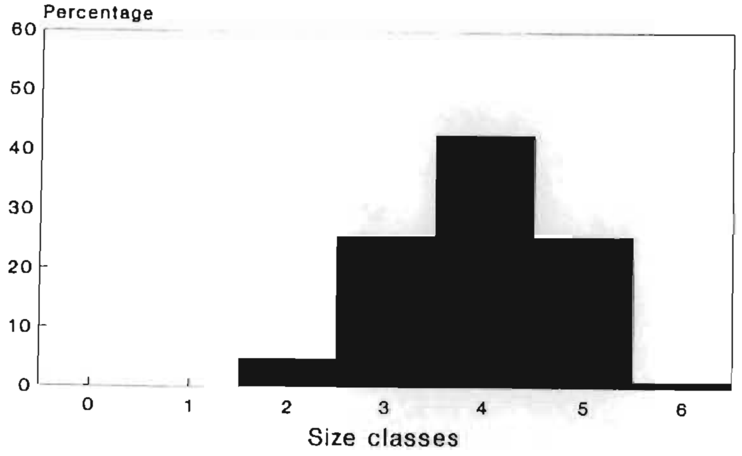
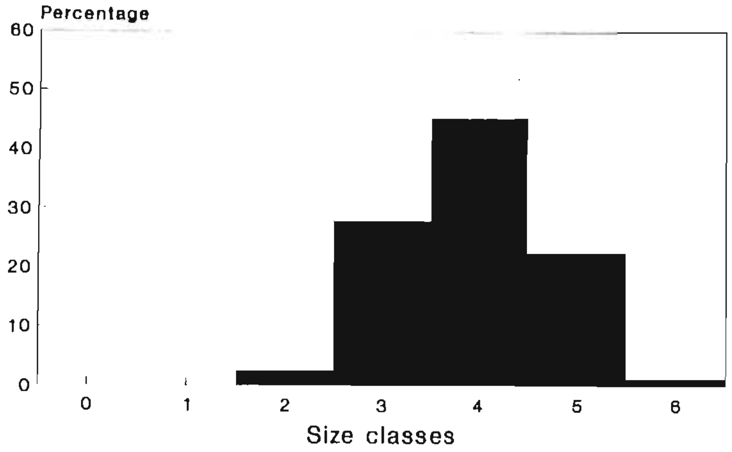
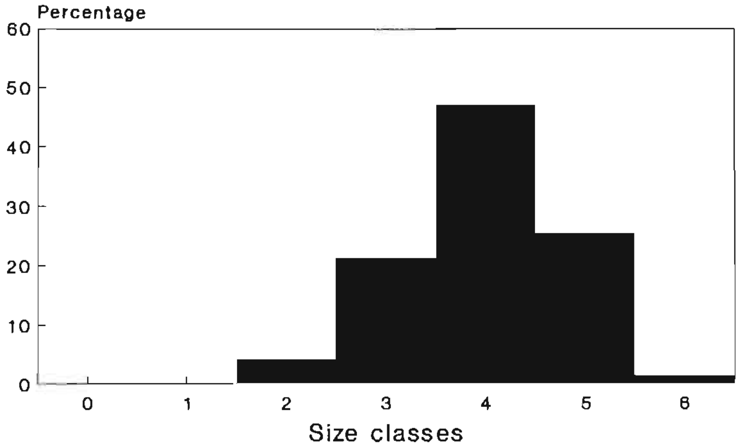


