BIOLOGICALLY INDUCED ALTERNATIVE STATES IN TWO ROCKY SUBTIDAL BENTHIC COMMUNITIES

by

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Thesis submitted in the Faculty of Science,
University of Cape Town, for the degree of
Doctor of Philosophy. March 1987.

To my parents Ruth Barkai and the late Meir Barkai
and to my wife Revital.

'Ecology is the study of plants and animals in relation to their environment and to one another. But it is also more than that: it is the main intellectual discipline and tool which enables us to hope that human evolution can be mutated, can be shifted onto a new course, so that man will cease to knock hell out of the environment on which his own future depends.'

Max Nicholson, 1972.

ACKNOWLEDGEMENTS

When I arrived in South Africa four years ago I firstly discovered that my English was very poor and secondly that I had no idea of what it meant to dive on the West Coast. There is no way I could have coped with these two problems without the help of many people who made this project possible.

Special thanks are given to the following: my supervisor Professor G M Branch who gave extensive advice, encouragement and support. His endless patience and help in my "bitter battle" with the English language was greatly appreciated; Dr C L Griffiths gave advice and assistance and was always friendly and ready to help; Prof J G Field helped me through my first steps of this project especially with the Scientific Diver Certificate and in introducing me to the variety of computers available in the department.

Shallow water diving in the harsh sea conditions of the West Coast can be tricky and sometimes dangerous. I would therefore like to thank the following: Chris Heineken, Tony Gardiner, Antonio Tonin, Shael Harris, Gerry Rule, Andrea Pulfrich, Jean Harris, Diane White and Pete Friede, the enthusiastic divers who helped me with the many hours of diving that were necessary to complete this project and also to Ken Findlay (for his beautiful underwater photographs). Special thanks however, go to Paul Hanekom, head of the

University of Cape Town Diving Unit and to Pete Fielding. They were always prepared to help with diving despite their busy schedules and the frequent adverse sea conditions.

The writing up of this project was not easy in a foreign language and it would have been much more difficult had it not been for the help of many people. Cheryl Ozinsky, Maria Steurer, Geoff Hoy and Sue Burchell spent a lot of their time assisting me with this task.

Special thanks go to Mandy Lombard, Christopher McQuaid and Steve Tugwell who devoted a lot of their time both to the diving and with my English. The cheerful help of two lovely ladies, Venetia Stuart and Patti Wickens is specially appreciated as they lightened some difficult moments during this project.

Many thanks go to Coleen Moloney for her useful advice with computing, statistics and English. Lesley McQuaid, Carlos Villacastin-Herrero, Helen Veldhuis and the staff of Computer Centre contributed a lot of effort in assisting me with the large amount of computer work required to analyse my data.

I would like to thank Sandy Tolosana who typed most of the thesis. The hospitality and help of Philip and Althia Steyn from Langebaan and Uncle Bill from Saldanha Bay is greatly appreciated.

Many thanks also go to : Dave Pollock for his advice and his help with the tagging of rock lobsters; Phil Hockey and Alison Bosman for introducing me to Marcus Island; the Department of Sea Fisheries, and in particular the Saldanha Bay branch, their inspectors, skippers and crew members of the patrol boats; the National Research Institute of Oceanology for technical advice, supplying current meters and for analysing the recorded data; Richard Simons, Rob Anderson, John Bolton and Nigel Jarman for advice and identifying algae; Leonora Fox for typing parts of the thesis; Helen McMurray for assisting with the field work; Koos Williams for technical assistance and all the members of the Zoology Department for their friendly welcome when I arrived in the department and encouragement during the course of this project.

Financial support was given through the Benguela Ecology Programme of the South African National Committee for Oceanographic Research, and a University of Cape Town Postgraduate Scholarship.

But most of all I would like to thank my wonderful little wife, Revital, who accompanied and helped me right from the beginning with every aspect of the project. Without her love, continuous support and encouragment I would not have been able to complete this project.

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ABSTRACT

This thesis is concerned with the contrasting communities that occur in the subtidal zones of two closely situated islands in Saldanha Bay on the west coast of South Africa:

Marcus (17°55'E/33°03'S) and Malgas (17°55'E/33°'S). Both are guano islands, supporting substantial populations of seabirds. They have a similar bottom topography and experience similar physical conditions. Despite these similarities their subtidal benthic communities are, however, radically different. Marcus Island has prolific beds of the black mussel *Choromytilus meridionalis*, accompanied by a large number of other species, notably the sea urchin *Parechinus angulosus*, the holothurians *Pentacta doliolum*, *Thyone aurea* and *Trachythyone insolens*, large population of whelks, mostly *Burnupena spp.* and the barnacles *Austromegabalanus cylindricus* and *Notomegabalanus algicola*. In contrast, Malgas Island is dominated by a large population of the rock lobster *Jasus lalandii* together with a dense seaweed flora, and has small numbers of the ribbed mussel *Aulacomya ater* and the whelks *Argobuccinum pustulosum* and *Burnupena papyracea*.

Similar larval stocks supply both Marcus and Malgas Island. However, many of the recruited species never pass their primary stages at Malgas Island because of predation

by rock lobsters. They do, however, play a significant role in the trophic web of the established benthos. Recruiting barnacles, for instance, are a major source of food for the rock lobsters.

Key interactions that occur between the adults of benthic species include the effects of rock lobster predation on mussels, competition between barnacle and mussels and algae, the reversible predator-prey relationship between rock lobsters and a whelks, and a seemingly competitive interaction between holothurians.

Of the barnacle species, *Notomegabalanus algicola* is a better coloniser having short-lived populations with a high rate of turnover. *Austromegabalanus cylindricus* is more tolerant of biological stresses (predation and competition for space) and large individuals survive for longer periods. In the absence of rock lobster predation, mussels outgrow barnacles. Giving such predation, mussel numbers are severely reduced while barnacles (notably *N. algicola*) are capable of maintaining a continuous presence by recruitment, even if their biomass is never appreciable. When the level of predation is low, *Choromytilus meridionalis* is a better space competitor than *Aulacomya ater* and more tolerant of siltation and other physical stresses. It is capable of rapidly excluding other species (barnacles, seaweeds, Pyura, sponges and others) from the primary subtratum. On the other hand *large individuals of A. ater* can survive even in the presence of a dense rock lobster population, and occurs in small clumps at Malgas Island while C. *meridionalis* is excluded by the rock lobsters.

Rock lobsters have multiple effects on the relationships between major space competitors, notably mussels and algae. They exclude grazers, thereby promoting survival of recruited sporelings; and they free primary space for algae by preying on mussels. Other unpalatable or inedible species such as Pyura and Porifera also benefit from the latter effect.

Burnupena spp. (notably *B. papyracea*) and the rock lobster have a reversible predator-prey interaction which depends partly on their relative densities and partly on the protection that B. papyracea gains from the bryozoan *Alcyonidium nodosum*, which encrusts its shells. This reversible relationship is central in understanding the contrasting communities at Malgas and Marcus Islands: At Malgas the dense rock lobster populations control most of the fauna and there are only small numbers of *B. papyracea*, which are protected by their symbiotic relationship with *Alcyonidium*. At Marcus Island the *Burnupena* spp have attained a density at which they prevent colonisation by rock lobsters. Sublittorally. *B. papyracea* is the most abundant species of whelk, probably because of its symbiotic relationship with the encrusting bryozoan.

At Marcus Island there is an apparent competition for space between the holothurians *Pentacta doliolum* and *Thyone aurea*. In reality they are not competing: *Pentacta* provides an anchorage for the loosely attached *Thyone* and is essential for its survival in areas where water movement is strong. This type of coexistence is more likely to occur in an environment where food is plentiful, predation pressure is low and other environmental factors become dominant.

Both Marcus and Malgas Island support stable benthic communities, in spite of frequent physical disturbances at both islands (wave action, storms), and because of biological disturbance (predation) at Malgas. The Marcus Island mussel population provides a food source for many predators (notably whelks) which, in turn, resist colonisation by rock lobsters. Mussels, whelks and sea urchins at Marcus Island, and rock lobsters at Malgas Island, are "keystone" species. These species determine the special characteristics of the two islands. Although stable, these represent alternative states of the same ecosystem.

The rock lobster is one of the the top predators in the shallow-water benthic Benguela ecosystem. According to past evidence, they have dominated almost the entire west coast from Cape Point to the Orange River. Commercial and illegal exploitation has considerably reduced their numbers in many localities, and the effects of this have not yet been established. It is concivable that any substantial reduction in the number of rock lobsters from particular areas may create other stable communities in the Benguela ecosystem which are capable of resisting recolonization by rock lobsters. The nature of shallow-water hard-substrate benthic communities of other regions in the Benguela ecosystem will probably reflect the size of the rock lobster population in these areas. It may be possible to assess the state of the rock lobster population in an area by sampling and observing the diversity and distribution of particular benthic species. Apart from the practical applications of this research it seems that alternative stable states do occur among benthic communities. Opposing stable states can even exist in close proximity to one another and maintain long-term stability despite being exposed to high energy environmental forces.

INTRODUCTION

There are two major difficulties which confront the modern ecologist. Firstly, most of the systems which he deals with are very old, with few historical facts to rely upon. Even when the system is very dynamic, any changes may easily exceed the researcher's life span. Secondly, since the mid 1800's, there have been increasing affects of human activity on the surroundings, introducing many new and "unnatural" factors to the existing system.

In relatively closed systems, where the community habitat and structure are well defined and the trophic relationships are easy to follow, small scale perturbations are often used to overcome these problems eg. caging (Dayton 1971; Menge 1978a; 1978b; Schmidt and Warner 1984), or the exclusion of one or more key species (eg. Connell 1961; Paine 1966; 1977; Branch 1981; Kitching 1985). Another approach is to simulate changes in components of the ecosystem (biotic or abiotic) in the laboratory (eg. feeding studies, or analyses of the effects of fluctuations in water temperature etc.).

A major problem with all these methods is that in conducting the experiments,the natural habits or habitats of the organisms are perturbed. This introduces more variables or "side effects", which require extreme caution in the interpretation of the results in order to avoid self-introduced errors (Underwood and Denley 1984; Sebens 1985;

Underwood 1985). As a result, population modelling and biological interactions are often restricted to only a few species, with limited application to the natural environment.

A unique opportunity to overcome some of these problems arose following the discovery of two sublittoral habitats (at Marcus and Malgas Islands, in Saldanha Bay, on the west coast of South Africa) which are geographically very close to one another and have similar environmental conditions, yet support contrasting benthic comunities.

This thesis consists of comparative work on these two contrasting communities, conducted over a four-year period. Several experimental methods were employed to study the benthic communities in detail and to test various theoretical hypotheses relating to stability, equilibrium, and predator-prey relationships.

Very few sublittoral experimental studies (if any) have been undertaken on the completely exposed coasts of the Atlantic Ocean. Although Marcus and Malgas Islands are both located in the vicinity of a bay, they are nevertheless often exposed to the full violence of the Cape storms. This fact predetermined the manner in which the diving work was carried out and the type of equipment which could be used. Consequently, the experiments were designed to minimise any long-term routine monitoring or sampling and, instead, an emphasis was placed on using the local benthic organisms as indicators of environmental parameters (water quality, food avaiability etc.), in addition to studying their role in the community structure.

The thesis is divided into seven separate chapters, each of which forms a separate unit.

Chapter 1 is a general description of Saldanha Bay including a review of much of the research on the physico-chemical characteristics of the water and the biological research which has previously been done, with special attention to the area surrounding Marcus and Malgas Islands. This information was supplemented by several additional short-term experiments to obtain more accurate comparative data on water movements and temperatures at the precise localities where experiments were undertaken.

Chapter 2 is a summary of three years' annual sampling of the benthos and is used as a descriptive chapter to introduce the two communities and the local species. There is also a discussion of the role of biological interaction versus physical factors in determining and maintaining these two divergent benthic communities.

In **Chapter 3** some of the hypotheses which were raised in chapter two, are tested and the assumption that the two benthic communities are alternative stable states of the same ecosystem is examined. This was accomplished by monitoring recruitment and succession of a large variety of species under different conditions ie. on settlement plates which either were or were not protected by cages and which had different types of substrata.

In **Chapter 4** measurements of growth and mortality rates of two common mussel species (*Choromytilus meridionalis* and *Aulacomya ater*) are presented. Each of these species occurs only at one of the islands, although both settle at both islands. Reasons for their mutually exclusive distribution are discussed.

Chapter 5 examines the special predator-prey relationship between rock lobsters and whelks and their major role in maintaining the alternate stable states of the two benthic communities.

In **Chapter 6** the energetic requirements and food resources of the rock lobster population at Malgas Island are analysed and nonconventional sources of food suggested for these rock lobsters.

Chapter 7 summarises the entire thesis and proposes two models of biological and trophic interactions for the benthic communities of the two islands.

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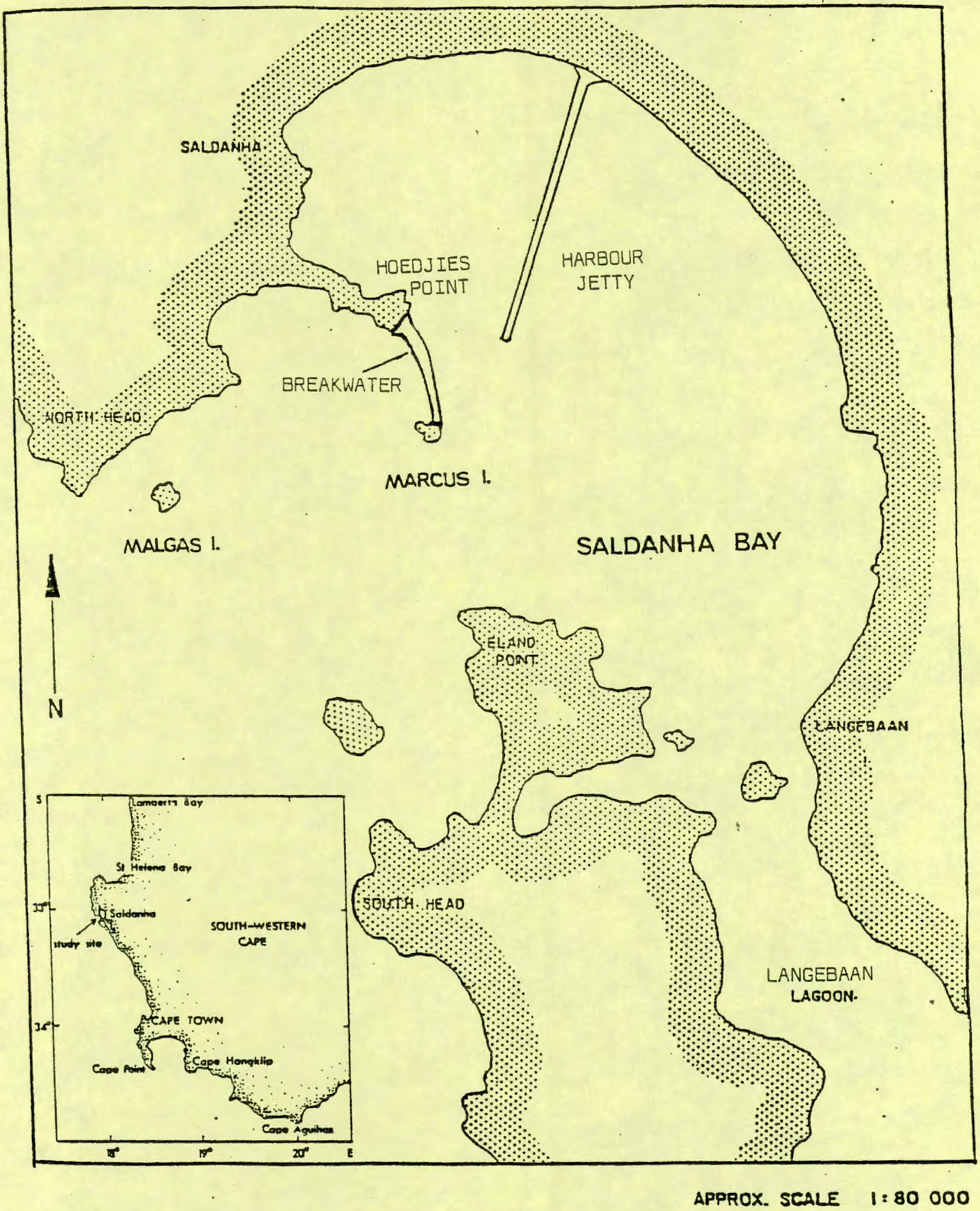

Fig. 1.1 A map of the study sites in Saldanha Bay showing the positions of Marcus and Malgas Islands.
Inset shows The position on the west coast of South Africa.

CHAPTER 1 - SALDANHA BAY: THE RESEARCH AREA

GENERAL DESCRIPTION

PHYSICAL REVIEW

Saldanha Bay (33°S/18°E) is situated on the Western shores of South Africa about 100 km North West of Cape Town, and is influenced by the cold stream of the Benguela current (Fig. 1.1).

Flemming (1977) has described the physical aspects of Saldanha Bay, such as the climatic, hydrological, geological and geomorphic features. There is evidence that the sea-level stood near to its present level and higher, number of times during the period 140,000-80,000y B.P. During the period 80,000 to 20,000y B.P it was below the present sea level most of the time although there is school of thought which claims higher sea levels on some occasions during this period (Milliman and Emery 1968). It was only 18,000 to 20,000 B.P that the sea started to rise from to its present level (Du Plessis and De La Cruz 1977) and there are suggestions that it stabilised at its present high position only some 6400y B.P (Flemming 1977). Both sides of the mouth of the bay are protected by granitic barriers which maintain the shape of the bay mouth. Because of this the inshore section of the bay, and probably most of the remaining bay as well, are "in equilibrium with the energy spectrum of ocean waves entering the system" (Flemming 1977) and only very limited erosion is detected (Du Plessis and De La Cruz 1977).

The climate of this part of the west coast is very dry and no rivers feed into the bay or the lagoon, so the bay is entirely marine in origin, and is composed of sea water without any fresh water dilution as occurs in estuaries (Day 1959; Boucher and Jarman 1977).

The bay is open to the sea at its South Westerly point and is jointed in the South East to the long shallow, narrow Langebaan lagoon. Strong South Westerly winds during the summer and North North Westerly winds in the winter are typical of the bay region. The water temperature fluctuates between 10°C and 15°C in the winter and between 8°C and 13°C in the summer. The bottom of the bay is mostly sandy, although parts of the shallow shore regions are comprised of granite rocks (Day 1959).

Extensive research was conducted in the bay during the years 1974-1977, in preparation for a massive harbour and industrial development in and around the bay. Shannon and Stander (1977) found that the physical and chemical characteristics of the water in the bay are basically similar to those of the Benguela ecosystem, except for the lagoon region which has higher water temperatures and salinities in the summer. Shannon and Stander separated the bay into three sub-ecosystems: a) the lagoon; b) the bay, and c) the Benguela current, with little differences between the latter two. Willis et al. (1977) found that the sediment in the bay is composed mainly of $CaCO_3$ and SiO_2 (over 93%). Other aspects of the sediment were investigated by Birch (1977), Flemming (1977) and Du Plessis and De La Crus (1977). Physical aspects were also described by the Council for Scientific and Industrial Research (CSIR report 1976/1 1976/2). The latter report examined the potential effect of the (then) future construction of a breakwater connecting the mainland at Hoedjies Point to the North Eastern region of Marcus Island, particularly in relation to the dynamics of the bay which considerably influence the direction and strength of the tidal currents. The average maximum and minimum tide in the bay is 1.76m and 0.26m spring, and 0.76m and 0.26 neap, respectively (S. A. Navy 1987). Five percent of the total winter swell in the bay is above 5.5m and 1.2% of the total summer swell. Eighty-five percent of the total swell is above 2m, mainly from South South West, South West and West South West, and so the Westerly-directed points of the bay are exposed to strong swells most of the year (CSIR report 1971).

BIOLOGICAL REVIEW

From a biological point of view, most previous research in the region has concentrated on the littoral region or on the plankton. The little research done on the benthos, is concerned only with the soft substrata of the bay. The balanoid species that are typical of the shores of the bay were described by Stephenson (1948) who gives a detailed description of the littoral species of the western shores of South Africa including Saldanha Bay. Day (1959) described in detail the faunistic composition of the shore in the bay and the lagoon and points out the considerable difference between species diversity and density in protected and exposed areas. While rocky shore communities are far more diverse in regions of strong wave action than in the shelter of the lagoon, the reverse is true of the communities of soft bottoms. Grindley (1977) summarizes data collected during 1946-76, on the zooplankton of the bay and indicates a dominance of typically marine zooplankton although there are some species typical of the lagoon. Henry et al (1977) found that the rate of phytoplankton production is 28.0-125.7 $mg/cm^3/h^{-1}$ which is characteristic of the productive Benguela upwelling system. Their research did not indicate a large seasonal fluctuation in production, contrary to the earlier research of Lazarus (1974). Du Plessis (1977) investigated different aspects of the biology of the black mussel *Choromytilus meridionalis*, a common constituent of the benthos of the bay. He found large fluctuations in the quantity of planktonic mussel larvae during different seasons and in different regions of the bay. He also found that recruitment and growth rate of the mussels differed significantly in different regions of the bay and were highest near the mouth of the bay and lowest in the sheltered lagoon.

The benthos of the soft substratum has been sampled mainly by dredging or by SCUBA divers. (Day 1959; Christie and Moldan 1977b). Research carried out by Christie and Moldan (1977a) showed a significant reduction in the quantity of benthic soft-substrate communities in areas that were then affected by organic pollution originating from the fish factories in the area. An extreme example of massive benthic mortality was researched by Newman and Pollock (1973) who found that the oxygen level in the water decreased to almost zero in areas adjacent to the fish factories. Since then methods of dry loading have considerably reduced the pollution and nowadays the oxygen level is normal (8ml/liter) (Gardner _et_ _al_. 1983). Marcus Island is closer to the factories than Malgas and it is possible that the benthic fauna at Marcus was adversely affected in the early 1970's. Altough all recent measurements of oxygen taken close to the fish factory reveal normal levels (Gardner _et_ _al_. 1983), the construction of a breakwater does restrict water flow in the harbour, and a recent mass mortality of benthic organism was recorded in Hoedjier point (Pollock, pers. comm.). There is, however, no evidence that this localised event had any effect on the benthos at Marcus Island.

Moldan (1978) examined the influence of the artificial movement of sand in the bay area during dredging accompanying the construction of the break-water and harbour jetty and found that the benthic biomass decreased in quality significantly adjacent to the work site. However, recovery and recolonisation began even before the construction was completed. Beckley (1981) compared the benthic biomass adjacent to the jetty, where iron loading takes place, with a control area deeper in the bay, and with further data obtained by Christie and Moldon (1977b). Beckley found that the macrobenthic biomass decreased considerably in the area near to the jetty and an exceptionally tolerant species of polychaete worm, *Prionospio sexoculata*, became the dominant species. In contrast, the meiofaunal and bacterial biomass increased considerably comapred to the control area.

The marine floral community of the bay was described in detail by Simons (1977) who reviewed data on the local algal community over the last 90 years. Simons disagrees with the opinion of Isaac (1937) who claims that the marine fauna in the bay differs from that typical of the Western shores of South Africa and is supported by eurythermal species that are characteristic of the warmer waters of False Bay ($18^{\circ}40'E/34^{\circ}15'S$). Simons claims that only those areas adjacent to the lagoon differ from the Benguela system. An important fact is the almost total dominance of one species of kelp, *Laminaria pallida*, over the other common species of kelp normally found in the system, namely *Ecklonia maxima*; this perhaps being due to the relatively wave protected habitat of the bay.

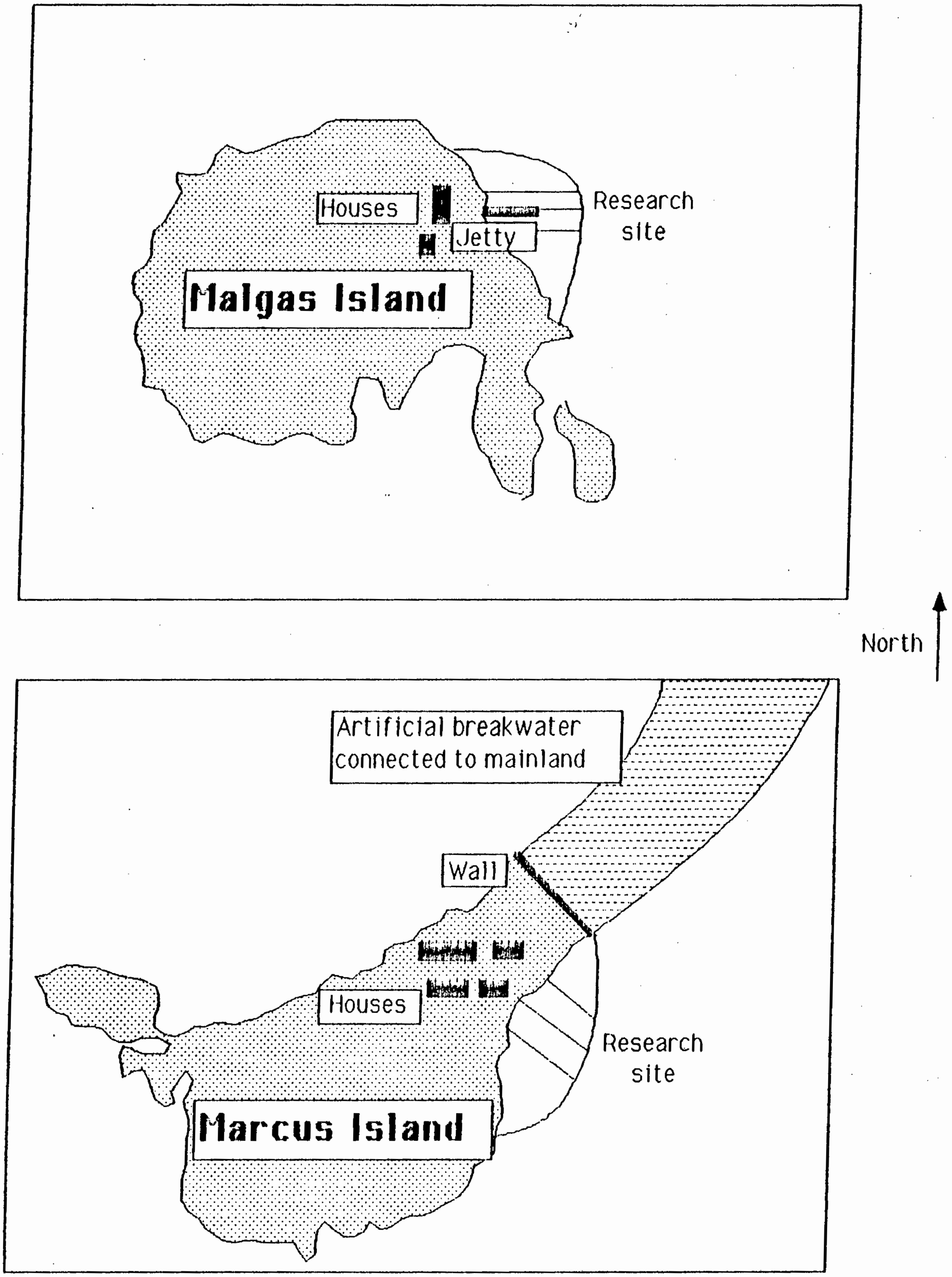

Fig. 1.1a
Detail maps of the research sites showing their postion at the islands. Parallel lines running through the research sites show positions of transects (scale 1 - 4.000).

DESCRIPTION OF THE ISLAND SITES:

Five islands are situated in the bay (Fig. 1.1 and 1.1a), two of which, Marcus (17°58'E/33°02'S) and Malgas (17°55'E/33°03'S) were chosen for comparative research on the processes of settlement and survival, together with analyses of community interactions between some of the benthic species typical of the shallow (down to 10m) hard substrata of the bay. The two islands are situated in the North Western region of the bay. Malgas island is closer to the Western region of the bay, while Marcus Islands is closer to the centre of the bay. In 1976 Marcus island was connected to Hoedjies Point (Fig 1.1) by a breakwater.

The South West regions of both islands are exposed to the entire force of the swell during most of the year, although certain more easterly regions are more protected and enable SCUBA diving on frequent occasions. These latter regions are however also exposed to strong wave action during storms (a common phenomenon, especially in winter) so that the research sites represent an exposed coastal ecosystem. Both islands are guano islands, populated by numerous species of seabirds. A large quantity of guano is swept into the sea during stormy and rainy weather. Bosman et al. (1986) found that guano solutes in the water considerably increased the production of intertidal algae although their influence on the shallow subtidal region has not yet been measured.

The islands are situated on a granite substratum that penetrates sublittorally to a depth of 10m, about 50-100m from the shore. Some of the rocks are covered by sand giving the bottom a patchy rocky sandy appearance. Deeper water is characterised by a sandy bottom. This isolates the rocky-substrate fauna of the islands and makes the islands somewhat different from open-coast rocky shores where the rocky substratum decends to greater depth. At Malgas Island the sublittoral is steep up until a depth of 3-4m and then becomes more moderate, while at Marcus Island the slope is uniformly moderate.

water Physico-Chemical conditions

Three sources of information are available on the physical and chemical nature of the water around the two islands. Firstly, there is information in the published litrature and in unpublished reports. Secondly, records of sea swell and wind in the bay are kept by the local port authority. Finally, measurements were made of water currents and temperatures at the precise sites where experiments were undertaken.

The tidal currents in the bay near Malgas Island are not strong (0.01 - 0.03 m sec^{-1}) whereas in the vicinity of Marcus Island the average tidal current is higher [0.1 m sec^{-1} (Shannon and Stander 1977; Huizing 1982)].

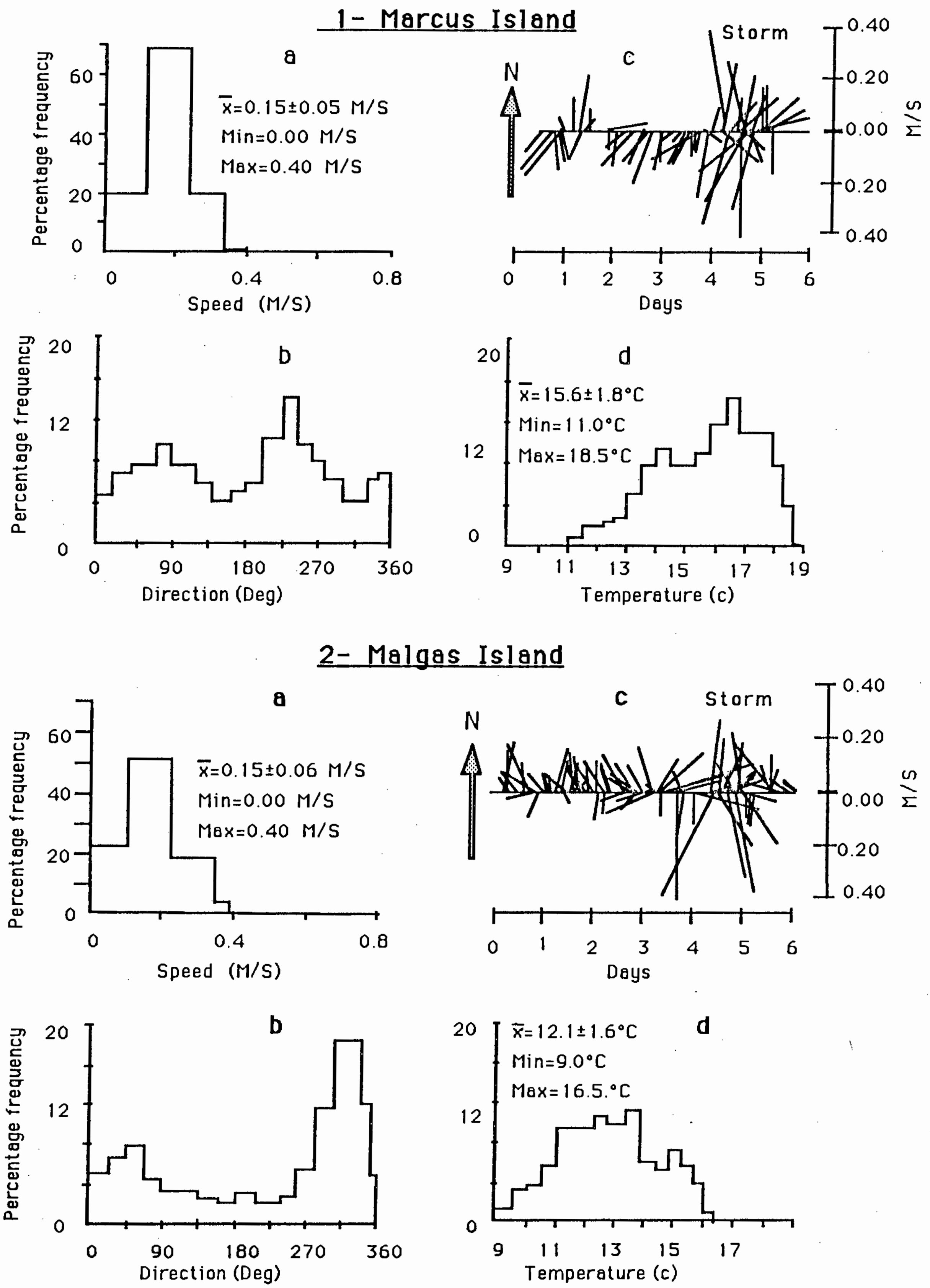

Fig 1.2

Mean daily percentage frequency of water speed (a), and direction (b), with a combined "stick graph" of speed plus direction (c), and temperature (d) as recorded by a RCM4 (recording current and temperature meter) at 15 minute intervals on Marcus (1) and Malgas (2) Islands during February 1984.

Two RCM4 recording current meters, adjusted to measure at 15min intervals, were placed at the research sites at a depth of 10m. The data on current speed and direction and on temperature were limited to short periods because of heavy fouling on the current meters by a common barnacle, *Notomegabalanus algicola*. Painting the RCM with a highly active anti-fouling (D920-0001: Rubamarine) partly solved the problem. However violent storms, together with some damage caused by boats anchoring on the equipment at Malgas Island, caused the loss of one recorder with several months data. Even so, the data derived from the relatively short period when both recorders were functional are of interest because of their comparative value.

The data show that there was practically no difference between the currents at the research sites at both islands (Fig 1.2a). At Marcus Island, the strongest currents were mainly South West (high-tide currents) with a further smaller peak in a East North East direction (low-tide currents). At Malgas Island, the strong (high-tide) currents were mainly West North West, while the low tide currents were less notable (Fig. 1.2b), perhaps because of the opposing swell direction. On both islands, single maxima of 0.4 m sec^{-1} were recorded.

Huizing (pers. comm.) estimates from data collected in the bay area, from the CSIR report (1971) and from the mathematical model of the bay's water circulation (CSIR Report 1976/1, 1976/2), that Malgas Island as an entirety is more exposed to the Westerly swell and therefore to shore currents. The data on water movement shown in figure 1.2 were taken at a single point near each island, close inshore in shallow water, and are therefore influenced to a large extent by the rise and breaking of waves on the beach; however, these are the actual forces of interest since they are the source of most of the hydrodynamic energy acting on the shallow-water benthos. During the period 08/02/84 to 09/02/84, a storm broke out in the bay. Wind velocity was above 40 knots and the swell height was nearly 5 meters even in the shelter of the bay (recorded at the local port control station). Figure 1.2c show the similar effect of the storm on total water velocity at both islands, with maximum speeds of 0.4 m sec^{-1}. Such a storm obviously does not reflect the more severe effects of winter storms when the average swell height is 8-9 m in the bay and it certainly does not compare with the extreme case of May 1984 when a maximum swell height of 17m and a strong North Westerly wind reaching 60 knots were recorded just in the mouth of the bay (Fraser 1984; Jury _et_ _al_. 1986).

The water temperatures at the two sites show a large daily fluctuation, characterictic of much of the upwelled Benguela ecosystem. Around Marcus Island the water is slightly warmer during summer (13-17°C) than at Malgas (11-15°C). This is probably due to the tidal flow of warmer water from the lagoon. Over the period the recorders were deployed, the average water temperature around Marcus Island was 15.6°C, approximately 3.5°C higher than that of Malgas Island (12.1°C) (Fig. 1.2d).The range of temperatures recorded was however wide and fluctuated considerably each day as tidal movements occurred: the mean differences between the islands were eclipsed by these fluctuations. In winter the mean differences between the islands are smaller (Shannon and stander 1977). Measurements of water clarity were obtained using a method similar to that of Lythgoe (1971). A red float of 20cm diameter, fixed to the sea bottom at a depth of 7m, and the maximum distance over which it remained visible was recorded. Visibility in the water is better at Malgas island (8-9m on average) than that at Marcus Island (4-5m) during most of the year. On many occasions large quantities of planktonic crustaceans (mysids) reduce the visibility tremendously at Malgas. Based on 29 recordings during different seasons of the year visibility averaged 4.7m (3.2 s.d) at Marcus Island and 8.3m (4.1 s.d) at Malgas Island. The salinity around both islands is similar (34.85°/oo - 34.90°/oo) as is the concentration of dissolved oxygen in the water (8ml/liter) (Shannon and Stander 1977). The waters around Marcus Island are now clear of the pollution that typified the area until the early 1970's (Gardner et al. 1983), which caused a drastic decrease in the oxygen concentration of the water (Newman and Pollock 1973).

The chlorophyll and nutrient levels of the bay were measured by Henry and Mostert (1977). Generally, there is a decreasing gradient in nutrient and chlorophyll concentration from the mouth of the bay to its centre and a further decline as one moves down the lagoon. The waters surrounding Malgas Island have slightly higher levels of primary production than those around Marcus Island. Variations in nutrient concentration from one site to another within the bay are, however, greatly exceeded by seasonal fluctuations, and there is usually a very uniform dispersal.

In general physical conditions around the two islands seem very similar. Certainly there are no obvious differences that could explain the contrasting biological communities found on the two islands (see Chapter 2).

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CHAPTER 2 - BENTHIC COMMUNITY STRUCTURE OF THE HARD SUBSTRATA AT MARCUS AND MALGAS ISLANDS

INTRODUCTION

The stability and equilibrium of the community and the ability of the species to actively choose a suitable niche, are questions that have occupied ecological thought from the end of the past century. Up until the seventies of the present century, most researchers dealing with environmental interactions tended to assume that any community which has existed for an extended period will finally reach equilibrium with its environment: aclimax community. Clements (1916), one of the founders of this approach, compared this process with embryological development. Scheer (1945), Margalef (1963), Odum (1969), Dayton (1971) and to a lesser extent Meadows and Cambell (1972), are some of the many ecologists supporting this approach. Margalef (1963) established the terms "immature community" and "mature community" to describe the early and unstable period of a community and the final and stable state of the ecosystem respectively. Odum (1969), using similar terms to those of Clements (1916), compared the development of a community to the development of an organism. In addition, Odum gives an energetic expression to the process, supposing that a community will grow and develop as long as excess energy is available. As soon as the energetic needs required to maintain a community at a particular size equal the amount of energy available and flowing into the system, the community will reach the final stable state. A sudden increase of one of the population components because of a chain of events (eg. an algal bloom), will cause the destabilisation and even destruction of the system, followed by regeneration. According to this theory the process of regeneration will bring into being a similar community to that which has been destroyed (as long as the abiotic characteristics have not been fundamentally changed). This process is, according to Dayton (1971), predictable and measurable. Meadows and Campbell (1972) support this approach in essence and also suggest the ability of the species to select its future niche. However they also describe a phenomenon that is difficult to explain - that many aquatic organisms select a habitat that is "well within their lethal limits". Moore (1974) refutes this approach, he suggests that the establishment of a habitat and the consequent development of the community therein, is only a matter of "habitat availability and ecological opportunity". In contrast to this approaches, Osman (1977) claims that a state of equilibrium probably exists for only a short while in most communities, until a disturbance of sufficient intensity interrupts it. This is a constant repeatable process and the characteristics of most habitats will depend on the nature, intensity and frequencies of the disturbances acting on it. Connell and Slayter (1977) suggest that a mature community is simply an established community that has grown. An analogy they give is that a young tree occupies a much smaller space in the ecosystem that the same tree a few years hence; simply because it has grown. In summary Connell and Slayter (1977), propose three succession models that have become very well known in a short time: a) The facilitation model suggests succession is a continuous process in which "later succession species are dependent upon early ones". b) The tolerance model suggests that community structure is determined by those species which are most efficient at exploiting the available resources, or more capable of resisting environmental pressures. c) The inhibition model is based on the concept of "first come first win", early colonists inhibiting the establishment of later arrivals. Connell (1978) has also tested the classic stability and equilibrium theories in two ecosystems which appear stable and constant over a very long period. These are the rain-forests and coral reefs. In his opinion, a detailed observation of the above ecosystems, will show that each system is composed of many subunits of which none are stable. These units are permanently involved in the processes of destruction and rebuilding and, as a result, different species occupy the same area as time goes on. This results in a large variety of species and continually changing dynamics. Buss and Jackson (1979) propose that the mode by which species share space in a habitat is determined by the opportunities that have been given to them in the past when free space becomes available. The competitive value of the species is then determined by its initial quantity at the time of settlement. This process is random and the nature of the community will therefore change from disturbance to disturbance. Sousa (1979a, 1979b, 1980), and Paine and Levin (1981) suggest that in areas of frequent, high disturbance, the community developing will be poor in species diversity, while areas showing medium disturbance will develop highly dynamic communities with a large number of species. The latter authors also impart great importance to the size of the space that has been freed. Supporting results were obtained by Taylor and Littler (1982) for rocky intertidal organisms which experience different intensities of disturbance in the form of sand. From the above it is apparent that there is a tendency to withdraw from the classical theory or at least to limit its bounds to a certain habitat and to small scale units of space and time. In a review, Connell and Sousa (1983), try to establish acceptable time-scales that will permit judgement whether the system is stable or not. Special attention is paid by these authors to the possibility of communities existing in "multiple stable states" at the same time in different places or in the same place at different times. Their conclusion is that in most cases "there is no clear demarcation between assemblies that may exist in an equilibrium state and those that do not". They further state that no evidence has been found for communities in "multiple stable states". For the same reasons, Connell (1985) refused to use the term "stability" for long-term succession because this term assumes that equilibrium exists.

It is in the light of these contrasting views that the present work was initiated on the contrasting shallow subtidal communities of two adjacent nearshore islands on the West Coast of South Africa, Marcus and Malgas Islands (Fig 1.1).

Preliminary research carried out during March 1983 on the eastern side of Marcus and Malgas Islands, showed that Marcus Island has a benthic fauna consisting of dense mussel beds (*Choromytilus meridionalis*), holothurians (*Thyone aurea, Pentacta doliolum, Trachythone insolens*), sea urchins (*Parechinus angulosus*) and whelks (*Burnupena cincta, B. papyracea, B. limbosa, Nucella cingulata, N. squamosa, Afrocominella capensis*) and a cryptic fauna of small animals associated with the mussels (eg. amphipods, isopods and polychaetes). There were, however, very few rock-lobsters and seaweeds.

Conversely, the second island, Malgas, has an enormous number of rock-losters (*Jasus lalandii*) and a rich community of seaweeds, and very few other benthic organisms. Both islands are situated in the Saldanha Bay rock lobster sanctuary, and we believe that the differences in the rock lboster populations of the two islands cannot be explained by poaching or exploitation.

During three years of research (1983-1985) at the above two sites, three annual sampling surveys were carried out at different depths. The purpose of this chapter is to describe these contrasting communities, together with information on physical factors at the two sites, and how they relate to the theories of stability and succession. In later chapters I experimentally test some of these speculations.

MATERIALS AND METHODS

SAMPLING OF THE BENTHOS

During 1983-1985 samples were taken from 2, 6 and 10m (Fig. 1.1a) depths. At Malgas a 2m sample was not obtained in 1983 due to the steepness of the reef. As a result, during 1984 and 1985 the position of the shallow sampling site was moved slightly (50-100m) to facilitate sampling at 2m. Depth was measured using a capillary depth gauge of the type normally used in sport diving. Two different quadrat sizes (0.11m^2 and 1m^2) and two different lengths of rope (6m and 10m) were used to sample and count different species of benthic organisms depending on their size and abundance. The large quadrat (1m^2) was used to count the sea squirt, *Pyura stolonifera*. Octopuses and the spiny starfish *Marthasterias glacialis* were counted using the 10m rope, which was also used at Malgas Island to count the whelks (*Burnupena papyracea* and *Argobuccinum pustulosum*) that are widely dispersed. The rock lobsters were counted using 6m ropes. All the other species were sampled and counted using the small quadrat ($0.11m^2$). The subtidal community at the Marcus Island study site was extremely patchy, 10 to 20% being almost bare rock alternating with virtually complete mussel cover. These patches constantly change in size and position and poor conditions of visibility make mapping impossible. Inclusion of bare patches in a random sampling technique would only give an accurate estimation of biomass if an unmanageably large number of samples were to be taken. Consequently the benthos at Marcus Island was sampled using a stratified random technique by sampling randomly within areas covered by mussels. The sampling methods using quadrats was as follows: a SCUBA diver on the sea bottom swam in a straight line from shore until he reached the first sampling depth. The quadrat was placed on the sea bottom as the first sample and a further two samples were taken 1m from each side of the first sample. In cases where the quadrat fell on a sandy bottom or bare rock, it was then moved to the nearest point covered by biota. The entire sample within the quadrat was collected in plastic bags and fixed on the shore with 4% formalin in seawater. All the macroflora and macrofauna above 2mm was then sorted, identified, counted, weighed and the sizes of dominate species measured.

The method of sampling using the 10m rope was as follows: two divers stretched a weighted rope on the sea floor parallel to the shore line at each sample depth. They then swam along the line and counted the number of individuals of any particular species found within 1m on either side of the rope. The rock lobsters were counted using a 6m rope, knotted at 1m intervals and tied at one end to a fixed point at the required depth. The two divers then swam with the rope in a circle around the point of attachment with the sea floor, increasing the radius of the circle by 1m each time and counting the quantity of lobsters in each circular sample. Three replicate samples were taken at each site. The results were transferred to units of wet biomass per m^2. The weight of *Pyura stolonifera* was estimated from data obtained by Zoutendyk (unpublished). Octopus weights were estimated using the data of Buchan and Smale (1981). The weights of the starfish *(Marthasterias*) and rock lobsters were estimated by using a subsample of 3 replicates (n=50 in each case). Large kelps (mainly *Laminaria pallida*) were excluded from the measurements of biomass at Malgas Island because most of their biomass is in the form of a canopy, and I was concerned primarily with the benthic community.

During March 1983, the first samples were taken after a relatively long period of storm-free weather. In June 1984, samples were taken after one of the strongest storms ever recorded in the area (May 1984). This storm caused massive disturbance of benthic life. In April 1985, the final set of samples were taken. The sampling at Malgas was completed on one day, after a relatively long period of calm. At Marcus Island the shallow samples (2 and 6m) were taken under similar conditions, but during the night strong swell conditions developed (8-9m , port control data) and the 10m sample could only be collected 48 hours later, in heavy seas. Massive benthic disturbance was observed during this dive.

In 1984 separate samples were taken at Marcus Island in order to examine the different layers of benthos at different depths within the mussel beds. These were compared with samples from rocks bare of mussels. The samples were obtained using 0.11m^2 quadrats. Each sample was divided into three layers, an upper layer visible to the eye, a bottom layer directly adjacent to the rocky substrate and a middle layer between the two. Each layer was removed separately and transferred to a plastic bag for sorting in the laboratory.

NUMERICAL ANALYSIS

Since treating the entire data set at the level of individual species (see appendix 1) would have been cumbersome, whole groups have been treated as units. Dominant species were, however, treated separately. Major groups recognised were as follows:

Porifera - 4 spp.

Actiniaria - 3 spp.

Polychaeta - 16 spp.

Cirripedia - 2 spp., but dominated by *Notomegabalanus algicola*.

Small Crustacea - 35 spp., predominantly isopods and amphipods.

Large Crustacea - 5 spp., dominated almost entirely by *Jasus lalandii* at Malgas, but largely by hermit crabs and mud prawns (*Upogebia capensis*) at Marcus.

Bivalvia - 5 spp., but consisting almost entirely of the mussels *Choromytilus meridionalis* at Marcus and *Aulacomya ater* at Malgas.

Gastropoda - 19 spp., at Marcus mainly three species of *Burnupena* but at Malgas mostly *B. papyracea* and *Argobuccinum postulosum*.

Octopoda only - 1 species of the common octopus *O. granulatus*.

Echinodermata - 13 spp., of which only one species at Malgas while Marcus is dominated largely by the echinoid *Parechinus angulosus* and the holothurians *Pentacta doliolum* and *Thyone aurea*.

Ascidiacea - 4 spp., but dominated by *Pyura stolonifera*.

Algea - 21 spp., all at Malgas but kelp which is common at Malgas but also occurs at Marcus Island.

A Sperry Univac 1100 computer were used for all the statistical analyses, using the BMDP and SPSS-X statistical packages. Ln (x+1), (x = wet weight m^{-2}) transformations were used for graphical presentation and also for ANOVA tests in order to achieve a normal distribution of the data. For regressions, size distributions and t-tests, the original values of wet biomass were used. These latter tests were conducted only for samples collected with the small 0.11m^2 quadrat.

The mean wet biomasses of sixteen major groups, were selscted for more detailed analysis and presented graphically after Ln (x+1) transformation. Two way ANOVA was used to test the affect of depth and date of sampling on the wet biomass of each of these groups and on total biomass per m^2, within each of the islands .

One-way ANOVA was used for a number of groups which were common to both islands, with the independent factor being the location of the sample, while depth and date of the sampling were used as covariates in order to isolate their effects. A similar test was used for the comparison of total biomass per m^2 between the islands.

Simple linear regressions and multiple linear regressions were used to estimate the significance of any functional relationships between the biomass of particular groups (as a dependent variable), and the depth of the sample or its **biotic** substratum as independent variables. (At Marcus Island the biotic substratum is of mussels and at Malgas seaweeds constitute the major biotic substratum). In the special case of the holothurians *Pentacta* and *Thyone*, we added the biomass of *Pentacta* as an independent variable since it appeared from observation that *Thyone* might be dependent on the presence of *Pentacta*. The values R and r and their probabilities were calculted in order to estimate the strength, the direction and the significance of any dependence (R = the multiple regression correlation coefficient and r = simple regression correlation coefficient). The affect of each of the variables in the multiple regression equation independent was determined by its contribution to the value R^2 (coefficient of determination).

The size distribution of *Choromytilus* on Marcus Island was measured at different depths and dates of sampling to test for the influence of these factors on mussel size. T-tests were used in order to determine whether a significant difference existed between a) mean size at different depths at any particular date of sampling and b) between the mean size at a fixed depth but at different dates of sampling (Sokal and Rohlf 1969).

RESULTS

In a picturise manner, Fig. 2.1 and 2.2 summarize the visual impression gained in the subtidal zones of Marcus and Malgas Islands. Fig. 2.4 provided a more quantitative summary of the average depth distribution of the dominant species at the two islands.

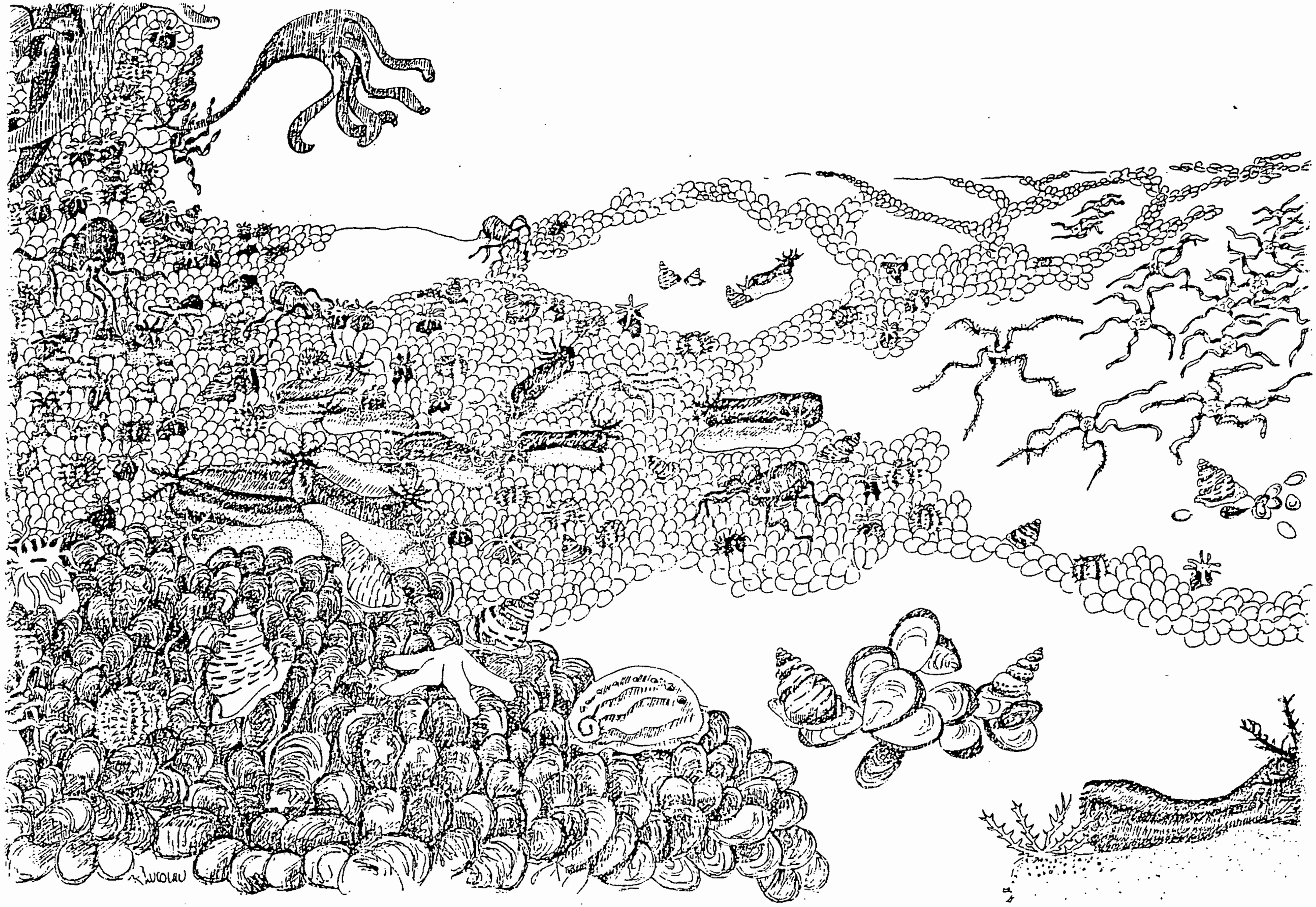


Fig. 2.1 Artistic impression of the sublittoral study site at Marcus Island.

GENERAL DESCRIPTION OF THE BENTHOS:

Benthos Of Marcus Island (Fig. 2.1)

At the shallow depths of 2-4m, the rock surfaces is covered by a single layer of black mussels, *Choromytilus meridionalis*, which dominates over the common littoral species *Mytilus galloprovincialis* and the ribbed mussel *Aulacomya ater*. Between the mussels, are expanses of the sandy sea anemone, *Bunodactis reynaudi* and smaller densely populated patches of the ascidiacean *Pyura stolonifera*. The mussels are mostly large and carry numerous small barnacles *(Notomegabalanus algicola)* on the edges of their shells. On the mussel beds there are abundant whelks *(Burnapena* spp.), concentrated together in clumps, as well as large numbers of the echinoid *Parechinus angulosus*; but only isolated individuals of the three common species of holothurians, *Pentacta doliolum*, *Trachthyone insolens* and *Thyone aurea* are present. Other species of echinoderms found in shallow water are small species of ophiuroidea, such as *Ophiactis carnea*, and *Amphiura capensis*, and larger species such as *Ophioderma wahlbergi* and *Ophiothrix fragilis*. In very shallow water close to the tidal line, a strip of kelp, *Laminaria pallida*, exists and amongst it are a few species of stunted red algae.

On going deeper, 5-7m, the rock structure becomes more complex; the flat granitic base is overlain with large boulders, while all the horizontal surfaces are covered by black mussels. The top layer of mussels consists of relatively small individuals, while beneath them larger individuals exist. These mussels dominate almost the entire landscape and provide a base for a large number of sea-urchins, whelks and other species. Almost every concavity in the rocks is occupied by *Octopus granulatus*. At the opening of such octopus holes there are many empty mussel shells. Around the octopus holes numerous specimens of *Burnupena* collect, probably feeding on remains of the octopuses' prey. Sometimes they settle on top of the octopus, even to the extent that they completely cover the octopus.

Amongst the holothurian, the black coloured *Pentacta* is most obvious and forms almost continuous sheet on top of the mussels. Isolated bright red patches of *Trachthyone* are evident. This picture is, however, misleading, since beneath *Pentacta* large numbers of pale orange *Thyone aurea* exist. In between the mussels especially on calm days numerous red and white isopods, *Exosphaeroma planum*, accumulate in dense aggregations around organic food remains. In early winter one species of ophiuroid, *Ophiothrix fragilis*, is dominant and covers large areas of mussel beds, although by the end of winter, or the beginning of summer it is replaced by another ophiuroid, *Ophioderma wahlbergi*.

At a depth of 10m, the black mussel remains dominant. In many cases it appears as if the mussels are settling on

Fig. 2.2 Artistic impression of the sublittoral study site at Malgas Island.

the sandy layers of the sea bottom although in actual fact they develop on a deposit of dead shells of the giant barnacles *Austromegabalanus cylindricus* and of dead mussels. Fragments of shells, large quantities of organic matter and silt are, accumulated and held together by the byssus threads of the mussels. At this depth, *Thyone* is found in large quantities, and is no longer associated with *Pentacta* as it is at the shallower sites. Its orange tentacles dominate the scenery. On going deeper, the layers of rock are replaced by a sandy substratum, covered by different species of Ophiuroidea which vary seasonally.

Notable in its absence from the entire sublittoral zone of Marcus, is the ribbed mussel, *Aulacomya ater*. Likewise the relatively small number of spiny starfish *(Marthasterias glacialis)* is curious, considering that the amount of their prey is substantial. However, the most significant feature is the almost complete absence of rock lobsters from this sublittoral ecosystem.

In summary, the benthos is dominated by the black mussel *Choromytilus*, but the community is rich in other species. Higher order predation form only a small part of the biomass, and rock lobsters are virtually absent.

Benthos of Malgas Island (Fig. 2.2)

At Malgas Island, the separation of species by depth is less clear. The kelp, *Laminaria pallida*, is the dominant species at first sight. Amongst the kelp, the rock surfaces are covered by large quantities of red algae and few species of Porifera which cover single patches of the rock. *Pyura stolonifera* characteristically occurs, in large patches which are dense but isolated; and is restricted to shallow water. Between the algae, rock lobsters crawl in huge numbers.Those that are visible represent only a small fraction of the real population size. Most of the population is concentrated in crevices under and between rocks, in quantities that may reach several hundreds per square netre, sitting one on top of the other, their antennae turned towards the opening of the crevice. The number of rock lobsters is especially high in the shallow areas, perhaps because the more complex structure of the rock there provides them with many hiding places.

The rock surfaces are bare of many of the species that are commonly present at Marcus Island: notable absentees are the black mussel, *Choromytilus*, all three holothurians, the urchin *Parechinus*, and ophiuroids. In contrast, the bivalve *Aulacomya ater*, does occur in the subtidal zone at Malgas, even although it is not common, forms only isolated clumps. The gastropod *Burnupena papyracea* is found in small groups, mainly in shallow waters, hidden between layers of red algae. Another gastropod which survives in relatively large quantities at Malgas Island is *Argobuccinum postulosom*. Large numbers of Octopus were also counted at Malgas Island. The general impression obtained at Malgas Island is one of greater uniformity, with two groups of

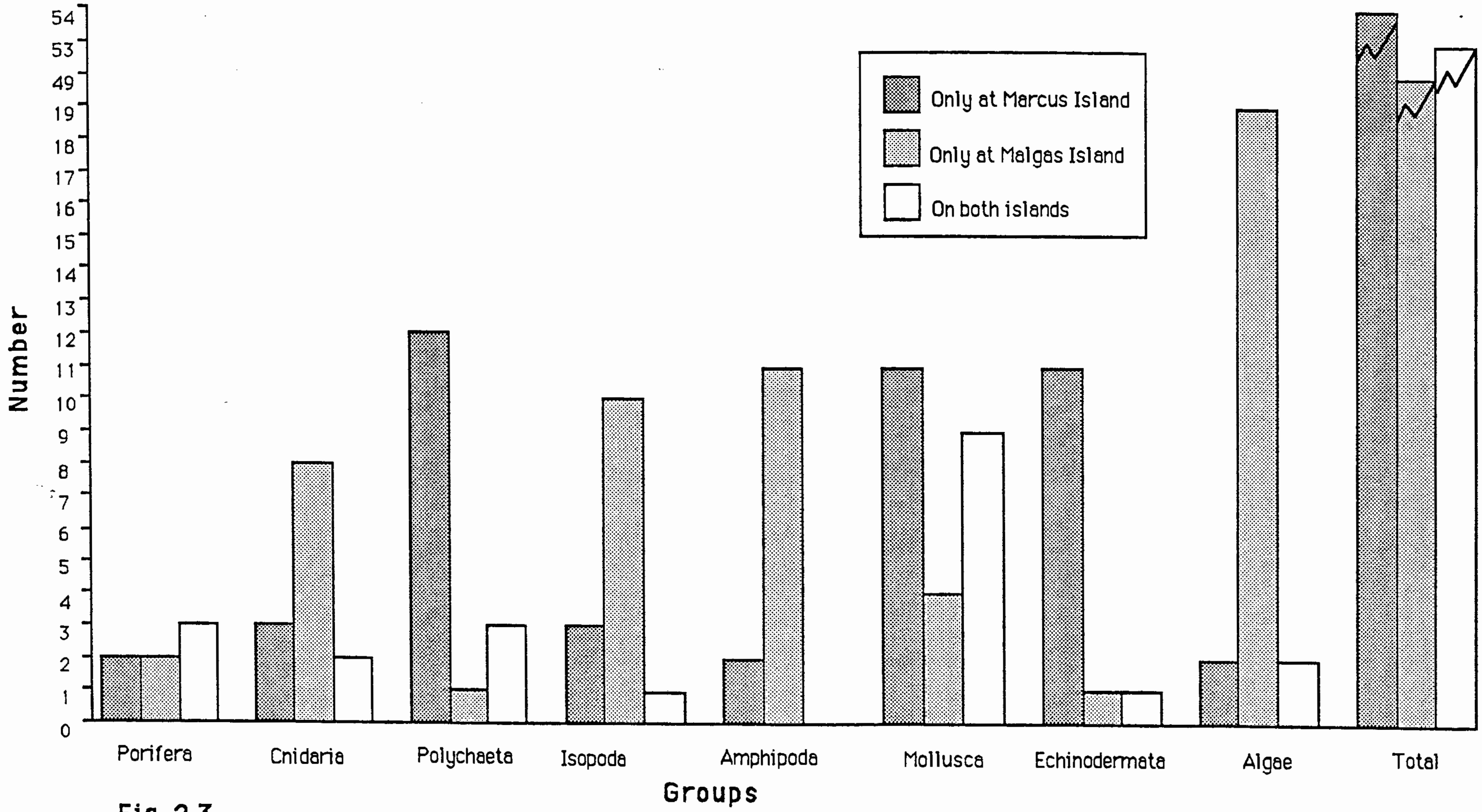


Fig 2.3

Number of benthic species, divided into major groups, at Marcus and Malgas Islands.

organisms dominating the entire environment: seaweeds and rock lobsters.

SPECIES DIVERSITY AND BIOMASS

Species diversity

156 different species were identified from both islands. Of these 49 species were only found at malgas Island and 54 only at Marcus Island, while 53 species were common to both islands (Fig. 2.3). At Malgas Island most of the species fell into two major groups: seaweeds (21 species, 80% of which belonged to the division Rhodophyta) and amphipods (11 species most of which were associated with seaweeds and differed from the amphipods typical of the mussel beds at Marcus Island. Notable were the relatively large number of mollusc species at Malgas Island (13 species), only four of which, the gastropods *Argobuccinum postulosum* and *Burnupena papyracea*, the bivalve *Aulacomya ater* and *Octopus granulatis*, were significant in terms of the total biomass. *B. papyracea* and *A. ater* existed in small quantities but were very large in size. All the other mollusc species were tiny bivalves or gastropods; either species which never attain any size or juveniles of larger species. Most of them settled on seaweeds.

At Marcus Island there was a larger variety of molluscs (20 species). Of them, the dominant mollusc was the bivalve *Choromytilus meridionalis* while the gastropods *Burnupena spp* also characterized the benthic fauna of Marcus Island.

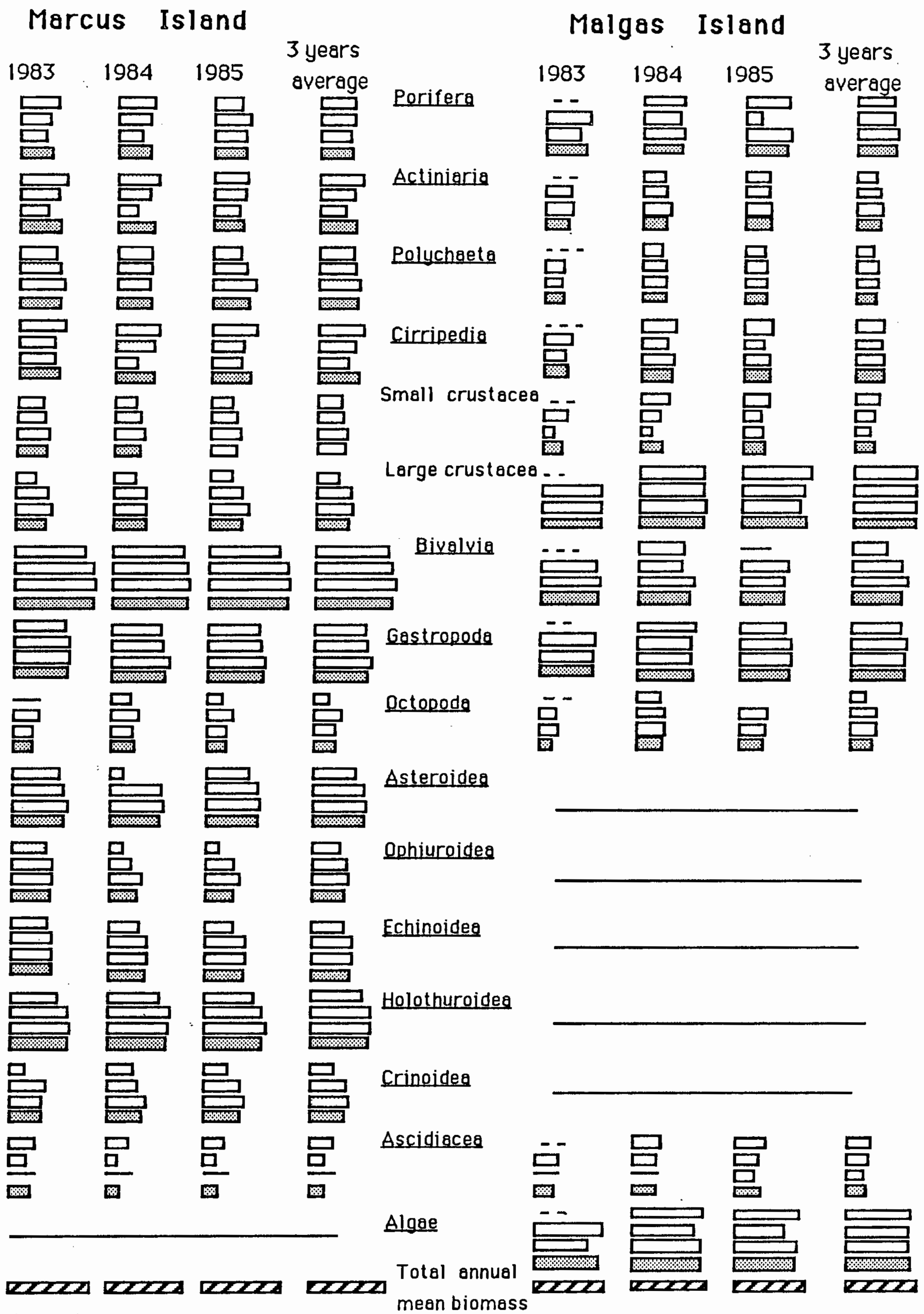
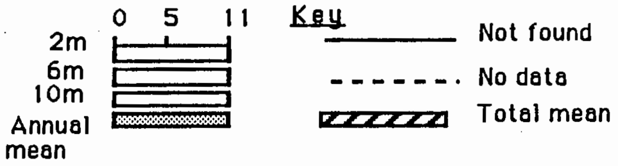


Fig 2.4
Mean annual wet biomass ($Ln(x+1)$, $x= g\ m^{-2}$), of the major benthic groups over 3 years, at 3 different depths at Marcus and Malgas Islands. The shaded areas represent the annual means of the 3 depths (see key).



The number of amphipod and isopod species at Marcus Island was relatively small (4 species each). Of the isopods *Exosphaeroma planum* was dominant. A number of polychaetes (12 species) were also typical of Marcus Island. Eleven Species of echinoderms were identified at Marcus Island. Of them, the dominant species were the echinoid *Parechinus angulosus* and the holothurians *Thyone aurea* and *Pentacta doliolum*. At Malgas Island only one species of echinoderm, *Henricia ornata*, was identified.

In summary, the number of species on both islands is similar, although algae (and their associated amphipod and isopod species) predominate at Malgas while a far greater diversity of animals is found at Marcus Island, and algae are almost completely absent.

Biomass (Fig. 2.4)

The biomass of the major species present at Malgas and Marcus Islands remained remarkably constant over the three years of observation, indicative of the stability of the two communities. Results of the one way ANOVA tests (Table 2.1) show that there were highly significant differences between the total wet biomass per m^2 at Marcus and Malgas Islands (with mean values of 41357.3 gm^{-2} and 10199.5 gm^{-2} respectively). At Marcus Island, the molluscas made up most of the biomass with *Choromytilus meridionalis* contributing almost 96% of the biomass of this group (35955.2 gm^{-2}). At Malgas Island, on the other hand, the bivalve biomass

Table 2.1: One way ANOVA of the mean wet biomass of the major species groups sampled at Marcus and Malgas Islands. Depth and date of sampling were held as covariates. Location of sampling (Marcus or Malgas) was the independent variable, and the dependent variable (mean biomass) was transformed to Ln(x+1), (x = wet biomass in grams per square meter). N.S= $p > 0.05$; S*= $p \leq 0.05$; S**= $p \leq 0.01$; S***= $p \leq 0.001$).

Factors: **Groups**	Marcus	Malgas	1 way ANOVA
Porifera	4.43	5.17	N.S
Actiniaria	5.03	3.20	S*
Polychaeta	5.20	2.75	S***
Cirripedia	5.43	3.54	S***
Small Crustacea	3.79	2.68	S***
Large Crustacea	4.40	8.26	S***
Bivalvia	10.49	6.73	S***
Cephalopoda	2.99	2.88	N.S
All Gastropoda	7.47	7.02	N.S
Burnupena spp.	7.11	4.82	S***
Argobuccinum	5.27	6.96	S**
Echinodermata	8.36	0.00	S***
Ascidacea	2.16	2.73	S*
Algae	0.00	8.39	S***
Mean total	10.63	9.23	S***

(largely *Aulacomya ater*) was only 837.2 gm^{-2}. The dominant groups contributing to the biomass of Malgas were the large crustacean *Jasus lalandii* (3867.1 gm^{-2}) and algae (4402.8 gm^{-2}) while at Marcus Island the biomass of large crustaceans was only 82.5 gm^{-2} and algae were virtually absent.

At Marcus Island the weight of all the species of echinoderms combined was on average 4273.7 gm^{-2} while at Malgas Island it was almost zero.

At Marcus Island, the mass of cryptic species (eg. polychaetes, isopods, amphipods and other crevice dwellers, was significantly higher than that of Malgas Island and the same was true of barnacles. It is especially interesting to note the biomass of the different gastropod species at the two islands. In total the gastropod biomass at Marcus Island was not significantly higher than that at Malgas Island. However if we separate the gastropods into their two main genera, *Burnupena* and *Argobuccinum*, the biomass of the former is much higher at Marcus Island than at Malgas Island, while with the latter the opposite holds true.

The effect of depth and date of sampling on biomass

About 70% of the species at Marcus Island showed a significant difference in biomass per m^2 when comparing samples taken at a depth of 2m and those taken in deeper water. In some cases, there were also differences in

Table 2.2: Two way ANOVA of the mean wet biomass (dependent variable) of the major species groups, at Marcus and Malgas Islands against depth and date of sampling (independent variables). Biomass was transformed to Ln(x+1), (x = biomass in grams per square meter). (N.S= $p > 0.05$; S*= $p \leq 0.05$; S**= $p \leq 0.01$; S***= $p < 0.001$).

Marcus Island

Factors:	Depth			Date			2 way ANOVA	
Categories:	2m	6m	10m	1983	1984	1985	Depth	Date
Groups								
Porifera	4.74	4.51	3.83	4.50	4.35	4.44	N.S	N.S
Actiniaria	5.75	4.70	3.45	5.56	4.88	4.17	S**	N.S
Polychaeta	4.65	5.10	5.62	5.67	4.71	4.98	S*	S*
Cirripedia	6.13	5.07	4.23	5.67	5.32	5.25	S***	N.S
Small crustacea	3.23	3.68	4.21	3.90	3.74	3.71	S***	N.S
Large crustacea	3.01	4.53	4.87	4.24	4.49	4.44	S***	N.S
Bivalvia	9.76	10.53	10.91	10.65	10.20	10.57	S***	S**
Gastropda	6.95	7.29	7.93	7.33	7.41	7.55	S***	N.S
Cephalopoda	0.74	4.01	3.96	2.67	3.30	2.74	S*	N.S
Asteroidea	5.90	7.04	7.35	7.04	6.79	6.92	S*	N.S
Ophiuroidea	3.78	4.78	5.05	5.42	3.78	3.89	N.S	S*
Echinoidea	4.42	5.56	5.54	5.46	5.09	5.30	S***	N.S
Holothuroidea	6.28	7.99	8.24	7.69	8.01	7.79	S**	N.S
Crinoidea	3.04	4.77	5.13	4.24	4.60	4.94	N.S	N.S
Ascidiacea	4.71	1.76	0.00	2.81	1.83	1.84	S*	N.S
Mean total	9.93	10.70	11.07	10.83	10.48	10.75	S***	S**

Malgas Island

	2m	6m	10m	1983	1984	1985	Depth	Date
Porifera	5.33	5.01	5.20	5.38	4.92	5.23	N.S	N.S
Actiniaria	2.88	3.12	3.43	3.19	3.15	3.26	N.S	N.S
Polychaeta	2.51	2.74	2.90	2.53	2.83	2.81	N.S	N.S
Cirripedia	3.95	3.21	3.49	3.24	3.88	3.30	N.S	N.S
Small crustacea	3.41	2.55	1.75	2.53	2.72	2.73	S*	N.S
Large crustacea	8.53	8.17	8.20	7.90	8.43	8.30	N.S	N.S
Bivalvia	5.06	6.68	7.20	7.62	6.43	5.54	N.S	N.S
Gastropda	7.04	7.13	6.88	7.17	7.19	7.03	N.S	N.S
Cephalopoda	1.86	3.26	3.18	1.80	3.40	3.08	N.S	N.S
Ascidiacea	4.28	2.89	0.89	2.54	2.80	2.86	S*	N.S
Algae	8.80	8.24	8.15	8.43	8.70	7.88	S*	N.S
Mean total	9.49	9.41	9.16	9.28	9.47	9.02	N.S	N.S

biomass between the sites at 6m and 10m (Table 2.2; Fig. 2.4) with the exception of the bivalves, all the sessile suspension feeders, including the Porifera, Actiniaria, Cirripedia (mostly the barnacle *Notomegabalanus algicola*) and the Ascidiacea (notably *Pyura stolonifera*) were more concentrated in shallow waters. The remaining groups, all of which consisted of mobile species, displayed the opposite trend. A comparison of the biomass per m^2 in different years shows a significant difference only in three of the groups, the bivalves, the polychaetes and the ophiuroids. Of these, the black mussel (*Choromytilus meridionalis*) which constituted 87% of the total biomass, displayed the most obvious changes, principly in response to storms. In the years 1983, 1984 and 1985 the bivalve biomass (combining the three depths together) was 42193.6 gm^{-2}, $26904.2m^{-2}$ and 38949.7 gm^{-2} respectively. The same pattern recurred in some of the other groups even though the trends were not statistically significant. The fact that a number of species that were directly associated with the mussel beds (ie. some small crustaceans, gastropods and some echinoderms) did not show a significant difference in biomass from year to year, is surprising. The explanation is, perhaps, their mobility, which enables them to find shelter during storms and to rapidly colonise patches cleared by storms (Branch 1984). This will be discussed further in the discussion.

Table 2.3: Simple and multiple regression analyses of the major benthic groups with we weight (g 0.11m^{-2}) as the dependent variable. Depth (m) and the biomass of algae / bivalves (wet weight g 0.11m^{-2}) are the independent variables (algae at Malgas Island and bivalvia a Marcus Island). r is the simple linear correlation coefficient, R the multiple correlation coefficient, p the significance level (N.S= $P>0.05$; S*= $P\leq0.05$; S**= $P\leq0.01$; S***= $P<0.001$) R^2 the coefficient of determination. The contribution to R^2 is the amount by which R^2 would be reduced if one of the independent variables was removed from the multiple regression equation [appllicable only when correlation is significant; (+ is 50-90% contribution; ++ is > 90% contribution; = indicates both contribute approximately the same N/A Not applicable)].

Marcus Island

	Simple linear regression				Multiple linear regression			
Predictors:	Depth		Bivalves		Depth and Bivalvia		Contribution to R^2	
	r	p	r	p	R	p	Depth	Bivalvia
Dependent variables								
Porifera	-0.26	N.S	-0.04	N.S	-0.4	N.S		
Actiniaria	-0.53	S**	-0.42	S*	-0.53	S**	++	
Polychaeta	0.45	S*	0.67	S***	0.68	S***		++
Cirripedia	-0.74	S**	-0.55	S**	-0.75	S***	++	
Small Crustacea	0.66	S***	0.82	S***	0.82	S***		++
Large Crustacea	0.83	S***	0.63	S***	0.83	S***	++	
Bivalvia	0.87	S***	N/A		N/A			
Gastropoda	0.75	S***	0.71	S***	0.75	S***	=	=
Ophiuroidea	0.31	N.S	0.40	S*	0.40	N.S	=	=
Echinoidea	0.53	S**	0.61	S***	0.61	S**		+
Holothuroidea	0.58	S***	0.39	S*	0.60	S**	++	
Crinoidea	0.41	S*	0.17	N.S	0.51	S*	++	

Malgas Island

	Simple linear regression				Multiple linear regression			
Predictors:	Depth		Algae		Depth and Algae		Contribution to R^2	
	r	p	r	p	R	P	Depth	Algae
Dependent variables								
Porifera	-0.02	N.S	-0.03	N.S	-0.07	N.S		
Actiniaria	0.19	N.S	-0.01	N.S	-0.24	N.S		
Polychaeta	0.18	N.S	0.07	N.S	0.19	N.S		
Cirripedia	-0.16	N.S	0.27	N.S	0.27	N.S		
Small Crustacea	-0.62	S***	0.93	S**	0.93	S***		++
Algae	-0.54	S***	N/A		N/A			

At Malgas Island, however, the results were qualitatively and quantitatively different from those at Marcus Island. Only three groups showed significant differences at different depths, and of these the only group with substantial biomass was the algae. Small crustaceans, most of which were associated with algae, followed suit. In part I ascribe the uniform depth distribution of almost all species to the predatory activities of the rock lobsters, for they have reduced the biomass of most groups to a low level. Likewise, not a single group displayed significant differences in the biomass per m^2 between the different years of sampling.

The results of the regression tests (Table 2.3) show that the biomass of most of the species at Marcus Island was linearly and positively dependent on depth (except for ophiuroidea and porifera) while the actiniaria and cirripidea show a negative dependence. These results confirm the patterns seen in figure 2.4 (for the averaged annual wet biomass) and in table 2.2 (two-way ANOVA test).

Interactive effect of depth and substratum on biomass.

Both depth and the amount of mussel or algal biomass (at Marcus or Malgas respectively) appeared to influence the biomass of several groups of animals. The multiple regression analyses provides measure of the relative influence of each of these factors (depth and mussel or algea biomass) on the biomass of other groups. Table 2.3

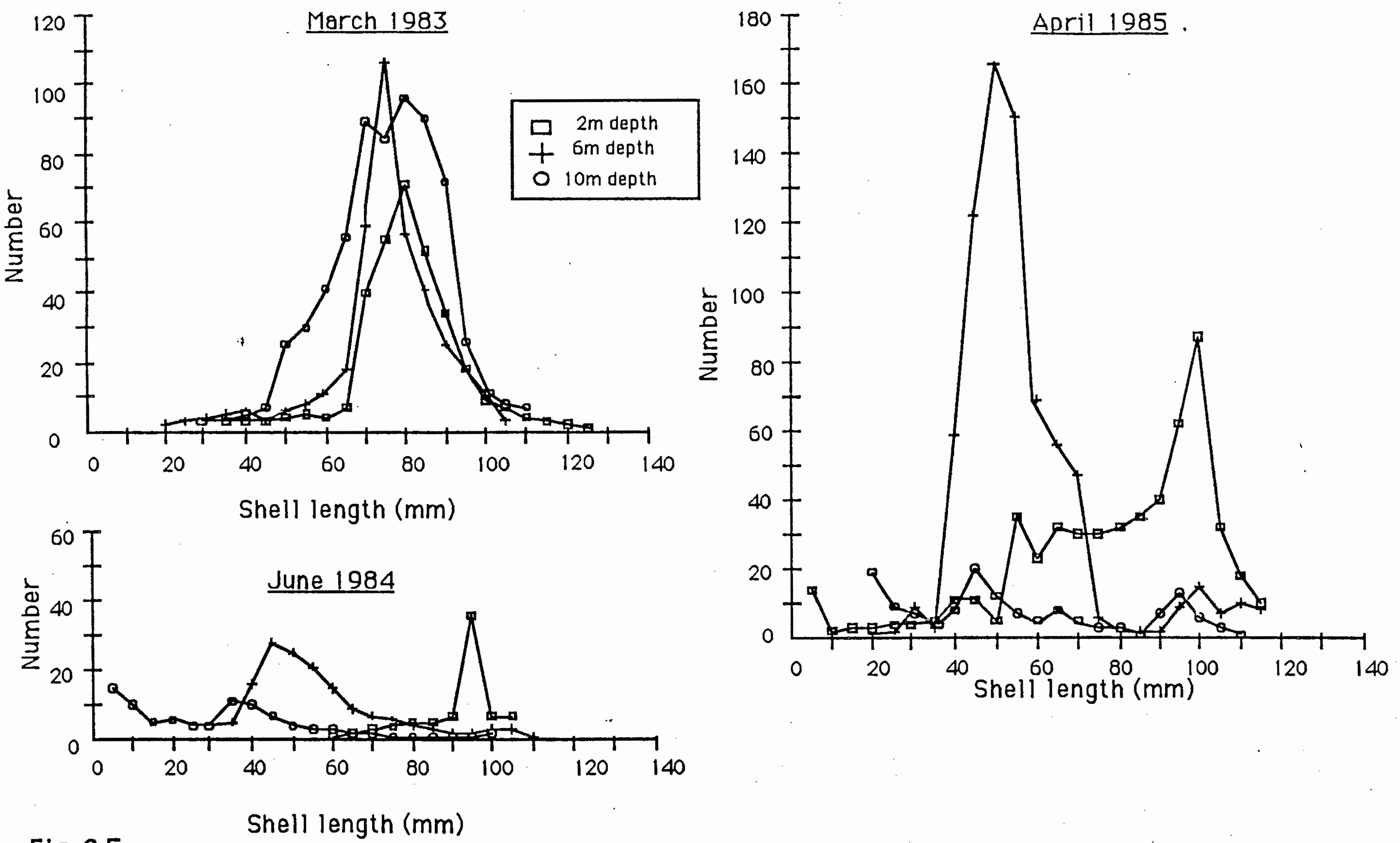
Table 2.4: All subsets linear regression analysis of the holothurian *Thyone aurea* wet weight (g 0.11 m^{-2}) as the dependent variable. Depth (m) and the other holothurian *Pentacta doliolum* and bivalves (wet weight g 0.11 m^{-2}) are the independent variables. In the table R^2 is the coefficient of determination and p is the significance level (N.S= $P>0.05$; S*= $P\leq0.05$; S**= $P\leq0.01$; S***= $P<0.001$) . The contribution to R^2 is the amount by which R^2 would be reduced if one of the independent variables was removed from the multiple regression equation.

Independents variables	R^2	p	Contribution to R^2
Depth	0.26	S**	0.06
Bivalvia	0.11	N.S	0.03
Pentacta	0.64	s***	0.38
Depth+Bivalvia	0.32	S**	
Depth+*Pentacta*	0.67	S***	
Bivalvia+*Pentacta*	0.64	S***	
Depth+Bivalvia +*Pentacta*	0.70	S***	

shows that the groups actinaria, cirripedia, large crustacea, holothuria, and crinoidea were mainly influenced by depth, with the first two groups showing a negative dependence. In contrast, the polychaetes, small crustaceans and echinoids were mainly dependent on mussel biomass.

Setting aside the proven effect of mussels and algae on the biomass of other organisms, correlations were sought between all the dominant species. Only in one case was a significant correlation detected: The holothurian *Thyone aurea* was positively associated with *Pentacta doliolum*, especially in shallow water. A separate multiple regression analysis was undertaken to test this association further. Table 2.4 shows that the biomass of *Thyone* was significantly dependent on the biomass of *Pentacta*. A similar but lesser dependence was observed between *Thyone* and depth of sampling, but no correlation existed between the biomass of *Thyone* and the biomass of mussells. Of the three independent factors explaining *Thyone* biomass, *Pentacta* biomass was the major contributor to the coefficient of determination (Table 2.4)

Multiple regression analyses were also performed for the major groups at Malgas Island, with depth and biotic substratum as independant variables. This time, however, seaweed biomass replaced mussel biomass as the biotic substratum. Table 2.3 shows that algae and small crustaceans were the only groups having a dependence on


March 1983

June 1984

April 1985

Fig 2.5

Size distribution of *Choromytilus meridionalis* from Marcus I., at 3 different depths. Sampled once a year over three years.

depth of sampling. In both cases the dependence was negative. Small crustaceans were also significantly dependent on the biomass of seaweeds, which were also the major contributors to the coefficient of determination for the small crustaceans (Table 2.3). All the other groups did not show any dependence on depth or seaweed biomass and their biomass seems to be either competely random or dependent on other factors that were not examined.

SIZE DISTRIBUTION OF CHOROMYTILUS AT MARCUS ISLAND.

Figure 2.5 summarises the combined effect of depth and date of sampling on the number and length of mussels over the years 1983, 1984 and 1985. Short explanation is giving for each one of the tested combinations, assuming that the length and number of mussels reflects the intensity of recent perturbations (storms) and the resistance of the mussels to these disturbances at the different depths. The results of t-tests for mean shell length (Tables 2.5 and 2.6) show that mussel lengths and numbers changed significantly from depth to depth and between the different years of sampling. Shallower mussels were significantly larger in size but less densely packed than those in deeper water. Both sizes and densities were, however, greatly dependent on the time that had elapsed since the last major storm. Following storms the number of mussels and their average sizes reduced significantly, notably in deeper water (6-10m).

Table 2.5: Number (N) and mean shell length in mm (x) of *Choromytilus meridionalis* at the three different depths and dates of sampling.

	March 83		June 84		April 85	
	N	X	N	X	N	X
Depth (m)						
2	252	81.21	64	93.94	361	76.53
6	332	76.34	110	54.57	651	53.62
10	529	75.36	68	32.34	133	43.94

Table 2.6: T- tests for differences between mean lengths (mm) and average numbers of the bivalve *Choromytilus meridionalis* , from three different depths at Marcus Island, (2,6,10m) and three years of sampling (1983,84,85). The sign > indicates that the average length or number of mussels in the left hand columns is significantly greater (t-test, $P \leq 0.05$) than in the right hand columns. The number of > signs indicates the magnitude by which the left hand columns are greater than the right. Short, assumed, explanations for these differences are listed, and are discussed further in the text (Some rows in the table summarize results of few separate t- tests).

Average length

Depth	Year	T- test	Depth	Year	Assumed explanation
2m	83,84,85	>	6m,10m	83,84,85	*Stronger attachment.*
6m	83	>	6m	84,85	*Detached by May 1984 storm.*
6m	83	N.S	10m	83	*No big storms for a long period.*
6m	84,85	>	10m	84,85	*Shallower, stronger attachment*
10m	83	>	10m	84,85	*No big storms for a long period.*
10m	85	>	10m	84	*Post May 1984 storm cohort.*

Number

Depth	Year	T-test	Depth	Year	Assumed explanation
10m	83	>	2m,6m	83	*No big storms for a long period.*
10m	83	>>	10m	85	*Immediate post storm sample.*
10m	84	=	2m,6m	84	*Similarly affected by May 1984 storm.*
Total	83	>>>	Total	84	*No big storms at 1983, Post May 1984 storm.*
2m,6m	85	>>	10m	85	*Immediate post storm sample (10m 1985).*

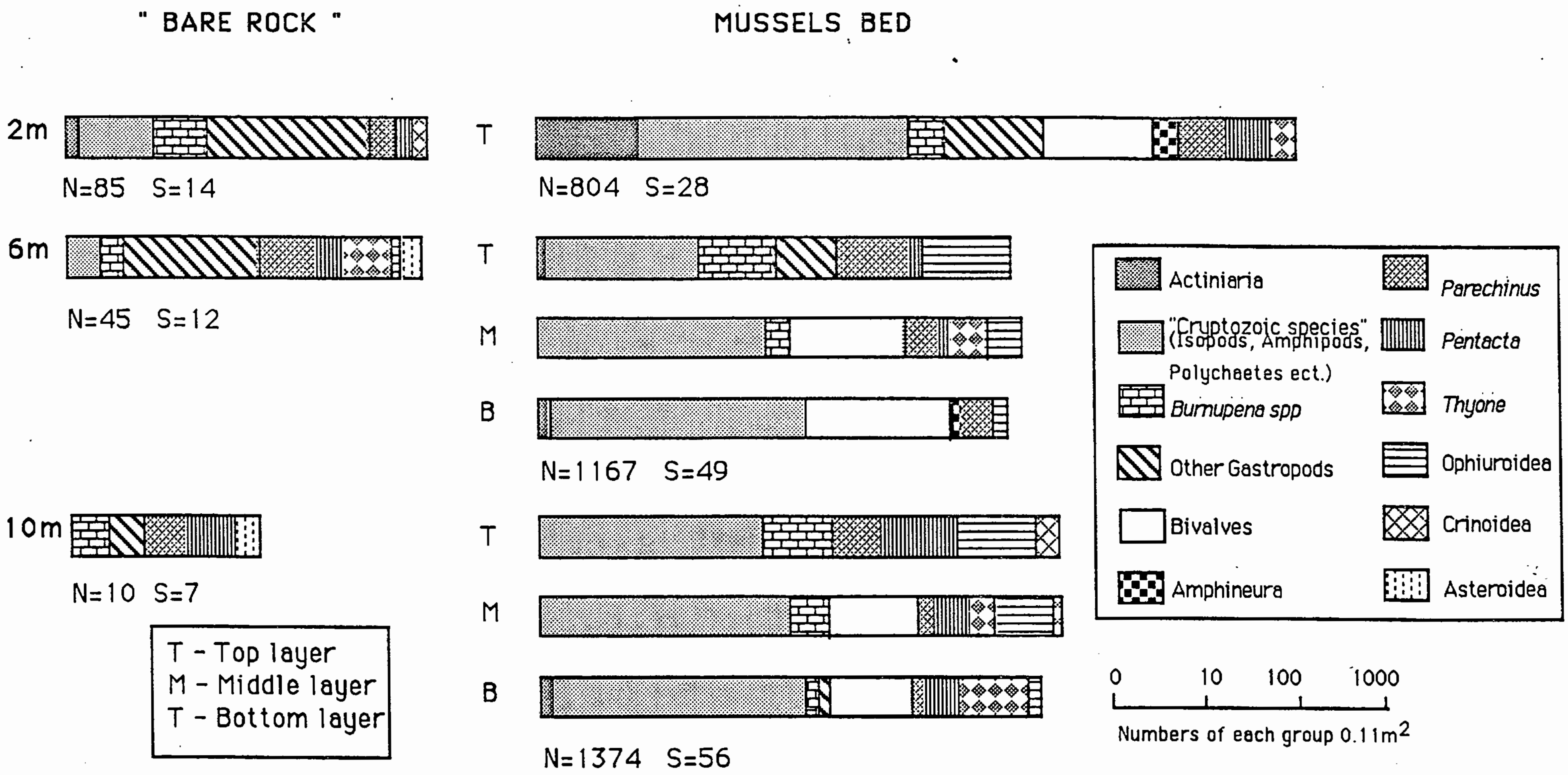


Fig 2.6

Number of individuals of the major benthic groups (natural log scale) per $0.11m^2$ at Marcus Island. The benthic fauna was sampled from "bare rock" (without mussels) and from three layers within mussel beds, at three different depths (2,6,10m). N is total number of individuals and S is total number of species (for each depth and place of sampling).

THE MUSSEL - BED STRUCTURE AT MARCUS ISLAND

Analysis of the fauna associated with different layers within the mussel bed (a "top" superficial layer, "middle" layer and a bottom layer attached to the substratum) and a comparison with the fauna occuring in areas of "bare" rock (ie devoid of mussels). Fig. 2.6 demonstrates the central role of mussels as a secondary substratum and habitat for many species. "Bare rock", (unoccupied by mussels) had a single-layered biotic structure and was composed of a poor variety of species and relatively few individuals. At all those depths, bare rock supported a density of animals one to two orders of magnitude lower than that in the mussel beds. In shallow water due to constant wave action only small number of mussels settle in a single layer, accommodating relatively small number of other species. In deeper water about half of the mussels are not attached directly to the rock substratum, but layered on top of other mussels. Actiniarians, "cryptozoic species" (isopods, amphipods and polychaetes), bivalves, amphineurans and ophiuroids showed a strong preference for the mussel bed. In terms of numbers "cryptozoic species" dominated the whole depth of the mussel bed although their mass contributed only slightly more than 0.5% to the biomass (Table 2.1). *Pentacta* was found mostly on top of the mussels but also appears on bare rock even in the very shallow water. *Thyone* on the other hand was limited mostly to deeper water and it was very rarely found on the top layer, usually being covered by some of the other species of the benthos, notable *Pentacta*.

DISCUSSION

It has been well recorded that sublittoral rocky hard substrates on semi-exposed coastal shores are capable of supporting a large number of species, and that completely different communities can develop in what appear to be very similar conditions, even within small geographic distances (Mann 1972; Craig & Mann (in press.); Hiscock & Mitchell 1980; Hiscock 1985). The most immediate result that emerges from the present analysis is that the communities are entirely different. The major purpose of this discussion is to explore and speculate on the reasons for those diferences. In later chapters specific aspects of those speculations are tested by experiments.

ABIOTIC FACTORS

Results from the present work (water speed, direction and temperature and from other published and unpublished work on the physical and chemical characteristics of the water in the bay (see chapter 1 and Fig. 1.2 for review) have failed to distinguish even one markedly different abiotic factor that could explain the difference between the benthic communities of the two islands. Despite this, five abiotic aspects still need further discussion, because of differences in the nature of the two islands and because one of the factors, organic pollution, might have affected the benthic fauna around Marcus Island in the past, and therby contributed to its present biotic structure.

Temperature

The average water temperature at Marcus Island is higher by ($3.5^{\circ}C$) than that of Malgas Island in summer while in winter they have very similar temperatures (see Chapter 1). However, on both islands, the temperature is within the limits of the cold Benguela current (Andrews 1974, Simons 1977, Brown and Jarman 1978) and is different from that of the lagoon system (Day 1959, Simons 1977). Furthermore, the Benguela upwelling system is characterised by fluctuations of temperature which can exceed $7^{\circ}C$ in a single day (Shannon et al. 1981), so that the differences between the islands are insignificant relative to normal fluctuations. It is not possible to explain the differences in community structure on the basis of differences in water temperature. For instance, a number of research projects show that the production and growth rates of some typical algal species is higher when the water temperature is $3-4^{\circ}C$ above the average Benguela water temperature (Bolton and Luning 1982, Bolton 1983, Anderson and Bolton 1985). Thus their absence from Marcus Island is inexplicable on the basis of temperature.

The rock lobster, *Jasus lalandii*, which is one of the key species that has radically different densities at the two islands, is known to be affected by fluctuations in water temperature. Heydorn (1969), found a significant decrease in moulting activity of *Jasus* males with a decrease in water temperature. However, the massive rock lobster population of the colder waters of Malgas Island, negates the possibility that the difference between the two islands has its origin in the different water temperature. Many of the other benthic species of the shallow sublittoral zone inhabit the littoral zone as well, and are resistent to extreme temperature fluctuations. Thus difference in temperature can be abandoned as an explanation for these contrasting communities on the two islands.

Water clarity

Water clarity establishes the level of radiation penetrating the water, which is essential for the process of photosynthesis. The question is whether the poor visibility is the cause of the absence of seaweeds at Marcus Island, while they are prevalent at Malgas Island. Anderson and Bolton (1985) explored the affect of water clarity on seaweeds production at Oudekraal on the West Coast near Cape Town. They found that at a 6m depth in seas of poor visibility (3-4m) similar to those typical for Marcus Island (see Chapter 1), that the amount of radiation reaching the sea floor was 9% of the radiation reaching the surface waters. This value is still, however, nine times higher than the value of 1% which is considered to be the critical minimum, below which no kelp will survive, and is 90 times higher than the value of 0.1% taken as the critical minimum for foliose red algae (Norton et al 1977; Hiscock 1985). Bolton (pers. comm.) rejects the possibility that water clarity of the order of that measured off Marcus Island, can limit the growth rate of red algae or kelp, although it might, however, affect the species composition. Apart from this, direct observations made at the islands, show that the visibility was often less at Malgas that at Marcus caused by large swarms of planktonic mysids; which also argues against light limiting algal growth at Marcus. In addition, an incidental observation was made of a large quantity of red algae growing on a rope stretched between two measuring instruments at 8m depth, and at a height of about 30cm above the sea floor at Marcus Island. Clearly light was not limiting at this depth, and it most likely that algae were able to grow on this rope because it was out of the reach of the urchins which abounded on the substratum below.