1.1 *Stomopneustes variolaris*

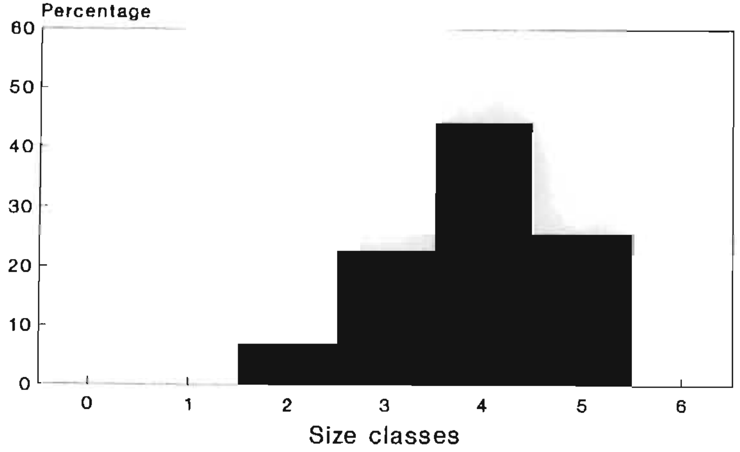
JANUARY 1992



APRIL 1992



June 1992



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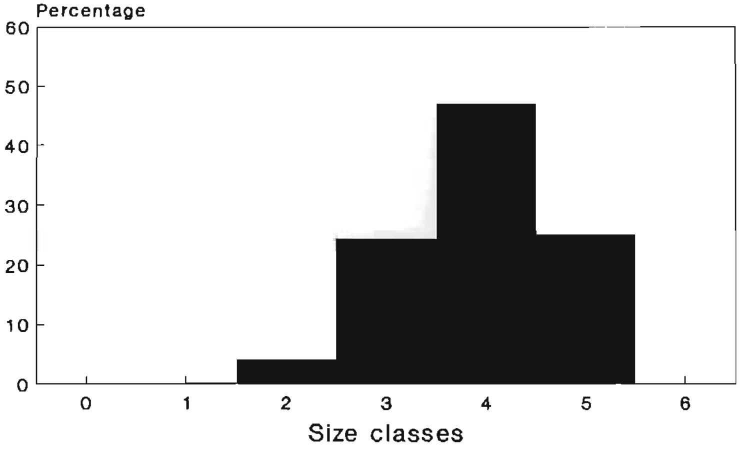
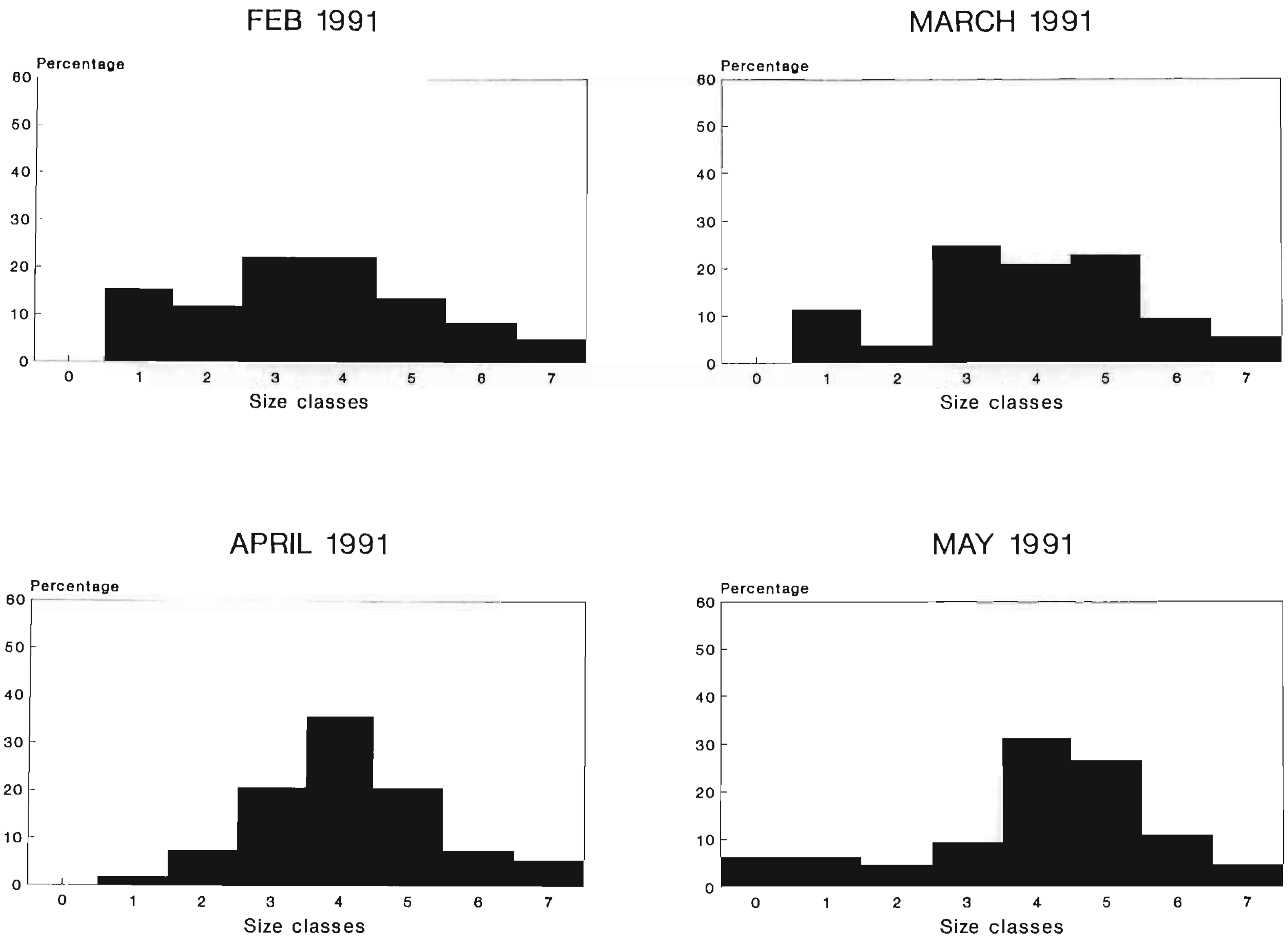