Substratum

The granite surface at Marcus Island slopes more gently in the sublittoral zone than at Malgas Island. Vertical rock surfaces are differently populated from horizontal rock surfaces (Sebens 1985). However, even at Malgas Island, the vertical surfaces appear only in shallow areas and, in any case, the samples were taken only from horizontal surfaces, which predominate on both islands. Although difficult to quantify, it appeared that the substratum at Malgas Island provides more hiding places and rock crevices than at Marcus Island. Crevices and holes are of considerable importance to the rock lobsters, which hide in their hundreds in rock crevices where they are protected from predators and sheltered during storms (Heydorn 1969). However, the rocky substratum at Marcus Island also contains a considerable number of hiding places and, in addition, the new breakwater near the research site provides an infinite number of crevices, all of which are not exploited by the rock lobsters. As part of the research project (to be reported in more detail in Chapter 5), artificial shelters were introduced to Marcus Island and 1000 lobsters were transferred there. Despite the presence of these shelters, the rock lobsters disappeared within a few days, excluding the possibility that lack of shelter and hiding places are the reasons for the chronic scarcity of rock lobsters from Marcus Island.

Pollution

A number of pollutant sources exist in Saldanha bay and are more likely to affect Marcus Island because of its proximity to the harbour. The major pollutant sources are the iron-ore terminal, the dredging activities deepening the entrance canal into the harbour, and fish factory waste. Effects of the former have been researched by Beckley (1981) and Gardner et al (1983). Beckley found that the iron ore terminal has only a local effect which extends nowhere near either island. The latter authors, however, found a large increase in the concentration of iron in the body of *Choromytilus meridionalis*, near to the terminal (three times higher than values typical of the West Coast), although no pathological effects on the black mussel were found. The large population of the black mussel at Marcus Island is testimony of the absence of any adverse effects of iron are on the mussels. Dredging obviously affects the benthos of the soft substratum at the work site though it does not seem to affect the adjacent hard substrata. A further effect is the suspension of organic and inorganic material and silt (Windom 1972; Moldan 1978). This organic material, together with silt, provides a food source for bivalve filter feeders and also increases their digestive efficiency (Winter 1976; Kiorboe at el. 1980). This may be advantageous for the growth of filter feeders off Marcus Island. Dredging is, however, an intermittent event, and no intense dredging has been undertaken in the bay since the mid 1970's.

Organic pollution from fish factory waste causes a drastic decrease in the oxygen level during calm and hot days, together with the release of methane and hydrogen sulphide which are toxic to most benthic species

(Nachenieus et al. 1968; Newman and Pollock 1973; Hicks 1975; Christie and Moldan 1977). Since 1974, however, the situation has improved considerably following the introduction of dry off loading from the fishing boats to the factories, and the oxygen level are now normal most of the year even near the fish factories (Gardner et al. 1983). Strangely enough there is evidence that organic runoff, composed mostly of fish waste, is not an attractive source of food for mussels and results in a decrease in their dry weight together with high mortality (Winter 1974, Murken 1976). Likewise, Christie and Moldan (1977) found a decrease in populations of *Choromytilus meridionalis* near the source of pollution in Saldanha Bay. However, as stated before, the large populations of black mussels off Marcus Island, negates the possibility that they are significantly affected by the pollution in the harbour. In a series of experiments conducted on both islands (see Chapters 3 and 4 for details) it was found that *C. meridionalis* and other benthic species typical of Marcus Island, can settle and grow without difficulty at Malgas Island when protected from predators and likewise rock lobsters can live for many months when held in cages at Marcus Island, where they are normally practically absent (Chapters 3, 5 and 6). This also argues that pollution is not a factor that can be invoked to explain the differences in community structure at the two islands.

Water movement

Hydrodynamic energy is the most intense and consistent physical pressure acting on shallow sublittoral communities. However, comparative measurements of water velocities at Marcus and Malgas Islands (Chapter 1, Fig. 1.2) show that both islands experience similar water velocities. This conclusion is supported by the work of Shannon and Stander (1977) and Huizing (1982 and pers. comm.).

PHYSICAL DISTURBANCES (WAVE ACTION), BENTHOS STRUCTURE, COMPLEXITY AND STABILITY

The effects of strong physical disturbance on species diversity has been well researched (Day, 1959; Taylor and Littler, 1978; Sousa, 1979a, 1979b; McQuaid, 1981, 1982; Lissner, 1983; Hiscock 1983; McQuaid and Branch, 1984, 1985). Similar to the effects of predation, when physical disturbances can reduce interspecific competition for food and space. This occurs because less resistant species, which are otherwise superior competitors, are prevented from dominating space freeing limited resources for more tolerant (although otherwise inferior) species. As a result, species richness and biomass decrease in areas exposed to intense wave action (Dayton, 1971; Sousa, 1979a, 1979b; Branch, 1984) where the biomass of filter feeders is relatively high.

several authors (Connell & Sousa, 1983; Pimm, 1984; Connell, 1985) have criticised the loose way in which the term "stability" is used. In the present context, community stability is considered over three years, a period that exceeds the life span of many of the organisms in the community. In addition, severe storms, capable of changing an unstable community,occurred during this period.

Connell (1985) also claims that much research on stability has been performed using unsuitable scales. Scales in time and space are of course important. However, ecosystems are open and change with time, and scales are to a large extent an arbitrary matter.

Different communities maintain stability in different ways depending on the types and levels of stress and disturbance which they are exposed to. Dayton et al. (1984) define three major types of stability: a) resistance - referring to a communitiy which resists displacement by disturbance or invasion by other species; b) resilience - referring to the ability of a community to recover to its original structure following disturbance or invasion by new species; c) persistence - referring to a constant community composition (by either resistance or resilience) through at least one generation of the dominant species. Pimm (1984) suggests that highly complex and integrated communities are more vulnerable to changes and disturbances and thus are less stable.

Different depths and dates of sampling at Marcus and Malgas Islands bracket the intensity and the frequency to which the benthos is exposed to wave action and storms. Quantitative changes in the number of species and total biomass were observed at different depths and different dates of sampling (mainly at Marcus Island), (Table 2.2, Fig 2.4). However the present work suggests that Marcus and Malgas Islands, although so different from each other, have a stable although dynamic benthic comunity. During the three years of research, **qualitative** changes were not detected in the fauna and flora on the sublittoral hard substrata of the islands, in spite of constant disturbance by waves, and intermittent chronic disturbance by storms. Using Pimm's (1984) terminology, it seems that the differing species composition and complexity of the benthos of Marcus and Malgas Islands are stable, but I believe that different processes maintain the stability on the two islands.

The benthic community of Malgas Island has a relatively simple structure with very few biological interactions and, although it contains a similar number of species to Marcus Island (Fig 2.3), all of them are over shadowed by the high biomass of the major predator, *Jasus lalandii*. The mobility of these rock lobsters enables them to seek the protection of deeper water and rock crevices, thus allowing them to survive severe storms without any significant effect (Table 2.2). Other benthic species common to Malgas Island (Porifera, Ascidiacea) are sessile and well adapted to wave action. With refence to the definition in the preceding paragraph, the Malgas Island benthic community can be described as maintaining stability through resistence to physical disturbance.

Marcus Island exhibits a much more complex benthic structure with many more biological interactions. The mussel *Choromytilus meridionalis* is the dominant benthic species. This species, and some of its associated macrofauna such as polychaetes and ophiuroids, are more vulnerable to wave action than the bentos at Malgas Island. As a result, the benthic biomass of Marcus Island fluctuates significantly with depth and, to a lesser extent with time (Fig.2.4, Table 2.2 and 2.6). In particular, the mussels are very susceptible to storms, and their average density and size composition change are a reflection of the time that has passed since the last major storm (Table 2.6).

For example, samples of mussels (with their epifauna) taken at Marcus Island from a depth of 2m, weigh 50% less than sample from 6m and 66% less than those from the 10m sample. In deeper waters, the number of species and their biomass increases significantly, as a result of decreased wave action (Table 2.2). However, the groups Porifera, Actiniaria, Cirripedia and Ascidiacea are more abundant in shallow water (Fig. 2.4, Table 2.2). These sessile or sedentary groups comprise filter-feeders or species which specialize in capturing wave-tumbled prey and they are adapted to resist strong wave action and share the shallow sublittoral space with black mussels. *Choromytilus meridionalis,* in the absence of its major predator, the rock lobster, covers the entire depth range available to it, from the shallow zone down to a depth at which rock gives way to sand. It contributes approximately 90% of the total biomass at all the depths. It does however lose its primary place to *Mytilus galloprovincialis* when exposed in the littoral zone (Grant _et_ _al_. 1984; Clark and Griffiths in press).

The size distribution of *Choromytilus meridionalis* at different depths and dates of sampling (Fig. 2.5, Table 2.6) clearly demonstrates the effect of different levels of disturbance on the species. In shallow water the mussel bed is single layered, with a large average size but small density of mussels. These mussels are strongly attached to the substratum and substantial force is needed to detach them. This constantly present community appears to invest much of its energy in attachment to the substratum, building dense and thick byssus threads (Martella 1974; Witman & Suchanek 1984). As a consequence this shallow-water mussel community can tolerate severe storms that develop quickly and thus survives for long periods of time. In deeper waters, however, the frequency of disturbances is less, and mussels form stratified layer, and often attach to fractions of shells, silt and various other species

(Fig. 2.6). The mussels are thus precariously attached to their substratum. Unpredictable and intermittent storms, can arise very quickly [eg. the storm of May 1984 reached a climax in less than 12 hours: (Jury et al. 1985)] and wash away these deeper mussels in large quantities. Consequently the deeper water communities are dynamic, often youthful and constantly changing.

Despite this, the overall community remains remarkably constant from year to year. Only three of the fifteen groups examined showed any significant change from 1983 to 1985. There appear two reasons for this: storms never eliminate more than a fraction of the existing mussel bed; and the many mobile species which occur in the mussel beds can rapidly colonise bare patches to maintain the status quo when storms create new patches.

The Marcus Island benthos therefore exhibits two different ways of maintaining stability. The shallow water community, which is relatively poor in species and well adapted to wave action, but has few biological interactions, achieves stability by resistance (Pimm 1984). The deeper water community is richer in species and is complex with many biological interactions (eg. *Thyone aurea* relies on *Pentecta doliolum* to hold it and protect it against wave action, and cryptozoic species use mussels for shelter). This community is more vulnerable to sudden storms and to removal of one or more of its species. It can, however, recover quickly and achieves stability by resilience (as defined by Dayton et al. 1984; Pimm 1984).

The physical pressures at Marcus Island, contrary to the predation pressure at Malgas Island, causes the biomass of many species to increase with depth, increases their dependency on the nature of the substratum and on the presence of other biotic components which assist their attachment to the substratum. In a physically unsteady environment, many of the species tend to respond by a) differentially developing power of attachment in response to differences in the level and frequencies of disturbance,or b) selecting more predictable and protective micro-habitats (Hubbell 1979; Pain and Levin 1981). There is special interest in the development of measures for survival which occur only in restricted circumstances, especially when they involve interactions between species. These measures are characteristic of the highly populated environment of Marcus Island: for example the dependence of *Thyone* on *Pentacta* in order to attach itself to the substrate in the face of wave action; the dependence of many species on the mussels for a protective microhabitat; the unusual clumping of whelks near to octopus holes, probably because they can scavenge on what was left of the octopuses' prey.

The situation at Malgas Island is entirely different. I believe that community structure there is dominated by the presence of dense rock lobster populations, which dictate the nature and number of species that can survive there. Many of the species that are common at Marcus are precluded from surviving at Malgas. Those that do live there are specialised to resist predation. In the chapters that follow, more specific experiments are undertaken to test ideas that flow from the present description of these contrasting communities. Specifically:

1. If rock lobsters control community structure at Malgas, then in areas at Malgas that are protected from predation, recruitment should lead to a community similar to that at Marcus.

2. Similarly, if mussels are transplanted to Malgas and protected against predation, they should survive and grow there as well as at Marcus.

3. If the two communities are stable, then some factors should prevent rock lobsters from simply invading Marcus Island and establishing a community like that existing at Malgas.

4. If the rock lobsters at Malgas are to maintain stable populations despite an apparent absence of sufficient food, they must be able to utilise unsuspected and unorthodox sources of food.

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CHAPTER 3 - RECRUITMENT AND SETTLEMENT

INTRODUCTION

Communities that develop on subtidal hard substrata are determined in the first instance by the larvae and spores that settle and subsequently by physical and biological factors that influence the survival and growth of these organisms. The present chapter is concerned with the contrasting communities that occur in the subtidal zones of two closely situated islands in Saldanha Bay on the west coast of South Africa: Marcus (17°55'E/33°03'S) and Malgas (17°55'E/33°'S). Both are guano islands, supporting substantial populations of seabirds, and the enriching effect of the guano runoff has been shown to enhance intertidal productivity (Bosman and Hockey 1986; Bosman _et al_. 1986) .Both have a fairly similar bottom topography and experience similar physical conditions (Chapter 1 & 2). But despite these similarities their subtidal benthic communities are radically different (Chapter 2). Marcus Island has prolific beds of the black mussel *Choromytilus meridionalis*, accompanied by a large number of other species, notably the echinoid *Parechinus angulosus*, the holothurians *Pentacta doliolum*, *Thyone aurea* and *Trachythyone insolens*, large population of whelks, mostly of the genus *Burnupena*, and the barnacles *Austromegabalanus cylindricus* and *Notomegabalanus algicola*. In contrast, Malgas Island is dominated by a large population of the rock lobster *Jasus lalandii* together with a dense seaweed flora. There are few animals, although there are small numbers of the ribbed mussel *Aulacomya ater* and the whelks *Argobuccinum pustulosum* and *Burnupena papyracea*.

In this chapter I describe experiments using settling plates which explore some of the possible reasons for these differences. Artificial settlement plates of various materials or designs have previously been used in two main lines of research. First are those concerned with the actual materials used, ie. the inavastigation of how different materials and paints resist fouling. Most of these results are published in internal reports, many of which have been reviewed by De Chalain (1979) and Henschel (1981). Secondly there are those concerned with the organisms themselves, for example, the searching by larvae for a suitable settlement site prior to metamorphosis (see review by Meadows and Campbell 1972 and also Moore 1974), or by mobile adult organisms for suitable substrata offering protection, shelter, or an adequate food source.

This second approach has gained much attention amongst ecologists, since it has enabled them to follow the processes of recruitment, succession and survival of species from the initial stages of colonisation until some sort of stability is achieved (Sutherland 1974; Osman 1977; Karlson 1978; Russ 1980; Keough 1983; Schmidt & Warner 1984; Witman 1985 and many others). Kindred studies have been undertaken on succession on naturally or artificially denuded rocks (eg. Jackson 1977; Sousa 1979a; 1979b; Paine & Levin 1981; Taylor & Littler 1982; Dayton 1985). The effects of physical and biological factors, such as wave action, storms, the stability of the substratum, competition and predation, have also been analysed in terms of their impact on succession and the ultimate composition of shallow marine ecosystems (Day 1977; Osman 1977; Sousa 1979a; 1979b; Taylor & Littler 1982; Dayton 1985).

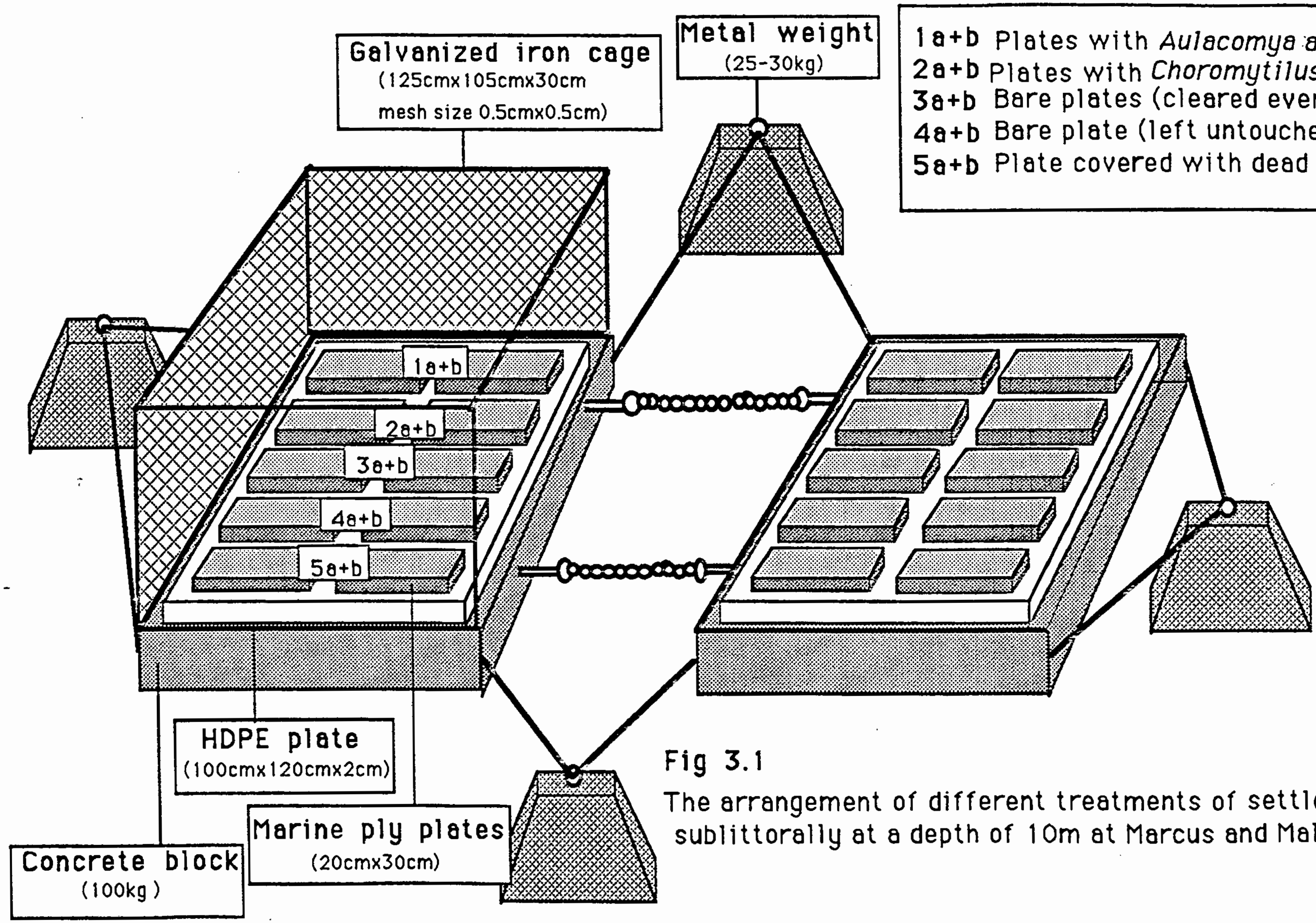
The effects of predation (or grazing) on littoral or sub-littoral fauna have been tested either by excluding major predators or grazers (eg. Dayton 1971; Paine 1974; 1984) or by protecting smaller areas by cages or anti-fouling paint (eg. Mook 1981; Underwood 1985). Results arising from such manipulations need to be cautiously interpreted because the treatment may have side effects. For instance, cages designed to exclude predators may also reduce light and waterflow and accumulate silt. In spite of this, such manipulations are a powerful means of testing factors that may influence settlement and subsequent survival. In this paper settling plates have been used in conjunction with cages to test (a) whether similar settlement and recruitment occurs at Malgas and Marcus Islands, and (b) whether settlement at Malgas Island leads to the development of a community similar to that of Marcus Island if rock lobsters and other large predators are excluded.

Since previously established organisms often influence the intensity and success of subsequent settlement (Odum 1969; Connell and Slatyer 1977; Grosberg 1981; see also chapter 2) I allowed live mussels to attach to some of the plates before they were installed, left some bare, and glued dead shells of the giant barnacle *Austromegabalanus cylindricus* onto others. This allowed me to compare settlement on bare substrata with that on plates with established mussels or dead barnacle shells.

MATERIALS AND METHODS

CONSTRUCTION OF CAGES AND SETTLEMENT PLATES

40 marine-ply settling plates (20 x 30 cm) were covered with GRP (glass-reinforced polyester) and sprayed while still wet with fine sea sand and shell fragments in order to provide a rough surface. Sets of 10 of these plates were connected to larger plates (100 x 120 cm) made of inert HDPE (high-density polyethylene). No settlements occurs on HDPE so the settling plates were effectively isolated. The smaller settling plates were attached to the HDPE plates by means of nylon screws and nuts, which resist marine fouling and corrosion for long periods. At each island, two of the HDPE plates were mounted horizontally on 100 kg concrete blocks positioned on the seabed at 10 m depth. Each of the concrete blocks was attached by chains to very heavy metal weights (old engine blocks), thereby adding further stability. At



Key for the plates

1a+b	Plates with *Aulacomya ater*
2a+b	Plates with *Choromytilus meridionalis*
3a+b	Bare plates (cleared every 2 months)
4a+b	Bare plate (left untouched)
5a+b	Plate covered with dead barnacle shells

Fig 3.1

The arrangement of different treatments of settlement plates placed sublittorally at a depth of 10m at Marcus and Malgas Islands.

each island one set of plates was protected by an iron cage while the other set was left unprotected (Fig. 3.1). The mesh size of the cage was initially 2.5 x 1.5 cm but was later reduced to 0.5 x 0.5 cm by means of plastic netting, in order to reduce penetration of smaller predators such as whelks. Strong to violent wave action is the norm at both islands (waves reaching up to 17m in extreme conditions (see chapters 1 & 2)): hence the extraordinary measures necessary to secure the cages. Cage controls (roof only, sides only) proved futile since they were not strong enough; mounting and maintaining the plates and cages was in itself a major operation.

Each set of plates was divided into five duplicated treatments to test recruitment and settlement of marine organisms on different types of hard substrata (Fig. 3.1). In the first treatment live tagged ribbed mussels, *Aulacomya ater*, were allowed to attach to the plates before they were installed. Self dissolving bandages, which disintegrate after two to three days submergence in sea water, were used to bind the mussels to the plates to allow them time to attach securely. In the second treatment, live tagged black mussels, *Choromytilus meridionalis*, were similarly established on the plates. In the third and fourth treatments, the plates were left bare, while in the fifth, dead shells of the giant barnacle *Austromegabalanus cylindricus* were attached. The plates were inspected after they had been submerged for 66, 123 and 189 days which, for convenience, are hereafter referred to as 2, 4 and 6 months respectively. (Longer-term experiments were planned but after 6 months the experiment was destroyed in a storm). In the case of treatments 1, 2 and 3 the plates were removed from the water to record settlement, and settled organisms were removed, counted and identified, before the plates were reinstalled. The plates in treatments 4 and 5 were inspected under water and all recruits were recorded: all settled organisms were left untouched throughout the period of observation. There were two reasons why the plates were processed in these two different ways. Firstly, the plates in treatments 1, 2 and 3 could be used to obtain a picture of seasonal settlement and, secondly, I was primarily interested in obtaining a detailed picture of the development and growth of mussel communities on these plates, which demanded removal of the plates to obtain accurate information on the numbers and size compositions of the mussels. Plates in treatments 4 and 5, on the other hand, allowed me to monitor the accumulative settling that took place over the entire period.

All species that settled on the plates were identified and counted and, for convenience, they were divided into two functional sub-groups: (1) species that compete for space, including sessile species such as barnacles, sedentary species such as sea anemones and mussels, and very slow-moving species like the holothurians, and (2) active mobile organisms, which do not seem to depend on the substratum. These divisions are, of course, arbitrary, but facilitate isolation of different aspects which affect species distribution.

NUMERICAL ANALYSIS

A number of different numerical methods was used to compare and test differences in settlement at the two islands and in response to the different treatments.

Cluster analysis

Cluster analysis was used to illustrate the percentage similarity between the various settlement plates at both islands (the dependent variable being the percentage cover of organisms that colonized the plates). The Bray Curtis measure of similarity and group-average sorting (Field et al. 1982) were used.

Student Newman Keuls test

Following one way ANOVA tests, the Student Newman Keuls test (SNK) (Sokal and Rohlf 1969) was used to subdivide the plates on each island into subgroups that were statistically different on the basis of either the percentage cover of each of the species (or taxonomic groups), or the number of species.

Two way ANOVA & multiple classification analysis

To estimate the relative importance of each predictor (eg. the importance of caging vs. type of plate) in terms of its effect on the community developing on the plates,and of the different categories within each predictor (eg. with or without a cage; with mussel-coverd, barnacle-covered or bare plates), Multiple Classification Analysis (MCA) was applied (Andrews 1973) using a SPSS-X programme. This analysis gives an Eta value of between 0 and 1 for each of the predictors, according to its relative influence on the percentage cover of the species. It also gives the negative or positive deviation of each category from the grand mean, in order to rank the importance of the different treatments according to their negative or positive influence on the number of species settling or their percentage cover. A 2-way Anova was applied to the MCA table to quantify the effect of predation (ie the presence or absence of a cage) and the type of substratum (while keeping the duration the plates had been in the sea as a co-variate).

Linear regression

Linear regression was used to test if the numbers of *Thyone aurea* on the settling plates were correlated with those of *Pentacta doliolum,* since there is a possibility that *Thyone* requires *Pentacta* to anchor itself to the substratum and their numbers are correlated in the natural community at Marcus (Chapter 2). The regression test was applied to different combinations of plates to determine the effect of caging and type of substratum on the presumed relationship between the two species.

Interactions between predation and substratum

Three-dimensional graphs were used to portray the effects of predation and type of substratum on species diversity and on biomass. Predation pressure (x axis) was ranked from 1-4, representing increasing levels of predation. Rank 1 was represented by sites at Malgas Island within cages, where predators and grazers were completely absent. Rank 2 represented the condition within cages at Marcus Island, where small predators such as drilling whelks, and grazers such as urchins and small starfish were present (since they were capable of penetrating the cage). Marcus Island plates that were not caged represented the third rank, while the fourth rank was allocated to Malgas Island plates which lacked a cage and experienced the greatest level of predation because of the huge rock lobster population there. This ranking was based on the mean (wet) biomass of predators that were either present in the cages or had access to the uncaged plates: Malgas Island, uncaged = 3867 gm^{-2}, caged = 0 gm^{-2}; Marcus Island uncaged = 1199 gm^{-2}, caged = 1318 gm^{-2}). The Y axis of the graphs was ranked according to the spatial complexity of the settling plates: Rank 1 - bare plates which were cleaned after each

Table 3.1: Number of species and cumulative % cover of a) spatial competitors, b) mobile species and c) all species combined, which settled on the settlement plates at Marcus and Malgas Islands after 2, 4 or 6 months. Cumulative % cover is the sum of the % cover of all species and may therefore exceed 100%. The sequence is organized according to the amount of predation experienced on each of the plates, from no predation (Malgas Islans with cage), to low levels of predation (Marcus Island with cage), to moderate predation (Marcus Island without cage) and, finally, extreme predation (Malgas Island without cage). Each of the 4 different predation levels was then further divided into 5 levels of substratal complexity, in descending order from very complex substrata (*Choromytilus* and *Aulacomya* plates*) to less complex (barnacle plates) and, finally, bare plates which were either untouched throughout the whole period of the experiment (6 months) or cleaned after each inspection.

	Spatial competitors		**Mobile species**		**Total**	
	Number	% cover	Number	% cover	Number	% cover
2 months						
Malgas with cage						
Choromytilus	10	243	1	17	11	260
Aulacomya	9	221	3	28	12	249
Barnacles	2	43	0	0	2	43
Bare untouched**	2	10	0	0	2	10
Bare cleared	2	10	0	0	2	10
Marcus with cage						
Choromytilus	3	174	11	53	14	227
Aulacomya	4	166	10	60	14	226
Barnacles	3	95	1	30	2	125
Bare untouched	2	75	0	0	2	75
Bare cleared	2	69	4	11	6	88
Marcus no cage						
Choromytilus	2	110	5	70	7	180
Barnacles	2	81	4	81	6	162
Bare untouched	2	35	3	42	5	77
Bare cleared	2	33	2	37	4	70
Malgas no cage						
Barnacles	2	40	0	0	2	40
Bare untouched	2	20	0	0	2	20
Bare cleared	2	15	0	0	2	15
4 months						
Malgas with cage						
Choromytilus	12	227	4	36	16	263
Aulacomya	11	208	4	64	15	272
Barnacles	4	183	0	0	4	183
Bare untouched	2	90	2	20	4	110
Bare cleared	2	168	3	15	5	183
Marcus with cage						
Choromytilus	6	68	9	108	15	176
Aulacomya	5	63	7	90	12	153
Barnacles	3	140	2	9	5	149
Bare untouched	3	105	3	66	6	171
Bare cleared	4	75	5	53	9	128
Marcus no cage						
Choromytilus	2	10	3	56	5	66
Barnacles	2	160	1	15	3	175
Bare untouched	1	103	2	10	3	113
Bare cleared	1	45	1	10	2	55
Malgas no cage						
Barnacles	3	110	0	0	3	110
Bare untouched	3	190	0	0	3	190
Bare cleared	3	142	0	0	3	142
6 months						
Malgas with cage						
Choromytilus	6	165	8	159	14	324
Aulacomya	6	165	9	153	15	318
Barnacles	5	165	8	120	13	285
Bare untouched	7	165	8	120	15	285
Bare cleared	6	165	9	115	15	280
Marcus with cage						
Choromytilus	8	147	6	15	14	162
Aulacomya	8	95	5	40	13	135
Barnacles	2	100	3	28	5	128
Bare untouched	2	100	1	17	3	117
Bare cleared	2	49	0	0	2	49
Marcus no cage						
Barnacles	2	130	3	29	5	159
Bare untouched	2	75	2	10	4	79
Bare cleared	2	4	2	17	4	41
Malgas no cage						
Barnacles	3	105	0	0	3	105
Bare untouched	3	125	0	0	3	125
Bare cleared	3	123	0	0	3	123

* There were no unprotected mussel plates at Malgas Island (the mussels being predated by rock lobsters); no unprotected *Aulacomya* plates at Marcus Island (where the mussels died); and no unprotected *Choromytilus* plates after 4 months at Marcus Island (due to death of the mussels).

inspection; Rank 2 - bare plates which were left untouched throughout the experiment period; Rank 3 - barnacle plates; and ranks 4 and 5 the mussel plates (*Aulacomya ater* and *Choromytilus meridionalis* respectively). Ranked values for predation and spatial complexity were plotted against (a) number of species and (b) the total % cover of all species on each of the plates.

RESULTS

Figures 3.2 and 3.3 summarise the recruitment of the most important pecies or groups of species to the settling plates, in terms of their percentage cover. Data on species richness appear in Table 3.1

MARCUS ISLAND. (FIG. 3.2 AND 3.1)

After 2 months the number of species and the percentage cover of the major groups were higher on plates that were protected by the cages than those that were unprotected. The *Aulacomya* that had been established on uncaged plates soon disappeared, so no further results are reported for this particular treatment. Inside the cages the mussel-covered plates had a markedly richer community than either the bare or barnacle plates. Most of the surface of the caged mussel-plates was covered by a dense settlement of tiny (7 mm) juveniles of the holothurian *Thyone aurea* which were absent

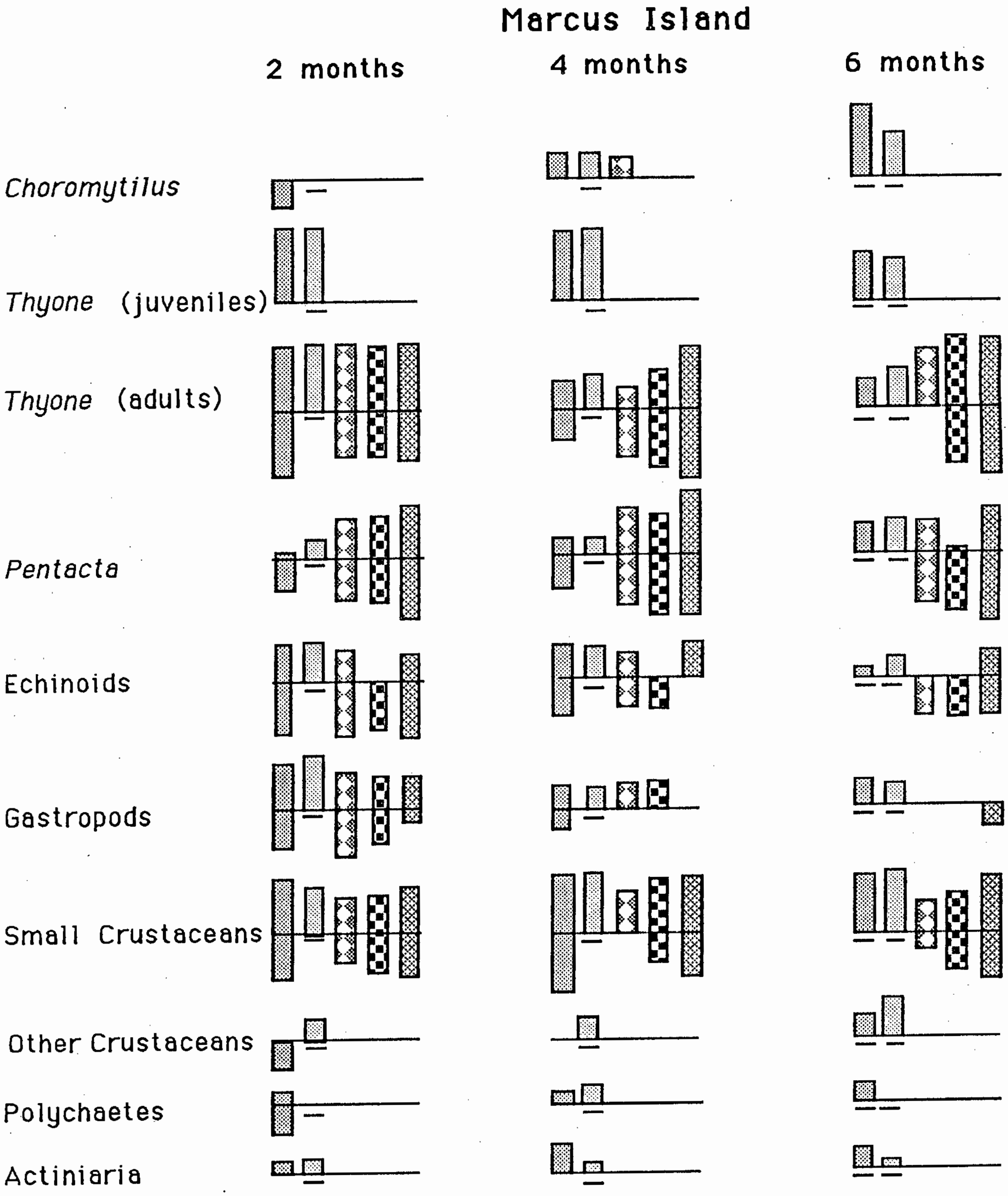
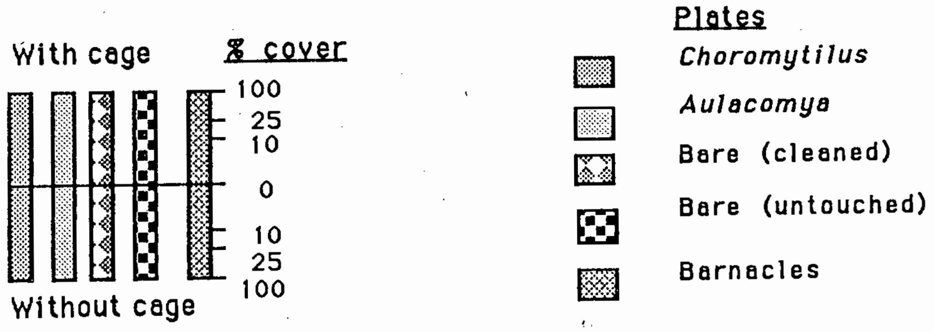


Fig 3.2
Percentage cover of species (Ln+1) which settled on the plates at Marcus Island after 2, 4 and 6 months. Dashes indicate lack of data for particular treatments, because of the deth of uncaged *Aulacomya* within the first two months, and of *Choromytilus* after 5 months.



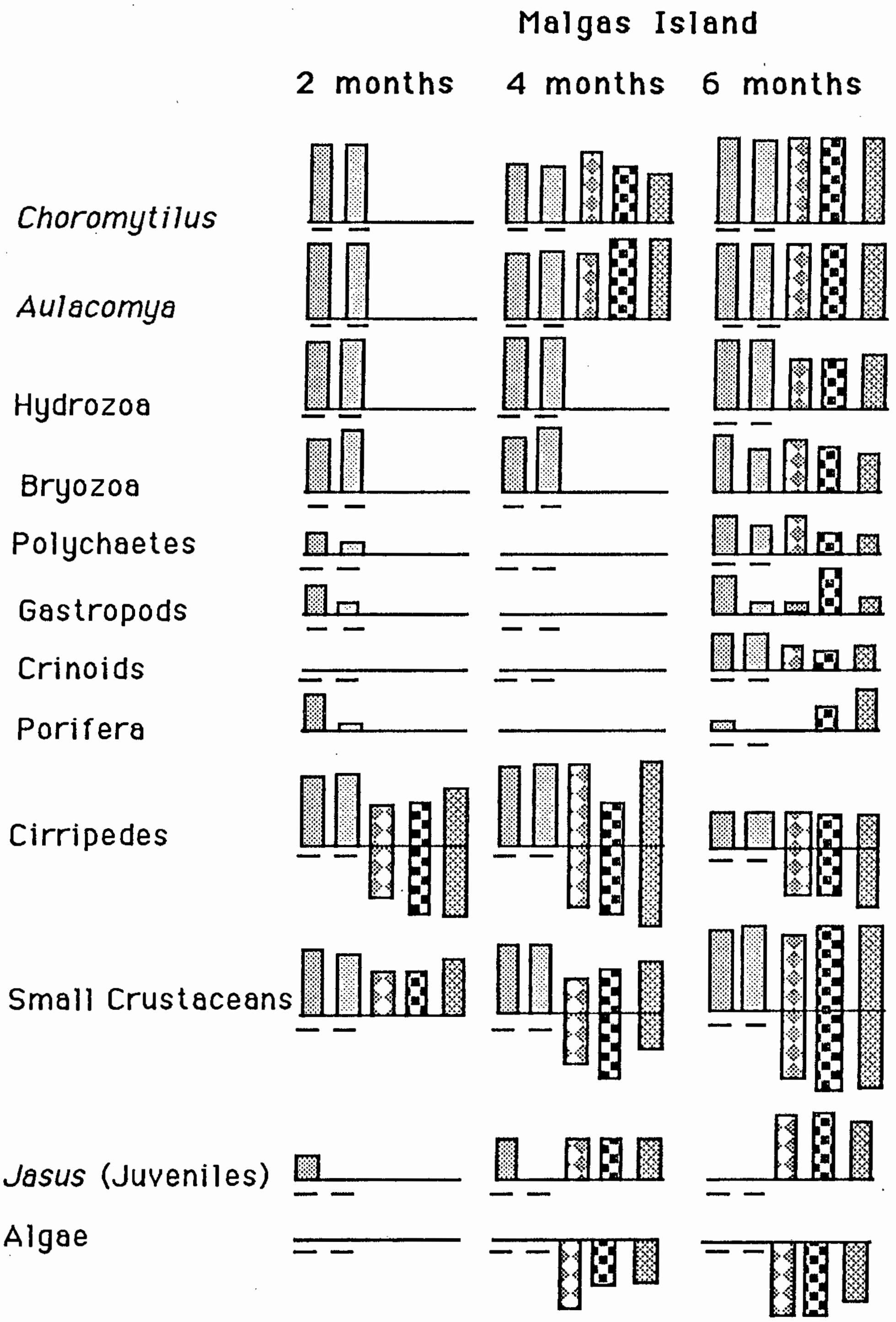
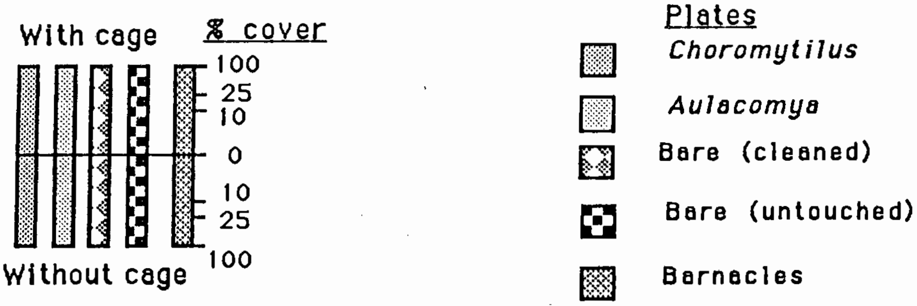


Fig 3.3
Percentage cover of species (Ln+1) which settled on the plates at Malgas Island after 2, 4 and 6 months. The two mussel plates were stripped of their mussels immediately after the plates were placed in the water, so there are no data for these two treatments which are indicated by dashes.



from the other caged plates and from all the uncaged plates. Smaller numbers of adult *Thyone aurea* and *Pentacta doliolum* and a few individuals of *Trachythyone insolens* had immigrated through the cage mesh and settled on the plates. While their numbers were approximately equal on all the plates (caged and uncaged) their relative spatial distribution differed in and out of the cages. Inside the cages *Thyone* was distributed randomly with respect to *Pentacta*, but outside it was concentrated beneath *Pentacta* - a pattern previously noted when the natural communities were sampled (see Chapter 2).

Other species that were more common on the mussel plates (particularly the caged plates) were two anemones, a series of gastropods (*Burnupena spp.*, *Crepidula porcellana*, *Afrocominella capensis*, *Gibbula zonata*), the cushionstar *Patiriella exigua*, the ophiuroids, *Ophioderma wahlbergi* and *Ophiothrix fragilis*, the crinoid *Annametra occidentalis* and juveniles of the rock lobster *Jasus lalandii*. The last named is of particular interest because adults of *J. lalandii* are scarce at Marcus Island. The mussel plates, particularly those in the cages, accumulated silt. Associated with this habitat was a range of isopods, amphipods, a mud prawn (*Upogebia capensis*), the crab *Hymenosoma orbiculare*, a number of polychaetes, a pycnogonids (Notably *Tanystylum brevipes*), a bivalve (*Venerupis corrugatus*) and a sipunculid (*Golfingia capensis*). Small individuals of the urchin *Parechinus angulosus* occurred on all the plates, but larger individuals were excluded from the caged plates.

Adults of *Pentacta* were the only organisms that occurred more commonly on plates without mussels: a trend that persisted in subsequent months.

The bare plates and the barnacle plates supported far fewer species - notably a few *Burnupena spp.*, the urchin *Parechinus angulosus*, and adults of both *Pentacta* and *Thyone*.

After 4 months the pattern was similar, with diversity and cover higher on the caged plates than on the uncaged plates and notably on the mussel-covered plates rather than on the bare or barnacle-plates. The juvenile *Thyone* had now grown to 20 - 25 mm and although concentrated on the mussel-plates had extended on to the other caged plates. On the uncaged plates juvenile *Thyone* were still absent. The spatial arrangement of adult holothurians remained unchanged, *Thyone* being randomly arranged within the cages but clustered beneath *Pentacta* outside the cages.

After 6 months a comparable picture existed, except that a massive settlement of juvenile *Choromytilus* had occurred within the cages, specifically on the mussel-plates. Outside the cages no settlement occurred on the plates, although small numbers of adult mussels moved onto the plates from the surrounding substratum. In addition, the barnacle

Notomegabalanus algicola settled on the large pre-established mussels. All the mussels were lost from plates outside the cages. On the remaining uncaged plates, *Pentacta* was more abundant on the barnacle-plates than on the bare plates and clustered in rings around the bases of the barnacles.

MALGAS ISLAND. (FIG. 3.3)

Recruitment to the plates at Malgas Island was strikingly different inside and outside the cages. On plates that were not protected by cages, the pre-established mussels were rapidly preyed upon by the rock lobsters and totally eliminated, most within a few hours. No animals were subsequently recorded on the uncaged plates except for a thin scattering of tiny freshly settled barnacles, which was evident on all the plates throughout the six months of observation. After 2 months these barnacles were the only life on those plates but by 4 months red algae (notably *Pachymenia carnosa*) covered much of the surface. By 6 months this alga dominated the uncaged plates and housed an associated fauna of small crustaceans such as amphipods and isopods. The uncaged barnacle-plate had significantly less algal growth than the bare plates.

On the plates inside cages dense recruitment of *Choromytilus* and *Aulacomya* occurred on the mussel plates within the first 2 months, together with large numbers of the barnacles *Notomegabalanus algicola* and a few idividuals of *Austromegabalanus cylindricus*. Although unquantified, it was noticeable that *Choromytilus* settled on those segments of the plates where silt had accumulated, whilst *Aulacomya* settled on the clearer parts of the plates. Two amphipods (*Ichnopus thaurus* and *Aristias symbiotica*) and an isopod (*Exosphaeroma planum*) recruited to the silt beneath the mussels. The mussels soon became covered by a variety of hydrozoans (particularly *Symplectoscyphus arbriformis* and *Amphisbetia operculata*), and by bryozoans (notably *Onchoporella buskii* and *Bicellariella ciliata*). The bare plates and barnacle plates supported a dense settlement of barnacles.

After 4 months the mussels that had recruited had grown to an average of 6 to 8 mm, developed a clumped pattern, and spread from their original site of settlement (ie the mussel plates), to cover much of the surface of the bare and barnacle plates within the cages. By 6 months further growth of the mussels (now averaging 22mm in length) continued their spread so that they thickly covered almost 100% of all the plates within the cages. *Aulacomya*, although still abundant, became smothered by the faster-growing *Choromytilus* which overgrew them. Thus all the plates within the cages became 'mussel plates' because of the progressive spread of recruited mussels from their first site of settlement on the original mussel plates. Barnacles that had settled on the bare and barnacle-plates were increasingly

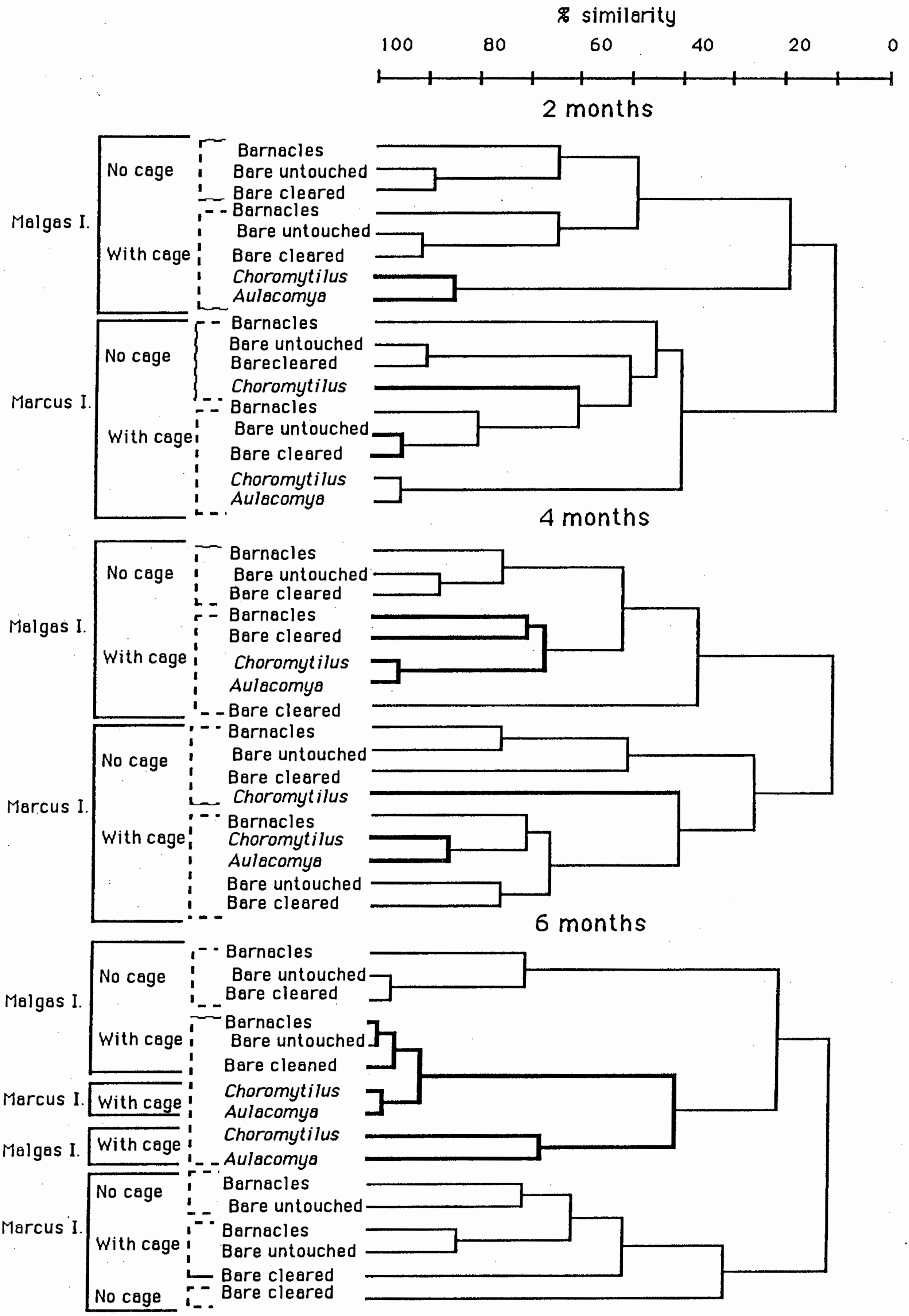


Fig.3.4 Dendrogram of % similarity (using % cover of all species after 2,4 and 6 months) of the different settlement plates from both islands, calculated using the Bray Curtis measure of similarity and group-average sorting. Dark lines distinguish plates which were either originally mussel plates or become dominated by mussels due to the spreading of mussel recruits.

smothered by the mussels and after 6 months occupied only the edges of the plates, which were, by then, the only portions of the plates that remained uncovered by mussels. As the mussels established themselves, so an epifauna of hydroids, bryozoans, sponges and sea anemones developed on them. Large numbers of tiny crayfish (20 mm carapace length) also accumulated in the cages, but were too small to prey on the mussels. No algal growth developed on any of the caged plates.