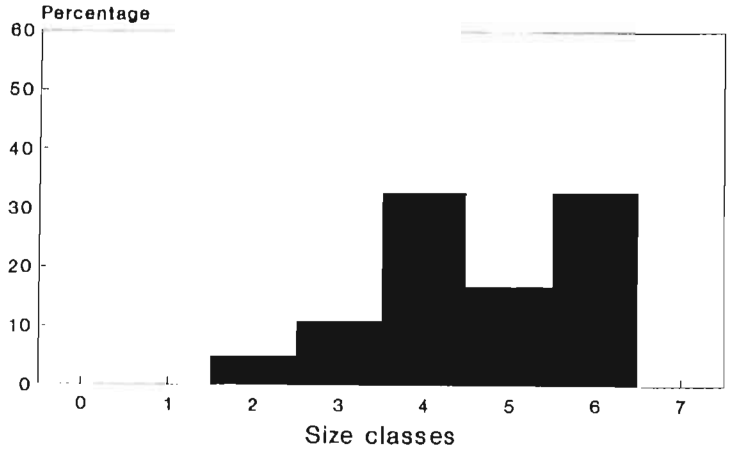

FEB 1991

MARCH 1991

APRIL 1991

MAY 1991

1.2 *Diadema savignyi*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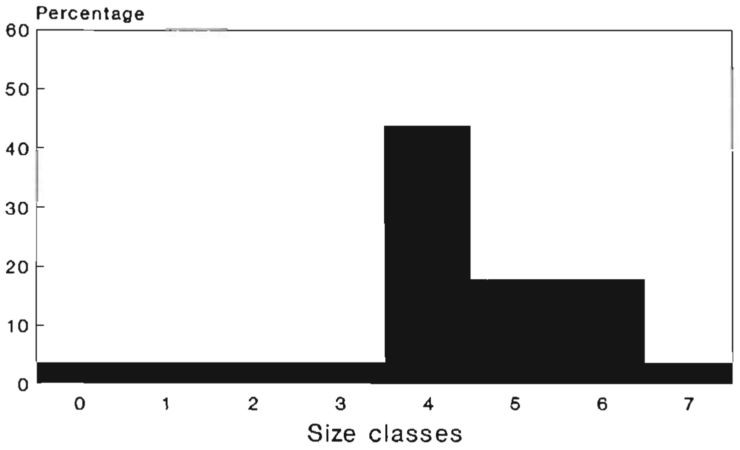
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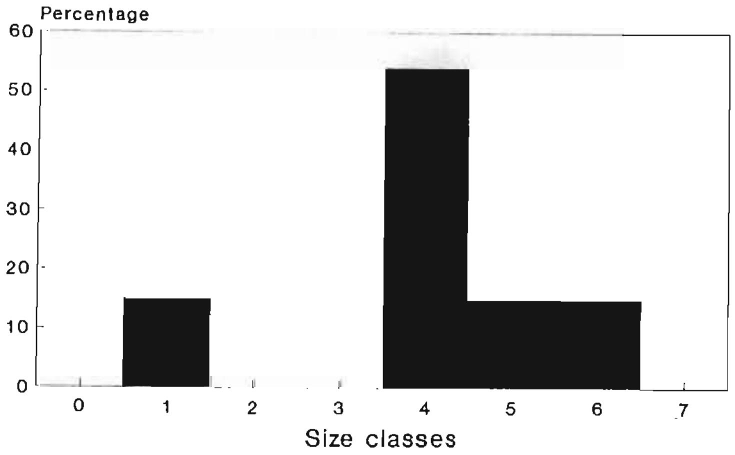
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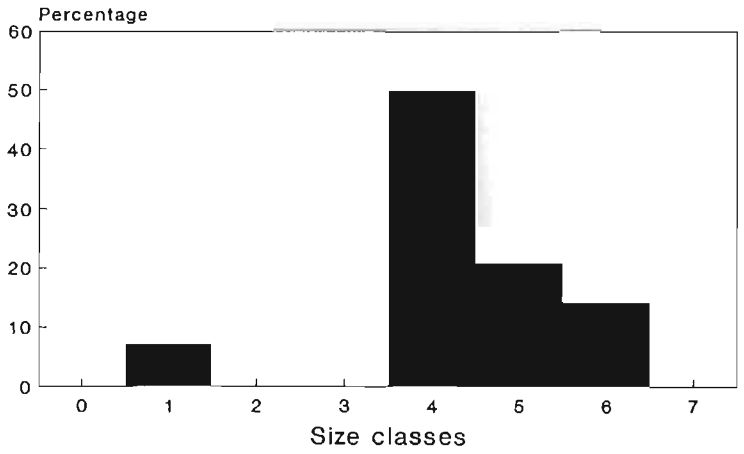
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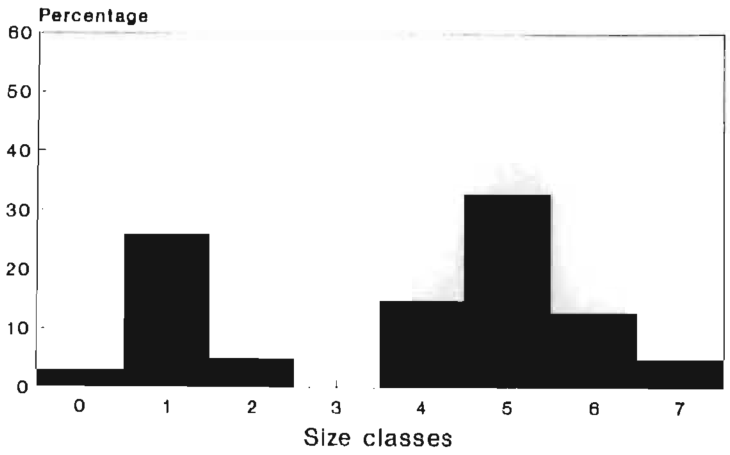
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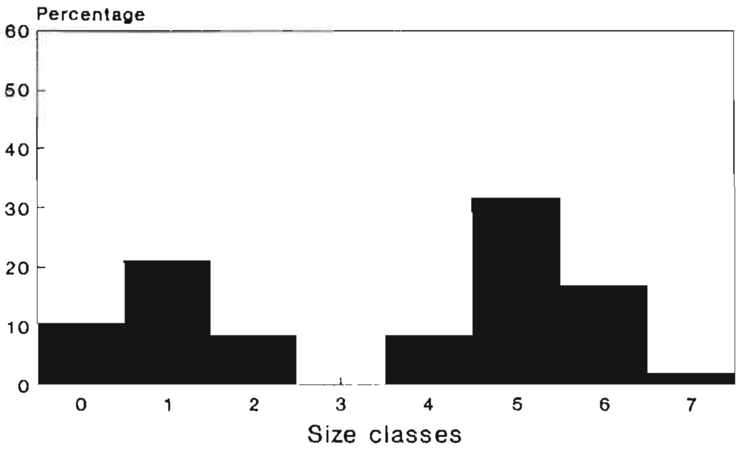
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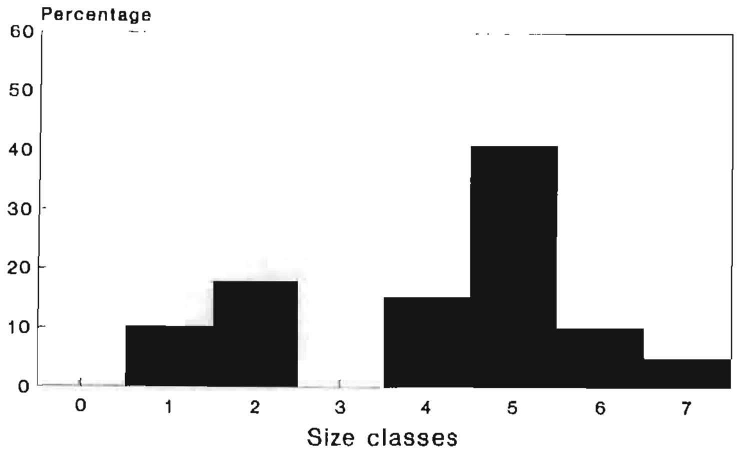
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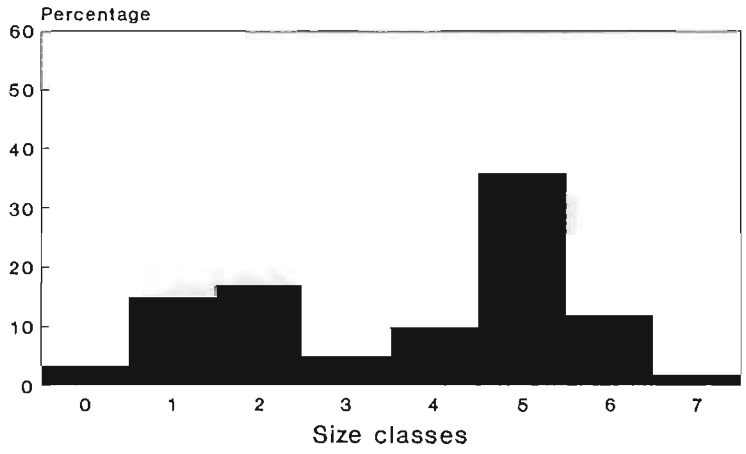
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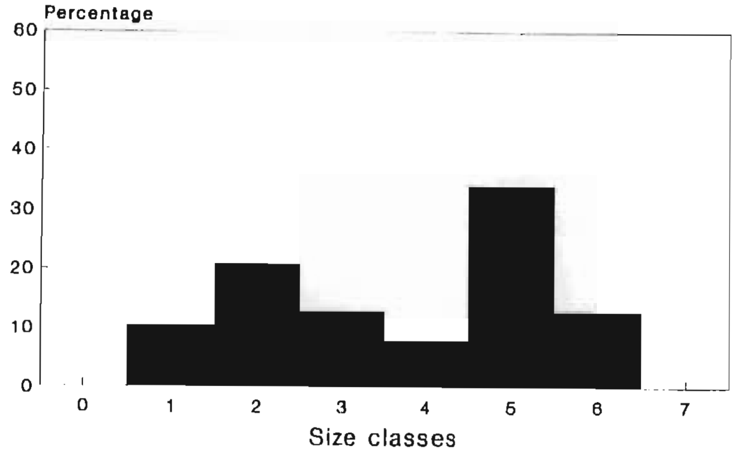