A notable feature of the community developing on the caged plates was that several of the species recorded were not normally found at Malgas Island. These included the mussel *Choromytilus*, both species of barnacle, the gastropods *Gibbula zonata, Nucella cingulata* and *Burnupena cincta*, a crinoid, *Annametra occidentalis*, and a brittlestar, *Amphipholis squamata*.

COMPARATIVE NUMERICAL ANALYSES.

Cluster analysis.

An analysis of the similarity between the communities developing on the plates (Fig. 3.4) shows that after 2 months there were two primary clusters - those at Marcus Island forming one group and those at Malgas Island another - with very little similarity between them. Each of these groups divided further into two subgroups ie. the caged mussel plates versus the remaining plates; the latter were in turn divisible into caged and uncaged plates. At this stage the primary distinction was between the islands, while within each island the two caged mussel plates (one initially comprising *Choromytilus* and the other *Aulacomya*) had very similar communities.

After 4 months the primary distinction between plates at Marcus and those at Malgas remained, but within each island the caged mussel plates were not longer so distinctive and formed part of a cluster with the other caged plates.

After 6 months the pattern had changed subtantially, with the caged mussel plates at Marcus now forming a discrete cluster together with all the caged plates at Malgas, which had become 'mussel' plates by virtue of the spread of recruited mussels from the original mussel plates on to the bare and barnacle-plates. This result is of particular interest, for it shows that if mussels are allowed to develop at Malgas, the associated community that becomes established has strong similarities with that associated with the mussel beds found at Marcus Island.

SNK Tests.

SNK analyses (Table 3.2a and b) were used, following a one way ANOVA test, to distinguish plates (or groups of plates) that were significantly different in terms of: (a) the total number of species present; (b) the number of mobile species (which did not compete for space); (c) the number of sedentary or sessile species (which were spatial

Table 3.2: Student Newman Kuels analyses of the number of species or percentage cover of the dominant groups of organisms settling on plates. Groups of plates that are not significantly different (P>0.05) are united by underlining. Within groups of underlined plates, those with the lowest values are placed on the left and those with the highest on the right. Groups that are significantly different are shown in successive rows, the first row giving plates with the least number of species or % cover and the last row those with the greatest.

Marcus Island (a)

Duration in sea:	2 months	4 months	6 months
Total Number of Species	4 5 7 8 3 9 6 1 2	7 8 9 6 5 4 4 3 1 2	3 4 7 8 5 9 1 2
Number of Mobile Species	4 5 7 8 3 9 6 1 2	7 9 5 8 6 4 3 5 8 6 4 3 2 2 1	3 4 5 7 8 9 4 5 7 8 9 1 2
Number of Species of Spatial Competitors	3 4 5 6 7 8 9 2 1	7 8 6 9 6 9 4 5 4 5 3 2 1	7 3 4 5 8 9 1 2
Choromytilus % Cover	1 2 3 4 5 6 8 9 7	1 2 3 4 5 6 7 8 9	4 5 7 8 9 1 2
Gastropoda % Cover	9 3 4 5 8 6 1 2 6 1 2 7	5 7 8 9 4 6 4 6 1 2 3	3 4 5 7 8 9 1 2
Thyone (Juvenile) % Cover	3 4 5 6 7 8 9 1 2	6 7 8 9 2 3 1 4 5	3 4 5 7 8 9 1 2
Thyone (Adult) % Cover	7 8 9 4 3 5 1 2 6	6 3 1 2 4 5 7 8 9	7 1 2 8 3 9 5 4
Pentacta % Cover	2 1 6 3 4 7 8 5 9	2 1 6 4 3 7 5 8 9	2 3 1 4 5 7 8 9
Parechinus % Cover	4 5 3 3 2 1 8 7 2 1 8 7 6 9	4 9 3 7 8 6 5 2 1	3 4 2 1 5 7 8 9

Malgas Island (b)

Duration in sea:	2 months	4 months	6 months
Total Number of Species	3 4 5 7 8 9 2 1	7 8 9 4 5 3 1 2	7 8 9 3 4 5 2 1
Number of Mobile Species	3 4 5 7 8 9 2 1	1 5 7 8 9 2 4 3	7 8 9 3 4 5 2 1
Number of Species of Spatial Competitors	3 4 5 7 8 9 1 2	4 3 3 7 8 9 2 5 1	7 8 9 4 3 5 2 1
Cirripedia % Cover	3 4 7 8 5 9 2 1	3 4 5 7 1 2 8 9	1 2 3 4 5 7 8 9
Aulacomya % Cover	3 4 5 7 8 9 1 2	7 8 9 3 2 1 4	7 8 9 1 2 3 4 5
Choromytilus % Cover	3 4 5 7 8 9 2 1	7 8 9 5 2 4 1 3 5	7 8 9 1 2 3 4 5
Algae % Cover		1 2 3 4 5 9 9 7 8	1 2 3 4 5 9 8 7
Other* % Cover	7 8 9 4 3 5 1 2	7 8 9 4 3 5 5 1 2	7 8 9 1 2 3 4 5

* Other : Hydrozoa, Bryozoa, Polychaeta, Gastropoda, Echinodermata and small crustaceans.

Key to plates:

	With Cage	Without Cage
Mussel plates-*Aulacomya ater*.	1	-
Mussel plates-*Choromytilus meridionalis*	2	6
Bare plates (cleaned).	3	7
Bare plates (untouched).	4	8
Barnacles plates.	5	9

competitors); and finally (d) the percentage cover of a series of important species or functional groups of species, notably the mussels *Choromytilus meridionalis* and *Aulacomya ater*, predatory gastropods, algae, the holothurians *Pentacta doliolum* and both juvenile and adult *Thyone aurea*, and the urchin *Parechinus angulosus*. The data on which these SNK analyses are based are shown in Table 3.1 (number of species) and in Figures 3.2 and 3.3 (% cover).

The total number of species was always highest on the caged mussel plates at both Marcus and Malgas Islands (plates 1 & 2), although after 6 months all the caged plates at Malgas (plates 1 to 5) formed a statistically indistinguishable group, associated with the spread of mussels onto other caged plates. The number of mobile species revealed a less clear-cut but similar pattern, the caged mussel plates usually housing the greatest richness. The diversity of spatial competitors was invariably highest on the caged mussel plates (and, ultimately, on all the caged plates at Malgas as they effectively became mussel plates). This is of particular interest, for it shows that at least over the first 6 months of colonisation, the mussels promoted the recruitment and development of other spatial competitors, even although they covered 100% of the surface of the plates.

Of the mussel species, recruits of *Aulacomya* never settled at Marcus Island, and only after 6 months was a settlement of *Choromytilus* recorded. This occurred almost exclusively on the two mussel plates (1 & 2), irrespective of whether they originally supported *Choromytilus* or *Aulacomya*. At Malgas Island both species of mussels initially recruited preferentially (and almost exclusively) to the mussel plates (1 & 2), but after 6 months they had recruited to all of the caged plates (1 to 5) which were by then equivalent to mussel plates).

Barnacles settled too sparsely at Marcus Island for any significant differences to be detected between the plates. At Malgas, highest recruitment was initially associated with the caged mussel plates (1 & 2) and the uncaged barnacle plate (9). With the growth of mussels on the caged plates this pattern changed, and after 6 months, all the uncaged plates (7 to 9) had significantly higher recruitment than the caged plates (1 to 5). In part this result is due to competitive exclusion of barnacles from the caged plates. However the dense recruitment of barnacles onto the uncaged plates also reflects the predatory activities of rock lobsters, which continually scraped the uncaged plate clean, clearing space for more recruits. Consequently recruitment was highest on these uncaged plates, but survival very low. Inside the cages fewer barnacles recruited, many were smothered by the mussels, but some survived and grew to maturity.

Algae recruited to the plates only at Malgas Island, and almost exclusively to the uncaged plates there (7 to 9), which were effectively bare plates because the rock lobsters had removed all animals apart from the perpetual scatter of continually recruiting newly settled barnacles.

Several species recruited only to plates at Marcus Island. Of these, the predatory/scanenging gastropods, *Burnupena spp.*, initially occurred in significantly higher numbers on both caged and uncaged mussel plates (plates 1,2 & 6) but by 6 months were more abundant in the caged mussel plates (1 & 2). Newly settled juveniles of the holothurian *Thyone aurea* occurred significantly more abundantly on the caged mussel plates after both 2 and 6 months. Adults of *Thyone aurea*, however, showed no pattern, their apparent preferences varying from one observation to the next. The urchin, *Parechinus angulosus*, similarly showed no pattern, which is scarcely surprising considering its mobility. The holothurian *Pentacta doliolum* departed radically from the pattern shown by most species, its numbers being significantly lower on the mussel plates (1, 2 & 6) than elsewhere, and often significantly higher on the uncaged barnacle and bare plates (7, 8 & 9).

The overall pattern revealed by the SNK tests was for the caged mussel plates to house the highest species richness (whether one considers total species or mobile species and spatial competitors separately) and to attract the highest recruitment of most species, including mussels. Ignoring the two groups for which recruitment seemed random (adult *Thyone aurea,* and *Parechinus*) the only departures from this pattern were: the barnacles at Malgas Island (settlement highest outside the cages, even although survival there was low); the algae at Malgas (settlement exclusively on uncaged plates); and *Pentacta doliolum* at Marcus (recruitment mainly to the uncaged bare and barnacle-plates and least to the mussel plates).

Multiple Classification Analysis (MCA).

The MCA analysis allows one to rank the factors (predictors) which determine the distribution and percentage cover of particular species or groups of species. The test was applied separately to Marcus and Malgas islands to determine the relative influence of caging versus the nature of the substratum.

At Marcus Island (Table 3.3a) the numbers of species (total, mobile species only, or spatial competitors only) were influenced primarily by the nature of the substratum rather than by the presence or absence of a cage (higher Eta values being associated with 'substratum' rather than 'cage' in seven out of nine sets of comparisons). Similarly, the percentage cover of most of the major species (or groups) was influenced more by substratum than cage effects. The only exeption was the urchin *Parechinus angulosus* (after 2

Table 3.3: Multiple Classification Analysis (M.C.A) which yields Eta values that are an indication of the ability of the the predictors ("cage" and "plate") to explain variations in the dependent variables. Each predictor is divisible into categories (with and without cage for "cage", and different types of substrata for "plate"). The effect of each category on the positive or negative deviation of the dependent variables from their grand means is indicated by plus or minus marks.

Marcus Island* (a)

Dependent variables

2 months Treatment	Total number of species	Number of mobile species	Number of species of spatial competitors	Cirripedia	Small crustaceans	*Choromutilus*	Gastropods	*Thyone* (juveniles)	*Thyone* (adults)	*Pentacta*	*Parechinus*	Other echinodermata
Cage (Eta)	.26	.21	.26		.47		.10	.48	.52	.44	.56	.47
Without Cage	-	-	-		-		+	---	-	++	+	---
With Cage	+	+	+		+		-	+++	+	--	--	++
Plate (Eta)	.82	.81	.73		.81		.72	.82	.88	.90	.46	.68
Aulacomya	+++	+++	+++		+		++	+++	+++	---	++	+++
Choromytilus	++	+++	+		++		+	+++	+++	---	+	+++
Bare Plate C	-	-	-		--		++	---	--	-	-	---
Bare Plate NC	--	--	-		--		--	---	--	-	--	---
Barnacles	--	--	-		+		---	---	-	+++	-	-
4 Months												
Cage (Eta)	.72	.62	.82		.48	.55	.58	.96	.25	.53	.21	.59
Without Cage	--	--	--		---	--	---	---	-	++	-	---
With Cage	++	++	++		+	+++	++	+++	+	--	+	+++
Plate (Eta)	.68	.66	.70		.89	.72	.70	.37	.77	.83	.67	.51
Aulacomya	+++	+++	+++		+++	+++	+++	+++	+	---	+++	---
Choromytilus	++	++	+		++	+++	+++	+++	--	---	++	---
Bare Plate C	-	-	-		---	-	-	-	---	-	--	++
Bare Plate NC	-	-	-		--	---	--	+	-	+	--	-
Barnacles	--	--	-		-	---	---	+	+++	+++	-	-
6 months												
Cage (Eta)	.35	.09	.47	.45	.49	.35	.37	.43	.21	.78	.51	.56
Without Cage	-	-	--	---	--	---	---	---	-	+++	+ +	---
With Cage	+	+	+	++	+	++	++	++	+	--	--	+++
Plate (Eta)	.97	.84	1.00	1.00	1.00	.98	.99	.97	.83	.67	.45	.94
Aulacomya	+++	+++	+++	+++	+++	+	+++	+++	---	--	--	+++
Choromytilus	+++	+++	+++	+++	+++	+++	+++	+++	---	---	++	+++
Bare Plate C	--	--	--	---	---	---	---	---	--	--	++	---
Bare Plate NC	--	--	--	---	--	---	---	---	++	+	+	--
Barnacles	-	-	--	---	-	---	--	---	+++	+++	---	--

Malgas Island** (b)

Dependent variables

Treatment	Total number of species	Number of mobile species	Number of species of spatial competitors	Cirripedia	Small crustaceans	*Aulacomya*	*Choromutilus*	Gastropods	Algae	Other
2 months										
Cage (Eta)	.44	.29	.45	.43	.62	.44	.45	.35		.93
Without Cage	--	---	--	--	---	---	---	---		---
With Cage	++	++	+	+	++	++	++	++		+++
Plate (Eta)	.98	.83	1.00	.99	.93	1.00	1.00	1.00		.21
Aulacomya	+++	+++	+++	+++	+++	+++	+++	+		++
Choromytilus	+++	+	+++	+++	+++	+++	+++	+++		++
Bare Plate C	--	---	--	--	--	---	---	---		---
Bare plate NC	--	---	--	--	---	---	---	---		-
Barnacles	--	---	--	--	--	---	---	---		---
4 months										
Cage (Eta)	.88	.54	.20	.50	.28	.89	.81		.79	.75
Without Cage	-	---	-	++	-	---	---		+	--
With Cage	++	++	+	-	+	++	++		---	+++
Plate (Eta)	.98	.55	.75	.54	.88	.36	.81		.55	.28
Aulacomya	+++	++	++	++	+++	++	+++		---	+++
Choromytilus	+++	++	+	++	+++	++	+++		---	+++
Bare Plate C	-	+++	-	-	--	--	-		++	---
Bare plate NC	-	++	-	-	-	-	--		+++	--
Barnacles	-	---	+	+	--	+	---		---	-
6 Months										
Cage (Eta)	.77	.20	.88	.91	.44	1.00	1.00	.10	.91	.99
Without Cage	-	---	-	+++	+	---	---	---	+++	---
With Cage	++	++	+	---	-	+++	++	++	---	+++
Plate (Eta)	.67	.68	.55	.50	1.00	.45	.45	.82	.50	.10
Aulacomya	+++	+++	+	---	++	+++	++	+++	---	+++
Choromytilus	+++	+++	+	---	+++	+++	+++	+++	---	+++
Bare plate C	-	-	-	-	--	-	-	---	+++	-
Bare Plate NC	-	-	-	-	-	--	-	---	++	-
Barnacles	-	-	-	+++	-	--	-	---	-	-

Key

Devation from grand mean.	±	1% - 33%
	±±	33% - 66%
	±±±	66% - 100%

* At Marcus Island the treatment "*Aulacomya* without cage" did not exist throughout the experiment and "*Choromytilus* without cage" only persisted for the first four months (due to death of mussels).

** At Malgas Island both treatments "*Aulacomya* and *Choromytilus* without cage" were eliminated at the outset of the experiment (the mussels being preyed by rock lobsters).

Other : Hydrozoa, Bryozoa, Polychaeta, Gastropoda, Echinodermata.

and 6 months) which, because of its mobility, was free to move on to uncaged plates, but was largely excluded from the caged plates by its rigid test.

A further break down of the two primary predictors into categories allows determination of whether either the presence or absence of a cage or the specific nature of the substratum have positive or negative effects on the organisms. In the MCA analysis this is expressed by positive or negative percentage deviation from the grand mean of each indicator. At Marcus Island the number of species was in all cases higher on caged than on uncaged plates, and higher on the two mussel plates than on the other three types of substrata (Table 3.3a). The percentage cover of the dominant groups of organisms followed the same pattern. One exception was *Parechinus angulosus* (commonest outside cages, for reasons given above). Another was *Pentacta doliolum*, which was commoner outside cages than inside, and was specifically associated with barnacle plates but avoided the mussel plates. Its exclusion from cages is understandable because it has a rigid body wall and is relatively immobile, but its avoidance of the mussel plates remains unexplained. Its preference for the barnacle plates over bare plates may reflect its greater ability to adhere to a complex substratum. The final exception was *Thyone aurea*, which conformed to the general pattern in being more abundant inside cages than out, but at months 4 and 6 it was strongly positively associated with the barnacle plates and, in most cases negatively associated with the mussel plates. This may be an indirect effect, because *Thyone* appears to be correlated with *Pentacta* (see chapter 2).

The MCA analysis needs to be interpreted cautiously when applied to Malgas Island because the mussel plates outside cages were almost immediatley stripped of their mussels, creating bare plates, while the barnacle plates and bare plates inside the cages were progressively encroached upon by recruiting mussels and became mussel plates. Because of these changes, the relative influence of cage and substratum changed with time. Initially (after 2 months) substratal effects were uniformly greater than cage effects (having higher Eta values), but after 4 months the two indicators influenced roughly equal numbers of different groups of organisms, and after 6 months the presence or absence of a cage was the dominant indicator (Table 3.3b).

Highest species richess was invariably associated with the caged mussel plates, as was the percentage cover of most groups of organisms. The single departure was the algae, which occurred exclusively outside cages. Their apparent avoidance of mussels is an artefact (since there were no mussel plates outside the cages). But their marked development on bare plates as opposed to barnacle plates was interesting. The only other exception was the barnacles, whose prevalent settling outside cages has already been discussed, and which settled more abundantly on the barnacle plates rather than on the bare plates after 4 and 6 months -

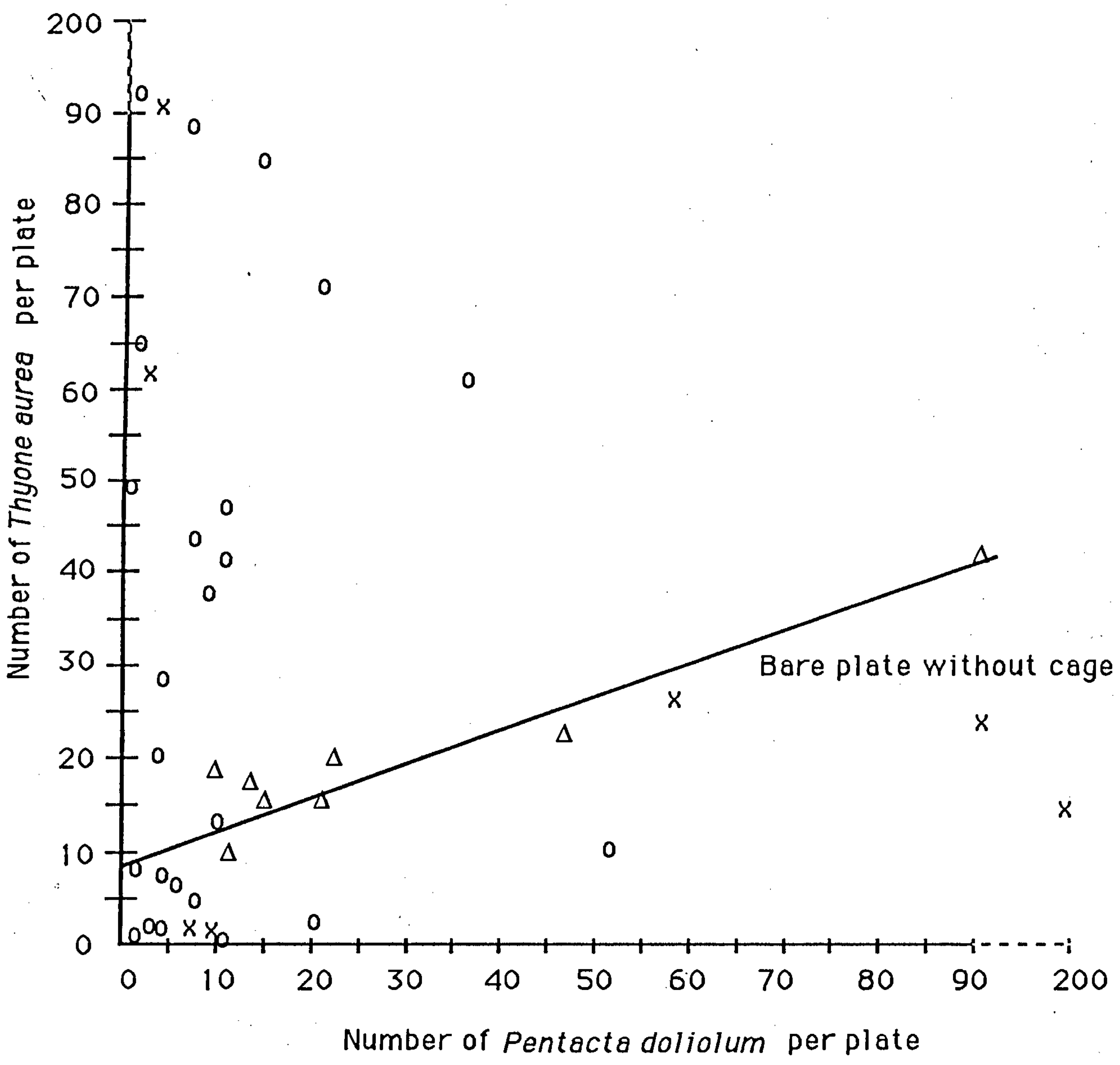


Fig 3.5

Corelations between numbers of *Thyone* and number of *Pentacta* on different types of plates.
N.S = Non significant, P > 0.05.

o - All plates within cages
Δ Bare plates without cages
x - "Mussel" and "barnacle" plates without cages

o + Δ + x	N=40	r=0.10	p=N.S	
o + x	N=31	r=0.14	p=N.S	
o	N=24	r=0.01	p=N.S	
x + Δ	N=16	r=0.04	p=N.S	
x	N= 7	r=0.29	p=N.S	
Δ	N= 9	r=0.78	p<0.05	Y =8.60 +0.29x

possibly because algal growth excluded them from the bare plates.

Correlations and Linear Regressions.

From all the subsets of plates and species present, the only combination of species showing a significant correlation was *Pentacta doliolum* and *Thyone aurea*, and then only on the uncaged bare plates ($r = 0.78$, $p < 0.05$). This finding agrees with previous observations (see Chapter 2) that the two are positively associated in the field ($r = 0.8$, $p < 0.01$). No correlation existed inside the cages, or on the mussel plates outside cages, but on the bare plates outside cages the regression relating *Thyone* numbers to *Pentacta* numbers was positive and significant (Fig. 3.5). The regression plots also revealed that by far the highest numbers of *Thyone* occurred within the protection of the cages.

DISCUSSION

The composition of the communities developing on the settlement plates differed between the islands, between caged and uncaged plates, and between the plates with different substrata. Three major factors played a role in this: the intensity of predation; the availability of recruits; and the nature of the substratum.

EXCLUSION OF PREDATORS

The clearest effect demonstrated was the overriding influence of the rock lobster *Jasus lalandii*. At Malgas Island where it is abundant (mean wet weight 3867 gm-2), uncaged plates that initially contained pre-established mussels were stripped within a few hours. All the uncaged plates subsequently supported virtually no animal life, sustaining only short-lived settlements of barnacle spat and, ultimately, a cover of algae with its epifauna of algal-dwelling crustaceans. Conversely, the plates inside the cages developed a diverse community (Fig. 3.3) which finally converged upon that found at Marcus Island (Fig. 3.2). SNK analyses (Table 3.2a and b) show the significantly higher diversity and the higher cover of almost all animals on the caged plates; and the MCA analysis (Table 3.3a and b) confirms that after 6 months the effect of predation (ie. the presence or absence of a cage) was the key variable influencing the community composition at Malgas Island.

At Marcus Island caged plates also supported higher numbers of species and a higher percentage cover than the uncaged plates, and most species (or groups of species) were more abundant on the caged plates (Fig. 3.2, Table 3.2a and b). Differences between caged and uncaged plates were, however, not nearly as striking as they had been at Malgas. There are several reasons for this. The level of predation outside the cages there was not as high as at Malgas and, in particular, the near-absence of rock lobsters substantially reduced the intensity of predation. Griffiths and Hockey (1987) have modelled the impact that predators are likely to have on a hypothetical cohort of mussels in the subtidal zone at Marcus Island, and concluded that predators account for an insignificant fraction of the mortality; thinning due to intraspecific competition for space is of far greater significance. The MCA analysis (Table 3.4) confirms that the influence of predation on the comunities developing on plates at Marcus Island is of secondary significance relative to the effects of substratum. A second factor influencing the outcome of colonisation at Marcus was the prevalence of mobile species at the island which rapidly colonised the uncaged plates. Those that were sufficiently small or flexible also penetrated the cages. These included small predators (notably the whelks *Nucella spp.*). Even although the biomass of these predators inside the cages was small (119 g wet mass m-2) in comparison with that on the uncaged plates (1199 g m-2), low-level predation did occur inside the Marcus Island cages. Finally, there were some species which quickly spread to the uncaged plates but could not penetrate the cages (particularly adult *Parechinus angulosus* and *Pentacta doliolum*) and these species increased the cover of animals on uncaged plates.

Cages often have inadvertant side-effects (see Schmidt and Warner 1984). We are confident that at at Island the differences between the uncaged and caged plates were almost entirely due to the presence or absence of rock lobster predation. Direct observation of predation by rock lobsters on uncaged mussel plates, the speed with which the pre-established mussels were removed, and the presence of characteristically crushed mussel shells all provided unequivocal evidence that rock lobsters removed the pre-established mussels from uncaged plates and prevented animals from subsequently becoming established on these plates. Furthermore, in a separate experiment, plates were maintained within cages with or without *Jasus lalandii*; within one month rich communities covered 100% of the surface of the plates that were in cages lacking rock lobsters, but in the presence of rock lobsters the plates were kept virtually bare (see chapter 6).

Nevertheless there are four possible cage effects influenced the communities developing within cages. Firstly, siltation occurred on all the mussel plates, fine sediment accumulating between the mussels. This was most obvious on the caged mussel plates. A characteristic fauna developed in this sediment, including amphipods, a sipunculid, a bivalve, an echiuroid, polychaetes and a burrowing prawn. All these species occurred commonly in the mussel beds at Marcus Island (Chapter 2), and although they were more abundant in the cages they were all also present on uncaged mussel plates. Siltation did not occur on any of the plates that lacked mussels, and appears to be a natural process in the mussel beds, whether caged or not.

A second cage effect is protection from wave action, and I believe that the prevalence of juvenile *Thyone aurea* inside the cages at Marcus Island is a consequence of this.

Thirdly, cages reduce light, and this is almost certainly why no algae developed inside the cages at Malgas Island, even in the early stages of the experiment, before mussels dominated the caged plates completely.

Finally, cages may exclude other species in addition to the predators they are intended to keep out. The only species apparently affected in this way were *Parechinus angulosus* and *Pentacta doliolum*, the adults of which were excluded from the cages.

Despite these cage effects, I am convinced that the major differences between the communities at Malgas and Marcus, and between caged and uncaged plates at Malgas, are due to the presence or absence of rock lobsters. The convergence of community structure on the caged plates of the two islands remains a key finding and demonstrates that if it were not for the effects of rock lobsters similar benthic communities could be anticipated at Marcus and Malgas.

AVAILABILITY OF RECRUITS

The availability of potential recruits - either planktonic larvae or mobile benthic post-larval stages - may influence the structure of the community developing on settling plates. In the short term, seasonal availability plays a major role, but in the long term proximity to a source of recruits can become more important (Meadows and Campbell 1972; Sutherland 1974; Osman 1977; Sousa 1979a; 1979b; Grosberg 1982; Keough 1983; Underwood and Denley 1984). Most species that did settle on the plates recruited to both Malgas and Marcus, including many that were not normally found on one or other of the islands. At Malgas Island, notable examples were *Choromytilus meridionalis*, many species of gastropods, a crinoid, several small crustaceans and polychaetes. All of these were not previously recorded from the island, but occurred commonly within the cages. They were also common at Marcus, both in the natural community and on caged and uncaged plates. At Marcus Island small post-larval juveniles of *Jasus lalandii* were recorded inside the cages despite the near-absence of adults in the benthos. These species collectively contributed to the convergence of the communities on the caged plates of the two islands.

Conversely, some species recruited to only one of the islands. Juveniles of the three holothurians (*Thyone aurea, Pentacta doliolum* and *Trachythyone insolens*) recruited only to Marcus Island (Fig. 3.2 and 3.3). It is possible that these species undertake only short-distance dispersal and that none of their larvae was present at Malgas. Algae never settled on the plates at Marcus even although they dominated the uncaged plates at Malgas. Almost certainly their absence at Marcus was due to the abundant grazers (particularly urchins) at Marcus, but contributing factors may have been the total domination of space by sessile animals, and filtration by mussels. Whatever the cause, the absence of algae on plates at Marcus and their sparsity in the benthos as a whole at this island had a ripple effect: ie. the exclusion of a suite of small algal-dwelling crustaceans which were found at Malgas but not at Marcus (see also Chapter 2).

There was one major difference between colonisation at the two islands. Because there is an extremely impoverished benthos at Malgas there were practically no mobile post-larval stages that could invade the plates, and recruitment was entirely by way of larval settling. Almost all the early recruits at Malgas were sessile species, including mussels, algae, sponges, hydrozoans and bryozoans.

At Marcus Island the rich benthic community in the vicinity of the plates included many mobile or sedentary species which moved onto the plates almost immediately after they were installed. Important participants were the urchin *Parechinus angulosus*, the holothurians, and the whelks

Burnupena spp. and *Nucella spp.* Larger individuals were excluded from the caged plates if they had inflexible bodies or shells, but small predatory whelks and juveniles *Parechinus* penetrated; and *Thyone aurea*, which is flexible, rapidly became more abundant inside the cages than outside. The rapid domination of plates by these mobile, often adult, organisms almost certainly influenced subsequent settling of larvae, because of their command of space and their grazing, filtering and predatory activities (cf. Keough 1983). While sessile species initially dominated at Malgas and mobile species at Marcus (Table 3.1) this distinction disappeared as the communities converged, and after 6 months the caged plates had similar numbers of both sessile and mobile species on comparable plates.

DIFFERENCES IN THE SUBSTRATUM

The plates initially comprised five different treatments representing (in the following order) decreasing surface complexity: a) covered with *Choromytilus*, b) covered with *Aulacomya* c) with attached dead barnacle tests, d) bare and never cleared, and e) bare and cleared every two months. In reality, these treatments changed once the plates were introduced into the water. Uncaged plates at Malgas were immediately stripped of their mussels leaving "bare" and "barnacle" plates. The caged plates at Malgas were progressively invaded by mussels and eventually all of them were effectively mussel plates.

Despite these limitations, clear distinctions existed between some of the treatments, the most obvious being between plates with or without mussels (Fig. 3.2 and 3.3, Table 3.3a and b).

Mussels potentially have both negative and positive effects on recruitment. On the negative side, the filtering action of mussels may inhibit recruitment of other organisms (Cowden et al 1984). Mussels also preempt primary space, as evidenced by their spread to all the caged plates at Malgas. In the natural community at Marcus Island they command almost all of the primary space (Chapter 2). They also smother other organisms which do succeed in occupying primary space. At Malgas they overgrew barnacles that had settled on the caged plates and, as a consequence, barnacles were amongst the few organisms to occupy more space on the uncaged plates than the caged plates, even although their survival there was brief. The MCA analysis (Table 3.3b) reveals the initially positive and finally strongly negative effect that mussels had on the distribution of barnacles at Malgas. Competitive displacement of barnacles by mussels has been well documented elsewhere (Dayton 1971; Paine 1974; Menge and Sutherland 1976; Menge 1976; 1978; Menge and Lubchenco 1981). Competitive interactions also occurred between the two species of mussel. *Choromytilus*, being the faster-growing species (Griffiths 1981; Wickens 1985 and see also chapter 4) overgrew and ultimately displaced most of the *Aulacomya* from the plates at Malgas; in the benthos of

Marcus Island *Aulacomya* is virtually absent and *Choromytilus* dominates. Small *Aulacomya* are found there but do not survive to an adult stage. Their dead shells are found enmeshed in the byssus threads of *Choromytilus*, testifying to their fate. Both species of mussel also appeared to have a negative effect on *Pentacta* (Table 3.3a) which had a significantly lower percentage cover on plates with mussels than on most other plates (Table 3.2a). The reason for this is unknown for *Pentacta* regularly forms a dense cover on top of mussels in the subtidal zone at Marcus (see Chapter 2).

Despite these negative effects, most species (or groups of species) responded positively to the presence of mussels (Table 3.3a and b). The total number of species and the total cover were consistently and significantly higher on the mussel plates (Figs. 3.2 & 3.3 and Tables 3.1 and 3.2). If the species are categorised into two functional groups (sessile or sedentary - spatial competitors, versus mobile species that do not occupy or compete for space) this trend persists, the mussel plates still supporting the highest diversity and cover of both groups (Tables 3.1, 3.2, and 3.3). This is of particular interest, for mussels often dominate space and reduce diversity by competitively excluding other spatial competitors (eg. Paine 1974). At least for the six months over which this experiment ran, the opposite was true, mussels clearly enhancing overall diversity and even the diversity of other space-occupying species. Witman (1985) describes similar positive effects that mussel beds have on a variety of species.

The positive influences of mussels are due to at least four different effects. Firstly, the mussels themselves recruited selectively and exclusively to other mussels: no settlement occurred directly onto the bare or barnacle plates. Only once the growing mussels spread to occupy bare and barnacle plates did settlement of new recruits take place on these plates. Such self-recruitment is known in many mussels (Suchanek 1978; Paine and Suchanek 1983).

Secondly, the mussels facilitated recruitment of many other species (Fig. 3.2 and 3.3). At Malgas Island these included the bryozoans, hydroids and sponges, all of which recruited by way of larval settling. At Marcus island juveniles of sea anemones, juvenile *Thyone aurea*, ophiuroids, all capable of post-larval movements, rapidly moved onto the mussel plates. I speculate that these species gained shelter on the complex surface of the mussel plates.

Thirdly, four species of small predatory gastropods (*Burnupena spp.*, *Nucella squamosa* and *N. cingulata*) were all first found on the mussel plates and, ultimately, were significantly more common on them (Fig 3.2 and 3.3, Table 3.2b). Mussels are a primary source of food for these whelks, the *Nucella spp.* in particular drilling through the shells (see Chapter 4). McQuaid and Branch (1985) have previously described positive correlations between the biomass of filterfeeders and that of predatory gastropods on intertidal rocky shores.

A fourth benefit accrues to species which capitalise on the sediment that accumulates between the mussels, notably amphipods, isopods and polychaetes.

Turning to the remaining plates (barnacle, bare and uncleared and bare cleared) there were few consistent or significant differences between them (Tables 3.1 and 3.3). Algae (which only settled at Malgas and only on uncaged plates) were significantly more abundant on the bare plates than on the barnacle plates (Tables 3.1b and 3.3b). I have no explanation for this and had, in fact, anticipated that the more irregular surface of the barnacle plate might enhance algal settling. Possibly the rough texture of the barnacles eroded the algal fronds thereby reducing algal cover. Underwood and Denley (1984) have shown that in the intertidal zone in New South Wales barnacles and other surface irregularities have no influence on algal recruitment. At Malgas Island the pattern of algal settlement had a secondary effect: the barnacle *Notomegabalanus algicola* settled less intensely on the bare plates than on the barnacle plates. It is unlikely that their apparent preference for the barnacle plates is a gregarious response triggered by the barnacle shells (which belonged to a different species - *Austromegabalanus cylindricus*), since *N.algicola* settled equally on all these plates after 4 months and only became less abundant on the bare plates once they had become dominated by algae.

Pentacta doliolum (which was restricted to Marcus Island and more common on plates outside cages than inside) occupied significantly more space on the barnacle plates than on either of the bare plates (Fig. 3.2 Table 3.2a) and clustered around the bases of the barnacles rather than on the bare spaces between the barnacles. Probably the relativly smooth surface of the bare plates was less suitable for attachment and provided no protection against wave action. Outside the cages, *Thyone aurea* also occurred more commonly on the barnacle plates than the bare plates (Fig. 3.2) and its numbers were correlated with those of *Pentacta*. Inside the cages *Thyone* was more abundant, showed no preference for barnacle plates rather than bare plates, and its numbers were no longer correlated with those of *Pentacta* (Fig. 3.5). *Thyone* can only attach itself weakly to the substratum. In the shallow wave beaten subtidal of Marcus Island it is found lying beneath *Pentacta* (only its crown of tentacles penetrating to the surface), and its numbers are correlated with those of *Pentacta* (see chapter 2). I suggest that it depends on the more firmly attached *Pentacta* to avoid being detached by waves. Indeed, if *Pentacta* is experimentally removed, the underlying *Thyone* are immediately washed away (personal observations). Within the shelter of cages, *Thyone* loses this dependency on *Pentacta*. Such facilitation between two ecologically similar co-existing species is interesting because it runs counter to the competitive interaction that might intuitively be expected. Other comparable examples have been described by Duggins (1980; 1981) for urchins and by Duggins & Dethier (1984) for grazing molluscs.

The few differences between the "barnacle" and "bare" plates that are described above are all quantitative differences between the amounts of particular species present, and stand in strong contrast to the much more radical differences between plates with or without mussels (Table 3.3). The positive influence that mussels have on diversity and abundance is still the most striking feature to emerge from the comparisons of plates with different surface textures.

COMBINING THE EFFECTS OF PREDATION AND SUBSTRATE COMPLEXITY

By ranking the intensity of predation and the complexity of the surface of the plates (see Methods) their integrated effects on diversity (ie. number of species) and on percentage cover could be portrayed three dimensionally (Fig. 3.6). For the first four months both diversity and cover peaked on plates with the lowest level of predation and the greatest complexity, emphasising the importance of both predation and substrate complexity on settlement and the early establishment of communities. After six months, however, substrate complexity became irrelevant at the two

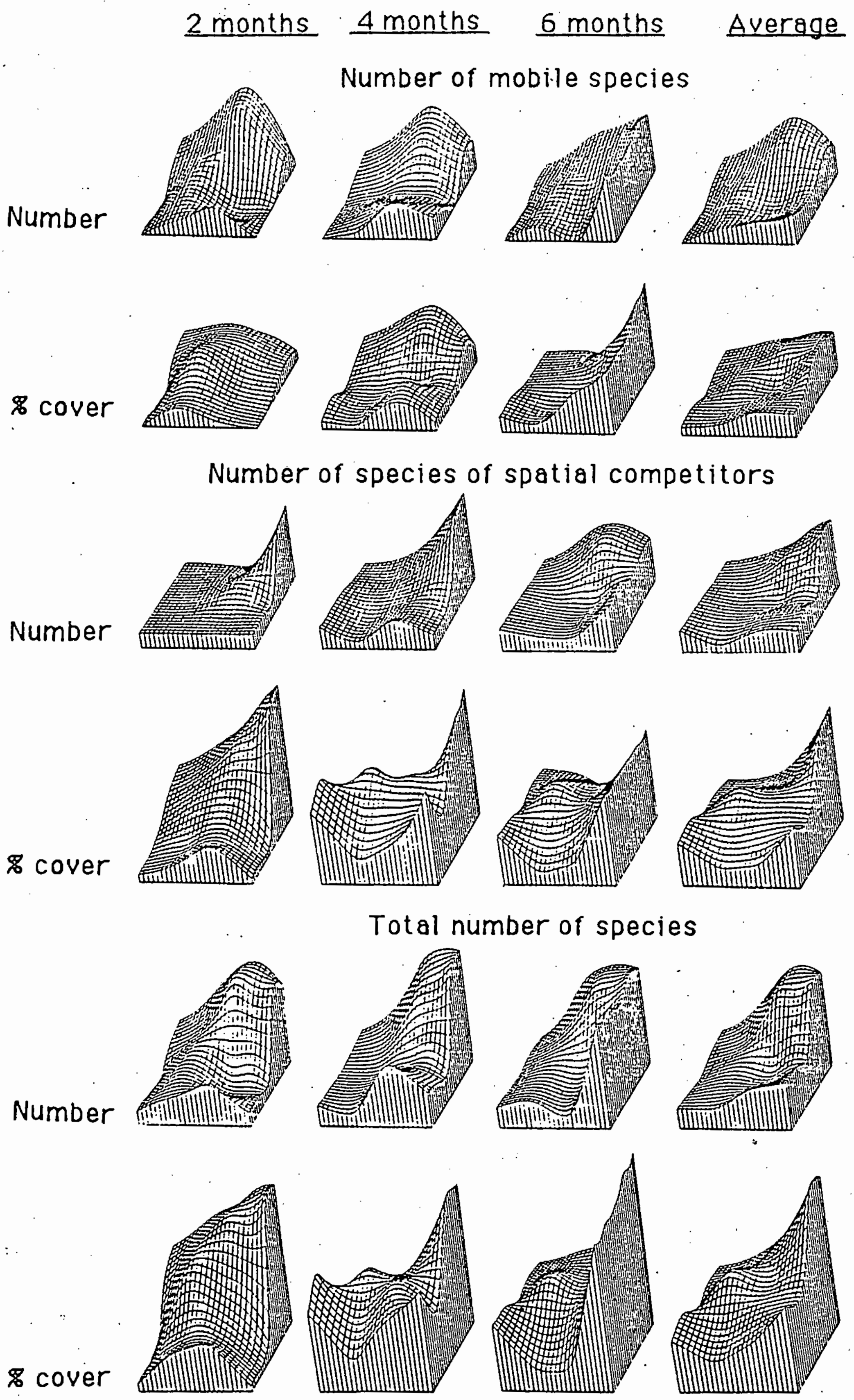
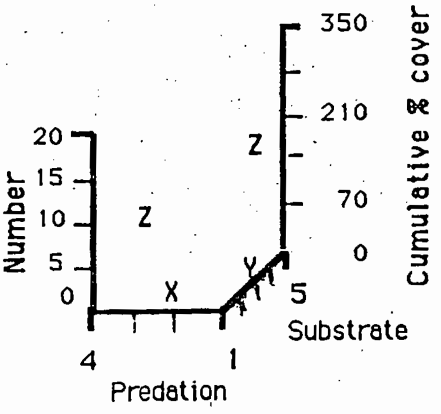


Fig. 3.6

A three dimentional graphic description of table 3.2, in which the x axis represents ranked values for the different levels of predation, rangingfrom 1 (minimal presure) to 4 (maximal presure). The y axis represents different tupes of substratal complexity, ranging from 1 (bare plate) to 5 ("mussels plate"). The dependent variable Z, is number of species and their total precentage cover.



extremes of predation (ie. caged versus uncaged plates at Malgas: ranks 1 and 4 in Fig. 3.6). There are two contrasting reasons for this. The caged plates at Malgas experienced virtually no predation and soon became uniformly covered with mussels and, hence, uniformly complex; comparable and equally rich communities developed on them. Conversely, the uncaged plates were almost immediately stripped of the mussels that had been pre-established on them. Furthermore, virtually everything that subsequently settled on the plates (with the exception of algae) was immediately removed by rock lobster predation, irrespective of the substratal complexity. All the uncaged plates therefore became and remained uniformly impoverished.

By contrast, at intermediate levels of predation (ie. at Marcus Island on caged versus uncaged plates: ranks 2 and 3 in Fig. 3.6) the complexity of the substratum continued to be an important factor enhancing diversity and percentage cover throughout the experiment.

If the species that settle on the plates are subdivided into mobile versus sessile or sedentary species, the picture changes and some of the processes involved are revealed. The diversity and cover of mobile species (Fig. 3.6) increased rapidly at Marcus Island, plates (which were the plates experiencing intermediate levels of predation: ranks 2 and 3 in Fig. 3.6) because of immigration from the surrounding rich community. Early colonisation of plates by mobile species was not possible at Malgas, even when predation was prevented by caging, because of the near-absence of mobile species (other than the rock lobsters). In the later stages of the experiment a few mobile species did accumulate slowly on the protected plates at Malgas, presumely recruited from larval stocks or by immigration from the intertidal community.

Sessile or sedentary species which compete for space and depend on recruitment by larval settling followed a different time course on the two islands (Table 3.2 and Fig. 3.6). Their early recruitment was restricted almost entirely to plates that were protected by cages and which had the greatest surface complexity (ie. the mussel plates within cages at Malgas Island).

At Marcus Island (both inside and outside cages) the recruitment of sessile or sedentary species was much slower, probably because of the rapid incursion of mobile forms which pre-empted space, disturbed the substratum by grazing and predation, and possibly filtered out potential recruits. This interaction between mobile species. (which can move in immediately from the adjacent community) and sessile species (which depend on larval dispersal), adds a new and important dimension to colonisation. Clearly the availability of mobile adults and planktonic larvae, and the accessibility of the plates to both will influence the rate and nature of community development. Branch (1985) has previously argued that the contrasts between mobile and sessile species (in terms of modes of competition, nature of limiting resources and responses to predators or disturbance) are vital to understanding competitive processes in the sea.

There are thus three major factors that influence the communities settling on the plates at Marcus and Malgas Islands: (1) intensity of predation; (2) the effect of substrate complexity on recruitment, and particularly on the early recruitment of sessile species; and (3) the availability of larvae and mobile adults.

GENERAL CONCLUSIONS

Quite clearly the rock lobster *Jasus lalandii* plays the major role in controlling the differences between the two islands; once it is excluded the communities converge as mussels settle and dominate. Similar "keystone" roles have been ascribed to other predators, including starfish (Paine 1969), sea otters (Simenstad et al 1978) and lobsters (Mann and Breen 1972).

In the virtual absence of *J. lalandii* at Marcus Island, mussels establish dense beds and other, often more subtle, interactions become important. For instance, intense grazing by urchins precludes development of dense algae. The mussels themselves increase substrate complexity and are associated with a high diversity and a cover of other species. At least in the early phases of recruitment the mussels facilitate settling of spatial competitors. And, as a final example, *Thyone aurea* appears dependent on *Pentacta doliolum* to gain protection from wave action. There is now increasing realisation that such positive relationships - mutualisms, and direct and indirect commensalisms - play important roles in structuring communities (see, for example, Paine 1974; Duggins 1980; 1981; Steneck 1982; Dethier and Duggins 1984).

I believe that Marcus and Malgas islands represent two alternative stable states (in the sense of Sutherland 1974). Underpinning the stability of the two communities are: the high density of *Jasus lalandii* at Malgas Island and its role as a keystone predator; the preferential recruitment of settling mussels to mussel beds; and the availability of mobile species at Marcus Island - an availability which permits almost immediate reoccupation of bare space when it is created by events such as storms (see also discussion in chapter 2). These islands have maintained their contrasting communities throughout the four years of study despite some record storms during the research period (Chapter 2). The ultimate key to understanding why they have remained alternative states probably lies in answering another question - why rock lobsters have not invaded the food-rich subtidal zone of Marcus Island. In part, this forms the subject of a separate study (Chapter 5).

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CHAPTER 4 - MUSSELS: GROWTH RATE AND MORTALITY

INTRODUCTION

The shallow hard substrate benthic communities of Marcus and Malgas Islands in Saldanha Bay (33^{O}S 18^{O}SE) share somewhat similar physical environmental conditions and yet are extremely different in their sublittoral communities. Marcus Island has a benthic community consisting of dense mussel beds, numerous sea urchins, holothurians and whelks, and many other species associated with the mussel beds. There are, however, very few rock lobsters (*Jasus lalandii*) or seaweeds. Malgas Island, on the other hand has large number of both rock lobsters and seaweeds, but very few mussels and an impoverished benthic fauna.

In previous chapters (Chapter 1 and 2), I compared both qualitatively and quantitatively, some of the biotic and abiotic characteristics of these sublittoral ecosystems. Chapter 3 dealt with mechanisms of recruitment, succession, competition and predation and the relative importance of these at the two islands. In summary, the main assumptions in these chapters were as follows: a) Massive predation on most benthic species by the rock lobster occurs at Malgas Island, and its almost complete absence at Marcus Island, is the main difference shaping these two contrasting benthic communities. b) Although very dynamic in the short term, both ecosystems are stable and consistent in time and space in the long term, so that the two systems represent alternative stable states (sensu Sutherland 1974)

Many ecological studies on benthic communities have used benthic macrofaunal species as indicators of environmental conditions (Field and McFarlane 1968; Dayton 1971; Konnecker 1976; Taylor and Littler 1982; McQuaid and Branch 1984). Filter feeders as a whole, and mussels in particular, have proved efficient and sensitive indicators of local environmental conditions (Roberts 1976; Pickwelll and Steinert 1984; Simkiss and Mason 1984). Moreover, mussels are also widespread, sessile, well investigated and sensitive to a wide range of physical conditions (temperature, wave action, substrate), chemical factors (oxygen, salinity, pollution) and biological interactions (competition for space, predation and food resources) (Black 1973; Yonge 1976; Pickwell and Steinert 1983; Simkiss and Mason 1983: Widdoes et al. 1984).

Mussels of the family Mytilidae are the most abundant bivalves in the rocky shore littoral and sublittoral ecosystems of most continents (Suchaneck 1985). *Choromytilus meridionalis* and *Aulacomya ater* often dominate sublittoral hard substrata on the South African west coast and both play an important role in the trophic web of this environment (Stephenson and Stephenson 1972; Velimirov et al. 1977: Griffiths and King 1979; Field et al. 1980; Griffiths 1981b; Suchaneck 1985).