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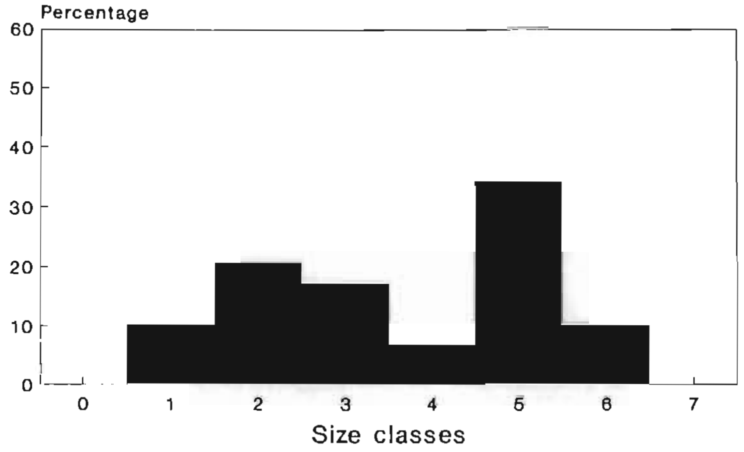
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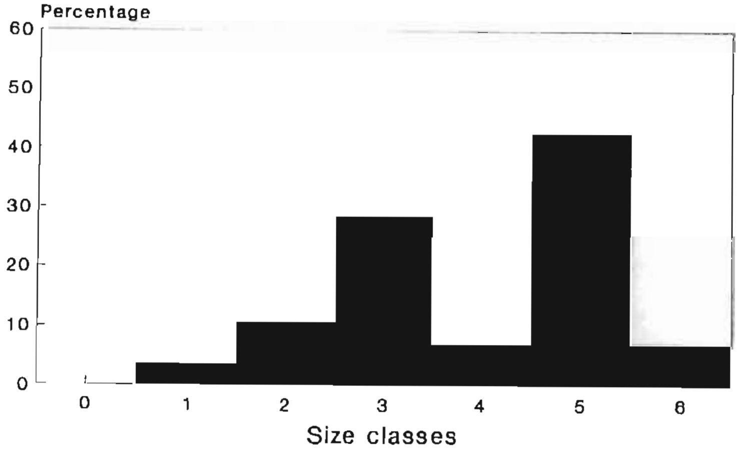
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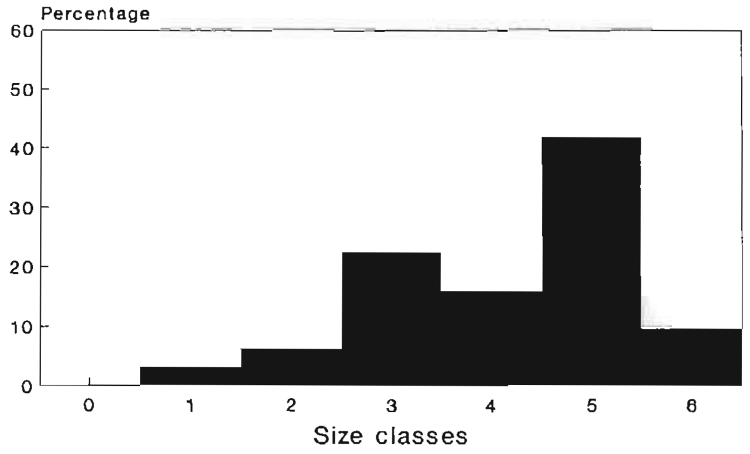
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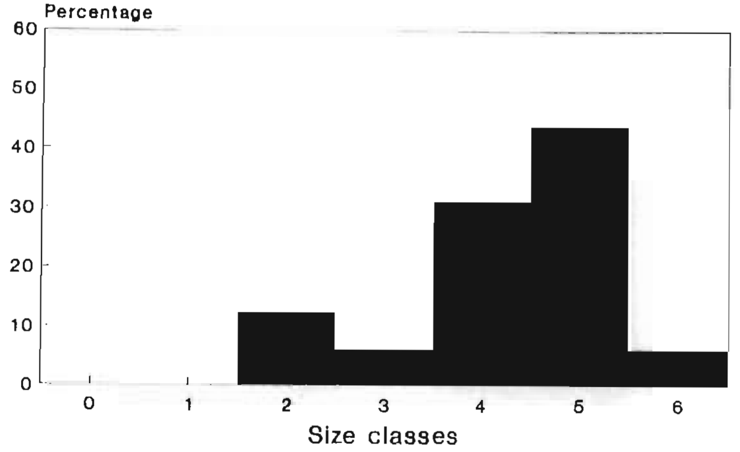