Preliminary observations on the benthic communities at Marcus and Malgas islands revealed an almost total dominance of the sublittoral region at Marcus Island by *C. meridionalis*, while *A. ater* was almost completely absent. At Malgas Island on the other hand, *C. meridionalis* is completely absent. The few mussels that do exist there are *A. ater*, and they are either hidden under stones or in kelp holdfasts, or of very large size (see Chapter 2 and 6).

The aim of this section of the thesis was to use these two species as comparative indicators in an attempt to understand some of the factors shaping these two presumably stable alternative states of the shallow benthic ecosystem. The characteristics of the two species of mussels were also investigated in an attempt to explain their differential distribution on the two islands. Special attention was paid to the potentially central role of the rock lobster *Jasus lalandii* in determining the structure of the shallow benthic ecosystems of the two islands.

MATERIALS AND METHODS

EXPERIMENTAL METHODS

Two groups of mussels, comprising 600 *Choromytilus meridionalis* and 600 *Aulacomya ater* were collected on the west coast near Cape Town and transferred to the laboratory. Each mussel was tagged with a numbered plastic label which was attached to the shell with a water-resistant epoxy glue.

The mussels were then subdivided into four sub-groups, each consisting of two replicates of 75 mussels. The average size of individuals in each subgroup of each specioes was statistically indistinguishable (~37mm for *C. meridionalis* and ~31mm for *A. ater*) and mussel size in all replicates was normally distributed around the mean.

The tagged mussels were then spread evenly over settlement plates and held in place with soluble nylon bandages (NE 400 white polyamide mussel netting) of the type used in commercial mussel farming operations. The plates were constructed of marine ply and separated by partitions. The bandages enabled the mussels to attach themselves to the plates but dissolved within two days, leaving the mussels attached by their own byssus threads. The plates, together with attached mussels, were then transported in tanks to Saldanha Bay where they were mounted subtidally at Marcus and Malgas Islands at a depth of 10m. The plates were bolted onto a large concete block anchored on the sea bed (see Chapter 3 for details of construction). One group of each of the species was protected from predation by a wire cage while the other group was left unprotected. The plates were removed from the water for inspection after 66, 123 and 189 days, between 7 September 1983 and 12 March 1984. After 189 days, the plates were destroyed by storm so that the experiment could not be continued.

At each inspection, the size and tag number of each mussel was recorded. The position of the mussels was also recorded to determine whether clumping occurred and exhibited any pattern.

Dead tagged mussels in the cages were also measured and checked to see if they had been drilled, to ascertain the relative importance of drilling predators (eg. the dogwhelks *Nucella squamosa* and *N. cingulata*), and whether these predators select prey on the basis of size. $0.33m^2$ quadrats were used to sample dead mussels trapped among living mussels in the natural community adjacent to the cages at Marcus Island. Note was made of mussel size and whether the shells were drilled or not. Only left or right valves were used, depending on which was most abundant. It was impossible to check the extent to which mussels on the uncaged plates were drilled, because most of the dead shells were lost from the plates.

NUMERICAL METHODS

Two-tailed t-tests were used to compare the mean sizes of mussels in different replicates and in different treatments, and test for differences in the sizes of drilled and undrilled dead shells.

To construct growth curves for *C. meridionalis* and *A. ater*, a computer programme, "growth", written by Wickens (1985) was used. In this programme, the time taken for an

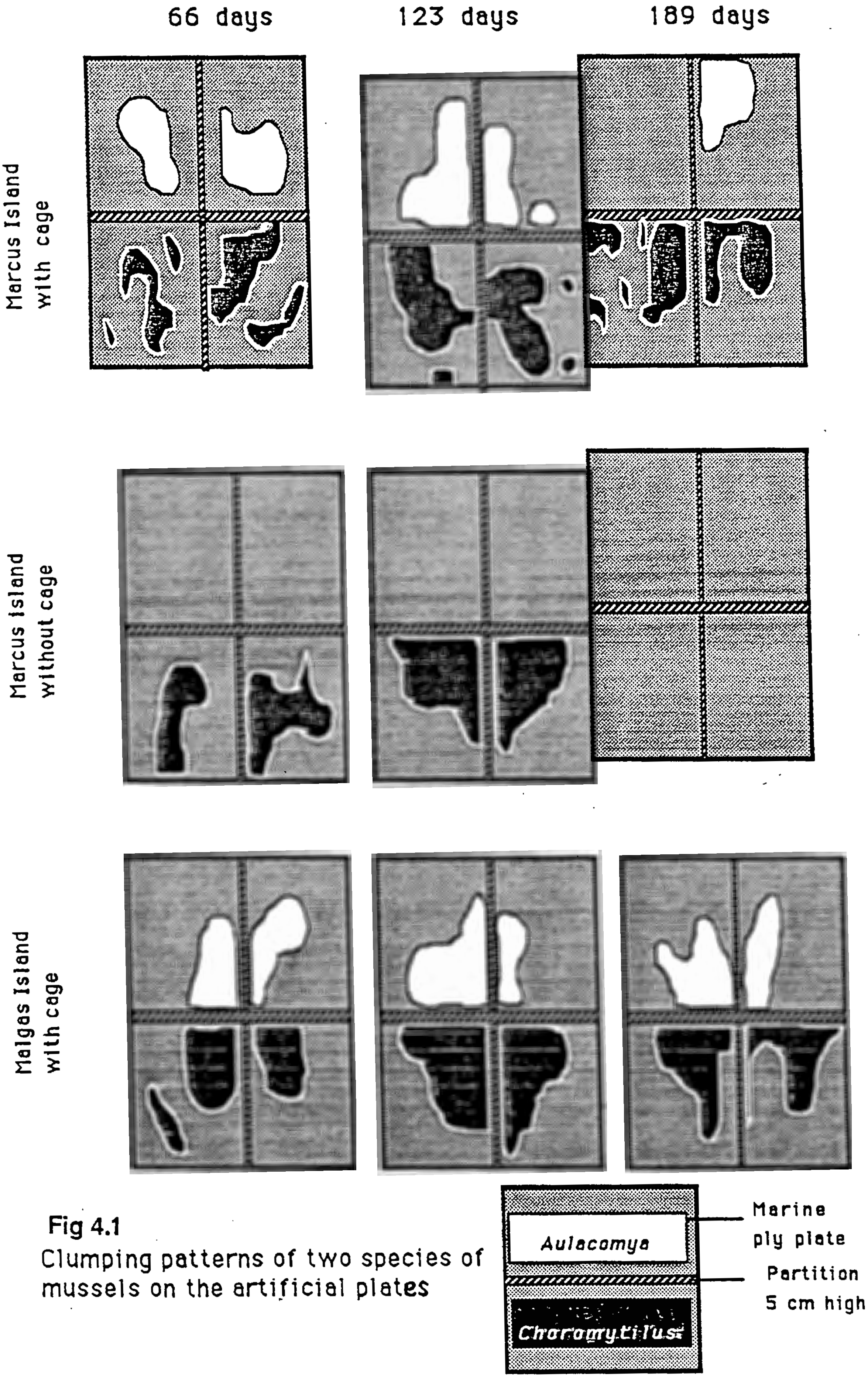

Fig 4.1
Clumping patterns of two species of mussels on the artificial plates

individual to grow through a size class is calculated from the average growth increment of each 5mm size interval. A "BMDP" package (P3R) was used to fit Von Bertalanffy, Gompertz and logistic growth curves to the age-length data obtained from the "Growth" programme. The Von Bertalanffy equation proved the most efficient predictor of growth for both species.

Chi-squared tests were used to test whether the proportions of shells killed by drilling gastropods was equal for both species.

RESULTS

CLUMPING AND OTHER OBSERVATIONS ON THE MUSSEL PLATES.

Some degree of clumping was always apparent with both species of mussel. Although the shapes of the clumps varied from plate to plate, in most cases at least part of the mussel clump was attached to one of the upright partitions (Fig 4.1) which provided them with some means of protection. When protected within cages, *C. meridionalis* formed several smaller clumps which were spread randomly over the plate. Unprotected *C. meridionalis* formed a single large clump in one corner of the plate. The clumps accumulated large amounts of silt, which provided a habitat for many small crustaceans, polychaetes and gastropods. The mussels themselves formed a substratum for many of the common epifaunal benthic species (see Chapter 3).

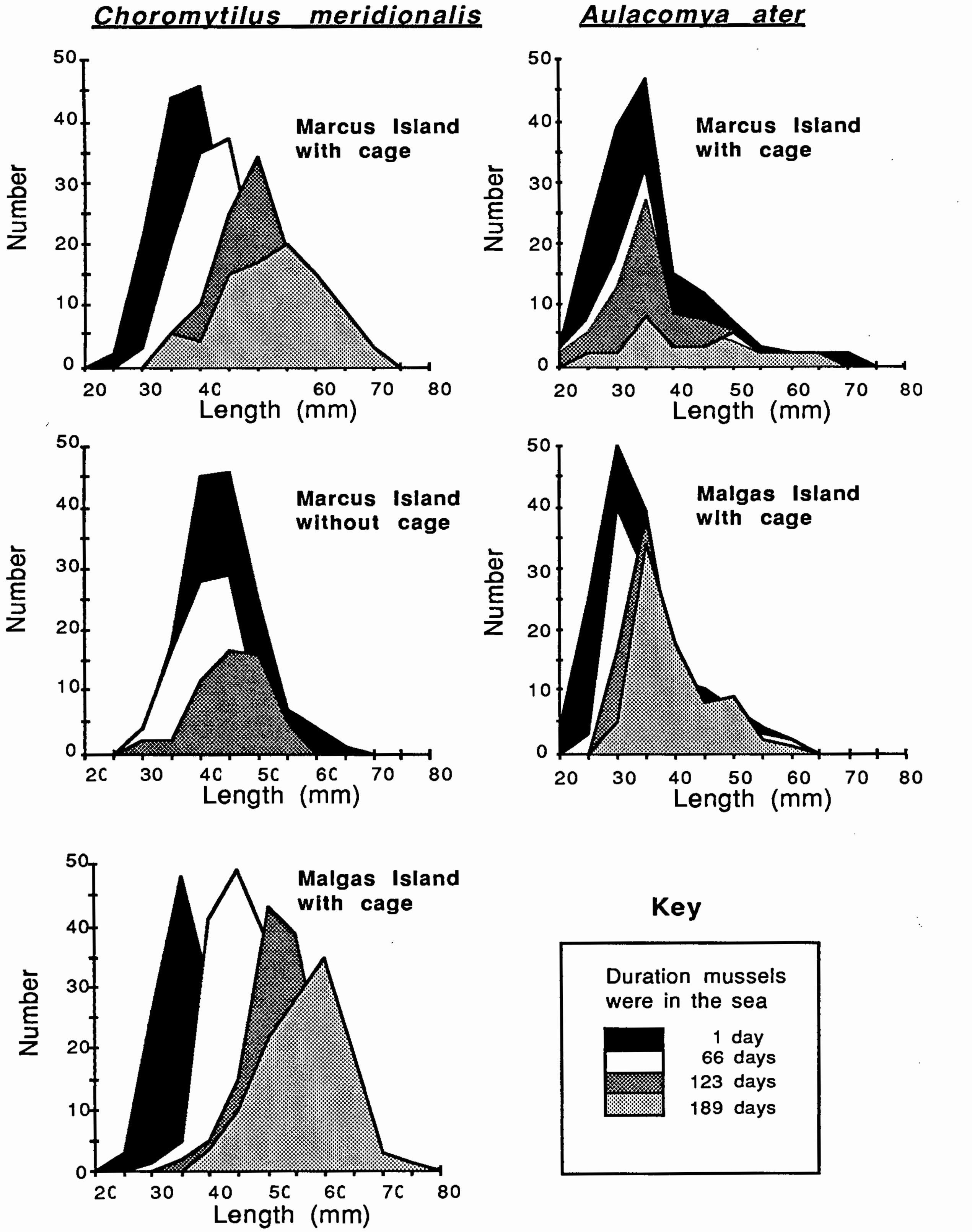

Fig 4.2
Size distribution of tagged mussels (*C. meridionalis* and *A. ater*), at Marcus and Malgas Islands. Half the mussels were protected by cages, while the other half were left unprotected.

MORTALITY

Figure 4.2 and Table 4.1 summarise the initial size distributions and numbers of the two species of mussels in relation to those after 66, 123 and 189 days. At Marcus Island, the mortality rate among caged *C. meridionalis* was 43% over a period of 189 days. Uncaged mussels had a mortality rate of 64% after 123 days (compared with only 31% for the caged mussels) and none of the uncaged mussels survived the whole period of the experiment ie. 189 days.

At Malgas Island, most of the caged *C. meridionalis* survived, only 21% mortality being recorded after 189 days. Of the uncaged mussels, none survived longer than a few hours, as a result of heavy predation by rock lobsters.

No uncaged *A. ater* survived the first 66 days at either island. At Malgas Island they lasted only a few hours due to rock lobster predation. At Marcus Island they survived for a longer period, as indicated by the increased size of some of the empty shells that were found but all of them died within the first 66 days.

Caged *A. ater* suffered heavy mortality before the first inspection at both islands: 48% at Marcus and 37% at Malgas. At Marcus Island high mortality rates continued for the whole duration of the experiment with only 13% of the original 150 mussels being alive after 189 days. At Malgas Island, after the initially heavy losses, the mortality rate

Table 4.1: Mean lengths (mm) of tagged mussels (*Choromytilus meridionalis* and *Aulacomya ater*) at Marcus and Malgas Islands, after time period of 66, 123 and 189 days. Fig. 4.2 shows the size distributions of these mussels.

Choromytilus meridionalis

	Marcus island				Malgas Island	
	Caged		Uncaged		Caged	
	N	Mean±s.d	N	Mean±s.d	N	Mean±s.d
0 day	150	37.2±7.5	150	36.4±6.2	150	36.1±6.9
66 days	121	41.0±6.7	89	39.1±5.7	144	42.9±5.3
123 days	104	46.8±6.7	54	42.8±5.8	123	49.8±5.6
189 days	86	50.7±8.2	0	______	119	54.0±7.0

Aulacomya ater

	Marcus island		Malgas Island	
	Caged		Caged	
	N	Mean±s.d	N	Mean±s.d
0 day	150	32.5±7.5	150	30.9±6.8
66 days	78	34.0±8.2	95	32.5±6.5
123 days	69	34.5±8.5	83	34.4±6.1
189 days	19	34.3±7.7	77	36.9±6.4

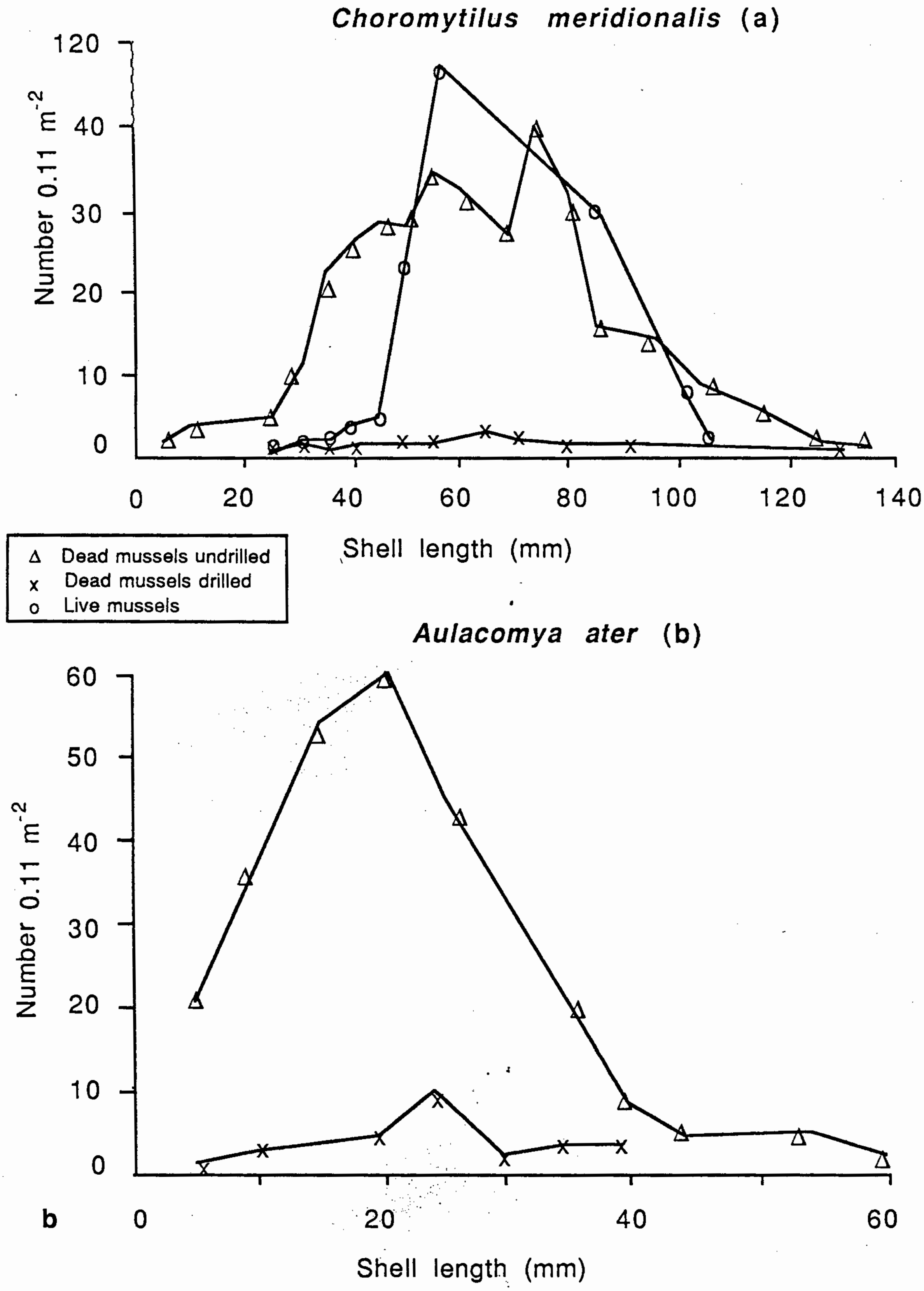

Fig. 4.3

Size distribution of dead and live mussels (*C. meridionalis* and *A. ater*), in the natural mussel beds at Marcus Island. The dead mussels are subdivided into those that were drilled and those that were not. No live *A. ater* were found in the sample.

dropped. Of those that survived the first two months, 81% were alive at the end of 6 months. A. ater was sensitive to the tagging procedure, and the initially heavy mortalities at both islands are considered to be due to this fact.

Causes of mussel mortality were in most cases very difficult to determine. Two causes, however, were obvious. Firstly, at Malgas Island the uncaged mussels were observed being eaten by rock lobsters. Secondly, at Marcus Island, small holes in some of the shells indicated that the mussels had been preyed upon by one of the drilling welks common to the area (most of which are *Nucella squamosa*).

None of the dead mussels found at Malgas Island was ever drilled. In contrast, at Marcus Island a large portion of the dead mussels of both species were drilled. In the extreme case, 83% of dead *C. meridionalis* and 45% of dead *A. ater* were drilled (Table 4.2, 66 days). For the entire duration of the experiment, averages of 58% of the dead *C. meridionalis* and 34% of the dead *A. ater* were drilled. A sample of dead mussels from the natural mussel population at Marcus Island revealed that only 7% of *C. meridionalis* and 9% of *A. ater* had drill marks (Fig 4.3). (Live *A. ater* are almost non-existent sublittorally at Marcus Island so it is possible that these shells might have come from the littoral zone.) A chi-squared test showed that in most cases the proportion of drilled *C. meridionalis* was significantly higher than that of *A. ater* in the experimental samples

Table 4.2: Mean size (mm) of dead and live mussels from the caged plates at Marcus Island, after 66,123 and 189 days, and of mussels from the natural mussel beds at Marcus Island. The dead mussels are subdivided into those that were drilled and and those that were not. Means which are joined by a vertical line are significantly different (t-test, P ≤ 0.05). Asterisks indicate significant differences between the two species in the proportions of shells drilled (chi-squared test, P ≤ 0.05).

Marcus Island

	66 days		**123 days**		**189 days**	
	N	Mean±s.d.	N	Mean±s.d.	N	Mean±s.d.
Experiment						
C. meridionalis						
Alive	121	41.1±6.7	104	46.8±6.7	86	50.7±8.3
Total dead	12	36.7±7.0	5	43.5±6.7	9	46.6±6.5
Not drilled	2	31.1±9.1	2	40.2±3.7	7	45.1±6.6
Drilled	10	37.8±5.3	3	45.7±8.0	2	51.8±1.2
% drilled	83.3*		60.0		22.2*	
A. ater						
Alive	78	34.0± 8.2	69	34.5± 8.5	19	34.3±7.7
Total dead	33	31.7± 9.8	10	35.3± 9.3	28	36.2±8.5
Not drilled	18	35.2±11.2	6	37.1± 8.6	23	36.6±9.0
Drilled	15	27.6± 5.6	4	32.7±10.9	5	34.5±6.1
% drilled	45.5*		40.0		17.9*	

Natural	N	Mean±s.d.
C. meridionalis		
Alive	529	75.4±13.7
Total dead	369	64.1±21.1
Not drilled	346	64.5±21.5
Drilled	23	58.9±22.1
% drilled	6.2	
A. ater		
Total dead	323	23.5±10.8
Not drilled	296	23.4±11.1
Drilled	27	24.2± 9.9
% drilled	9.1	

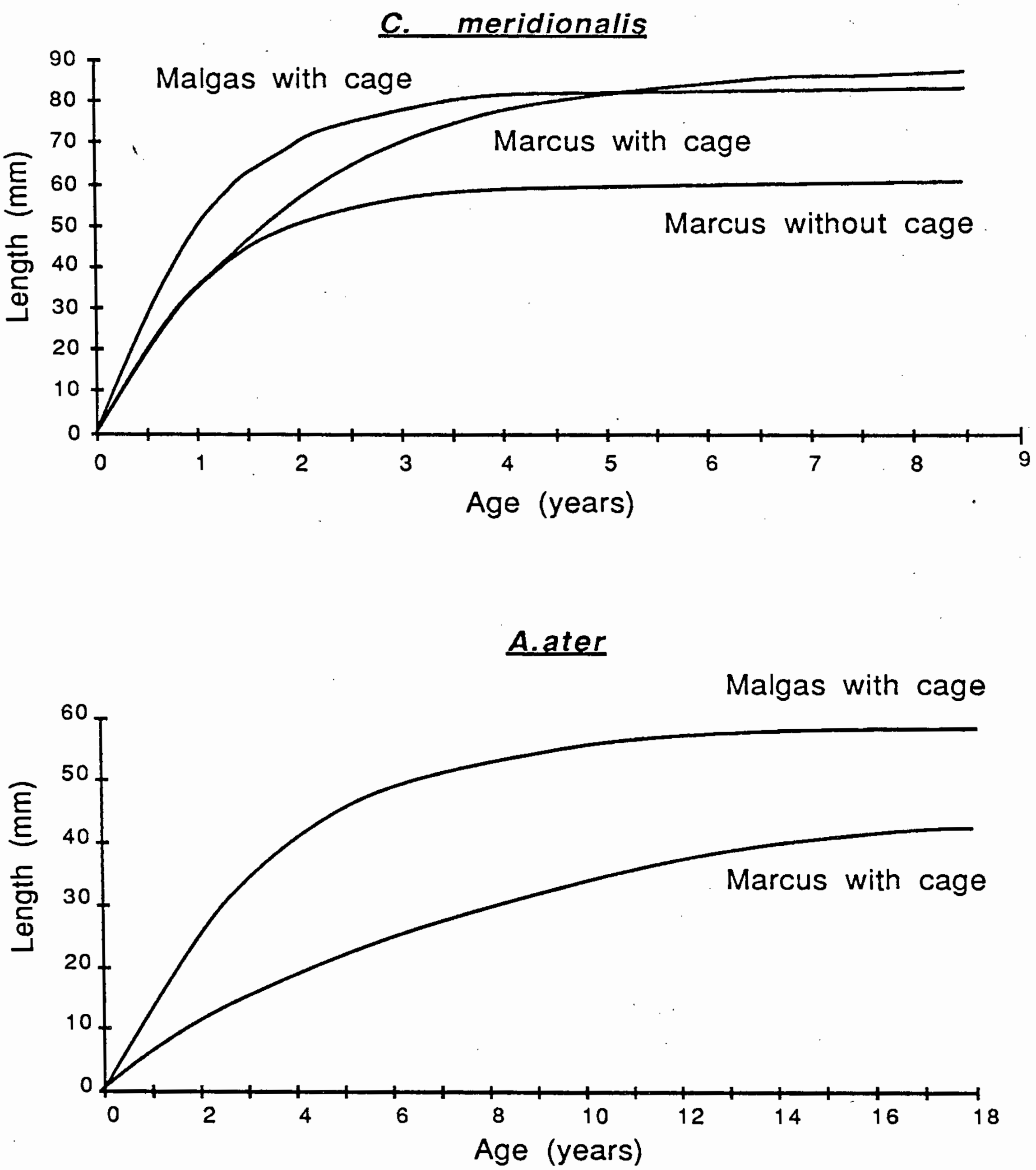

Fig. 4.4
Growth curves of *Choromytilus meridionalis* and *Aulacomya ater* under different experimental conditions at Marcus and Malgas Islands. The curves are described by Von Bertalanffy growth equations:

$L_t = L_{max}\,[1 - e^{-k(t-t_0)}]$; where t= age (years), L= length (mm).

	C. meridionalis			*A. ater*		
	Lmax(mm)	**K**	**to**	**Lmax**(mm)	**K**	**to**
Marcus caged	87.49	0.58	0.20	50.65	0.10	-0.83
Marcus uncaged	60.38	0.96	0.08	_._	_._	_._
Malgas caged	82.77	0.98	0.55	58.41	0.31	0.03

(Table 4.2). The same test applied to a sample from the natural population, however, revealed no significant difference between the species (chi-square test, P>0.05).

In both species most of the drilled mussels on the plates were similar in size to the drilled mussels in the natural population (Table 4.2).

GROWTH RATE

At Marcus Island the average size of caged *Choromytilus meridionalis* changed from 37.14mm to 50.70mm over the 189 days of the experiment ie. an average monthly growth increment of 2.37mm. Uncaged mussels at Marcus Island grow significantly slower (Table 4.3) and, from an initial average of 36.37mm, reached an average size of 42.86mm after 123 days (compared to 46.78mm for caged mussels after the same time period). This represents an average monthly growth increment of 1.58mm. At Malgas Island the overall growth of *C. meridionalis* was significantly faster than that of either the caged or uncaged mussels at Marcus Island (Table 4.3). The average size changed from 36.12mm to 54.04mm over 189 days, representing an average monthly growth increment of 2.84mm. On the basis of the growth data in Table 4.4, the Van Bertalanffy growth equations (Fig. 4.4) predicted similar maximum lengths for caged *C. meridionalis* at Marcus and Malgas Islands. However, the growth coefficient K, which indicates the speed with which the mussels reach Lmax, was

Table 4.3: T-tests comparing mean sizes of the tagged mussels (*Choromytilus meridionalis* and *Aulacomya ater*) at the two localities (Marcus and Malgas Islands) with two treatments (with and without cages). (N.S= no significant difference in mean length; $s^{*} = p \leq 0.05$; $s^{**} = p \leq 0.01$; $s^{***} = p \leq 0.001$; dashes indicate lack of data)

	C. meridionalis				***A. ater***			
Days in sea:	0	66	123	189	0	66	123	189
Treatments								
Marcus caged vs Marcus uncaged	N.S	S*	S***	—	—	—	—	—
Marcus caged vs Malgas caged	N.S	S*	S***	S**	N.S	N.S	N.S	N.S
Marcus uncaged vs Malgas caged	N.S	S***	S***	—	—	—	—	—

Table 4.4: Average growth increments (mm per month) *C. meridionalis* and *A. ater* at Marcus and Malgas Islands.

Choromytilus meridionalis

	Marcus caged		Marcus uncaged		Malgas caged	
Size classes (mm)	N	Mean±s.d.	N	Mean±s.d.	N	Mean±s.d.
20-25	__	_______	2	1.18±0.39	1	4.13
26-30	18	2.35±1.26	12	1.64±0.77	18	4.26±0.69
31-35	53	2.19±1.58	35	2.20±1.35	48	3.86±1.29
36-40	74	2.35±1.45	51	1.77±1.30	67	3.05±1.54
41-45	70	2.06±1.68	30	1.35±1.31	87	3.01±1.62
46-50	49	1.65±1.58	7	0.86±1.03	80	2.31±1.67
51-55	30	2.11±1.55	6	0.39±0.82	43	2.18±1.57
56-60	12	1.56±1.13	_	_______	22	2.63±1.55
61-65	3	1.40±1.92	_	_______	5	1.82±1.47
65-70	2	0.90±0.82	_	_______	1	2.73

Aulacomya ater

	Marcus caged		Malgas caged	
Size classes (mm)	N	Mean±s.d.	N	Mean±s.d.
20-25	15	0.39±0.63	17	1.31±0.55
26-30	33	0.13±0.25	78	0.84±0.63
31-35	64	0.08±0.17	84	0.67±0.60
36-40	18	0.17±0.31	29	0.67±0.56
41-45	16	0.03±0.07	19	0.44±0.61
46-50	7	0.05±0.07	20	0.20±0.42
51-55	5	0.01±0.08	_	_______
56-60	2	0.04±0.02	3	0.24±0.32
61-65	2	0.05±0.21	_	_______

almost twice as large at Malgas Island than at Marcus Island (0.98 and 0.58 respectively). Lmax for the uncaged *C. meridionalis* at Marcus Island (60.38mm) was much smaller than for the caged mussels (87.49mm) (see table in Fig. 4.4).

The average size of caged *Aulacomya ater* at Marcus Island changed from 32.54mm to 34.30mm in 189 days ie. 0.28mm per month (Fig. 4.2, Table 4.1). This figure is considerably smaller than that for Malgas Island, where the average size changed from 30.87mm to 36.93mm after 189 days, ie. an average monthly increment of 0.96mm (Table 4.1). This difference in growth rate is reflected in the parameters of the Von Bertalanffy growth equations (Fig 4.4). For caged *A. ater* at Marcus Island Lmax was 50.65mm and K only 0.1, whereas the same parameters for the caged mussels at Malgas Island were 58.41mm and 0.31 respectively. It is also significant that *A. ater* grew at a much slower rate than *C. meridionalis* in all cases.

DISCUSSION

MORTALITY

The sublittoral zone at Malgas Island supports no adult *Choromytilus meridionalis* and very few *Aulacomya ater*, because the rock lobster *Jasus lalandii* continually prevents successful settlement [although small number of very large *Aulacomya ater* can be found in unprotected situations at

Malgas Island (see chapters 2 and 6)]. When plates were introduced to Malgas Island with pre-established mussels growing on them, the mussels were almost immediately stripped off by the rock lobsters. If protection was provided in the form of cages, however, both species survived at Malgas Island for the full duration of the 6-month experiment.

Causes of mussel mortality within cages at Malgas Island are difficult to determine. The complete absence of predators that eat small mussels points to silt accumulation and at a latter stage (after 6 months), smothering by further mussels recruits and other sessile species (see chapter 3) as being major source of mortality, causing anoxia as well as preventing food from reaching the buried mussels (Seed 1976; Taylor and Littler 1982: Suchaneck 1985; Chapter 3).

At Marcus Island in the absence of rock lobsters, uncaged *C. meridinalis* survived for at least few months. The cause of their eventual disappearance is unknown. *A. ater*, however, was found to be extremely sensitive to the accumulation of silt and to smothering by benthic organisms, and its survival rate was very low whether they were caged or uncaged. Uncaged *A. ater* were rapidly covered by slow-moving but mobile species, particularly the holothurians and urchins and, although they survived long enough to increase in size, died within 66 days. Survival inside cages was higher, presumably because the cages excluded these large mobile species and the process of smothering retarded. Even *C. meridionalis*, which is very tolerant of anoxia (Currie and Cook 1975) and more capable of coping with silt and overgrowth by other species, suffered heavy mortality because of smothering by the high density of the sublittoral fauna at Marcus Island. As in the case of *A. ater*, survival of *C. meridionalis* was lower for uncaged mussels than for caged mussels, probably for similar reasons.

In the absence of predators, *A. ater* is an inferior competitor to *C. meridionalis* (see chapters 2 and 3), particularly in sand-abraded areas (Griffiths 1981b). In part this is because of its slower growth. However, *C. meridionalis* is more vulnerable to predation due to its weaker shell and weaker attachment (Griffiths & Seiderer 1980). As a result, *A. ater* often dominates large sections of the sublittoral zone where *Jasus lalandii* is present, whereas *C. meridionalis* is virtually absent from such areas (Griffiths 1977; Field et al. 1980). *C. meridionalis*, on the other hand, is prevalent in habitats which are less accessible to predators, or in areas where predators such as *Jasus lalandii* are absent.

At Malgas Island the rock lobster *J. lalandii* has displaced most other mussel predators, with the exception of *Octopus granulatus* which apparently preys on both rock lobsters and mussels.

In particular drilling whelks do not appear to contribute to mussel mortalities at Malgas Island: indeed, none of the dead tagged mussels found there had drill marks.

At Marcus Island drilling gastropods are a major source of mortality. The cages protecting the tagged mussels did not prevent entry by juvenile whelks, mostly *Nucella squamosa*, which is the most abundant of the sublittoral drillers at this island (Chapters 2 and 3).

Drilling whelks are found the world over in association with mussel communities and are regarded as major mussel predators, in some cases controlling the mussel population size and zonation pattern (Seed 1976; Griffiths, 1981a; Wickens and Griffiths 1985). During the present experiment, both species of mussel were more vulnerable to drilling whelks when they were caged, than in the natural populations: 18% to 83% of the experimental mussels were depredated by drilling whelks compare with only 7% to 9% of the mussels in the natural sublittoral community (Table 4.2 and Fig. 4.3) and 1.3% for littoral mussel populations (Wickens and Griffiths 1985). This drastic difference may have been due to the particular vulnerability of the experimental mussels immediately after they were replaced in the water subsequent to each inspection. Only a while after each inspection did clumping take place, and subsequent accumulation of silt and secondary settlement of other

Table 4.5: Review of different growth rates (mm per month) of *Choromytilus meridionalis* and *Aulacomya ater* from different localities.

AGE (Months):	3	6	9	12	15	18	21	24
				Choromytilus meridionalis				
LOCATION								
Malgas [1*] (caged)	9.07	7.10	5.56	4.35	3.40	2.66	2.09	1.63
Marcus [1*] (caged)	4.11	3.55	3.07	2.66	2.30	1.99	1.72	1.49
Marcus [1*] (uncaged)	4.10	3.23	2.54	2.00	1.57	1.24	0.97	0.76
Table Bay [2] (Melkbosstrand)	4.64	4.15	3.71	3.31	2.96	2.65	2.37	2.12
Table Bay[3] (Bloubergstrand)	2.02	2.01	2.00	2.00	1.99	1.98	1.98	1.97
False Bay [2] (Dalebrook)	2.21	1.89	1.62	1.39	1.19	1.02	0.87	0.74
False Bay [2*] (Bailey's cottage)	1.25	1.20	1.15	1.11	1.07	1.03	0.99	0.95
				Aulacomya ater				
Malgas [1*] (caged)	1.41	1.30	1.21	1.12	1.03	0.96	0.89	0.82
Marcus [1*] (caged)	0.38	0.37	0.36	0.35	0.34	0.33	0.33	0.32
Combined data[4**]								
Slowest	0.42	0.41	0.41	0.40	0.39	0.39	0.38	0.38
Fastest	0.82	0.80	0.77	0.75	0.72	0.70	0.68	0.65
Overall average	0.78	0.75	0.73	0.71	0.69	0.67	0.65	0.63

Source

1- Present work
2- Griffiths (1981)
3- Currie and Cook (1975)
4- Wickens (1985)

* - Sublittoraly

** - Combined data for *Aulacomya ater* from four different localities and sources.

organisms may result in a decreased vulnerability to drilling gastropod.

The whelks tended to drill *Choromytilus meridionalis* that were larger than the average size of the mussels that died, while attacking *Aulacomya ater* that were smaller than the average size in each sample (Table 4.2). This may be a reflection of the thicker shells possessed by *A. ater*. In the natural population at Marcus Island *C. meridionalis* reaches a much larger size than was avaiable within the cages, and there the drilling whelks fed on mussels that were smaller than the average size (Table 4.2). Drilling whelks are selective and will, if possible, choose prey yielding the greatest return per unit time. Very large mussels may, however, be unprofitable because their thick shells increase the time required to drill through the shell (Paine 1965; Harger 1972; Griffiths 1981b; Hughes and Dunkin 1984; Wickens and Griffiths 1985).

GROWTH RATE

Griffiths (1981b) and Wickens (1985) have reviewed most of the recent studies on the growth rates of *C. meridionalis* and *A. ater* at various localities on the South Africa coast. The results from these sources, together with those from the present research, are compared in Table 4.5. The growth rate is easiest to compare in the early stages of the growth curve, since in all cases the actual data obtained for mussel growth are from young individuals.

Provided they were protected inside cages, mussels of both species grew much faster at Malgas Island than any of the other mussels populations on the west coast for which data are available, including those at Marcus Island (Table 4.5).

At Marcus Island *C. meridionalis* tended to grow faster inside the cages than out of them, but both rates were similar to those recorded at Melkbosstrand on the west coast and much faster than in any other population. On the other hand, *A. ater* grew considerably slower in cages at Marcus Island than in any other population for which growth rate has been recorded.

Growth rate and survival rate of a species are indicators of the suitability of an environment. Both species of mussel grew faster and to a larger size and had higher survival rates when caged at Malgas Island, compared with either caged or uncaged mussels at Marcus Island. Clearly the physical environment and availability of food at Malgas Island are suitable for the mussels and their absence or sparcity at the island cannot be attributed to either of these factors. The high growth and survival rates in cages at Malgas must, however, be partly due to the absence of many of the spatial competitors and of most of the scavengers and drilling whelks which are so abundant at

Marcus Island. On the other hand, the uncaged mussels at Malgas Island were immediately consumed by rock lobsters.

At Marcus Island, *C. meridionalis* grew faster when protected by a cage than when unprotected, because of the exclusion of many of the species that smother it in the natural environment. Its fast growth may explain how it survives under such conditions of intense competition, while *A. ater* is outcompeted and eliminated.

CLUMPING

The habit that many mussel species have of clumping is well known but has hardly been investigated. Most popular explanations for this behaviour are derived from work conducted on intertidal mussel populations. Protection from desiccation, predation and wave action are the most widely accepted explanations (Dayton 1971: Harger and Landenberger 1971: Seed 1976; Suchanek 1985;).

Desiccation does not influence sublittoral communities and is not relevant to this work. However, the fact that clumping does occur among sublittoral as well as littoral mussels may suggest that its primary function is not to avoid desiccation. The fact that most of the clumps were formed near to the vertical partitions on the plates, and that more broken patchy clumps were formed by caged mussels (Fig. 4.1) may suggest that clumping provides protection from wave action. However, as discussed previously (Chapter 2), large, layered clumps of mussels are in fact more easily washed loose by waves (see also Dayton 1971; Paine and Levin 1981). Harger and Landenberger (1971) similarly found that smaller clumps are more firmly attached to the substratum than larger clumps. Harger (1970a) also found that mussels from quiet areas tended to create larger clumps than those in rougher environments. The observations that *C. meridionalis* forms a single-layered sheet on the rock face in shallow waters, but multiple layers in deeper, calmer waters (Chapter 2) supports Harger's findings. It may well be more correct to say that clumping occurs in spite of wave action rather than because of wave action.

Clumps of mussels accumulate large quantities of silt and are also favoured as a substratum by many other benthic species. The result is a reduction in the water circulation in and around mussel clumps. In large clumps, the inner mussels may also be covered by further layers of mussels, thus increasingly limiting their access to the surrounding water (Harger 1970b; Griffiths 1981b; Chapter 2).

In relation to this, clumping appears to have only adverse effects. Predation is thus the only factor left which may explain clumping behaviour. However, Harger and Landenberger (1971) found that large clumps of mussels (*Mytilus edulis* and *M. californianus* are more vulnerable than small clumps to the starfish *Pisaster ochraceus* and, probably, to other relatively large predators such as octopus, crabs, rock lobster and dogfish, which can more easily remove the looser mussels present in large clumps than the more firmly attached mussels in smaller clumps. Large loose clumps do, however, afford protection from one particular group of predators, the drilling whelks. Within clumps, only a small part of each mussel shell is accessible to the whelks, and siltation and overgrowth may further decrease the accessibility of the mussels to whelks. It is also possible that whelks cannot easily attach themselves to the exposed surface of a silted clump of mussels. Of course large clumps also reduce the probability of on individual mussel becoming a target for predation.

OVERVIEW

The results of this experiment proved that Malgas Island is physically suitable for mussel growth. The mussels cannot, however, survive there because of heavy predation by rock lobsters. On the other hand if they are provided with protection, their survival and growth rates at Malgas Island are higher than at Marcus Island, because smothering by other benthic species is minimal, and there are few other predators such as drilling whelks.

At Marcus Island, - in the absence of the massive predator population which characterises Malgas Island, environmental conditions such as siltation, smothering, wave action and inter-and intra-specific competition become much more important and influence the population dynamics of the mussels themselves.

Choromytilus meridionalis, is more vulnerable to rock lobster predation than *Aulacomya ater* but is a better spatial competitor and can tolerate harsher environmental conditions. Both species recruit to both islands. *C. meridionalis* survives the intensely competitive situation at Marcus Island whereas it is excluded from Malgas Island by intense rock lobster predation. *A. ater*, on the other hand fails to reach sexual maturity at Marcus Island, but small numbers do survive at Malgas and reach a size at which they are immune to the rock lobsters. In both instances, it appears as if biotic interactions (competition at Marcus Island, predation at Malgas) dictate which species prevails.

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CHAPTER 5 - REVERSAL OF ROLES BETWEEN A MARINE BENTHIC PREDATOR AND ITS PREY

INTRODUCTION

Perhaps the most conspicuous feature of shallow subtidal communities on hard substrata is the high degree of spatial variability of both species composition and standing stocks (Sousa et al. 1981; Connel and Keough 1985; Dayton 1985; Hiscock 1985). One of the most extensively studied and important causes of spatial variability is the localised effect of predation, including grazing (Luckens 1975; Garrity and Levings 1983; Tegner and Levin 1983; Dayton et al. 1984; Fairweather at el. 1984; Penney and Griffiths 1984; Hughes 1985; Thayer 1985), and several cases have been described of "keystone predators" which maintain a balance within the overall community between their preferred prey and species which are competitively dominated by these prey species (Mann and Breen 1972; Simenstad et al. 1974; Paine 1980). The role of predation as a driving force in the development and maintainence of alternate state communities has already been established (Simenstad et al. 1974; Sutherland 1974). However, I believe that the present paper is the first report of a prey species which has effectively exchanged roles with its chief predator and proved capable of maintaining a fundamentally different and stable community structure through the exclusion of that predator. Moreover the relationship between these two species was found to be mediated by a third species, symbiotic on the 'prey'.

This study is also relevant to the extreme contrast between the subtidal benthic communities surrounding two adjacent islands, Marcus and Malgas which lie 4 km apart in the Saldanha Bay area of South Africa (17°58'E:33°02'S). Apart from normal patchiness, the two communities are radically different in the trophic levels which dominate the biomass and, consequently, in the patterns of energy flow (Chapter 2).

The rock lobster *Jasus lalandii* is a ubiquitous, commercially fished top predator in kelp beds off the west coast of southern Africa (Field et al. 1977; Velimirov et al. 1977) and appears to function as a keystone species within this ecosystem. *J. lalandii* has been studied in some detail and consumes several prey species (with a preference for mussels), as well as scavenging (Heydorn 1969; Newman and Pollock 1974; 1979; Seiderer et al. 1982). Both of the islands studied lie within a rock lobster reserve and differences in physical conditions are slight or of a nature that cannot explain why the rock lobster is abundant at Malgas Island but conspicuously absent from Marcus Island (Chapters 1 and 2). Communities around the latter island are dominated by extensive beds of black mussels (*Choromytilus meridionalis*) as well as large populations of holothurians, sea urchins and especially whelks. Drilling whelks belonging to several species of *Nucella* are common but the majority of the whelks are scavengers: *Burnupena papyracea, B. limbosa* and *B. cincta* all occur in exceptionally high numbers. In contrast, communities around Malgas Island are dominated by extremely high densities of rock lobsters, which form approximately 70% of total faunal biomass, while most of its normal prey species are absent. Only two species of whelks occur there: *B. papyracea* and *Argobuccinum pustulosum*. The primary problem I wished to resolve was: why do these two islands support such different communities and which species are important in maintaining these two apparently alternate states?

METHODS AND RESULTS

SAMPLING

Initial quantification of species composition and biomass at the two islands was carried out as part of a broader project using SCUBA apparatus. Large, mobile species, including rock lobsters, were quantified using a series of belt transects running perpendicular to the shore, while smaller and sedentary species were sampled using quadrats (see Chapter 1 Fig. 1.1a). Only two species of whelks were recorded at Malgas Island, and total whelk densities were much lower than at Marcus Island (Table 5.1).

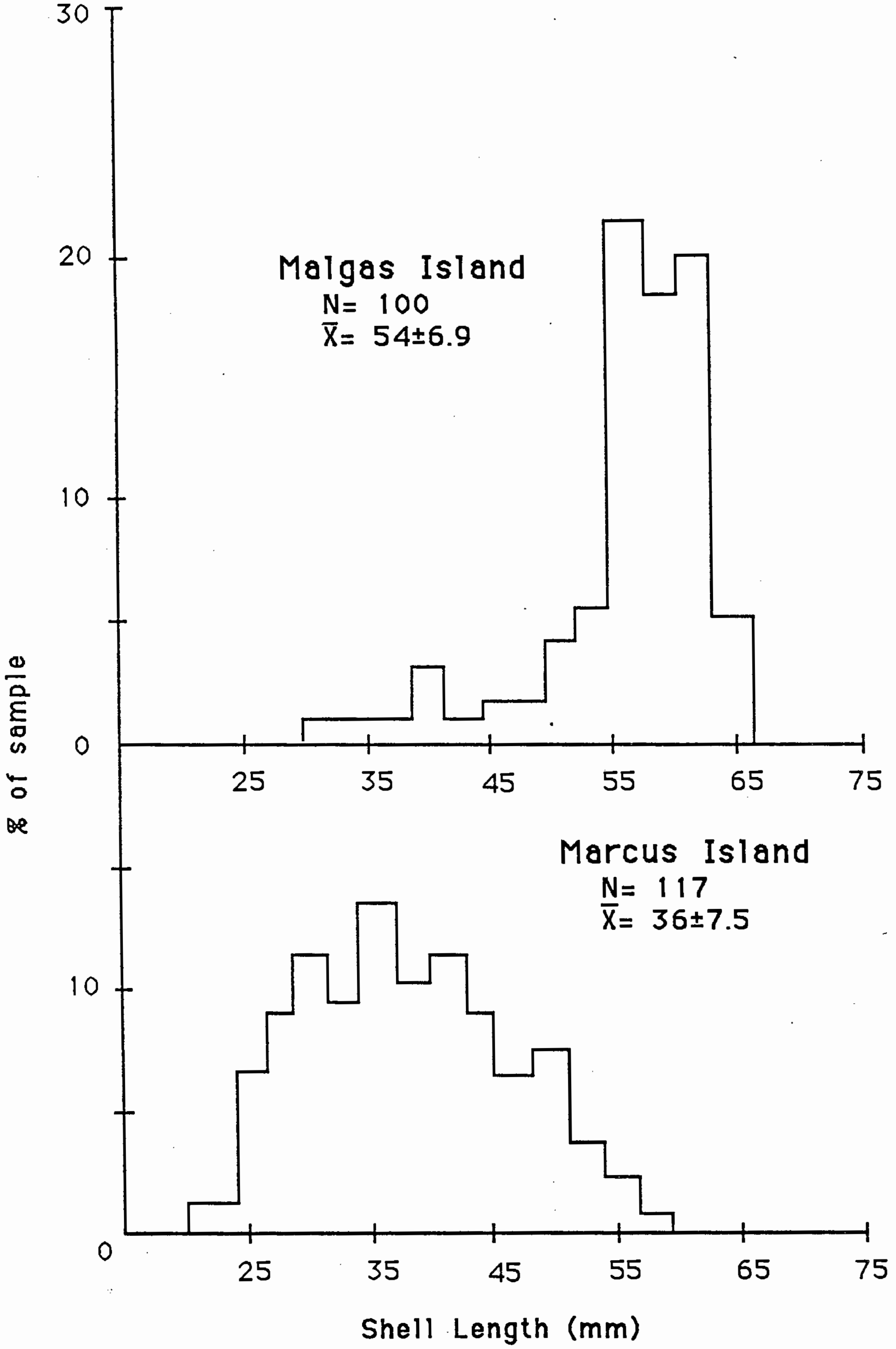

Fig 5.1
Size distribution of *Burnupena papyracea* at Malgas and Marcus Islands.

Table 5.1: Number of whelks species (m^{-2}) at Marcus and Malgas Islands.

Species	Marcus		Malgas	
	N	s.e.	N	s.e.
Argobuccinum pustulosum	12	6.1	40	8.5
Burnupena papyracea	141	4.1	14	4.7
Burnupena cincta	77	3.1	--	--
Burnupena limbosa	59	7.7	--	--
Total	289		54	

Burnupena papyracea, which occurs at both islands, exhibited a different size distribution at the two sites. Fig.5.1 shows that at Malgas Island where density was lower, average shell length (54mm, 6.9 s.d.) was significantly greater compared to Marcus Island [(average shell length 36mm, 7.5 s.d. (t-test P < 0.001)]().