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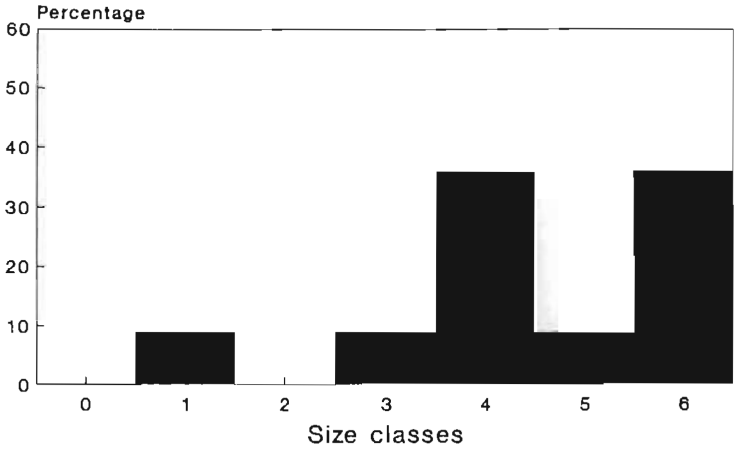

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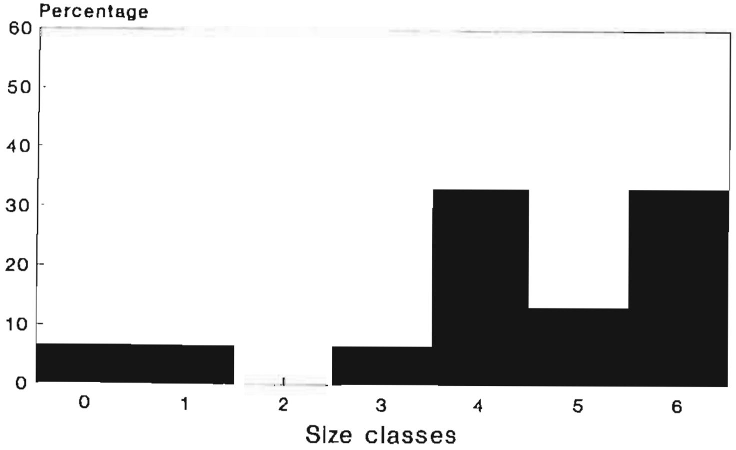

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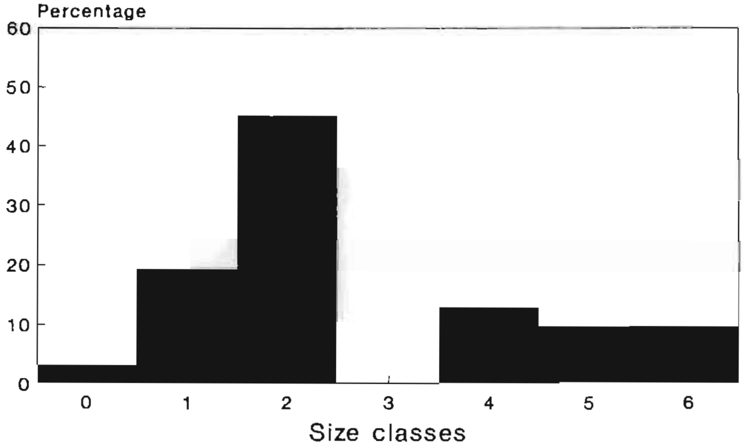

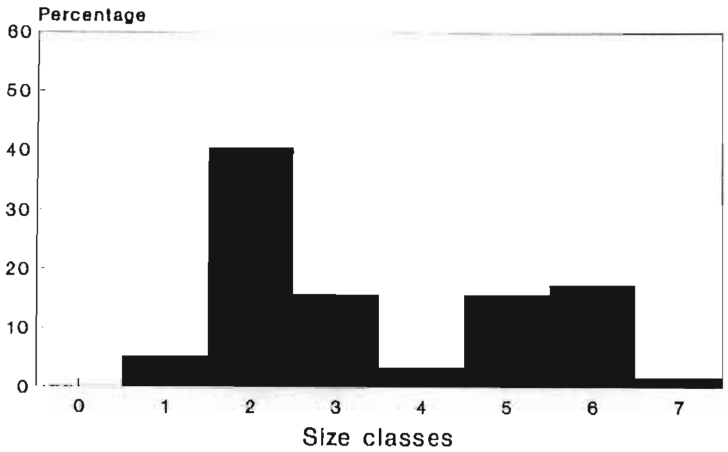

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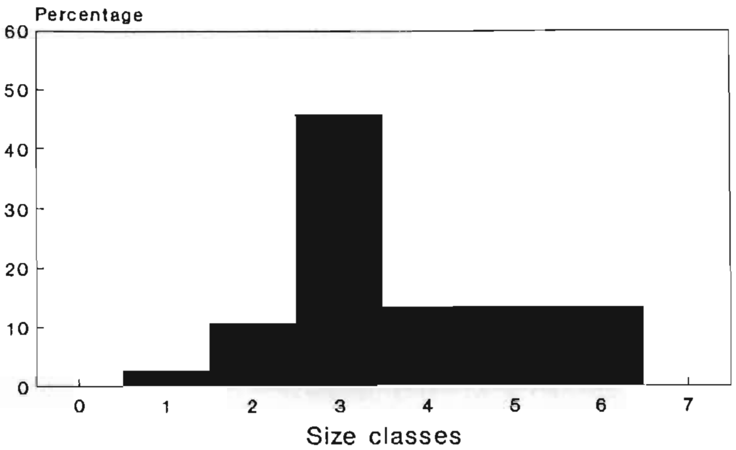