ROCK LOBSTER FEEDING

Twelve rock lobsters (average carapace size 77mm s.d. 5.4mm) captured at Malgas Island were placed in individual aquaria in the laboratory and offered mussels (*Aulacomya ater* and *Choromytilus meridionalis*, ranging from 30 to 90 mm in shell length) and whelks (*Burnupena* spp. and *Argobuccinum pustulosum*, ranging from 20 to 65 mm shell length). Although mussels were first to be eaten by the rock lobsters, whelks (*Burnupena spp.*) were also eaten, usually by chipping away the margin of the shell. This method of feeding results in

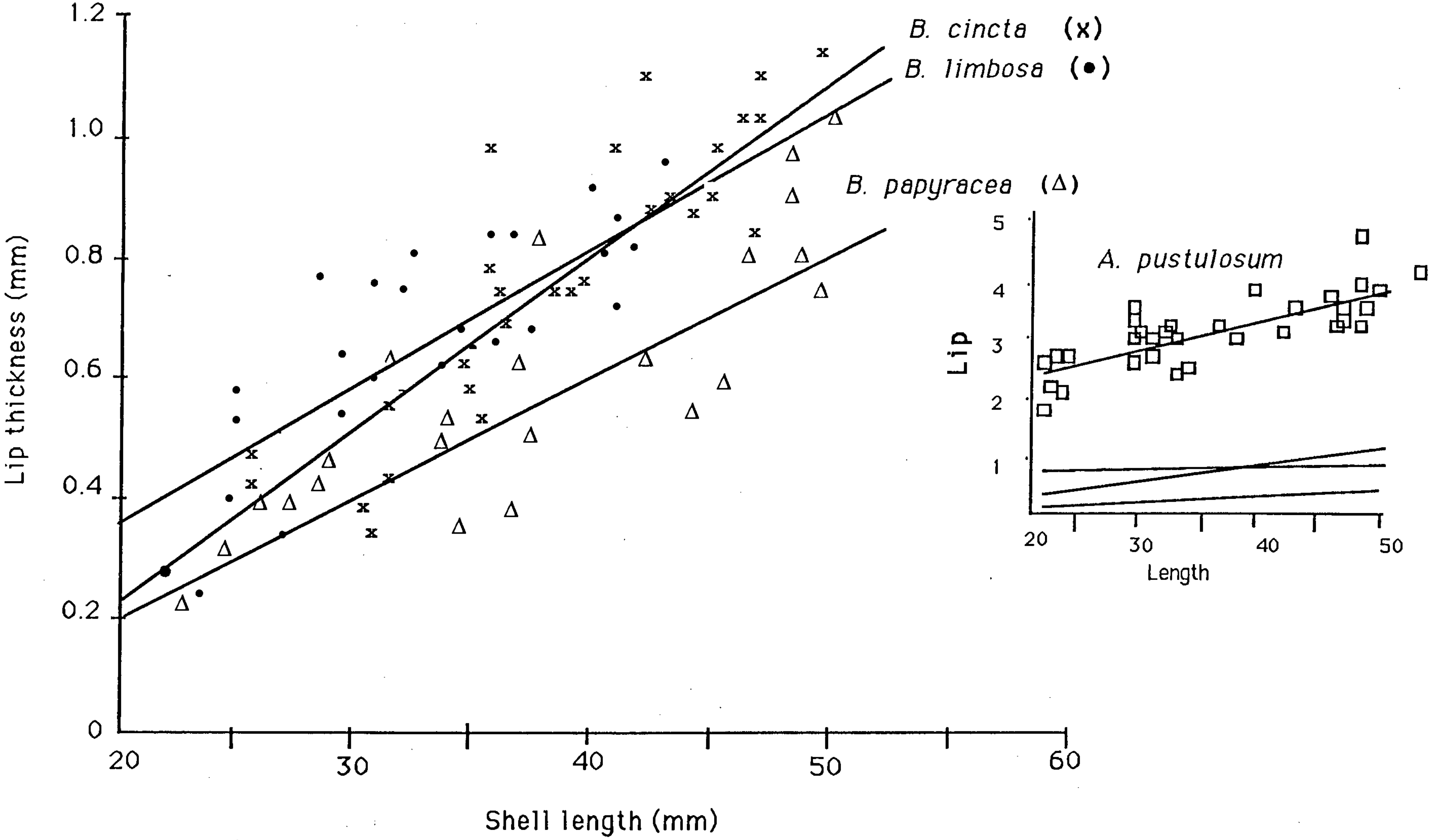

Fig. 5.2

Thickness of lip (mm) vs shell length in *Burnupena cincta, B. limbosa* and *B. papyracea*
The inset shows a comparison with the larger gastropod *Argobuccinum pustulosum.*

larger whelks, which have a thicker shell lip (Fig. 5.2), being less susceptible to predation. Although *Burnupena spp*. between 20 and 65mm shell length were offered as prey, the maximum size taken was 52mm. *Argobuccinum pustulosum* of all sizes were completely immune to predation due to their much thicker shell lips (Fig. 5.2). When *A. pustulosum* alone were offered as food, the shells showed minor damage due to rock lobster attacks, but no mortality was recorded over 3 months of experimentation.

Subsequently, the experiment was confined to *Burnupena spp*. to determine the feeding preferences of *J. lalandii* on *B. papyracea*, *B. limbosa* and *B. cincta*. Each rock lobster was offered similar sizes of three *B. limbosa* and three *B. papyracea* selected from the same size range (25-50mm). Whelks that were consumed were replaced daily. Because of the method of rock lobster attack it was possible to identify and measure the shells of consumed whelks. The experiment was terminated after 10 days and repeated using *B. papyracea* and *B. cincta*. Of the whelk species, *B. limbosa* and *B. cincta* were both preferred as prey to *B. papyracea* and were eaten in significantly larger numbers (Fig. 5.3) (chi square test; n=12, P<0.001 in both cases). Mean lengths of the *B. papyracea* eaten (27mm, s.d.= 2.4mm) were significantly smaller then those of either *B. cincta* or *B. limbosa* [32mm s.d=4.9mm; 32mm, s.d=4.5mm respectively, (one-way ANOVA; p<0.05)in both cases]. Maximum size of *B. papyracea* eaten (32mm) was also considerably smaller than

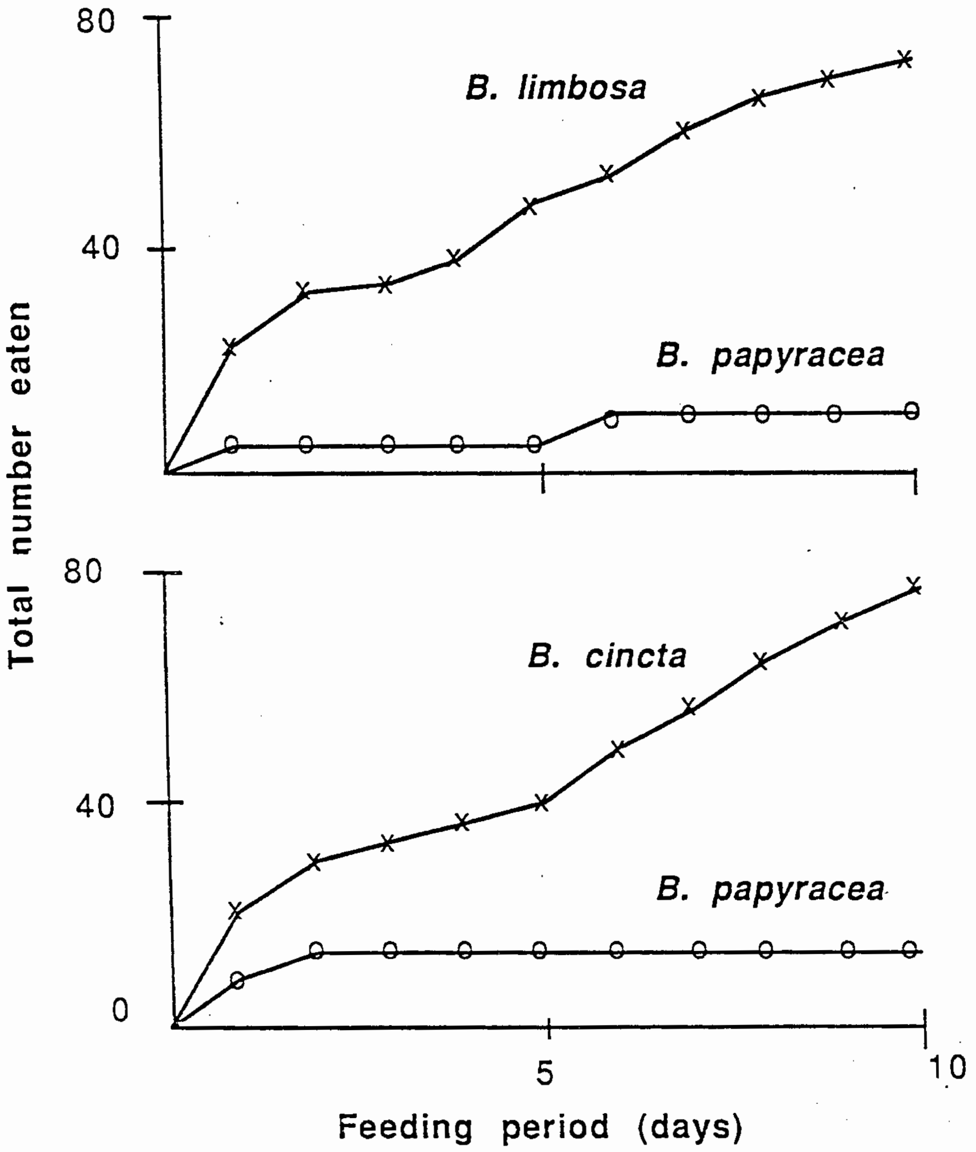

Fig. 5.3

Results of 10-day feeding experiment in which *Jasus lalandii* were fed on *Burnupena limbosa*, *B. cincta* and bryozoan-covered *B. papyracea*.

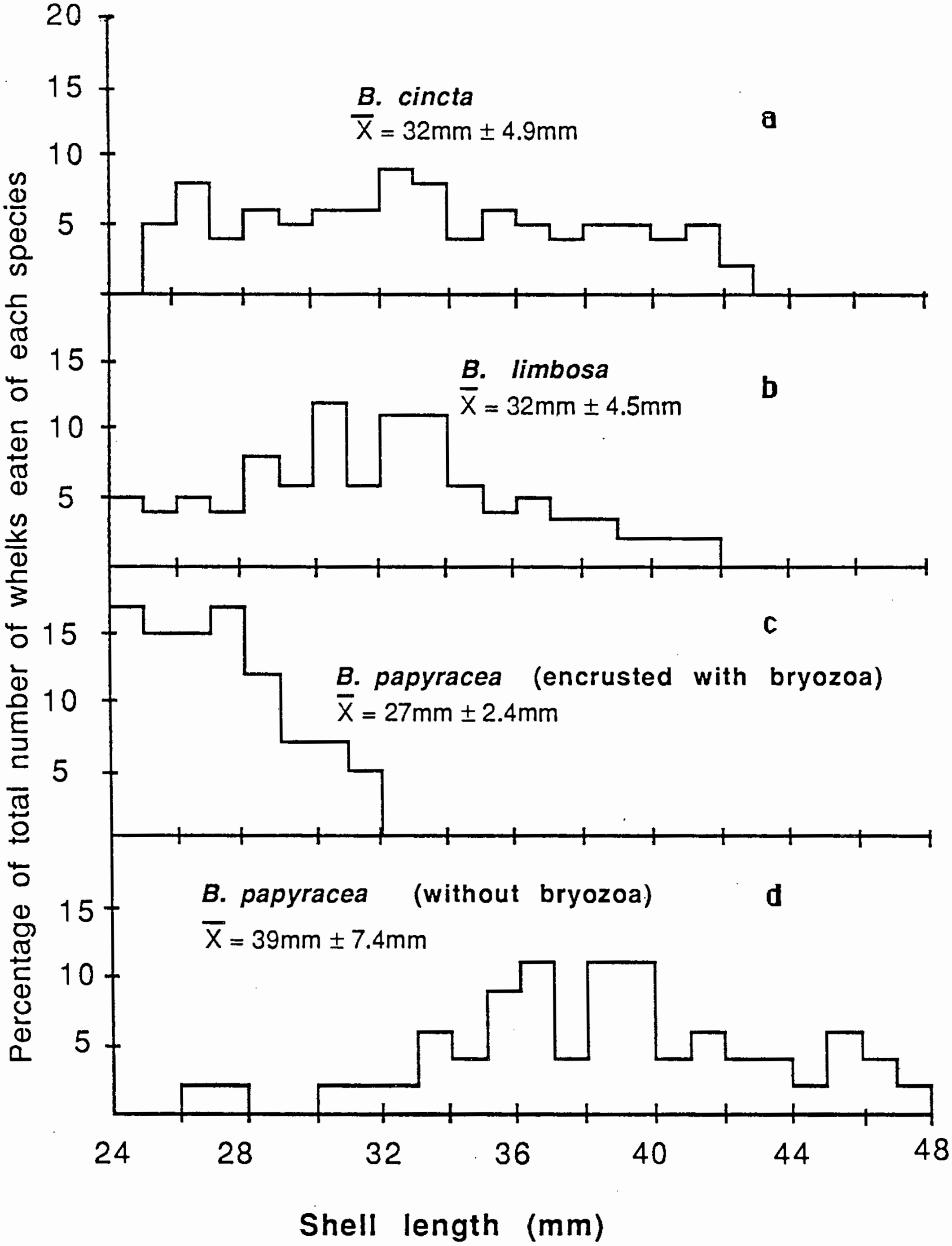

Fig 5.4

Size distribution of different *Burnupena* spp. eaten by rock lobster [*B. cincta* (**a**), *B. limbosa* (**b**) and *B. papyracea*, both with (**c**) and without (**d**) its encrusting bryozoa] The rock lobsters were offered the same sizes of whelks of each species.

that of *B. cincta* and *B. limbosa* (43 and 42mm respectively) (Fig. 5.4a, b and c).

The shell of *B. papyracea* is invariably covered by the commensal bryozoan *Alcyonidium nodosum* and the feeding preference experiment was repeated for 20 days using *B. cincta* and *B. papyracea* after the bryozoan covering had been removed from the latter. It was not posssible to perform a comparable experiment using *B. limbosa* for, after being damaged by rock lobsters, shells of this species were difficult to distinguish from those of *B. papyracea* which lacked a covering of *Alcyonidium*. Although more B. papyrecea were eaten after the 20-day experimental period (Fig. 5.5), there was no significant difference between the number of each species eaten (paired t-test, n=20, P>0.05). The consumption of cleaned *B. papyrecea* was consistantly higher than it was for *B. papyrecea* that had a covering of *Alcyonidium* (Fig. 5.5). The maximum size of *B. papyracea* taken by rock lobsters increased from 32mm to 48mm when the shells were cleaned (Fig. 5.4d). There was also a significant increase in the mean size eaten, from 27mm (s.d.=2.4mm) to 39mm (s.d.=7.4mm) (t-test, P<0.001) although this was still far below the mean size of 54mm (s.d.=6.9mm) for *B. papyracea* at Malgas Island (Fig. 5.1, 5.4c and d). The presence of symbiotic bryozoans thus decreases the minimum size which *B. papyracea* must attain before becoming immune to predation and decrease the rate of predation on *B. papyrecea*. As its size increases *B. papyracea* would

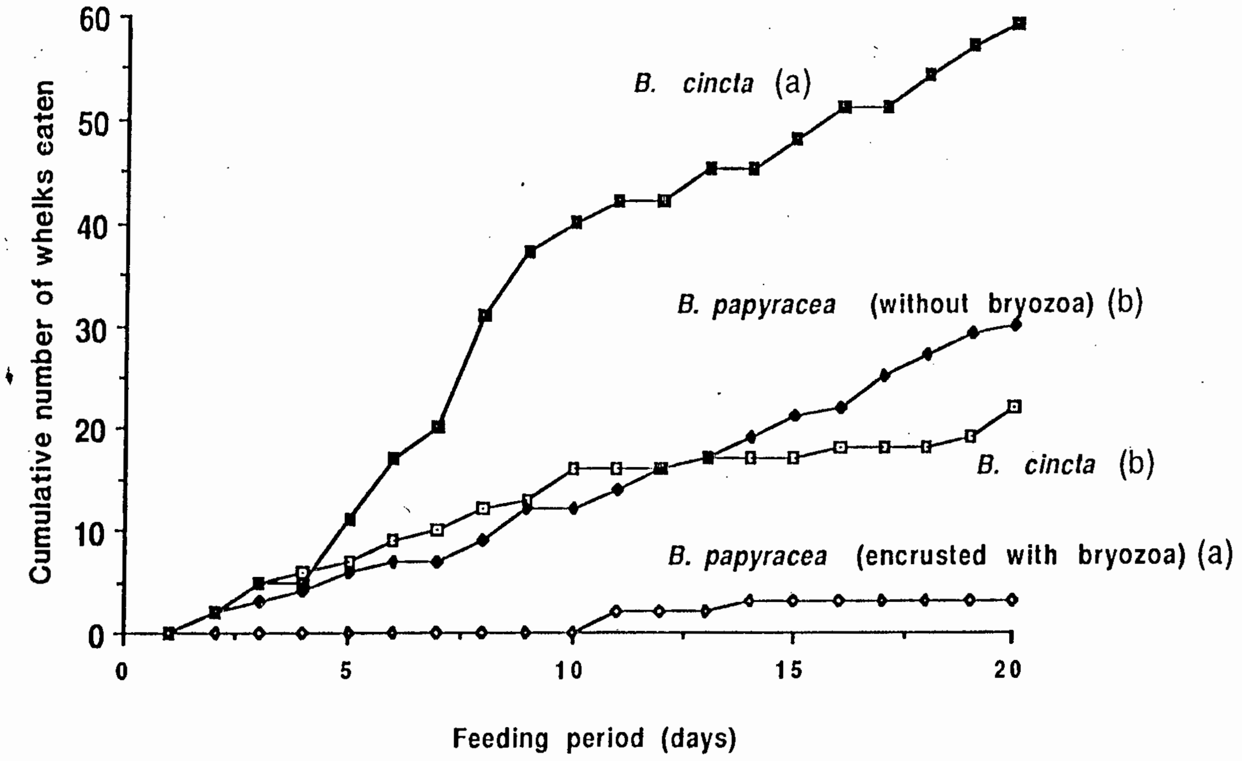

Fig. 5.5

Results of 20-day feeding experiments in which *Jasus lalandii* fed on: (**a**) *Burnupena cincta* and bryozoan-encrusted *Burnupena papyracea*, (**b**) *B. cincta* and bryozoan-cleaned *B. papyracea*. The graph shows the cumulative number of whelks of the different species and treatments eaten during the feeding period.

ultimately obtain a refuge in size when the shell becomes thick enough to discourage predation, but individuals that are smaller than this obtain partial protection through the presence of the bryozoan.

CAGING AND TRANSFER EXPERIMENTS

The ability of *Jasus lalandii* to tolerate physical conditions at Marcus Island was examined by caging specimens in situ at 10m depth in amongst the mussel beds around the island. Two cages were established at Marcus Island, with control cages at Malgas Island. Each cage was divided into four chambers and rock lobsters, collected at Malgas Island, were placed, two in each chamber. All the caged animals at both islands survived until released over 9 months later.

In an attempt to assess the impact of rock lobsters on the benthic community at Marcus Island, and to determine whether they could survive there without the benefit of cages, 1000 animals were captured at Malgas Island, tagged with numbered labels and released at 6-10m depth at Marcus Island. *Jasus lalandii* favours rock crevices so, in order to ensure that the transferred animals had sufficient suitable habitats at Marcus Island, shelters were first installed. These consisted of 0.5 ton, $1m^3$ concrete blocks with 20cm diameter passages running through them. During the initial transfer 10-15 animals were placed directly into each "crevice" and the remainder released in the vicinity of the blocks.

The result of rock lobster transfer was immediate and surprising. Although rock lobsters feed readily on whelks in the laboratory, their roles were reversed at Marcus Island. Apparently healthy rock lobsters were quickly overwhelmed by large numbers of whelks. Several hundred were observed being attacked immediately after their release and a week later no live rock lobsters could be found at Marcus Island. Recognising that some animals might have been damaged during tagging and so triggered the attacks, the experiment was repeated five times using smaller numbers (circa 20) of unmarked, undamaged rock lobsters. Pairs of animals were recovered at 15 minute intervals after release, the attached whelks collected and counted and the state of the rock lobsters assessed. The results were consistently similar. Temporary escape by swimming was possible for the rock lobsters but each contact with the substratum resulted in several more whelks attaching themselves until weight of numbers prevented escape. On average the rock- lobsters were killed within 15 minutes and all their flesh was removed in less than an hour, with over 300 *Burnupena spp.* attacking each individual.

WHELKS FEEDING

In a set of preliminary feeding experiments [conducted by McQuaid (unpublished data)] Burnupena species were maintained in aquaria with healthy mussels (Choromytilus meridionalis) for two months and did not feed unless the mussels were deliberately damaged. A similar experiment was conducted in the field at Marcus Island during the course of this present project using a cage similar to those described above. Four hundred black mussels were collected randomly from the local mussel population. One hundred mussels were placed in each of four separate chambers in the cage. In each of two of the chambers 100 Burnupena whelks, which were also randomly collected from the whelk population at Marcus Island, were placed together with the mussels while in the other two chambers there were only mussels. One month later the mussels were recovered from the cage and counted. Although the mortality rate was high (approximately 33% overall mortality), probably due to heavy siltation inside the cage, it was similar in all chambers both with and without the whelks (chi-square test, n=4 P>0.05).

DISCUSSION

The feeding experiments described account for the ability of both *Argobuccinum pustulosum* and *Burnupena papyracea* to survive at Malgas Island despite the presence of large numbers of rock lobsters. In the case of *A.*

pustulosum the shell is simply too thick and heavy to be successfully attacked (Fig. 5.2). *B. papyracea* was rarely attacked unless its bryozoan covering was first removed. Bryozoans have been observed to produce antibiotics which function as anti-fouling substances preventing epiphytic growth (Al-Ogily and Knight-Jones 1977). The presence of the bryozoan *Alcyonidium nodosum* as a shell-covering has two beneficial effects for *B. papyracea*. Slipper limpets (Crepidula porcellana) are virtually universal epibionts on all other species of *Burnupena* in this area, and up to five or six animals can be stacked on top of one another, presumably adding considerably to resistance to water movement. However, they never occur on *B. papyracea*. Secondly rock lobsters, having non-chelate pereiopods, break away the shell lip of whelks using their mouthparts. Since the removal of bryozoans from the shell renders *B. papyracea* vulnerable to rock lobster predation (Fig. 5.5) it seems likely that the bryozoan is distasteful, possibly due to the presence of anti-fouling compounds.

Larger individuals of *B. papyracea*, having thicker shells, are less vulnerable to predation than small individuals. Although the commensal bryozoans provide some defence for *small B. papyracea*, they are not always effective. *B. papyracea* is sometimes attacked but the size of animals taken is decreased significantly if the bryozoans are present (Fig. 5.4). Consequently commensal bryozoans offer increased protection to small *B. papyracea*, permitting the species to survive at Malgas Island under a regime of intense predation which excludes all other members of the genus. For the same reason *B. papyracea* becomes invulnerable to predation at a smaller size than its congeners, *B. cincta* and *B. limbosa* (Fig. 5.4). Nevertheless the population of *B. papyracea* at Malgas Island is skewed to the right and includes limited numbers of small individuals (Fig. 5.1). Although population density is also considerably lower at Malgas Island (Table 5.1), I believe that the difference in population structure between the two islands is a function of predation, rather than being explained by more rapid growth due to reduced intraspecific competition at Malgas Island. It is, however, true that the immediate reaction of whelks to the introduction of food at Marcus Island suggests intense competition.

The primary question in this paper concerns the absence of rock lobsters from Marcus Island, despite the availability of plentiful food there. Rock lobster fishermen resident in the area claim that populations of *Jasus lalandii* were similar at the two islands until at least 20 years ago. The cause of their original disappearance is unknown but there are records of a period when oxygen tensions were very low in the water near to Marcus Island (Newman and Pollock 1973; Christie and Molden 1977). Physical conditions are now clearly suitable for rock lobsters, as is evident from the survival of rock lobsters in cages at Marcus Island. But in their absence, various prey species appear to have attained very high densities; and the *Burnupena* spp. have reached densities at which they are capable of excluding rock lobsters directly by preying on them. *Burnupena spp.* are generally known as scavengers, although they will prey, at least intertidally, on small animals such as winkles (McQuaid 1982). Rock lobsters are generally predators, though they will also scavenge as well as resorting to cannibalism and there is obviously some overlap between these two modes of feeding. When predators are removed from a system, prey species often exhibit an increase in numbers (Paine 1969), sometimes followed by a crash as they eliminate their own food resources (Hairston et al. 1960; Caughley 1970; Klein 1970). At Marcus Island, however, community biomass is dominated by a filter-feeder, the mussel *Choromytilus meridionalis*, which forms 87% of total wet weight biomass (see Chapter 2). This species subsists on food imported into the system in the water column, so that it cannot eliminate its own food supplies (Branch 1985). Furthermore, as revealed from field (this study) and laboratory studies (McQuaid, unpublished data) Burnupena spp. are incapable of successfully attacking living mussels. Burnupena spp. have, however, been observed feeding on mussels damaged by other predators such as drilling whelks (Nucella spp.) and Octopus vulgaris (Chapter 2). Consequently C. meridionalis provides food for Burnupena spp. in the form of dead, dying or damaged mussels, but the whelks are, in turn, incapable of eliminating their own food

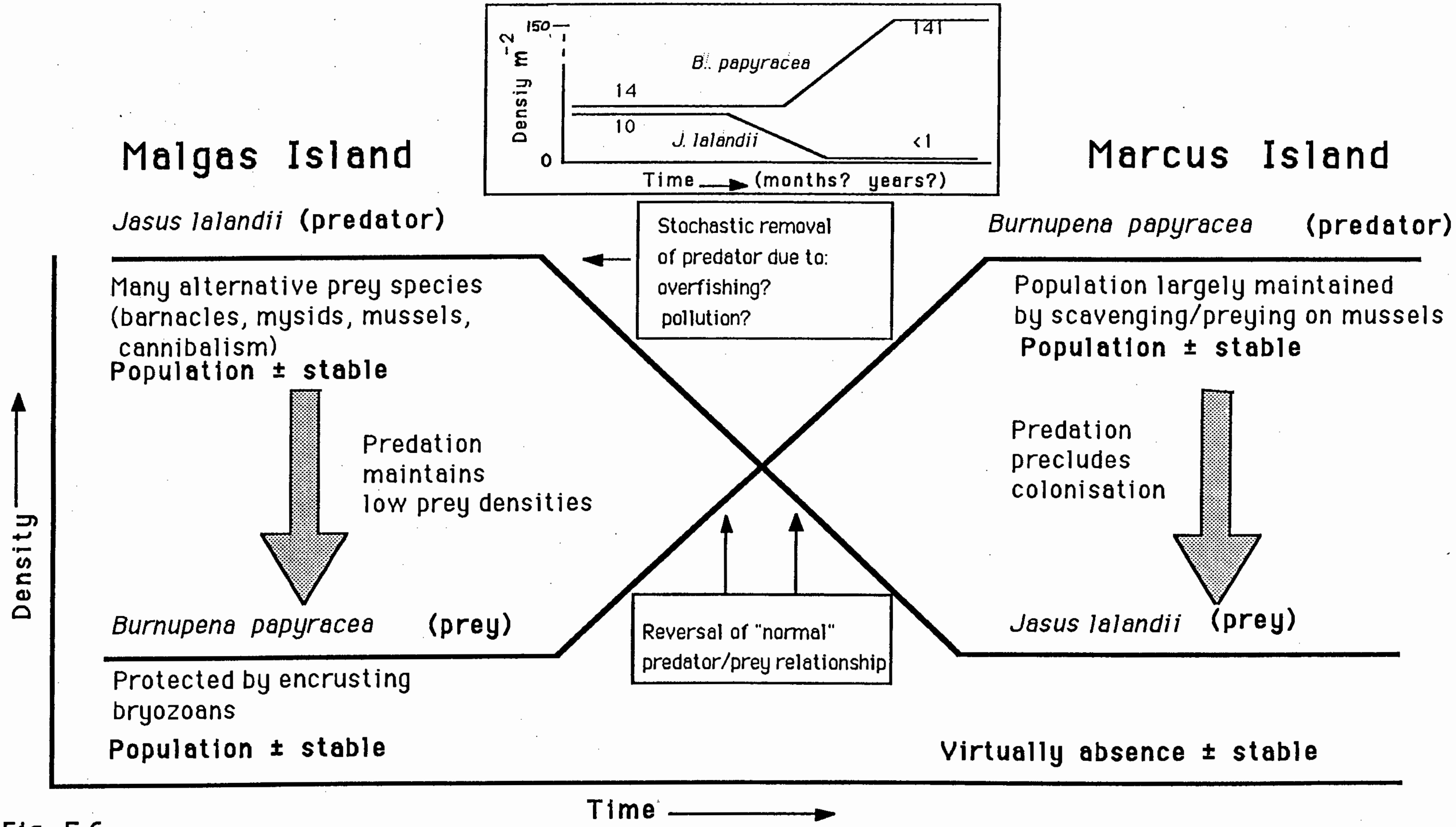

Fig. 5.6
Schematic description summary of rock lobster whelk predator/prey role reversal alternative states of benthic communities at Marcus and Malgas Islands. Inset gives correct proportions if actual densities are considered.

resource. As a result, both the whelk and mussel populations at Marcus Island are stable. Given that the whelks can be maintained at exceptionally high densities at Marcus Island, they are capable of preventing colonisation of the island by *Jasus lalandii*, a species that is normally regarded as a top benthic predator.

Figure 5.6 illustrates and summarizes the unusual prey/predator relationship between *Jasus lalandii* and *Burnupena papyracea*. Although neither whelks nor rock lobsters form a major dietary component for each other under normal conditions, the two species are capable of regulating their populations through predation. *Jasus lalandii* is a "keystone" predator and its presence or absence determines basic community structure. At Marcus Island this status has been lost as rock lobsters can no longer colonise the sublittoral zone. *Burnupena* spp. occur intertidally which provides them with a refuge from rock lobster predation. In the case of *B. papyracea* the bryozoan *Alcyonidium nodosum* provides a further refuge for subtidal populations, allowing them to expand enormously on the removal of predation pressure and numerically dominate sublittoral whelk populations.

An immediate implication of this work is that any drastic reduction in the numbers of rock lobsters may be irreversible and result in a new, stable configuration of the community. Apart from the theoretical interest of this effect, I feel that there are serious implications for rock lobster management strategies which often rely on santuaries as sources of re-population of depleted fishing grounds.

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CHAPTER 6 - THE ROCK LOBSTER POPULATION (JASUS LALANDII) AT MALGAS ISLAND: ENERGY REQUIREMENT AND SOURCES.

INTRODUCTION

In earlier selections of this thesis, the contrast between the subtidal benthic communities of Marcus and Malgas Islands have been highlighted. Although the two benthic ecosystems appear to be completely different, they probably represent two stable states of the same ecosystem (see chapters 2 to 4). Many of the benthic species that inhabit the two islands are typical of the shallow water communities of the cold Benguela ecosystem (Day 1959; Simons 1977; Field _et_ _al_. 1977; Brown and Jarman 1978; Field _et_ _al_. 1980), but the presence of a major predator (the rock lobster) at Malgas Island, and its near absence at Marcus Island, seem to be the major reason why the benthic communities have developed in different directions. One possible explanation for this difference is that, in the past, a combination of factors such as pollution, oxygen deficient water, poaching and construction work on the iron ore jetty in the bay, depleted the population of rock lobsters around Marcus Island (Newman & Pollock 1973; Christie and Moldan 1977; Beckley 1981; Chapter 2). The two benthic communities on the islands may then have developed into two different stable states. Today Saldanha Bay is a rock lobster sanctuary, the oxygen levels are normal and the sources of pollution are strictly controlled (Gardner et al. 1983; Chapters 1 & 2). Despite this, rock lobsters have not recolonised the area near Marcus Island.

In chapter 5 a description was given of an attempt to introduce rock lobsters to the study site at Marcus Island. One thousand rock lobsters were introduced and provided with artificial shelters. The attempt failed, however, due to heavy predation on the rock lobsters by the large population of whelks. This suggests that the "whelk-dominated" community at Marcus Island is in a stable state and capable of resisting recolonization by rock lobsters .

On the other hand, Malgas Island has a dense population of rock lobsters which have a considerable influence on the community. A major question that arises is how the high density of rock lobsters at Malgas Island can be maintained, when the benthic community there almost completely lacks food sources such as mussels and urchins, the normal prey of rock lobsters (Heydorn 1969; Newman and Pollock 1969; Griffiths and Seiderer 1980; Pollock et al. 1982; Pollock 1986).

The initial objective of this study was to answer this question, by determining (a) the energetic needs of the rock lobsters, (b) the availability of their normal food, notably mussels, and (c) the relationship between available food and the diet of the rock lobsters.

The findings that resulted from these objectives led to further exploration of unorthodox food sources and, more specifically, to an in-depth study of the productivity of freshly recruited organisms and a quantification of their energy input in relation to the energetic needs of the rock lobsters.

MATERIALS AND METHODS

GUT CONTENT ANALYSIS

During the research period (1983-1986), quarterly samples of gut content were taken from rock lobsters at Marcus and Malgas Islands, at different seasons of the year. The samples were limited to a total of 120 individuals per year in terms of the local Sea Fisheries permit. The proventriculus was separated from the remainder of the gut and fixed in 4% formalin in seawater. The contents of the proventriculi were examined microscopically and identified to the level of species. The prey species represented were then quantified using the method of Shepherd (1973). Following to this method, the relative abundance of each food item is calculated by estimating the relative volume that it occupies in the total volume of each gut (P). This value is multiplied by the estimated fulness of the gut (F), summed for all the guts, and divided by the total relative value of all food species from all the gut contents of the sample and multiplied by 100 to give a percentage.

eg. $(\Sigma PF/\Sigma\Sigma PF)100$ where

P = % of food item (i.e each species) relative to the total contents of the gut, and

F = fullness of gut (ranked from 1 to 10).

This analysis of gut contents is subject to the usual bias that shell remains persist longer than soft parts; the contribution of shellfish may therefore have been overestimated. Rock lobsters also tend to swallow fragments of shell and exoskeleton (Heydorn 1969; Aiken 1980), presumably to facilitate digestion and intake of calcium after ecdysis. Isolated fragments of shell or exoskeleton were therefore excluded from the analysis.

The thickness of pieces of barnacle shells in the rock lobster guts was measured from subsamples. Only relatively undamaged plates of the barnacles' shells were selected, and the thickness measured at the centre of the plates, to a hundredth of a millimetre. A regression curve relating shell thickness to barnacle growth rate was then used to determine the age of the barnacles in the sample.

ROCK LOBSTER SURVIVAL

Eight rock lobsters were captured and placed in pairs of cages which had an area of $1.31m^2$ and a height of 0.33m. The cages were placed at a depth of 10m at each of the islands.

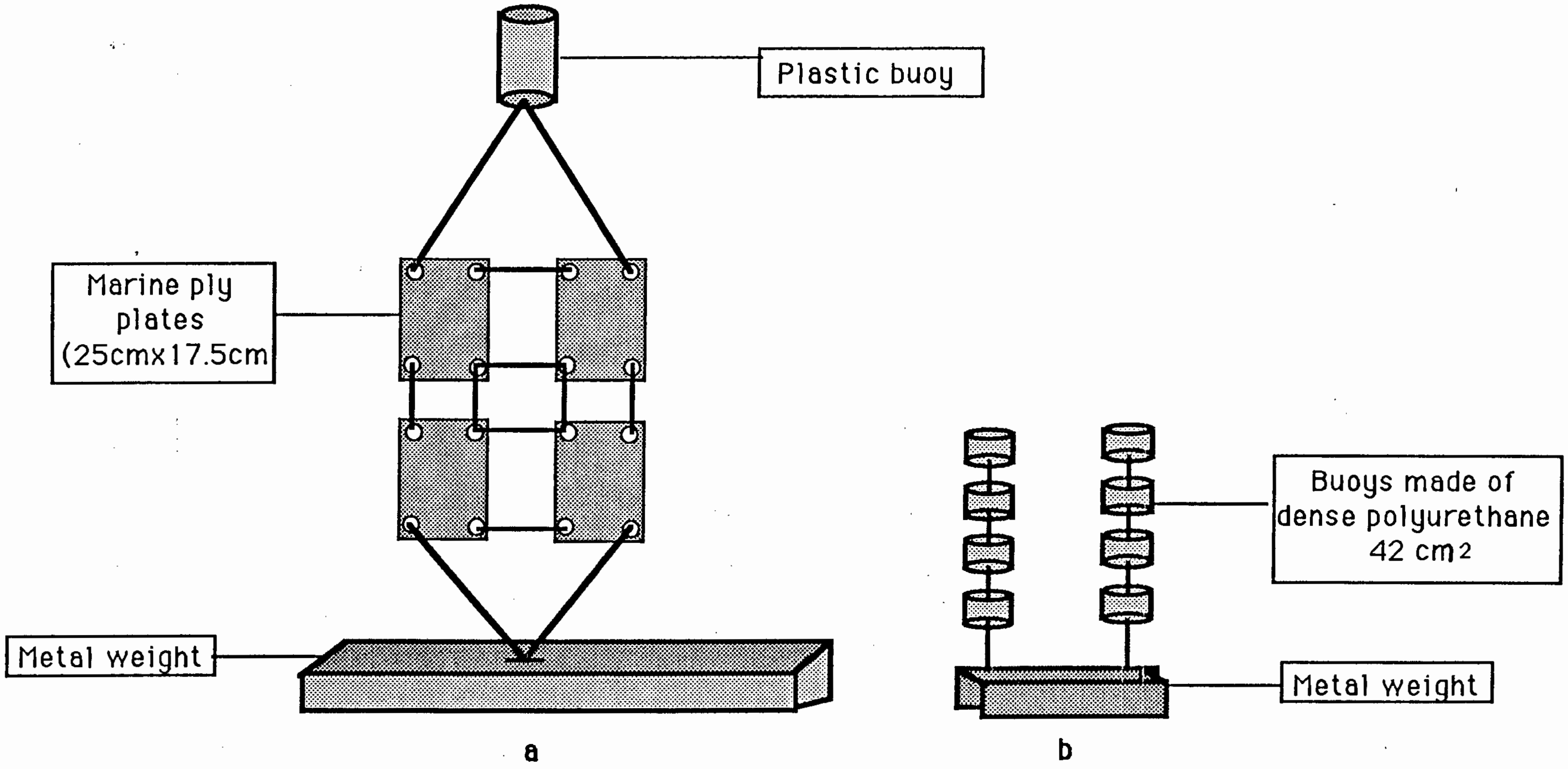

Fig. 6.1

Arangement of plates used to record (a) seasonal and cumulative recruitment, and small polyurethane buoys for daily recruitment (b).

Each cage was initially divided into four chambers. Two chambers in each of the cages were left undisturbed to act as controls, the other two chambers contained two rock lobsters each. The mesh of the cages was small enough (0,5cm x 0,5cm) to prevent the penetration of most of the macrobenthic species that might serve as prey for the rock lobsters. The condition of these rock lobsters was monitored regularly, as was settlement and growth of benthic species on the cage floor. All observations were done by means of SCUBA with as little interference as possible to the captured animals.

BARNACLE PRODUCTION

a) Monthly production by recruits of the most abundant subtidal barnacle, *Notomegabalanus algicola*, was monitored on settlement plates. Eight Marine ply settlement plates were cut to a size of 25cm x 17,5cm and coated with glass reinforced polyester (GRP) and sprayed with fine sea sand and shell fragments to make a rough surface. Each plate was placed in a container of sea water for two weeks and then dried on absorbant paper and weighed. The plates were then connected to each other by wire in sets of two's. The lowermost plates were anchored to the sea floor at a depth of 10m and the uppermost plates to a buoy (Fig. 6.1). Four plates were then left in the sea at each Island and replaced periodically by a similar set of plates. After removal from the sea, the plates were dried and weighed as above. The biomass of the barnacles was then calculated. To take account of other fouling species that had settled on the plates, subsamples of other species were cleared off the plate and weighed. The total weights of these other species were calculated using their percentage cover or total number and this weight subtracted from the total biomass to obtain the wet weight of barnacles per plate. This experiment took place between 23-11-1984 and 7-12-1985. Calculations of the monthly production of recruits was eventually based on the plates at Marcus Island, because those at Malgas Island were attacked and scraped by rock lobsters (in spite of the fact that they were suspended approximately one metre above the substratum).

b) Continuous accumulation barnacles was measured on similar marine ply plates. This time 32 plates were placed at each of the two subtidal localities. Approximately every forty days, four plates were removed and the barnacle wet weight calculated as in (a), while the remaining plates were left in place to permit continued growth and accumulation of barnacles. The duration of the experiment was 214 days (23-11-1984 to 25-06-1985) and was terminated when a severe storm eliminated the remaining plates.

c) Growth rate and production of barnacles during the first few weeks after settlement were also measured more intensively during the peak season of settlement, on the assumption, that over a 40 days or more, the biomass of the barnacles might peak and then drop due to intraspecific competition for space. A different technique was used to test this assumption. The artificial substratum chosen for settlement was buoys made of dense polyurethane (fishing net floats) with a surface area of 0,4m^2. A total of 32 buoys was used, in eight groups of four each. The buoys were tagged and placed in the sea near Marcus Island at a depth of 10m. They were then monitored at short time intervals (2 to 8 days) from the time recruits first appeared until the buoys were completely smothered and the biomass began to drop (after 40 days). Subsamples of the barnacles were removed at each interval to allow accurate measurement of shell thickness and length, and some of the buoys were sacrificed each time to accurately measure the biomass. The largest barnacles were measured in order to monitor growth rate of the founder generation only. Subsamples of barnacles of 20 to 40 days old were dried for 48 hours and their calorific value was established using a SP500 bomb calorimeter. This experiment was started on the 15- 11-1985 and terminated 61 days later.

MUSSEL PRODUCTION

The production of mussel recruits (of both *Choromytilus meridionalis* and *Aulacomya ater*) was monitored using the same plates as described in (a) above. The number of mussels per unit area was counted, subsamples wet-weighed, and the total wet biomass of mussels per plate calculated.

BIOMASS, SIZE DISTRIBUTION AND SEX RATIO OF *J. LALANDII*

The three-year average of *Jasus lalandii* biomass per square metre (as calculated in chapter 2) was used. The sex ratio and size distribution were established from the measurements of 1901 animals. [These rock lobsters were captured and tagged for use in the transfer experiment (Chapter 5)]. The male and female size distributions were converted to numbers of each size group per square metre.

FECUNDITY AND EGG PRODUCTION OF *JASUS LALANDII*.

Twenty nine female rock lobsters which were "in berry" were collected from Malgas Island on the 20-09-1986, close to the beginning of the reproductive season (Heydorn 1969). Their carapace size and wet weight was recorded. The eggs together with parts of the pleopods, were dried for 72 hours at 60°C using a method similar to that described by Beyers & Goosen (in press). The eggs were then removed from the pleopods and weighed. The calorific value of a sample of the eggs was measured using a CP500 bomb calorimeter.

AULACOMYA ATER SIZE DISTRIBUTION.

A total of 187 *Aulacomya ater* was collected off Malgas Island to determine its size distribution. Mean density was based on the average number of *Aulacomya* per square metre obtained from the annual benthic samples at Malgas Island (see Chapter 2).

ENERGY BUDGET FOR *JASUS LALANDII*

There is no comprehensive analysis of the energy budget of the rock lobster *Jasus lalandii*, and what information does exist is scattered and, in some cases, in disagreement. Some attempt has therefore been made by the author to calculate the energy requirements of *Jasus lalandii*, based on (a) respiration which has been measured in the laboratory (P. Zoutendyk pers. comm.); (b) reproduction, based on the calorific value of eggs, seasonal reproductive cycles and the relationship between body size and egg production (see above); and (c) various figures of growth rate (reviewed in Wickens 1985). In conjunction with the data on the size distribution and density of rock lobsters off Malgas Island, this information was used to calculate the mean energy requirements of the population, per square metre.

RESULTS AND DISCUSSION

ROCK LOBSTER STANDING STOCKS ON BOTH ISLANDS

During the years 1983-1985 both Marcus and at Islands were sampled annually for biomass of all benthic species including *Jasus lalandii* (see Chapter 2). However results of *Jasus* were seldom recorded off Marcus Island even though very small individuals (of 20-30 mm carapace size) were observed in deeper water on the mussel bed, occasionally in relatively large quantities, (group of about 50-100 individuals hiding in a deep hole). Larger rock lobsters

(100-120mm) were seldom seen, and then only in very small numbers (sometimes 1-5 individuals throughout the whole dive) and far away from the mussel beds which sustain a large whelk population (see Chapter 5). In contrast, Malgas Island has a very large rock lobster population with a mean density of 10.17 (7.24 s.d.) m^{-2}. In some cases more than 600 individuals per square metre were counted. The mean figure is very high when compared to some of the richer rock lobster grounds on the South African west coast [eg. an average of 0.81 m^{-2} with maxima of 2.19, 2.50, 2.37 and 1.9 m^{-2} at different depths and stations off Robben Island near Cape Town (Pollock 1979)]. Juvenile rock lobsters are usually found in shallow water aggregating in large numbers in deep crevices. Carlberg _et al_. (1979) indicate that an average of up to 40 juvenile rock lobsters can crowd into one square metre if provided with a three dimensional shelter. After reaching a carapace size of between 50 to 60mm they normally move to deeper water and disperse over a larger area (Heydorn 1969; Newman & Pollock 1974b; Pollock 1979). It seems that the narrowness of the rock bottom surrounding Malgas Island and its isolation from the rocky areas by the surrounding sandy bottom may stop or slow this dynamic process and this, together with other features discussed later, may account for the unusually high density of large rock lobsters around Malgas Island. The sex ratio of *Jasus* at Malgas Island is approximately 3 females to 7

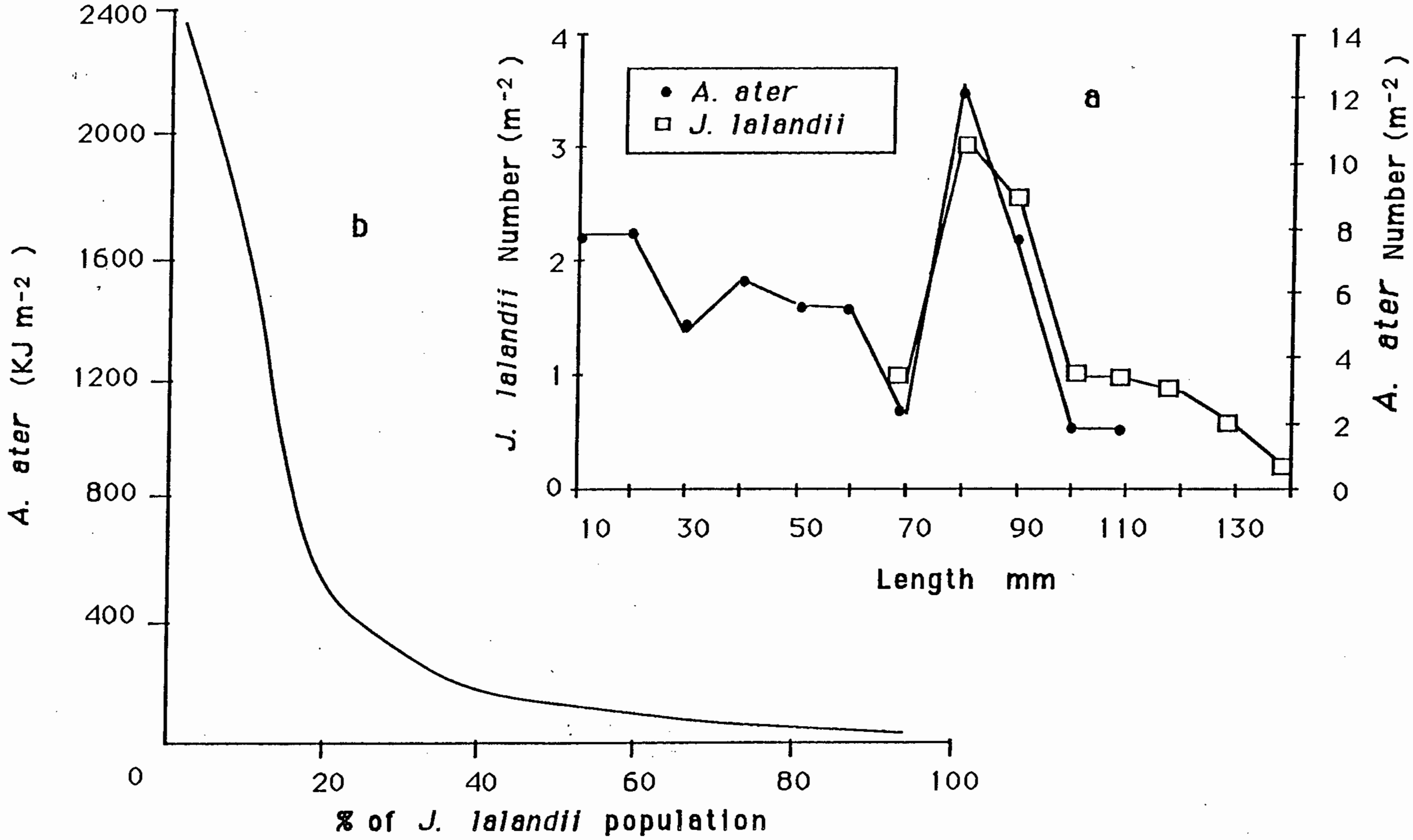

Fig.6.2

(a) Size distribution of the ribbed mussel, *Aulacomya ater* (shell length (mm)) and the rock lobster *Jasus lalandii* (carapace length (mm)) at Malgas Island. (b) Energy available for *J. lalandii* consumption from the standing stock of *A. ater* at Malgas Island, calculated from the critical prey size equation of Griffiths and Seiderer (1980), and the equation relating prey size to calorific value, given by Griffiths and King (1979).

males, a significant departure from equality (Chi squared analysis, $p < 0.001$, n=1901). Heydorn (1969) reported values of 76.3%, 75.3% and 72.1% males at Robben Island on different dates. The sex ratio fluctuated seasonally and varied at different depths. This is in keeping with other observations, and it is well established that in shallow water the number of females is normally larger than that of males, eg. 79% females at Elands Bay at a depth of 11m and 95% females south of Elands Bay at a depth of 9m (Pollock 1982). Shallow-water populations are also usually characterised by high density and a small average carapace length (Pollock 1982).