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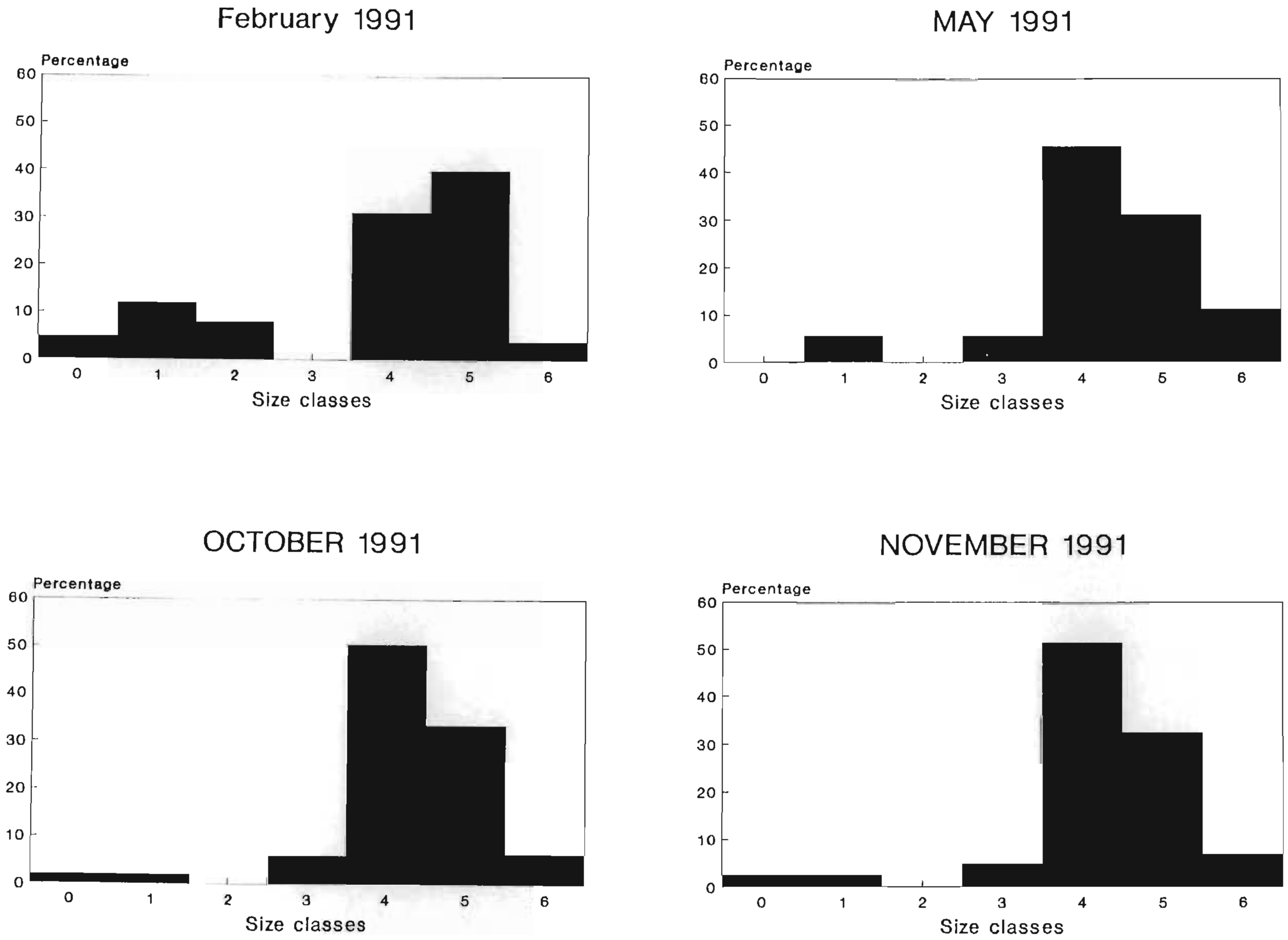
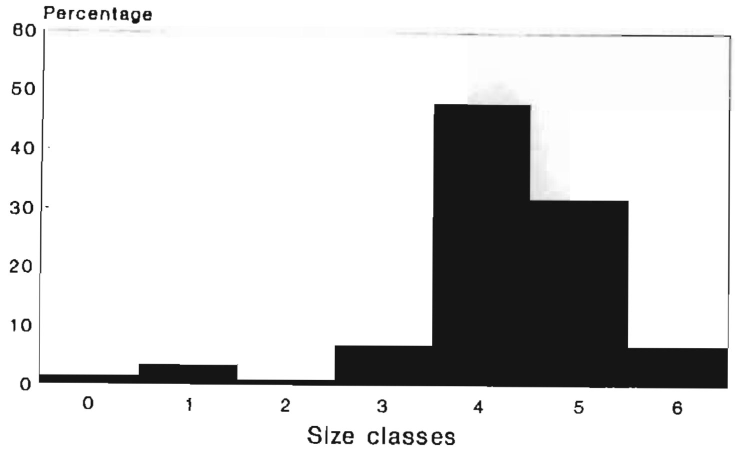


1.3 Echinometra mathaei

DECEMBER 1991



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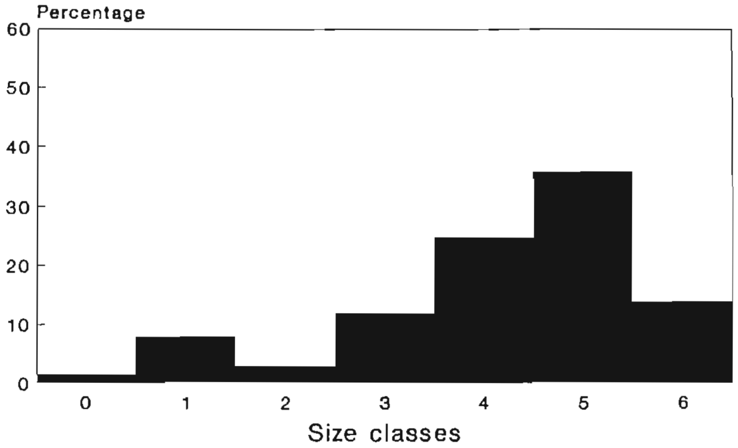