The carapace sizes of the individuals sampled at Malgas Island ranged between 58mm and 97mm for females (mean=75.42mm s.d.=8.53mm) and between 71mm and 134mm for males (mean=99.44mm s.d.=16.64mm). The overall size distribution is shown in Figure 6.2a. Almost no individuals under these size ranges were ever observed at Malgas Island, excluding the very small specimens found in the cages (see Chapter 3). The relatively high sex ratio of males to females, the large mean size and the high density of the population at Malgas Island, suggest that this population combines features normally typical of either shallow or deep-water rock lobster communities. (Heydorn 1969; Pollock 1979; Pollock et al. 1982; Pollock 1986). This may be a reflection of the fact that the rock lobsters cannot move into deeper waters as they would normally do (see above).

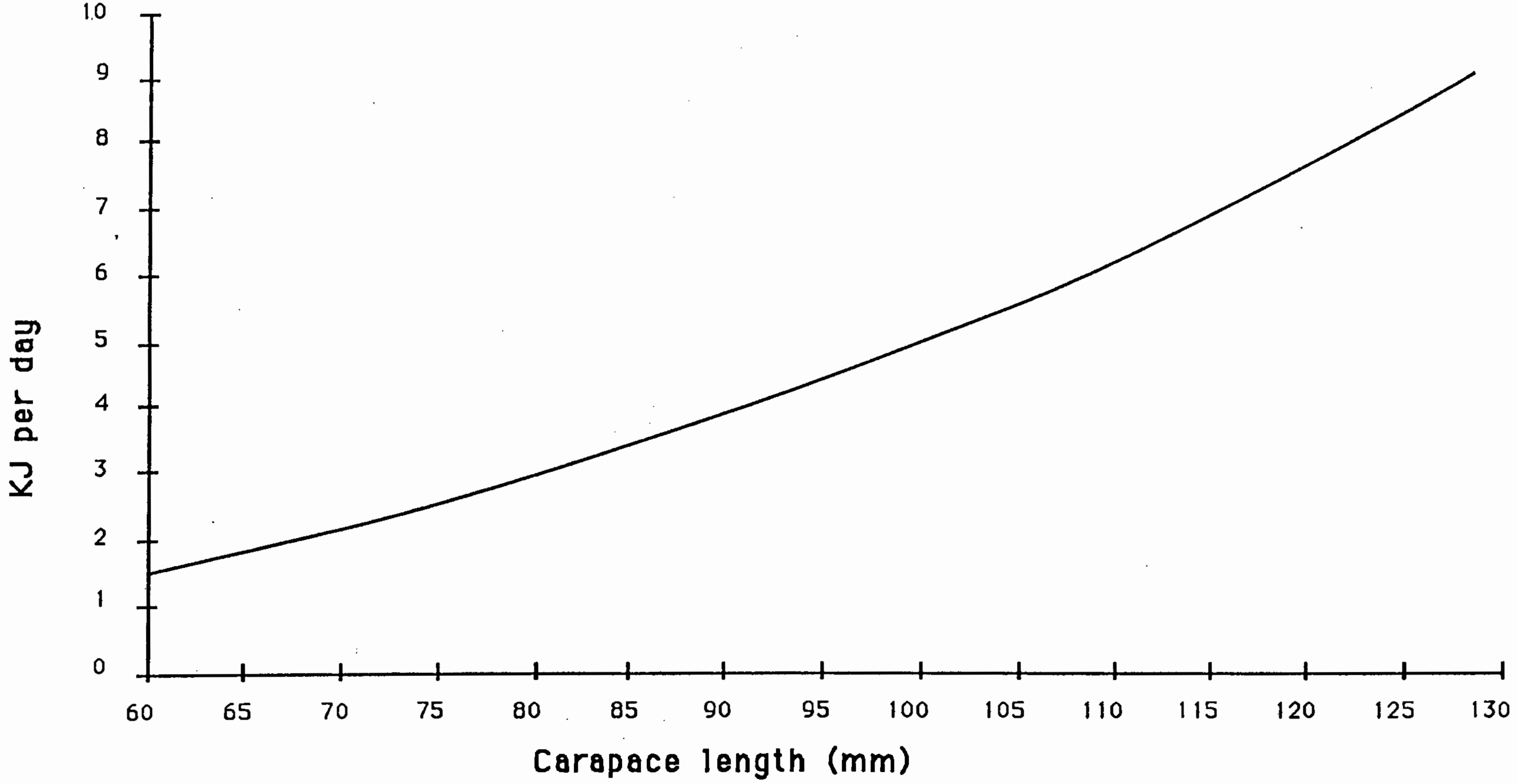

Fig. 6.3

Respiration rate of *Jasus lalandii* of different lengths (calculated from data obtained by Zoutendyk (unpublished)).

ENERGY REQUIREMENTS OF THE ROCK LOBSTER POPULATION AT MALGAS ISLAND.

In this section an attempt is made to estimate the minimum energy requirements of the rock lobster population off Malgas Island. To date no work has been done on the complete energy budget of *Jasus lalandii*. However, since this was not the objective of this research programme, use was made of variety of information obtained from other papers, from unpublished work by other researchers, or from research by the author.

Respiration

The respiration rate of *Jasus lalandii* was calculated from unpublished data (P. Zoutendyk pers. comm.), for male *Jasus* of different size classes held at different temperatures. Using the curve in Fig. 6.3, for respiration at 13°C (the average sea temperature at Malgas Island, Chapter 1) the energy cost of metabolism was calculated from the power equation:

$$y = 1.13\ (10^{-4}\ x^{3,32})$$

where y = respiration rate in kJ per day.

x = carapace length in mm.

The energy requirement of the *Jasus* population could then be calculated from the size distribution (Table 6.1). The final result was multiplied by 1.45, which is an estimate of the multiplication factor necessary to take into account the effect of nocturnal activity on respiration rate. This estimate is derived from Wingats' (1969) work on oxygen consumption of the spiny lobster, *Panulirus interruptus*.

The total calculated energy consumed by respiration rate is 50.51 $kJd^{-1}m^{-2}$ and the annual rate for the whole population is 18436 kJm^{-2} or an average of 4.97 kJ per 380g animal per day, approximately 85% of the total daily energy requirement of *Jasus*. By comparison Wingate (1969) obtained values of 6.28 and 10.46 kJd^{-1}, in winter and summer respectively, for oxygen consumption by 300g spiny lobsters (*Panulirus interruptus*) and McLeese (1964, 1968) recorded 2.53 and 7.47 kJd^{-1} at $5^{o}C$ and $21^{o}C$ respectively for *Homarus americanus*. Conover (1978) calculated the average maintenance cost for intertidal or subtidal invertebrates at approximately 77% of the total energetic needs.

Reproduction

The energy requirements for reproduction were calculated for female *Jasus lalandii* only, on the assumption that energetic output for reproduction is minimal in males. This presumption has previously been advanced as the reason why males have faster growth rates than females and may also explain their much greater average size (Beyers and Goosen in press). It is assumed that most of the energy input into

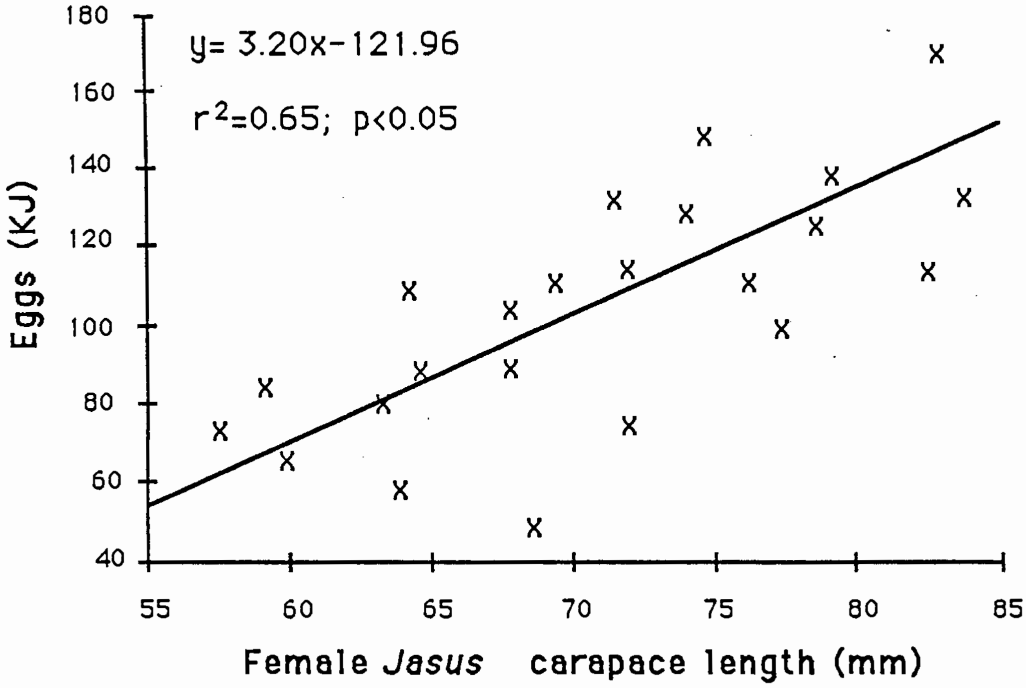

Fig 6.4
Calorific value of total eggs carried by female *Jasus lalandii* of different carapace lengths.

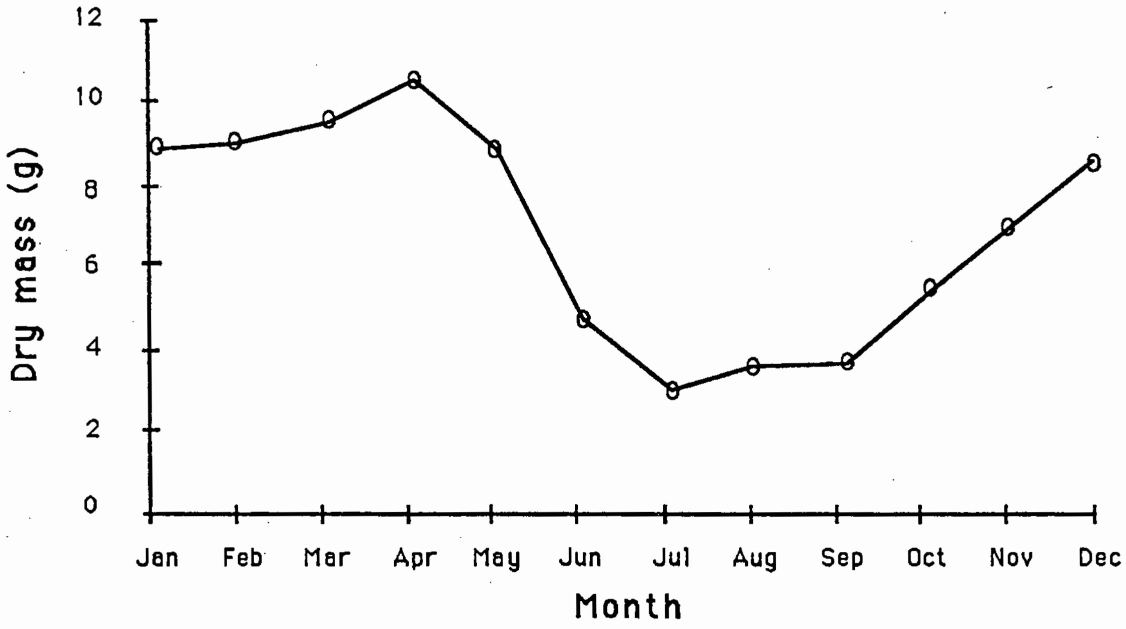

Fig. 6.5
Average monthly ovary dry weight of a female *Jasus lalandii* (70mm-90mm carapace length) calculated from the data obtained by Heydorn (1969).

reproduction in the female is in the form of the yolky eggs, their protoplasmic membranes and the spring-shaped funiculi that attach the eggs to the pleopods (see Silberbauer 1971, for details of the reproductive system of *Jasus*). In addition, Brafield and Llewellyn (1982) have suggested that 4% should be added to the calorific content of the eggs as an estimate of the costs involved in their production. Fig. 6.4 shows the regression of calorific value of the eggs against carapace size, from which it was possible to calculate the energy expended on eggs production by the entire population at Malgas (Table 6.1).

The average daily value of 4.84 kJm^{-2} was calculated for the whole population on the basis that the ovary develops over a period of about 213 days a year, a figure derived from Heydorn (1969) who gives seasonal fluctuations in ovarian dry weight for 70 - 79mm rock lobsters (see Fig. 6.5). The total daily requirement of female *Jasus* is thus 4.84 kJm^{-2} plus 4% (additional energy lost during synthesis) ie. 5.04kJm^{-2}, or an annual requirement of 1073 kJm^{-2}. This is about 8.5% of the total energy requirement of *Jasus* and can be compared with an average of 4.3% of assimilated energy, which Brafield and Llewellyn (1982) derived using the data of Conover (1978) for 20 aquatic invertebrates.

Growth.

Growth rate data for *Jasus lalandii* on the South African west coast have been reviewed by Wickens (1985). Wickens divided the data into two groups viz. slow and fast and also gave an overall growth rate. These data are summarized in the table below together with more specific information on growth rate in Saldanha Bay (Pollock et al. 1982) and at nearby Dassen Island (Newman and Pollock 1977).

Annual growth increment (carapace length, mm y^{-1})

Growth rate	**Male**	**Female**
Slow	2.8	0.9
Fast	4.8	1.5
Saldanha Bay	4.4	0.9
Dassen I.	4.4	0.6
Overall mean:	**3.8**	**1.3**

No data on growth rates are available for rock lobsters at Malgas Island specifically. Beyers & Goosen (in press) have correlated the growth rate of *Jasus* with the fecundity of females (number of eggs). They suggested that sexual maturity is reached at a large carapace size and that fecundity is high in areas with fast growth rates. The research site at Malgas Island was among the sites used by Beyers & Goosen (in press) in deriving this relationship. At this site they found that rock lobsters (of a given length) carry a larger number of eggs than at any of the other sites

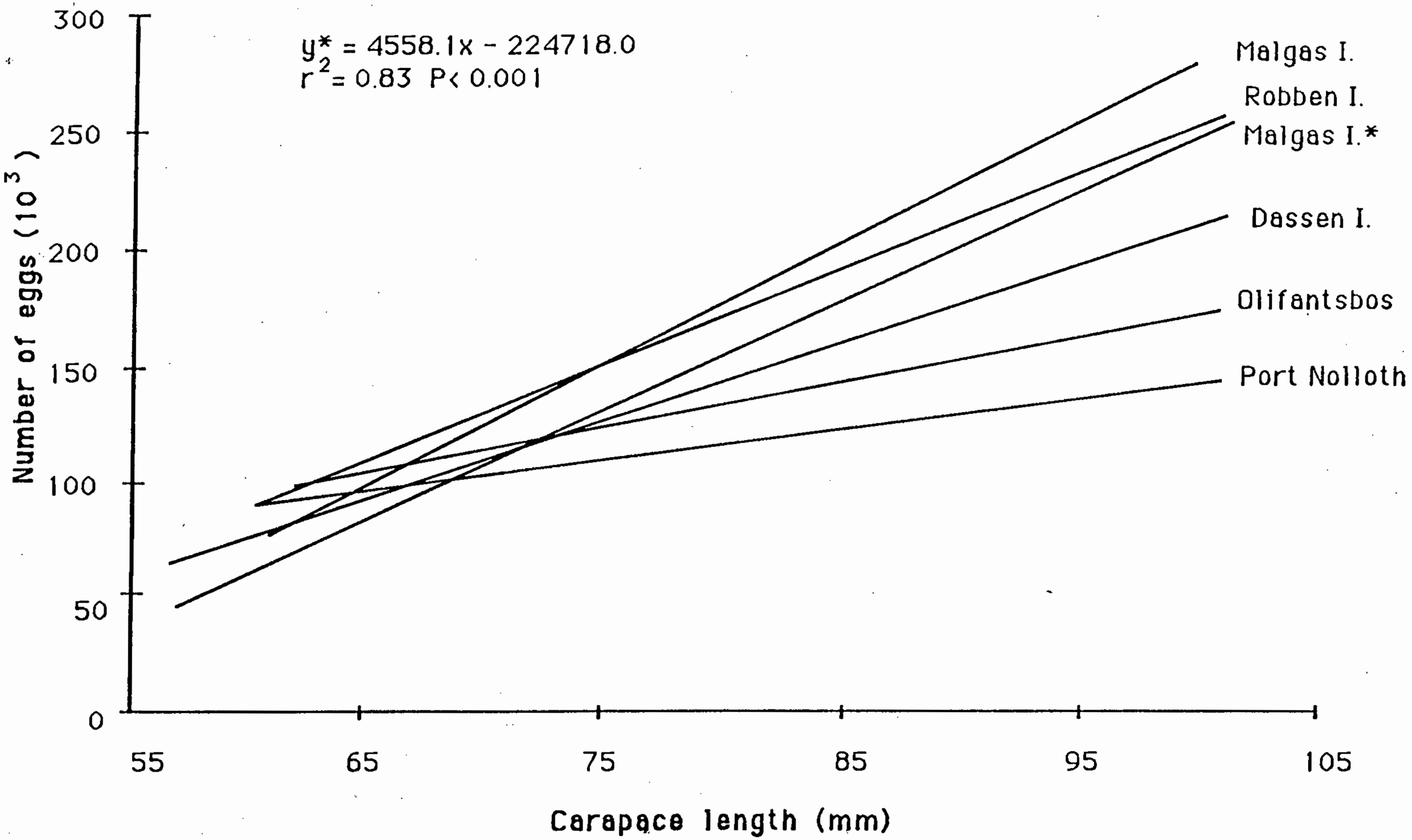

Fig. 6.6

Comparative regression lines describing the relation between carapace length and number of eggs carried by females *Jasus lalandii* at different localities (data from Beyers & Goosen in press).

*- Data obtained by the author.

examined on the West Coast, including Dassen and Robben Islands (see Fig. 6.6 for comparative curves of some of the sites). It is notable that Dassen and Robben Islands are considered to be among the sites with the fastest growing *Jasus lalandii* on the west coast (Newman and Pollock 1974a, 1974b; Wickens 1985; Beyers and Goosen (in press)). I repeated the observations made by Beyers & Goosen (in press), and found that over 77% of females in berry at Malgas Island were larger than 73mm (n = 153) and that the number of eggs they were carrying was positively correlated to their size and roughly equal to the numbers carried by rock lobsters at Dassen Island (Fig. 6.6). These results are similar to those obtained by Beyers & Goosen. Furthermore, the relatively large mean sizes of male and female *Jasus* at Malgas Island (99.44 and 75.42mm respectively) is close to the mean sizes found at Robben Island [males: 94mm, females: 84mm, (Heydorn 1969) and male: 88.53mm, female: 73.36mm (Pollock 1979)]. Several lines of evidence therefore suggest that the growth rate of rock lobsters at Malgas Island is very fast. Consequently the fast growth rate given by Wickens (1985) assumed as an estimation of the energy requirement for growth of the Malgas rock lobsters. To calculate this, the annual increment in Jasus' biomass was first calculated by converting the growth in size to weight, using the regression equation relating carapace size in mm to body wet weight in grams (Heydorn 1969):

Table 6.1: Summary table of energy requirement of *Jasus lalandii* population at Malgas Island (KJ m^{-2} d^{-1}).

Carpace size	Number m^{-2}		Respiration*	Reproduction**	Growth (both sexes)**		
midpoint (mm)	male	female	male+female	female only	slow	fast	overall
62.5	0.00	0.39	0.65	0.14	0.03	0.04	0.04
67.5	0.00	0.83	1.64	0.37	0.06	0.11	0.09
72.5	0.07	1.57	3.77	0.82	0.15	0.26	0.22
77.5	0.24	1.67	5.22	0.99	0.24	0.40	0.34
82.5	0.28	1.03	4.14	0.69	0.21	0.36	0.30
87.5	0.38	0.99	4.85	0.71	0.26	0.45	0.37
92.5	0.25	0.38	2.34	0.27	0.14	0.25	0.20
97.5	0.15	0.26	1.67	0.23	0.09	0.15	0.12
102.5	0.24	0.00	1.25	----	0.12	0.21	0.16
107.5	0.39	0.00	2.22	----	0.21	0.36	0.28
112.5	0.31	0.00	2.01	----	0.18	0.32	0.25
117.5	0.26	0.00	1.72	----	0.15	0.27	0.21
122.5	0.21	0.00	1.66	----	0.15	0.25	0.20
127.5	0.17	0.00	1.47	----	0.13	0.22	0.17
132.5	0.10	0.00	0.95	----	0.08	0.14	0.11
Total	**3.05**	**7.12**	**50.51**	**5.04**	**2.20**	**3.95**	**3.06**

Total daily requirement of *Jasus lalandii* is 59.50 KJ m^{-2}.

* Respiration in aquarium multipled by a factor of 1.45 to allow for activity (see text).

** Four percent added to allow for cost of synthesis. Ovarian development assumed to take 213 days (see text).

For Male $W = (L^{2.894})/1215.8650$

For Female $W = (L^{2.9729})/1600.7950$

where W = wet weight (g); and L = carapace length (mm).

The calorific value of *Jasus lalandii* is $14.53 kJg^{-1}$ (dry weight whole body) and 1g dry weight is equivalent to 3.6g wet weight, which means that for every gram increment in wet weight, the calorific content increases 4.04 kJ [calculated from data obtained by Field et al. (1980)].

Using this information, the total energy requirement for growth male and female *Jasus* at Malgas Island can be calculated, and amounts to $3.79 kJm^{-2}d^{-1}$. To this should be added 4% for the cost of synthesis (Brafield and Llewellyn 1982) which gives an annual requirement of $1441.75\ kJm^{-2}$ per individual (Table 6.1).

Summary of *Jasus lalandii*' annual energy requirement

By summing the above figures, and taking in account the size distribution and the sex ratio of the rock lobster population at Malgas Island, the annual energy required by an average of 10.17 individuals per square metre is:

$$R + P_r + Pg = 18436 + 1072 + 1441 = 20951\ kJm^{-2}y^{-1}$$

R = Respiration, P_r = Reproduction and Pg = Growth

Table 6.2: Calorific value (kJ m^{-2}) of standing stocks of benthic species at Marcus and Malgas Islands, considered as prey for *Jasus lalandii,* compared to the energy available from recruit sources (kJ m^{-2}) .

Standing stock (kJ m^{-2})

Place : Species	Marcus I.	Malgas I.
Porifera *	78	165
Polychaeta	332	27
Cirripedia	170	19
Small crustaceans	97	30
Other crustaceans	166	0
Choromytilus	42748	0
Aulacomya	26	2386
Burnupena spp.	4203	420
Other gastropods	218	0
Parechinus	378	0
Total:	48416	3049

Recruit species

Species	Energy value (KJ m^{-2} y^{-1})
Barnacles	25265
Mysids**	~94000
Mussel	295
Total:	**~119560**

* Porifera were found often in *Jasus* guts but are not normally considered as prey.

** Assuming total mortality of a single swarm, and assuming it sink to the bottom

This figure does not, however, take the absorption efficiency of *Jasus* into account. Since this has not been determined, the value of 64% for aquatic invertebrate carnivores (Bradfield & Llewellyn 1982) was used. Thus the rock lobsters must consume:

$$20951\ kJm^{-2}y^{-1}\ (100/64) = 32736\ kJm^{-2}y^{-1}.$$

In the laboratory the daily consumption of rock lobsters with unlimited food was found to be: $0.00004L^{3.75}$ kJd^{-1} [where L = carapace length mm, (Griffiths and Seiderer 1980)]. If this equation is used for the rock lobster population at Malgas Island, a much higher figure for annual consumption is obtained (approximately 87000 kJm^{-2}). However, ad lib feeding probably yields an much higher estimation of energy requirement compare with the actual intake of energy by *rock lobster* in the field.

FOOD SOURCES AT MARCUS AND MALGAS ISLAND

The standing stock (in KJm^{-2}) of rock lobster prey species at both Marcus and Malgas Islands is summarized in Table 6.2. The data are derived from the values for biomass (Chapter 2) which have been converted into units of energy. Most of the calorific conversions were taken from Field et al. (1980), but the value for *Choromytilus meridionalis* is from Griffiths (1981), this for *Aulacomya ater* from Griffiths and King (1979), and this for the Cirripedia was measured by the author.

From the values in Table 6.2 it can be seen that the benthic fauna at Marcus Island has about sixteen times more energy available for *Jasus* than that at Malgas Island. *Choromytilus* is the main energy source (88%) at Marcus Island, while at Malgas Island, *Aulacomya* is the main energy source (78%) apparent in the existing benthos. The standing calorific value of all the benthic prey at Malgas Island is very small, being only 9% of the calculated annual requirement of *Jasus lalandii*. *Aulacomya ater*, which provides 78% of this standing stock, is often considered a major food source for rock lobster (Heydorn 1969; Griffiths and Seiderer 1980; Pollock 1986). Heydorn (1969) found that in 64.8% of the 1200 *Jasus lalandii* be examined, the gut contents consisted of fragments of *Aulacomya*. Pollock (1979) recorded that in 97% of 118 stomachs of *Jasus lalandii*, mussel shell fragments were the major constituent. Indeed, the availability of mussels is, in many cases, considered as the main factor limiting the growth rate and population size of *Jasus*. For instance, Newman and Pollock (1974b) suggested that a correlation exists between benthic biomass (mostly *Aulacomya*) and rock lobster growth rate. However not all mussels are accessible to *Jasus lalandii*. When comparing the size composition of *Jasus* and *Aulacomya*, Pollock (1979) describes how *Jasus* at Robben Island, "are restricted to feeding only on mussels (*Aulacomya ater*) smaller than 60mm long", and that this size group constituted only 20% of the total mussel biomass. Griffiths and Seiderer (1980) found that for each size class of rock lobster there is a maximum critical size of *Aulacomya* above which the rock lobsters cannot prey on the mussels. They obtained the following regression equation describing this correlation: $Lm = -11.41 + 1.04Lr$.

When Lm = Critical length of mussel (mm) and

Lr = Carapace length of *Jasus* (mm)

Griffiths & King (1979) calculated the production: biomass ratio (P/B) of *Aulacomya* as 1.13. Using this figure, and the mean annual standing stock 2386.30 kJm^{-2} the annual production of *Aulacomya* at Island can be estimated at 2696.52 $kJm^{-2}y^{-1}$. This value is only 8% of the calculated minimal annual energy requirement of *Jasus* at Malgas Island. Furthermore given the size frequency of *Aulacomya* at Malgas Island (Fig. 6.2a), 83% of the *Aulacomya* standing stock at Malgas Island is above the critical size accessible to 80% of the rock lobsters (Fig. 6.2b), which means that the standing stock of *Aulacomya* at Malgas Island can only supply 1% of the annual energy requirements for most of the rock lobster population. One other factor influences the availability of *Aulacomya* to *Jasus*: recruits and individuals small enough to be eaten were almost all found either in inaccessible place under boulders, or within clumps amongst and under very large mussels. Although this was not quantified, it was clear that it further reduced the availability of small *Aulacomya* to rock lobster. Taken all

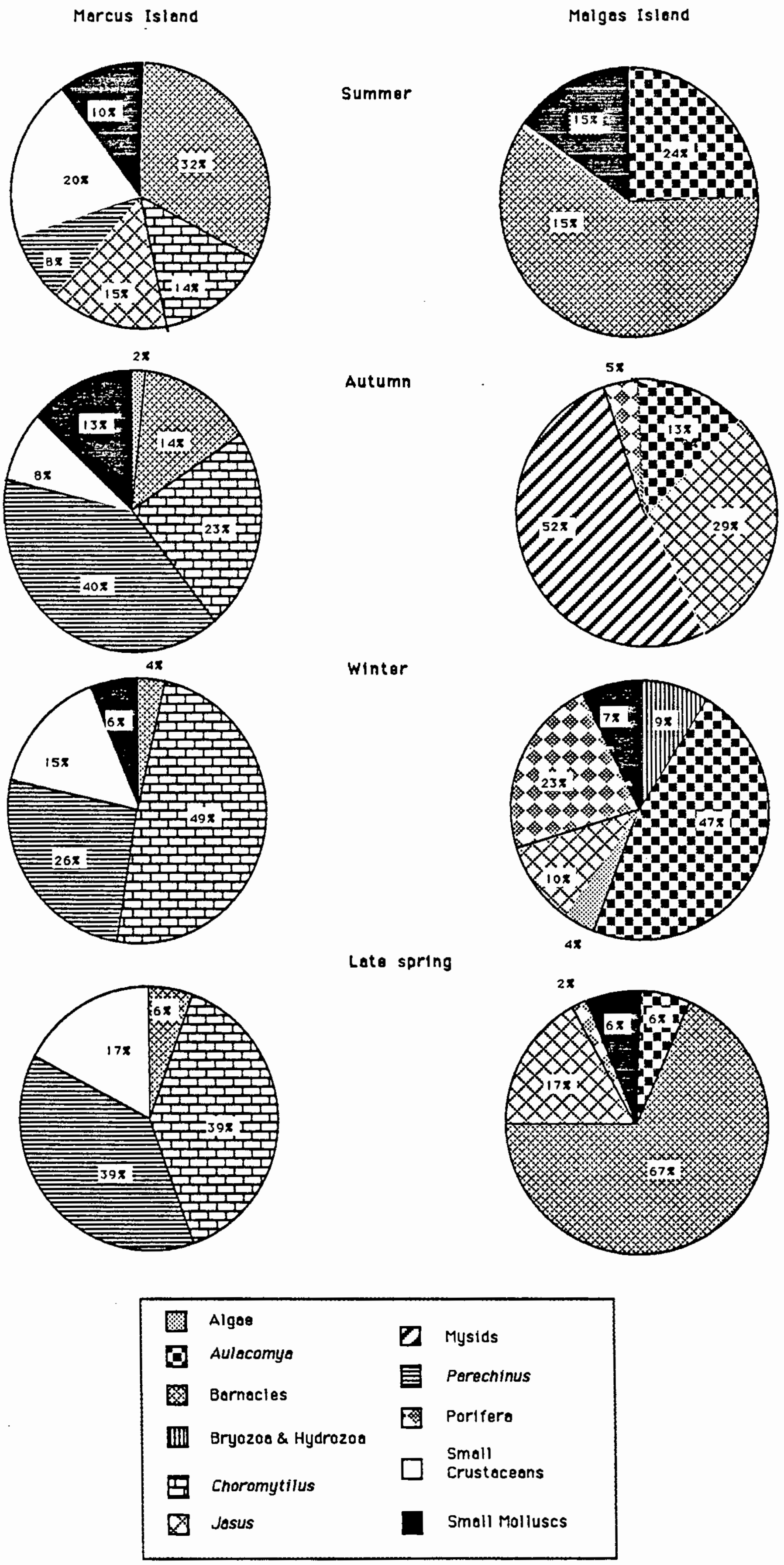

Fig 6.7

Relative volumes of different prey groups in the gut contents of *Jasus lalandii* (of all sizes) from Marcus and Malgas Islands, at different times of the year.

these factors into account, it is obvious that the standing stock of *Aulacomya* plays an insignificant role in the total energy requirements of the large population of *Jasus* at Malgas Island.

ANALYSES OF *JASUS LALANDII* GUT CONTENTS

Gut contents were taken from rock lobsters at both islands at different seasons between 1983 and 1986 (Fig. 6.7). At Marcus Island rock lobsters are scarce and occur only at the periphery of the mussel beds, where they feed throughout the year on common benthic macrofaunal species, particularly sea urchins (*Parechinus angulosus*), the black mussel (*Choromytilus meridionalis*), barnacles, small molluscs and crustaceans. This diet corresponds to the benthos that is locally available, and accords with previously published information on *the* diet of the rock lobster (Heydorn 1969; Newman and Pollock 1974b; Pollock 1979, 1982; Griffiths & Seiderer 1980;). The relatively large proportion of the small barnacle (*Notomegabalus algicola*) in the February (32%) and April (14%) gut samples was surprising, and is discussed in more details later in this section.

At Malgas Island the rock lobsters, not surprisingly, exhibit a completely different dietary pattern. In February and November (summer and late spring) the gut contents were dominated by tiny fragments of the barnacle *Notomegabalanus*

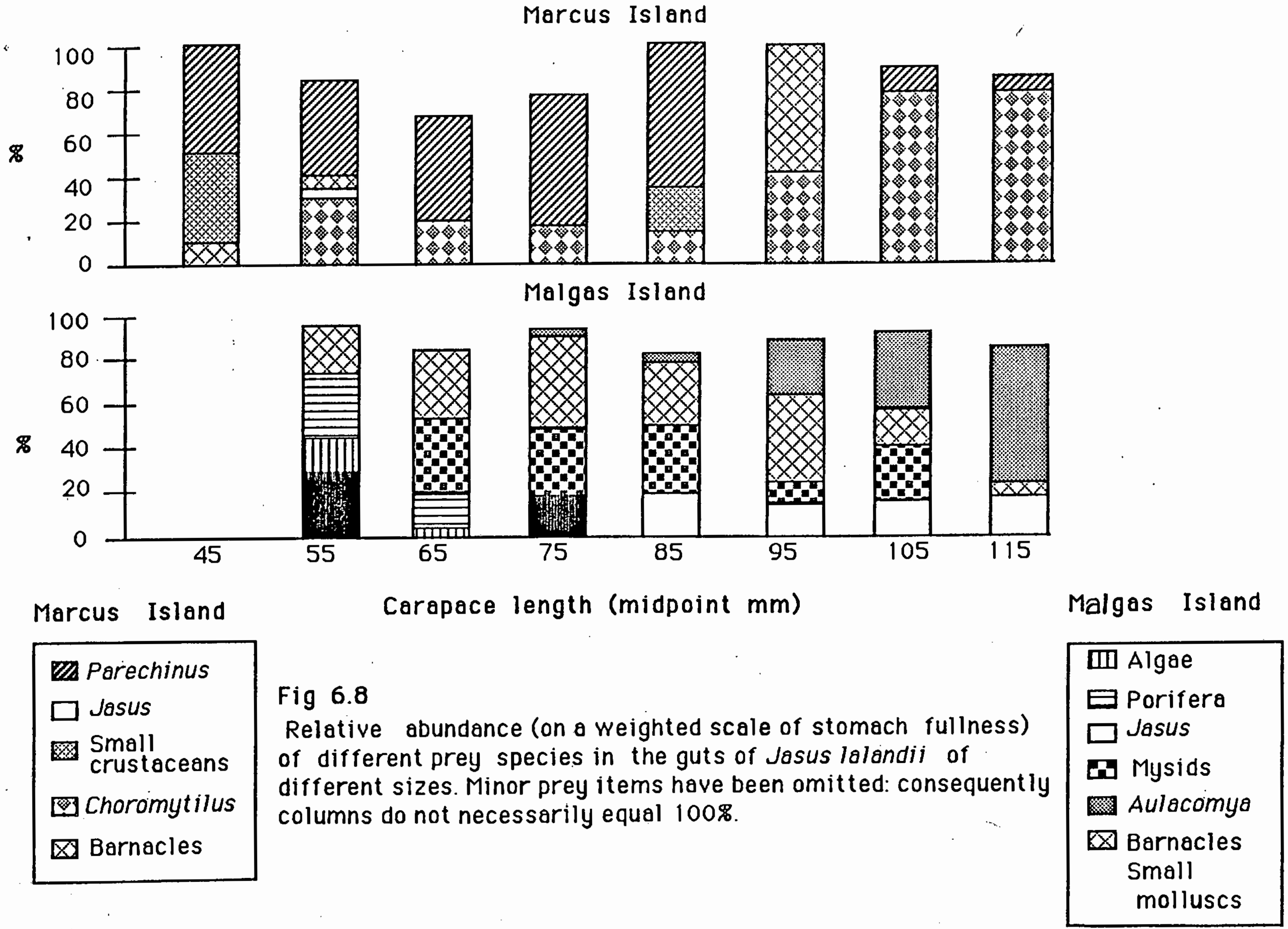

Fig 6.8
Relative abundance (on a weighted scale of stomach fullness) of different prey species in the guts of *Jasus lalandii* of different sizes. Minor prey items have been omitted: consequently columns do not necessarily equal 100%.

algicola (60% and 67% respectively). Additional material included small amounts of rock lobster exuvia and pieces of *Aulacomya* shell. In April (Autumn) more than 50% of the gut contents comprised planktonic mysids (*Mysidopsis schultzei*), while 29% consisted of hard remains of *Jasus* evidencing cannibalism. In August (winter) the diet was more diverse and included *Aulacomya* shell fragments (47%) and poriferan remains (23%), which were identifiable by the presence of spicules in the proventriculus. In addition to these major components, the gut contents of rock lobsters from both islands contained lesser amounts of small crustaceans, small bivalves and gastropods, and those from Malgas Island also included fragments of some algae, bryozoans and hydrozoans. These components occurred in most of the gut samples throughout the year and were a permanent feature of *the* diet, although some of this items may have been inadvertently consumed while the rock lobsters were feeding on other prey.

Analysis of diet could also be related to the size of the rock lobsters. At Marcus the black mussel *Choromytilus meridionalis* became increasingly important in the diet of large rock lobsters as they increased in size, while the urchin *Parechinus angulosus* was of greater importance to small rock lobsters (Fig 6.8). At Malgas Island though, smaller rock lobsters fed on barnacles, mysids, small molluscs and, to a certain extent, on algae and Porifera, largely depending on what was available seasonally. The larger rock lobsters also fed on these organisms but *Aulacomya* progressively dominated the diets of the larger size groups, which also showed a greater degree of cannibalism. This pattern of cannibalism is similar to that observed by Berry (1971) for the Natal spiny lobster (*Panulirus homarus*).

To summarize, at Marcus Island where prey species are abundant, the rock lobsters feed predominantly on two of the commonest species there, *Parechinus angulosus* and *Choromytilus meridionalis*. But at Malgas Island, where food resources were scarce, they feed on unusual food species. The diet appears to be completely dominated by seasonal fluctuations in the prey species. One surprise was that barnacles seem to play a major role in the diet of *Jasus lalandii*, even although they were never detected when the macrobenthos was sampled. Berry (1971) has, however, reported that barnacles play an important role in the diet of juvenile *Panulirus homarus*, but they have never been considered an important food source for *Jasus*.

Cannibalism also appears to be more important at Malgas Island, compared with other areas where food is abundant. Under artificial conditions it has been observed that a high population density tends to stimulate cannibalism, particularly of freshly moulted animals. In areas with low population density, cannibalism appears to be absent (Atena and Cobb 1980). The majority of *rock lobster* remains in the gut samples from Malgas Island were recorded in April and August, which coincides with the female moulting season but is slightly early for the male moulting season (Heydorn 1969; Newman & Pollock 1971; Pollock 1982, 1986). Shortage of food, high population density and moulting during the winter season (April - September) at Malgas Island may then stimulate cannibalism in the rock lobster community at that time of the year.

PRODUCTIVITY OF BARNACLES

As discussed above, the barnacle *Notomegabalanus algicola* occurred in large quantities in gut samples taken from rock lobsters during certain seasons at Malgas Island. However, very few were observed on exposed substrata during the three annual surveys of the benthic biomass (see Chapter 2), although they occur in large quantities on floating objects. This suggests that the rock lobsters prey on newly recruited barnacles with such rapidity that the barnacle population at Malgas Island is never capable of establishing itself on the rocky sea-floor. The question arises whether these tiny cirripedes, whose bodies consist mostly undigestable calcareous shell, are capable of providing enough energy to meet the needs of the high rock lobster population.

Recruitment of *Notomegabalanus algicola* had a distinctive seasonal pattern with peak setlement occurring

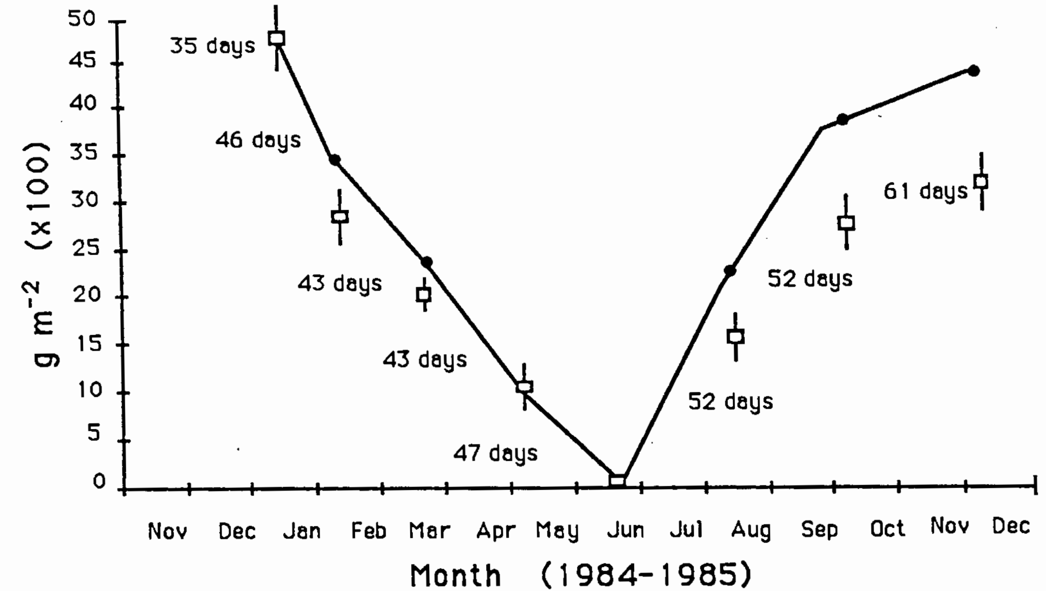

Fig. 6.9

Monthly biomass (wet weight m^{-2} ± s.d.), of recruited barnacles on the settlement plates. The empty box is the actual observations while the black dots are the adjusted results which take to account the drop in the accumulated biomass of the barnacles after 40 days (see text).

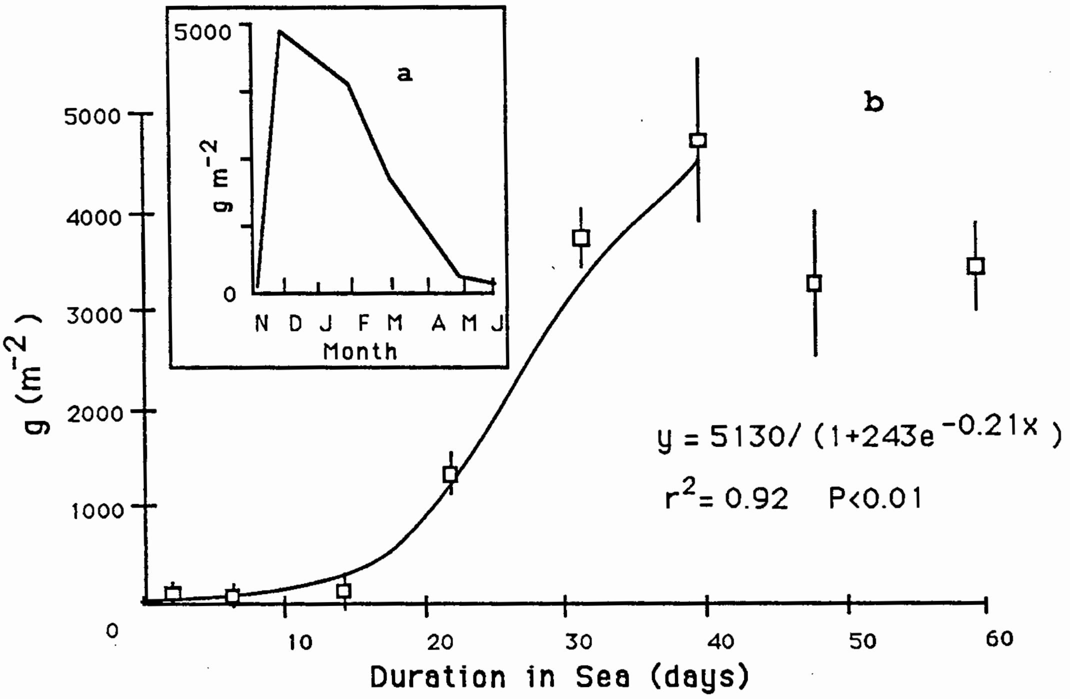

Fig. 6.10

Monthly (insert) and daily production of barnacles (wet weight gm^{-2} ± s.d.) during the peak season of settlement (November, December). The fitted logistic curve for the daily production describes only the early period (40 days) of settlement, before the accumulated biomass started to drop.

December and January when a maximum biomass of 4900 gm^{-2} (wet weight) was recorded (Fig 6.9). Recruitment then fell off until June, when no barnacle recruitment was recorded. As spring approached, recruitment again increased (Fig 6.9). On the plates that were continuously monitoring to quantify the cumulative effect of successive settlement and to estimate production, it was observed that barnacle biomass initially rose and then dropped sharply after about 40 days, once the settlement plates had been completely coverd. The biomass continued to decline over the 7 months that the plates were monitored (Fig 6.10a). Successive waves of recruitment smothered the first colonisers, so that the overcrowded barnacles became loosely attached to the plate and to each other and fell off. To calculate the initial production of recruiting barnacles more accurately, a 61-day experiment was initiated on the 15th of November 1984, when barnacle recruitment was close to its peak. It was assumed that over period longer than 40 days production would be restricted by the size of the plates. Furthermore, barnacles at Malgas Island are unlikely to survive as longer than 40 days, as discussed below. A logistic equation relating total wet weight (W, in grams) to age (A, in days) was fitted to the daily production of barnacles over only the first 40 days of the experimental period since after this period a sharp drop in the accumulated biomaas occured (Fig. 6.10b).

$$W=5130/(1+243e^{-0,21A})$$

After transformation of the data into units of energy, this could be expressed as

$$\text{Barnacle energy value } (kJm^{-2})=3403/(1+32047e^{-0.47302A})$$

To determine the age at which *Notomegabalanus* is consumed by *Jasus*, the thickness of barnacle shells found in the lobsters' guts was fitted into a regression equation relating shell plate thickness (T, in mm) to barnacle age (A, in days), which was determined by subsampling barnacles of known ages from the plates. The best fitted equation was again of a logistic type:

$$T=0.99817/(1+43.918e^{-0,17236A})$$

$(n=364,\ r^2=0.92,\ P<0.01)$.

Using this equation, and the data on the shell thickness of barnacles in the rock lobsters' guts, it was found that barnacles that were being eaten had an average minimum age of approximately 20 days and an average maximum age of approximately 38 days (Fig 6.11). This information was based only on unbroken barnacle plates extracted from the gut, but obviously very small juvenile barnacles were also consumed. There was no correlation between the minimum age of the barnacles eaten and the carapace size of the rock lobsters. The correlation between maximum age of barnacles and carapace size was, however, significant ($r = 0.75$; $p<0.01$, see Fig 6.11). This suggests that small rock lobsters can only feed on the younger (smaller) barnacles while the large rock lobsters can feed on full size range available.

At this stage it is necessary to calculate the relevant annual production of *Notomegabalanus algicola* that is available for consumption by the rock lobsters. The following assumptions were made in order to simplify this calculation but they all have the effect of making the estimation conservative: a) Jasus feeds on the barnacles when they are between the age of 20 to 40 days after first settlement, including secondary settlements; b) When feeding the rock lobsters clean the substratum completely; c) Jasus feed on one settlement a month (mean age of barnacles eaten equals 30 days; d) in the main season of recruitment (August to March) the biomass of barnacles reaches a peak after 40 days and they declines by about 35% over the subsequent 10 days. Production would therefore have been higher over the initial 40 days of recruitment than indicated by the biomass recorded over longer periods. This decline was used to estimate the degree to which production exceeded the recorded value for biomass (Fig. 6.9). This last assumption is important because, in many cases, due to bad sea conditions, the barnacle settlement plates were monitorded after periods exceeded 40 days (Fig 6.9).

Using the data in figure 6.9 a total annual production of 36285gm^{-2} (wet mass) was calculated (by summing the monthly production after adjusting the biomass to allow far declines when observations were made at intervals in excess of 40 days).

To convert this annual production to energetic units, the wet weights of *Notomegabalanus algicola* was converted to a dry weight. The average ratio of dry weight:wet weight was approximately 33%. The dry weight production of *Notomegabalanus* at Malgas Island was therefore 11975$gm^{-2}y^{-1}$. The calorific value of *Notomegabalanus* was measured using a bomb calorimeter and found to be 2.11 kJg^{-1} (dry weight). Annual production in calorific terms will thus be 25265kJm^{-2} which is about 77% of the calculated annual energetic requirements of the rock lobsters at Malgas Island

(25265/32737 kJm^{-2} = 0.77).

However one has to remember that 80% of the barnacle production is concentrated during the seven months of spring and summer, and during this period the barnacles can theoretically fulfill most of the rock lobsters' energy requirements.

MUSSEL PRODUCTION

After barnacles settle, they provide other benthic species with an attractive substratum which is rough and so provides better attachment and shelter to the new recruits, mostly mussels, small crustaceans and tunicates. While preying on the barnacles the rock lobsters also consume these other species. If the mussels are left undisturbed, they accumulate a substantial biomass, but this takes some time (Fig. 6.12). A rapid increase in mussel biomass starts only 80 days after the onset of recruitment, and prior to this there is very little accumulation of biomass.

Mussel recruitment is high in autumn, with a peak of 70g (wet weight) m^{-2} during April (Fig. 6.12). Du Plessis (1977) found a similar seasonal pattern for *Choromytilus* recruitment in Saldanha Bay during 1972-1975, but also recorded large fluctuations in the mass of mussels settling in different seasons and at different localities.

Using the same methods described above to calculate barnacle production, a value of 204.68 $gm^{-2}y^{-1}$ (wet weight) was obtained for mussel production. If 1g wet weight = 0.503g dry weight; and 1g dry weight = 2.870 kJ (the mean for *Aulacomya* & *Choromytilus*, based on data from Field et al. (1980) for *Aulacomya* and from Griffiths (1981) for *Choromytilus*), then annual production for mussels in the first days after recruitment is $295.48kJm^{-2}$. This is less than 1% for the annual requirement per square metre of *Jasus* at Malgas Island. Thus, mussels are capable of developing a very high biomass if they are not preyed upon, their early growth in the 30 days after recruitment at Malgas (by which time they will have been eaten by the rock lobsters) contributes only an insignificant amount of energy towards

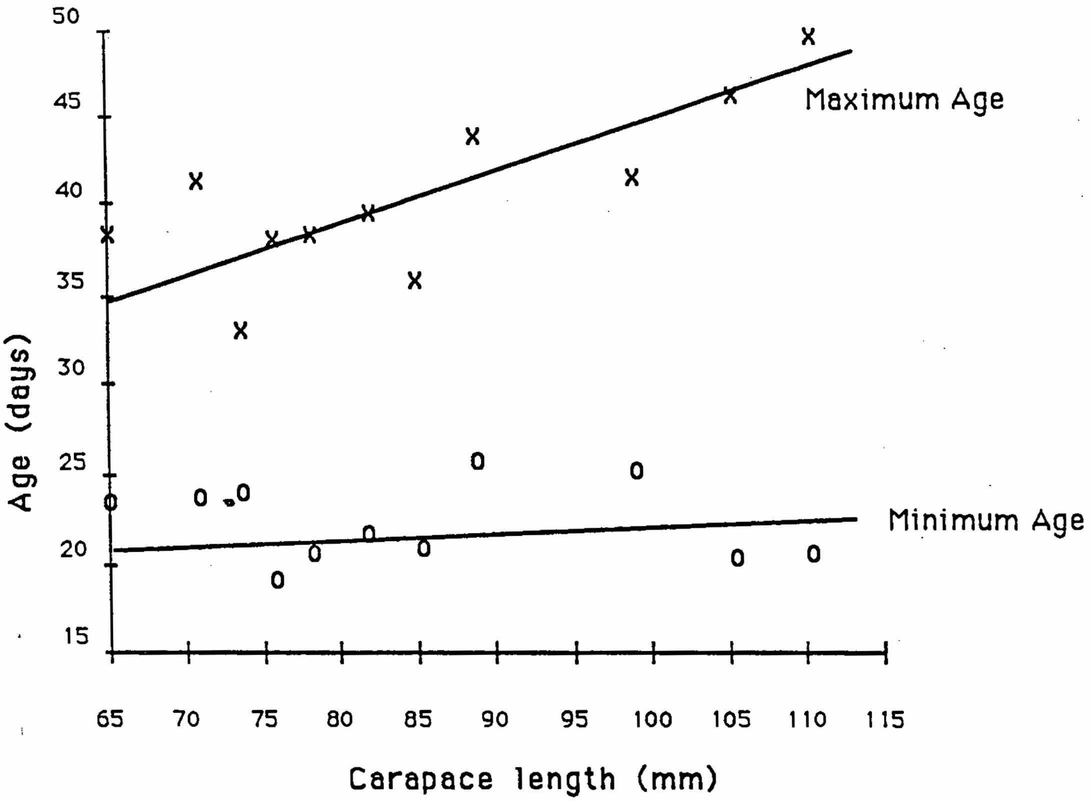

Fig. 6.11

Average minimum and maximum age of barnacles which were eaten by rock lobsters of different carapace length.

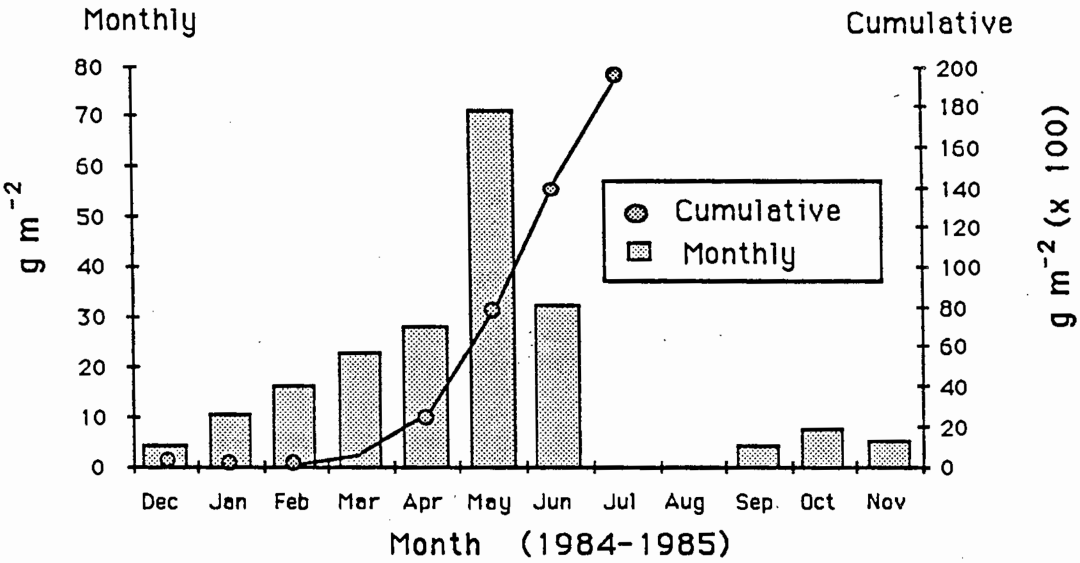

Fig. 6.12

Seasonal and accumulated biomass (wet weight) of recruited mussels on the settlement plates.

the needs of the rock lobsters - in contrast to the barnacle recruits.

MYSID PRODUCTION

As reported in chapter 2, large and dense swarms of mysids were often observed covering the rocky sea bed around Malgas Island. These swarms extended from the sea floor to about 2m below the surface. This phenomenon was observed throughout the year, but more often during the winter months. Mysids are common on the South African west coast especially near dense kelp beds (Carter 1983), but have never been reported as prey for rock lobster populations. Despite this, in the autumn gut samples more than 50% of the identified food was composed of the mysid *Mysidopsis schultzei*. The rock lobsters were never observed feeding on the mysids and there is no evidence of how they may capture mysids. Carter (pers comm.) has suggested that the sea of sand surrounding the narrow rocky belt at Malgas Island may have prevented the mysids from leaving the area. He also suggests that heavy mortality of mysids may deposit thick layers of them on the bottom, enabling *Jasus* to feed on them.

It was impossible during the present work to adequately research the actual annual production of *Mysidopsis* and its contribution to the annual energy consumption by *Jasus* at Malgas Island. However, in order to get some idea of the amount of energy available to *Jasus* from this source, data on a common and very similar species, *Mysidopsis major*, were used (Carter 1983 and pers comm.).

The estimated number of mysids in a 1 cubic metre swarm is between 1.6 X 10^5 and 5 X 10^5. The vertical spread of the swarm varies from 2 to 8 metres depending on the depth, and an average of 5m has been assumed. The mean dry weight of 1 mysid is 3.03mg and the calorific value 18.81 kJg^{-1} dry weight. A 5 cubic metre swarm will contain 1.65 X 10^6 mysids (assuming 3.3 x 10^5 mysids m^{-2}) with a total dry weight equal to $4.99x10^3$g and a calorific value of 9.4 X $10^4 kJm^{-2}$. Assuming that the whole swarm dies and sinks to the bottom, this figure for one swarm is equivalent to almost 3 times the annual energy requirement of *Jasus* at Malgas Island. It will, of course, only intermittently become available to rock lobsters. It cannot be suggested that the mysids are a regular food supply, or that the calculations made here are anything but a very crude estimation of their contribution to the rock lobsters. Nevertheless, their potential importance as a source of food is very high.

CAGING OF ROCK LOBSTERS

To test if *Jasus lalandii* could survive solely on fresh recruitment in the absence of macrobenthos, rock lobsters were caged for 8 months at Marcus Island and for 9 months at Malgas Island (before a severe storm destroyed the cages).

The bases of the cages were covered in plates similar to those used in the barnacle production experiment and the mesh was fine enough to exclude benthic species larger than a few millimetres. Regular checks on the condition of the caged rock lobsters at both islands showed that they all survived and were feeding on any recruits that colonised the plates within the cages. The control chambers that lacked rock lobsters were covered after a short time with a thick layer of benthic species, while the plates and walls in the experimental chambers remained completely clean because of rock lobster predation on recruits.

GENERAL CONCLUSIONS

One of the main conclusion drawn from this study is that it will be necessary to revise the conventional view that the maintenance and growth of rock lobsters is dependent on an adequate macrobenthic standing stock. At Malgas Island the standing stock of the macrobenthos is insufficient to support more than 9% of the energetic needs of the rock lobster population. Despite this, the rock lobsters are apparently fast growing, as shown by their high fecundity, the large size at which females become sexually mature and their large average size (Beyers & Goosen in press).

Much of the diet of the rock lobsters comprises young recently recruited barnacles, especially *Notomegabalanus algicola*, which provide enough energy input and annual production to support the energetic needs of the rock lobsters during most months of the year. Barnacles have not previously been recorded as an important source of food for *Jasus lalandii*, let alone considered sufficient to meet most of their energetic requirements. Rock lobsters which were kept in cages where they had no access to macrobenthic organisms survived for 8 to 9 months, consuming recruiting species shortly after they settled, and keeping the substratum bare in the process.

At times of low barnacle recruitment (winter and autumn) the rock lobsters turned to another unconventional source of food. Mysids then formed a dominant component of the gut contents of *Jasus* and, potentially, can supply more than enough to meet the energetic needs of the rock lobsters during certain periods. Once again, there have been no previous reports of rock lobsters feeding on mysids. It remains to be determined how the rock lobsters capture mysids, but it is conceivable that they are feeding on dead mysids that have deposited on the bottom.

It seems that cannibalism occurred more often among the rock lobsters at Malgas Island (Fig. 6.7, 6.8) than at other communities on the South African west coast (Heydorn 1969; Pollock pers. comm.), particularly during seasons when barnacle recruitment was sparce. Clearly rock lobsters are opportunistic and can capitalise on unorthodox sources of food which can sustain even the very dense populations found at Malgas Island.

Aulacomya ater, normally the most important prey species for rock lobsters, was important only to the large rock lobsters at Malgas Island and then only in periods when barnacle recruitment was at a low level.

Clearly it is no longer possible to quantify food availability for rock lobsters in terms of benthic standing stocks as has previously been done (Heydorn 1969; Newman & Pollock 1974b; Pollock 1979; Griffiths and Seiderer 1980; Seiderer <u>et</u> <u>al</u>. 1982; Wickens 1985; Beyers & Goosen in press). In fact, much of the biomass that is recorded in areas where rock lobsters are dense comprises species that are inedible or exceed the critical size available to rock lobsters. Conversely, biomass surveys almost invariable fail to detect (or, at best, underestimate) the importance of a continual input of recruits which can supply a substantial source of energy even though their biomass is not detectable. Substantial errors may arise in studies of energy flow which ignore the role of recruits which are consumed by carnivors shortly after settlement.

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CHAPTER 7 - SUMMARY

INTRODUCTION

Despite the environmental similarity of Marcus and Malgas Islands (Chapter 1), each supports a completely different benthic community (Chapter 2), representing extreme expressions of the same ecosystem (Chapter 3). While Marcus Island supports a huge population of black mussels (*Choromytilus meridionalis*) and many other epibenthic species eg. whelks (mainly *Burnupena* spp.), sea-urchins (*Parechinus angulosus*) and holothurians (mainly *Pentacta doliolum* and *Thyone aurea*) as well as large cryptic fauna of small animals such as isopods, amphipods and polychaetes but very few rock lobsters and seaweeds. Malgas Island is dominated by a very large population of rock lobsters (*Jasus lalandii*), many seaweeds and very few other species, notably two species of whelks (*Burnupena papyracea* and *Argobuccinum pustulosim*), sponges and tunicates.

The aim of this chapter is to summarise in two major models the information which has been gathered during the four years of research work (1983-1986) and is documented in the previous chapters. The models illustrate the processes by which the two, contrasting, benthic communities were developed and are maintained at Marcus and Malgas Islands (Figures 7.1 and 7.2). In addition a third model has been

Rock lobster depleted grounds

(Marcus Island)

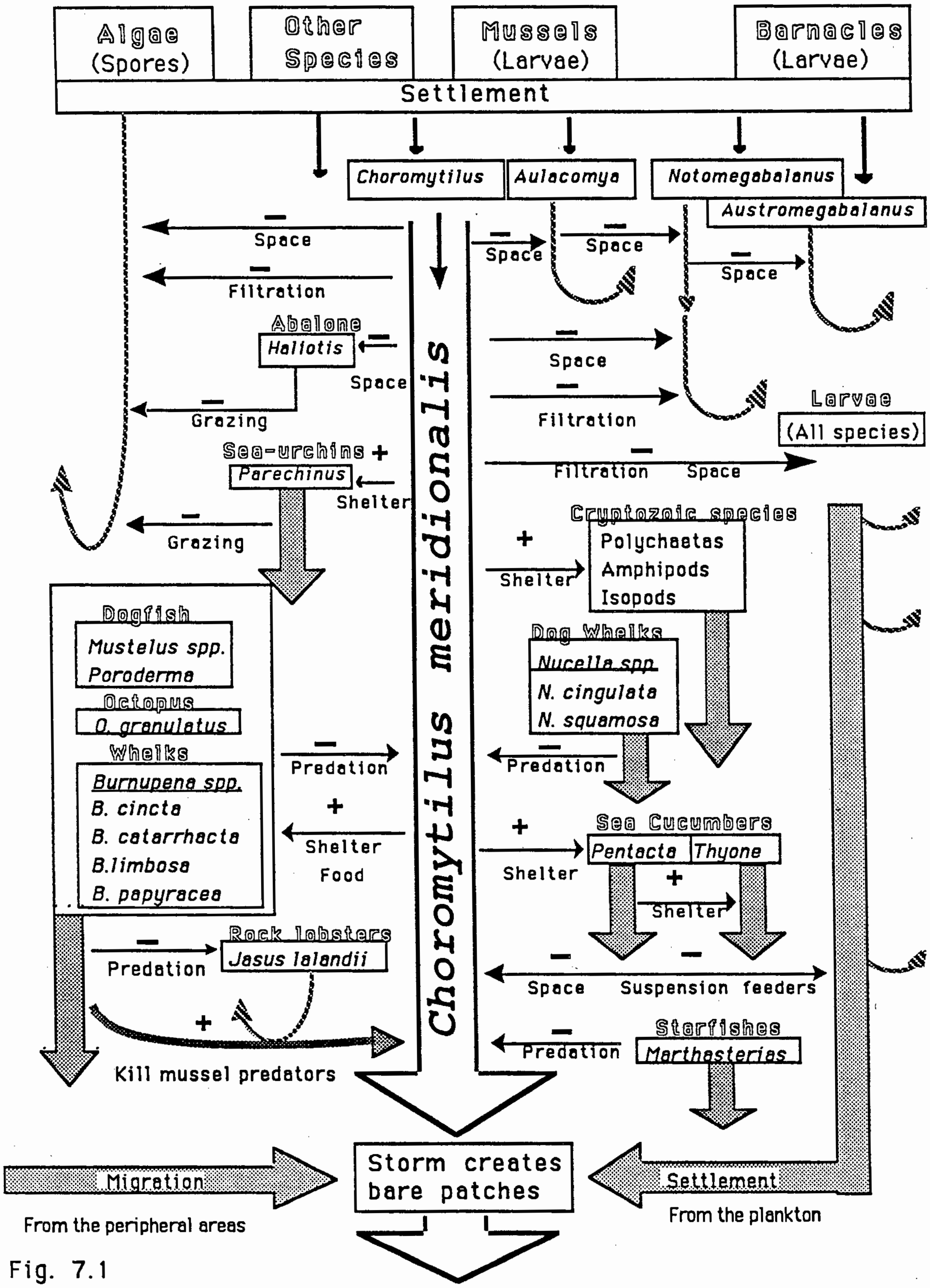

Fig. 7.1

Model of species succession and interaction at a site in the Benguela ecosystem where rock lobsters are depleted (Marcus Island).

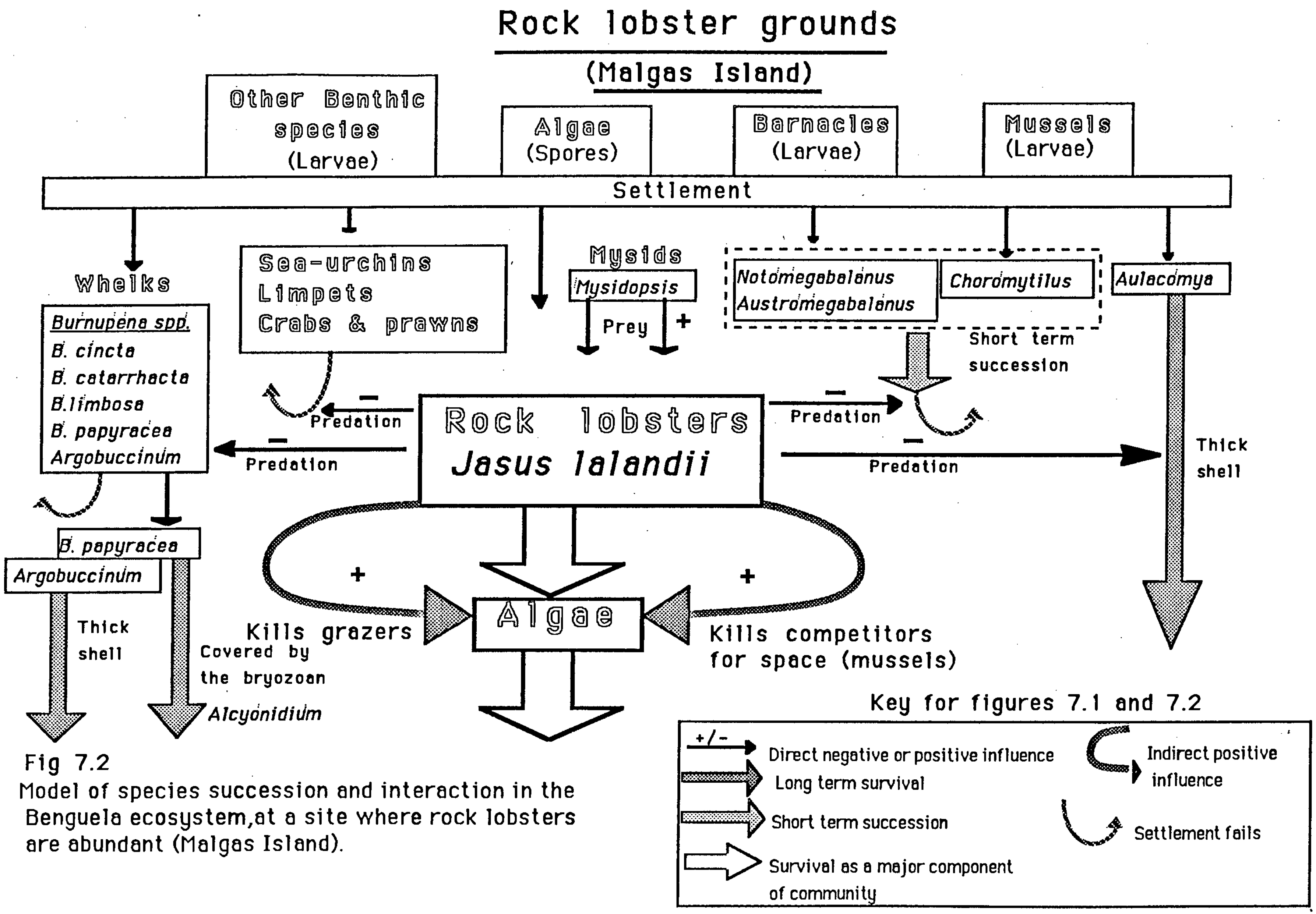

Fig 7.2
Model of species succession and interaction in the Benguela ecosystem, at a site where rock lobsters are abundant (Malgas Island).

included which describes a trophic web for each of these two benthic communities (Fig. 7.3).

By using these models it may be possible to analyse the functioning of other shallow-water benthic communities in the Benguela upwelling ecosystem without conducting a full-scale survey, but merely by sampling some of the major species. The idea is that qualitative information on the species hierarchy, rather than quantitative measurements, should be sufficient to understand how the communities functions. For example, in areas where the molluscs *Burnupena papyracea*, *Argobuccinum pustulosum* and *Aulacomya ater* are prevalent, one can assume that the areas are dominated by rock lobsters. By contrast, areas where other gastropod species and the black mussel exist, a small population of rock lobsters (*Jasus lalandii*) could be expected.

RECRUITMENT

Two sources of benthic recruitment supply the sublittoral benthos. First, there are benthic species which have a pelagic larvae stage which is dispersed in the plankton and can supply a number of widely spaced and differing habitats and benthic communities. secondly, there are species that lack larvae or have larvae which are not present in the water column but remain in the benthos itself

[Thorson 1950, 1966; Mileikovsky 1971; Meadows and Campbell 1972; Osman 1977; Paine and Levin 1981; Connell and Keough 1985; Gaines and Roughgarden 1985; Grahame and Branch 1985 (in review)]. The latter source is local and specific to each area, and is restricted to species in the existing adult benthic community. However, emigration of adults, strong wave action and currents can cause local benthos and larvae of the second type to disperse and expand these range even if their potential to colonise distant areas is restricted (Connell and Slatyer 1977; Connell and Keough 1985). In addition, some shallow-water benthic species are common both littorally and sublittorally so the fauna of both regions should be examined when considering the potential for recruitment. The ability of a recruited species to subsequently establish itself is largely dependent on existent occupants, assuming physical conditions are suitable (Keough 1983; Hiscock 1985; Branch et al. 1987)

At Malgas Island the establishment of newly recruited species is ruled predominantly by the enormous rock lobster population and only unpalatable species are able to reach maturity in any significant number [eg. *Pyura*, seaweeds and sponges (Chapter 2)]. Prey species are almost completely absent from the Malgas Island benthos although their larvae occur in the water column and both can and do recruit to the benthos. In fact, species which were never sampled as adults at Malgas Island appeared in areas as soon as they were protected by cages from rock lobster predation [eg. black mussels, some echinoderms, several gastropods and barnacles (Chapter 3)]. Another manifestation of this is the settlement of barnacles at Marcus Island on objects floating above the bottom, out of reach of rock lobsters. On the sea floor where the larvae are exposed to extensive filter feeding and other forms of predation, barnacles are rarely found. Similarly seaweeds, which are normally very scarce at Marcus Island, can establish themselves on objects above the sea floor away from the large populations of the grazing sea urchins (*Parechinus angulosus*) and filter feeders (Chapter 2). This continuous "invisible" flow of recruited species to the benthic ecosystem plays an important role in the energy cycle of the benthic communities (which has so far been ignored in most studies of energy flow. Examples include the role of juvenile mussels and barnacle in the rock lobsters' diet at Malgas Island and the presumed role of seaweed sporelings as a source of food in the diet of *Parechinus angulosus* at Marcus Island (Chapters 2 and 3).

PREDATION AND COMPETITION

Competition for space is directly affected by predation. The competitive ability of species depends largely on the amount of predation and environmental disturbance to which they are exposed (Dayton 1971; Paine 1974; Connell and slatyer 1977; Ayling 1981; Bernstein _et al_. 1983; Branch 1983; 1985; Sebens 1985). At Marcus and

Malgas Islands the competitive interaction between the major space-occupiers (barnacle, mussels, algae and holothurians) are all modified by the degree to which they are disturbed by predation and wave action.

INTERACTIONS BETWEEN MUSSELS

Aulacomya ater and *Choromytilus meridionalis* are the two most abundant species in the sublittoral zone on the west coast (Velimirov et al. 1977; Field et al. 1980; C. L. Griffiths 1981; Griffiths 1981). Although they have similar feeding habits and requirements (Griffiths 1980a, 1980b Stuart 1982) and occur in the littoral zone, together with an other dominant mussel, *Mytilus galloprovincialis*, they rarely occur together sublittorally. *C. meridionalis* is much more vulnerable to predation than *A.ater* because of its thinner and weaker shell (Griffiths and King 1979). It does, however, grow faster and seems a better competitor and more tolerant of stressful physical conditions (such as silt action, smothering by other animals and intertidal desiccation) than *A. ater* (Chapter 4). At Marcus Island where predation is low, *C. meridionalis* is the dominant species when both species settle equally on the same available space *C. meridionalis* outgrows *A. ater* in less than 6 months (Chapter 3 and 4). At Malgas Island where predation by rock lobsters is intense, *A. ater* is the dominant mussel, although it is not abundant and never forms continuous thick beds like those of *C. meridionalis* at

Marcus Island. Of the two species, it is *only A. ater* that utilizes refuges such as crevices and kelp holdfasts as a site for recruitment. This ability enables *A. ater* to survive the vulnerable juvenile period and reach the critical size at which it is no longer susceptible to rock lobster predation. Although *A. ater* does accur at Malgas Island, it does not dominate the rock lobster diet because only a small part of its biomass is accessible to these predators (Chapter 6).

BARNACLES AND MUSSELS

The first macrofaunal species to settle on bare hard substrata are barnacles, which create a secondary substratum for mussels whose attachment is not initially as firm as that of the barnacles. The mussels are, however, much faster-growing than barnacles and smother the barnacles in a short time (4-6 months) if there is little predation, as is the case at Marcus Island (Chapters 3 and 6). However when it is exposed to the intense predation that is experienced at Malgas Island, the black mussel, *Choromytilus meridionalis* fails to establish itself despite settling densely, while the ribbed mussel, *Aulacomya ater*, only occurs in small numbers (discussed later). Under those conditions the barnacle *N. algicola* then does form a thin veneer of small recruits on bare substrata, even although these are rapidly eaten and there is a high turnover of their populations.

BARNACLES

Both the small barnacle, *Notomegabalanus algicola*, and the giant barnacle, *Austromegabalanus cylindricus* are common in shallow sublittoral waters on the west coast (Day 1968; Field et al.1980). *N. algicola* normally settles on floating objects in larger numbers than *A. cylindricus* (Chapter 3), but is relatively scarce on the rocky bottom at Marcus and Malgas Islands. *A. cylindricus* occurs at both islands, but not in large numbers. Both species of barnacle, are preyed on by rock lobster and, when they are small, by some species of reef fish (Chapter 6; Joubert and Hanekom 1980; Bennett et al. 1983; Bennett and Griffiths 1986). *N. algicola* rapidly colonises bare space and initially dominates space in the early stages of succession. However, *A. cylindricus* achievs a size of over 50mm in diameter whereas *N. algicola* never reaches a size larger than 5mm in diameter. It seems likely that *A. cylindricus* can attain a refuge in size against predation, and even at Malgas Island where predation is intense small numbers of very large *A. cylindricuc* manage to survive while *N. algicola* never survives for long period (see Chapter 6). At Marcus Island the large size of *A. cylindricus* provides some advantage in the competition for primary space in the packed mussel bed. On the other hand, *N. algicola* has a very rapid growth to maturity which enables it to maintain a high output of larvae during its short lifespan and to opportunistically colonise bare space as it becomes available (Chapter 3 and 6).

HOLOTHURIANS

Two species of holothurians, *Pentacta doliolum* and *Thyone aurea*, can be considered as competitors for either space or food as they co-occur and occupy similar niches. Indeed, in many regions they exist together and even share the same available space (Field et al.1980; chapter 2). This relationship is particularly noticeable where there is strong wave action. At Marcus Island *T. aurea* lives beneath *P. doliolum*, and appears to depend on its greater power of attachment as a means of preventing being washed away by waves. This commensal relationship is not obligate. The two species are capable of surviving independently of each other and *T. aurea* was often observed using other forms of shelter from wave action (eg. mussels, crevices and artifacts). But wherever space is limited and water movement strong, *T. aurea* shelters under *P. doliolum*.

ALGAE AND MUSSELS

In the struggle for the limited primary space available on the rocky substrate, mussels and algae appear to be major competitors (Paine 1974; Suchanek 1985). Algae often recruit earlier than mussels, both littorally and sublittorally, although mussels usually overtake the algae in the long term (Payne and Levin 1981; Paine 1984; Suchanek 1985). Malgas Island is characterized by a large biomass of algae. The reasons for this are twofold. Firstly, rock lobsters exclude many of the major algal grazers, such as the sea urchin, *Parechinus angulosus*. Secondly, rock lobsters prey upon mussels thereby eliminating a major competitor for space. Other species such as Pyura and Porifera, which also compete for space with the mussels, similarly benefit from this last effect.

WHELKS

Two major genera of whelks, *Burnupena* spp. and *Argobuccinum* are found at Marcus and Malgas Island but are represented by different species and in different proportions at the two islands. At Malgas Island, *A. pustulosum* and *B. papyracea* are the only large whelk species that exist there. *A. pustulosum* survives because of its thick shell whereas *B. papyracea* is protected from rock lobster predation by an encrusting bryozoan which covers its shell (Chapter 5). The other species of whelk, being smaller, thin-shelled and unprotected, are preyed upon by the rock lobster and are completely absent from the benthos at Malgas Island. At Marcus Island two species of *Nucella* and additional species of *Burnupena* survive together with *B. papyracea,* which is the most common of the *Burnupena* species. *A. pustulosum* also occurs at Marcus Island although in smaller numbers than at Malgas Island. *A. pustulosom* feeds on the Cape reef worm, *Gunnarea capensis*, (Day 1969) but was observed scavenging on dead organic material at Marcus. Possibly it competes with *Burnupena* spp. for food, which may explain why its numbers are lower there (Chapters 2 and 5). The mussel bed at Marcus Island is exceptionally thick and supports an abnormally large population of *Burnupena* spp.. In this situation, the normal predator-prey relationship between rock lobsters and whelks is reversed and the whelks, which are normally considered to be scavengers, become aggressive predators on the rock lobster. It seems that this reversible relationship is controlled to a certain extent by the bryozoan *Alcyonidium nodosum* which coats the shells of *B. papyracea*. At Malgas Island *Alcyonidium* appears to grant *B. papyracea* relative immunity to predation. At Marcus Island the extraordinarily high numbers of whelks permit them to overpower the rock lobsters. It may well be that in intermediate situations the presence of *Alcyonidium* on the shells of *B. papyracea* tips the balance in favour of the whelks. Field et al. (1980) found that *B. papyracea* is the only *Burnupena* species that occurs sublittorally in many regions on the west cost near Cape Town in both the presence and absence of rock lobsters. Once *B. papyracea* has attained a high density it will be capable of excluding rock lobsters. Conversely, they seem unable to achieve this in areas where rock lobster populations are dense. Furthermore, there are other factors that contribute to this stability (see below).

ROCK LOBSTER DIET

As outlined in Chapter 6, the standing stock of *A. ater* at Malgas Island cannot support the energetic requirements of the dense rock lobster population. This fact highlights the opportunistic predatory habit of the rock lobster. Unorthodox and unexpected source of food, such as new recruits of barnacles and juvenile mussels, may play a major role in supplementing the diet of the rock lobsters in certain seasons of the year (Chapter 6). Scavenging and cannibalism are common in this isolated rock lobster population. They were even found to feed intensively on common planktonic mysids, utilizing this energy source particularly during period when barnacle recruitment is minimal.

COMMUNITY STABILITY

MARCUS ISLAND

Mussels dominate available space in areas with low predation, creating a habitat for many "cryptozoic" species which dwell among the mussels where they find food, shelter against predation and wave action and a diversity of microhabitats (Suchanek 1980; Dayton 1984; Witman 1985). There are several reasons why the mussels community at Marcus remains stable. In the first place, they derive their food from the water column and are never likely to be food limited in the productive turbulent waters of the Benguela upwelling ecosystem. The mussels are preyed upon by many predators including benthic species such as octopus (*Octopus granulatus*), whelks (*Burnupena* spp.), the drilling gastropods (*Nucella* spp. and *Natica* spp.) and starfish (*Marthasterias glacialis*), and a variety of fish (Griffiths 1981; Penney and Griffiths 1984). But none of these predators appears capable of controlling the mussel population at Marcus Island. Griffiths and Hockey (1987) have estimated that even their combined affects not of three can only acount for ~1.5 % of the mortality of mussels at Marcus Island: most die because of intraspecific competition for space, being thinned out as they grow and storms. Part of the reason why these predators have little impact on the mussel population is because many of them are not obligate predators but scavenge on mussels that have been injured by storms or other predators. However, rock lobsters have the potential to completely eliminate mussels or maintain them at very low levels. The near-absence of mussels at Malgas Island epitomizes this process. Many of the predators at Marcus Island also feed on rock lobsters. Notable are the octopus, dogfish and the *Burnupena* spp., which occur at such high densities that they prevent rock lobsters from colonising the island.

In deep-water at Marcus Island the mussels are seldom exposed to massive water movement and are loosely attached to the bottom. When a severe storm occurs, the whole layer of mussels is washed away together with most of its associated fauna, creating "free" space. This "free" space attracts two types of settlers: a) immigrants from the periphery-mostly active mobile species (sea urchins, whelks, sea cucumbers) as well as some sedentary species (mussels and sea anemones) and b) larvae from the plankton. However, even during very strong storms, the bulk of the mussel-bed community can survive, and recolonisation of bare rock by adult immigrants is therefore rapid and tends to inhibit larval settlement. The community thus remains unchanged, at least of species composition. Mussels from shallower water, where wave action is intense, attach themselves firmly to the bottom thus enabling them to survive sudden storms. Consequently, although the mussel bed is dynamic, it is also stable because the major "keystone" species always survive in large enough numbers to fill the gaps in the mussel bed rapidly and so maintain the typical character of the mussel bed.

MALGAS ISLAND

The rock lobsters at Malgas Island also appear capable of resisting very strong storms. They move into holes in large numbers and hold onto each other as a protection against wave action, or they move to deeper water (Heydorn 1969). Throughout the four years of observation, the rock lobsters at Malgas Island maintained a relatively stable population size, thereby continually dominating the species composition of the associated community.

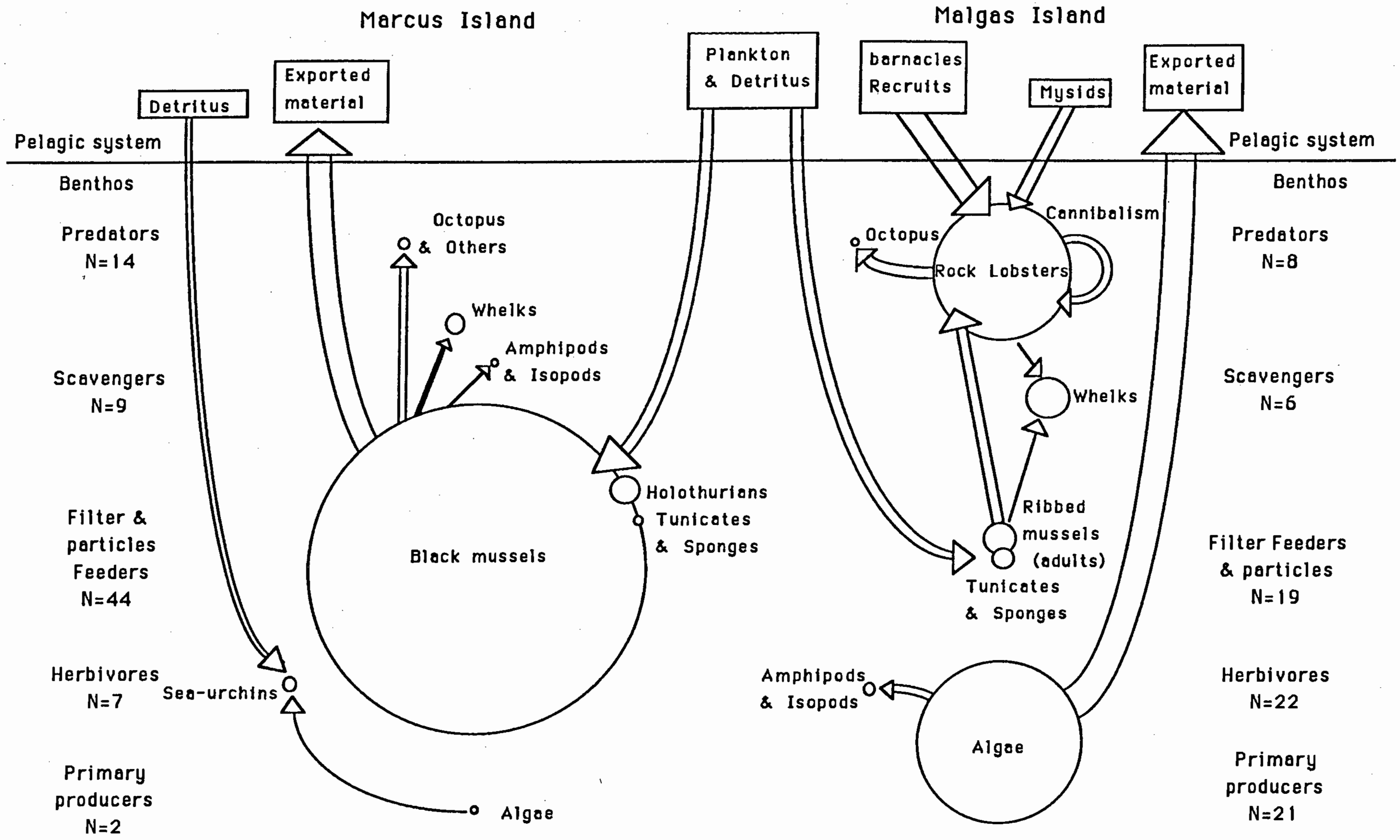

Fig 7.3
Comparison of energy flow through major groups in the benthos of Marcus and Malgas Islands. The diameter of each circle represents the relative percentage of biomass for each group of organisms. The thickness of the arrows, indicates non-quantitatively approximate importance of the energy flows. N indicates the number of species in each trophic group.

SPECIES DIVERSITY AND TROPHIC RELATIONSHIPS

Intense predation or extreme environmental stresses normally reduce species diversity and richness by only allowing adapted species to survive. Stable and protected environments have a similar effect on species diversity and richness, because a superior competitor may take over and exclude other species in the absence of disturbances (Paine 1974). An intermediate situation should then allow for maximum species richness and diversity [Connell 1978; Taylor and Littler 1982; Sebens 1985a, 1985b; Branch 1985 (in review)]. However the complexity of available substratum can reduce the effect of predation and physical disturbance (see Chapter 3). Under conditions of intense predation Malgas Island has a very low species richness of animals which are primary space competitors. Marcus Island also has a small number of species which are competitors for primary space: with a low level of predation the mussel *Choromytilus meridionalis* dominates almost all of the primary substratum. The total number of species is, however, similar at Malgas and Marcus Islands (107 spp v. 102 spp respectively), although different suites of spp occur at the two islands. At Malgas the algae and the associated herbivorous cryptic spp contribute largely to the species richness. The seaweeds act as a secondary substratum for many small species eg. amphipods, isopods, polychaetes and the juvenile stages of larger species such as mussels and gastropods. At Marcus these groups are of far less importance and more of the species are predators/scavengers or particle feeders associated with the mussel beds (Fig. 7.3).

Despite having a similar number of species, the trophic relationships and energy flow are entirely different at the two islands. The biomass at Malgas is dominated by algae and rock lobsters (Fig. 7.3), giving the appearance of an imbalanced trophic pyramid. Much of the food for rock lobsters is, however, in the form of newly settled barnacles which are imported to the benthos from the pelagic system. There is a low biomass of herbivores, and it happears that they can only have an insignificant effect on the large algae biomass. It is surmised that much of the algal production is exported. At Marcus Island mussels dominate the biomass. Algae are negligible, but herbivores (mainly urchins) contribute significantly in spite of this. How their energetic needs are met remains to be determined, but they are, known to be detritovores as well as herbivores (Greenwood 1980). A number of predators/scavengers depend directly on the mussels. By far the larger component of of the biomass is made up of particle feeders (filter, suspension and deposit feeders) which derive their food from imported material. Thus, although the animal biomass at Malgas is predominated by a top consumer and that at Marcus by particle feeder and secondary producers, both systems depend on imported material.

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APPENDIX A

TAXONOMIC LIST OF SPECIES WHICH WERE SAMPLED AND IDENTIFIED AT MARCUS (MAR.) AND MALGAS (MAL.) ISLANDS.

PHYLUM	SPECEIES	SITE
Porifera		Mal.
Cnidaria		
Hydrozoa	*Aglaophenia pluma* (Linnaeus)	Mal.
	Amphisbetia minima (Thompson)	Mal.
	Amphisbetia operculata (Linnaeus)	Mal.
	Antennela africana (Broch)	Mal.
	Campanularia integra McGillivray	Mal.
	Myriothela capensis Manton	Mal.
	Sertularella sp.	Mal.
	Symplectoscyphus arbriformis- (Mark.-Tarn.)	Mal.
Octocorallia		Mal.
Actiniaria	*Anthothoe stimpsoni* (Verr.)	Mal.Mar.
	Bunodosoma capensis (Less.)	Mal.Mar.
	Isanthus capensis Carlg	Mar.
	Pseudactinia flagellifera (Hertw.)	Mal.
Platyhelminthes		
Nemertea	*Zygonemertes capensis* Wheeler	Mal.

Sipunculida	*Golfingia capensis* (Teusch)	Mar.
	Phascolosoma spp.	Mal.
Echiurida	*Ochaetostoma capense* Stephen	Mar.
Annelida		
Polychaeta	Amphinomidae	Mar.
	Antinoe lactea Day	Mar.
	Arenicolidae	Mar.
	Cirriformia capensis (Schm.)	Mar.
	Lepidonotus semitectus Stimps.	Mal.Mar.
	Lumbrinereis sp.	Mar.
	Maldanidae	Mar.
	Marphysa sanguinea (Mont.)	Mar.
	Naineris levigtata (Grube)	Mar.
	Nereis sp.	Mal.Mar.
	Nicolea macrobranchia (Schm.)	Mal.Mar.
	Platynereis sp.	Mal.
	Sthenelias boa (Johnston)	Mar.
Hirudinea	*Helobdella* (?)	Mar.
	Pontobdella sp.	Mal.Mar.
Arthropoda		
Cirripedia	*Austromegabalanus cylindricus*-(Gmelin)	Mal.Mar.
	Notomegabalanus algicola Pilsbry	Mal.Mar.
Copepoda		Mal.Mar.

Isopoda	*Arcturella corniger* (Stebbing)	Mal.
	Cirolana hirtipes M.Edw.	Mar.
	Cirolana sulcata Hansen	Mal.
	Cirolona undulata Brnrd	Mar.
	Cymodocella eutylos Brnrd	Mal.
	Cymodocella magna Brnrd	Mal.
	Cymodocella sublevis Brnrd	Mal.
	Engidotea lobata (Miers)	Mal.
	Exosphaeroma planum Brnrd	Mal.Mar.
	Glyptidotea lichtensteini (Krauss)	Mal.
	Gnathia sp.	Mal.
	Paridotea fucicola Brnrd	Mal.
	Paridotea sp.	Mal.
	Sphaeramene polytylotos Brnrd	Mar.
Amphipoda	*Ampithoe ramondi* (Audouin)	Mal.
	Aristias symbiotica Brnrd	Mal.
	Atylus swammerdamei (M.Edw.)	Mal.
	Caprella danilevski Czerniavski	Mal.
	Cerodocus rubromaculatus (Stimps.)	Mal.
	Hyale saldanha Chilton	Mal.
	Ichnopus taurus Costa	Mal.
	Iphimedia capicola Brnrd	Mal.
	Leucothoe sp.	Mal
	Lysianassa ceratina (Walker)	Mar.
	Maera sp.	Mal.
	Melita orgasmos Brnrd	Mar.
	Temnophlias capensis Brnrd	Mal.

Tanaidacea	*Tanais philetaerus* Stebbing	Mal.
Leptostraca		Mar.
Macrura	*Jasus lalandii* (M.Edw.)	Mal.Mar
Anomura	*Paguristes gamianus* (M.Edw.)	Mal.
	Upogebia capensis (Kr.)	Mar.
Brachyura	*Dehaanius sp.*	Mal.Mar
	Hymenosoma orbiculare Desm.	Mar.
Pycnogonida	*Achelia guardridentata* (Hodgson)	Mar.
	Nymphopsis cuspidata (Hodgson)	Mar.
	Endeis clipeatus (Mobius)	Mal.
	Queubus jamesanus Brnrd	Mar.
	Tanystylum brevipes (Hoek)	Mal.Mar
Bryozoa	*Bicellariella ciliata* (Linn.)	Mal.
	Onchoporella buskii Harmer	Mal.
Mollusca		
Amphineura	*Ischnochiton bergoti* (Ve'lain)	Mar.
	Ischnochiton oniscus (Kr.)	Mal.
Pelecypoda	*Aulacomya ater* (Molina)	Mal.Mar.
	Choromytilus meridionalis (Kr.)	Mal.Mar.
	Kellya rubra (Mont.)	Mal.
	Monia squama Gmelin	Mal.
	Venerupis corrugatus (Gm.)	Mal.Mar.
Gastropoda	*Afrocominella capensis* (Dunker)	Mar.
	Amblychilepas scutellum (Gm.)	Mar.
	Argobuccinum postulosum-	

	(Light Foot)	Mal.Mar.
	Burnupena catarrhacta (Gm.)	Mar.
	Burnupena cincta (Bolten)	Mal.Mar.
	Burnupena limbosa (Lam.)	Mar.
	Burnupena papyracea (Brug.)	Mal.Mar.
	Crepidula porcellana Lam.	Mal.Mar.
	Fissurella mutabilis (Sow.)	Mar.
	Gibbula zonata (Wood)	Mar.
	Helcion pruinosus (Kr.)	Mal.Mar.
	Marginella biannulata (Fabr.)	Mar.
	Nassarius kochianus (Dunker)	Mar.
	Nucella squamosa (Lamarck)	Mar.
	Nucella singulata (Linn.)	Mar.
	Patella compressa Linn.	Mar.
	Siphonaria capensis Q.& G.	Mar.
	Tricolia capensis (Dnkr.)	Mar.
	Tricolia neritina (Dnkr.)	Mar.
	Turridae	Mal.
Cephalopoda	*Octopus granulatus* Lam.	Mal.Mar.
Echinodermata		
Asteroidea	*Henricia ornata* (Perrier)	Mal.Mar.
	Marthasterias glacialis (linn.)	Mar.
	Patiriella exigua (Lam.)	Mar.
Ophiuroidea	*Amphipholis squamata*- (delle Chiaje)	Mal.
	Amphiura capensis Ljungman	Mar.
	Ophiactis carnea Ljungman	Mar.

	Ophioderma wahlbergi Mull.& Trosch	Mar.
	ophiothrix fragilis (Abildgaard)	Mar.
Echinoioidea	*Parechinus angulosus* (Leske)	Mar.
Holothuroidea	*Pentacta doliolum* (Pallas)	Mar.
	Thyone aurea Q.& G.	Mar.
	Trachthyone insolens Theel.	Mar.
Crinoidea	*Annametra occidentalis* (Clark)	Mar.
Chordata		
Tunicata	*Ascidia sydneiensis* Stimps.	Mal.Mar.
	Ciona intestinalis (Linn.)	Mar.
	Corella eumyota Traust	Mar.
	Pyura stolonifera(Heller)	Mal.Mar.
Algae		
Chlorophyta	*Codium stephensiae* Dickinson	Mal.
	Ulva sp.	Mal.
Phaeophyta	*Ecklonia maxima* (Osbeck)Papenf.	Mal.Mar.
	Laminaria pallida Grev.ex J.Ag.	Mal.Mar.
	Splachnidium rugosum (Linn.)Grev.	Mal.
Rhodophyta	*Acrosorium sp.*	Mal.
	Arthrocardia sp.	Mal.
	Botryocarpa prolifera Greville	Mal.
	Carpoblepharis flaccida(Turn.)Kutz	Mal.
	Champia lunbricalis (Linn.)Desv.	Mal.
	Epymenia obtusa (Grev.)Kutz	Mal.
	Gigartia radula (Esp.) J.Ag.	Mal.
	Grateloupia filicina (Wulf.)	Mal.
	Hyemenena venosa (Linnaeus) Kylin	Mal.

Kallymenia agardhii J.Ag.	Mal.
Kallymenia schizophylla J.Ag.	Mal.
Pachimenia carnosa (J.Ag.)J.Ag.	Mal.
Plocamium cornutum (Turn.)Harv.	Mal.
Polysiphonia spp.	Mal.
Pterosiphonia cloiophylla-(Ag.)Falkenb.	Mal.
Trematocarpus flabellatus-(J.Ag.) De Toni	Mal.

APPENDIX B

LIST OF TAXONOMIC GUIDES WHICH WERE USED FOR SPECIES IDENTIFICATION THROUGHOUT THIS WORK.

Guide to the Benthic Marine Amphipods of Southern Africa 1976. By C. L. Griffiths. The Rustica Press.

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