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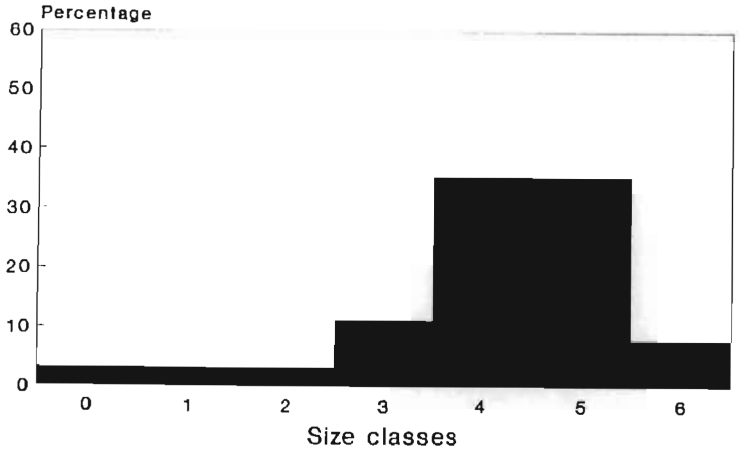

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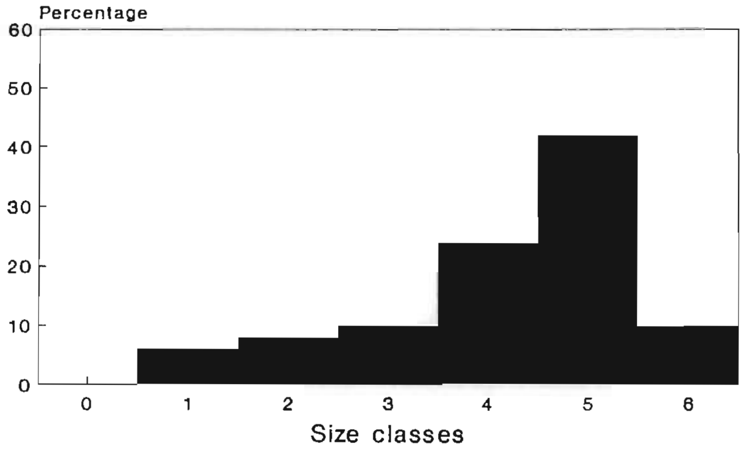

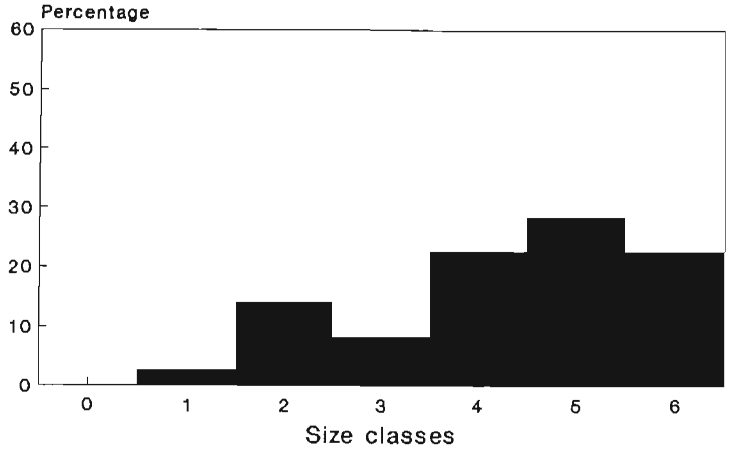

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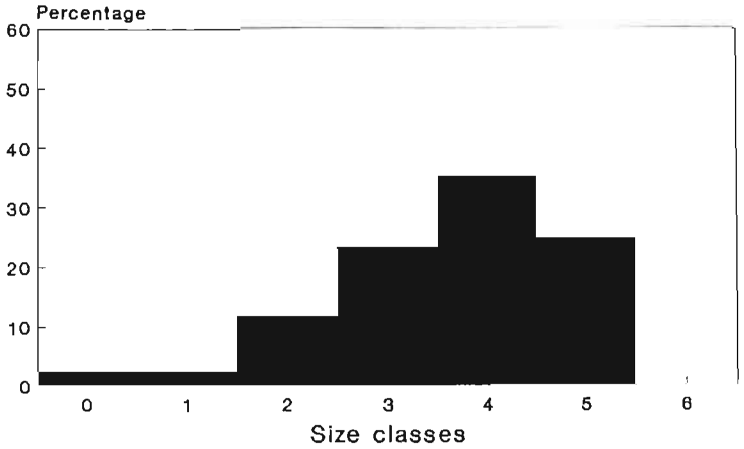

DECEMBER 1992