THE ECOLOGY AND BIOLOGY OF MOLLUSCS IN THE LITTORAL AND SUBLITTORAL ZONES AT MACQUARIE ISLAND, WITH SPECIAL REFERENCE TO PATINIGERA MACQUARIENSIS (FINLAY 1927)

by

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A thesis presented to the University of Adelaide
for the Degree of Doctor of Philosophy (November, 1972)

CONTENTS

SUMMARY

1. This study examines:

(a) the shore environment and the zonation patterns of rocky shores at Macquarie Island;

(b) the possible limiting factors at the upper margins of distribution of six species of molluscs (Amphineura: *Plaxiphora aurata*, *Hemiarthrum setulosum*; Gastropoda: *Patinigera macquariensis*, *Cantharidus (Plumbelenchus) coruscans*, *Laevilitorina caliginosa*, *Kerguelenella lateralis*);

(c) the behaviour, distribution, physiology, life history, and morphological variation of one of these molluscs - the limpet, *Patinigera macquariensis*; and

(d) the reproduction of other selected marine invertebrates, mainly molluscs and echinoderms.

2. A review of the literature of the following subjects is given:

collections and rocky shore ecology at Macquarie Island, zoogeography of Macquarie Island, comparable ecological studies of littoral molluscs in the sub-Antarctic and other climatic regions.

3. The geography, geology, climate, and weather of Mac-

quarie Island are outlined. The temperatures are low and have a small range. Winds are high and conditions are typically cloudy and wet.

4. A description of the zonation of the flora and fauna along the vertical aspect of rocky shores is given. Transects, one metre wide, are used to plot the positions of organisms. Six zones (Lichen, *Porphyra*, Bare, Upper Red, Kelp, Lower Red) local to Macquarie Island, as described by Kenny and Haysom (1962), are recognized as valid divisions. These are related to a universal zonation scheme formulated by Lewis (1964).

5. A number of environmental factors likely to be significant in the studies are recorded regularly over a period of one year.

6. Rock pools at different vertical levels along the shore are studied. The species of algae and the physical conditions in the pools vary with the different levels. The ranges of physical conditions widen progressively up the shore. The species of molluscs living in the pools are found to be related to (a) available food and (b) physical conditions. These relationships are noted as providing bases for further experimental investiga-

tion in both the field and the laboratory.

7. The distribution of the molluscs is described in reference to zonal boundaries. Abundances of each species are recorded, special habitats receiving particular attention.

8. A number of factors likely to influence the distribution and abundance of molluscs along the shore are studied. These include: food preferences, algal cover (particularly *Durvillea antarctica*), ability to recolonize an area, predators, reproduction, and tolerances to temperature, desiccation, and salinity. No one factor is found to limit the upper distribution of all species. The importance of each factor is assessed and is found to differ for each species. Combinations of factors limiting distribution are discussed, particularly in reference to sustained, sub-lethal, environmental conditions.

9. Studies on the limpet, *Patinigera macquariensis*:

These studies examine the adaptations of one species to the environment. Generally, limpets in different habitats show differences in activity, feeding, reproductive cycle, and shell shape.

9a. The feeding and activity responses of the limpets depend on whether they are submerged or emerged. Those in the eulittoral that are subjected to periodic emersion and submersion have increased rates of feeding and activity during periods of submergence in comparison to limpets continuously submerged. Limpets in the eulittoral move up with the incoming tide and down with the outgoing tide. Responses to light and water turbulence are shown to be operative during this movement. The upward movement is viewed as a response that enables more effective usage of the habitat at the upper range of distribution by the expansion of grazing areas. The movement of limpets with the tides is regarded as a response to environmental stimuli and not to a predetermined rhythm.

9b. Experiments with marked limpets show that they tend to live in a fixed area. No homing occurs. The re-establishment of original numbers in a measured area after the existing population had been increased by adding more limpets could indicate a constant pressure within a population to reach an optimum, stable level. There is no total migration of limpets down the shore at any season.

9c. The limpets lack osmotic control of the blood when subjected to abnormal salinities.

9d. The annual reproductive cycle is described using gonad indices supplemented by microscopical examination. After four months of gonadial development, spawning occurs over spring-summer; spawning is followed by a resting stage of three months. Correlations between environmental factors and the timing of stages in the reproductive cycle are shown but no causal relationships can be claimed. There is a phase difference of two months in the reproductive cycles of limpets from the eulittoral and from a depth of three to six metres.

9e. Lipids are important reserve materials and there is strong evidence that the digestive gland acts as a storage site. There is a large increase in the lipid content of gonads during reproductive development.

9f. Differences in shell height are correlated with the strength of water movement over the shell; the greater the turbulence the higher the shell.

10. The reproduction of some other marine invertebrates of Macquarie Island (mainly molluscs and echinoderms) is described. The type of reproductive development (i.e. whether by external larvae, egg case, or brooding) is determined for each species. In the case of those species collected at monthly intervals over a one year period, the reproductive cycles are outlined. Particular attention is paid to those species reported as brooding in previous collections from Macquarie Island. First records of brooding and egg case formation are noted.

DECLARATION

I declare that this thesis contains no material which has been accepted for the award of any other degree in any University and to my knowledge it contains no material previously published or written by another person except where due reference is made.

Rodney D. Simpson

November 1972

ACKNOWLEDGMENTS

I wish to thank my supervisors: Dr. R. Carrick, for his guidance and encouragement during this study and Dr. S. J. Edmonds and Prof. A. Stock for their helpful suggestions and criticisms on the writing of the thesis. Assoc. Prof. H. Heatwole also gave valuable criticism.

I am especially indebted to the Antarctic Division for the support, both logistically and financially, which enabled this study to be conducted. Equal indebtedness is extended to Dr. F. Jacka and Prof. A. F. O'Farrell for providing me with the facilities to work on the data after my return from Macquarie Island.

I am grateful to: A.N.A.R.E. personnel who assisted in the field, namely Messrs. T. Gadd, S. Harris, E. Jones, W. Hocking, D. James, J. Connelly, K. McCue, G. Johnson, and to all those who helped to launch and beach the diving platform; Mr. T. Gadd for assistance in laboratory experiments; and Mr. S. Harris for assistance in field photography and laboratory experiments.

Special thanks are due to Miss J. Snaps for assistance in the preparation of figures and photographs. I am grateful to Mrs. P. O'Hara, Miss E. Cherry, and Miss L. Henecker, for typing some of the preliminary work and to Mrs. M. Hague for typing the final draft.

Miss I. Bennett and Mrs. H. Black provided helpful guidelines prior to departure for the island. Dr. B. Smith provided access to sub-Antarctic collections housed in the National Museum of Victoria. Mr. J. Ottaway constructed the computer programme.

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I. INTRODUCTION

(a) Aims of the Study

The primary aims were (i) to define the factors that determine the upper distributional limits and abundance of molluscs in the littoral and sublittoral zones of a sub-Antarctic island and (ii) to examine further aspects of the biology of one of these molluscs.

The limiting factors considered were: (1) the nature of the habitat; (2) physico-chemical conditions (temperature, desiccation, salinity, light, pH); and (3) biotic interactions (food, predation, reproduction). Phosphate and chlorophyll levels in sea-water were not expected to be limiting but were determined at approximately monthly intervals in order to gauge their association with breeding cycles. While it may be possible for any one factor to be limiting, the combined effect of several often had to be taken into account. These factors could be proximate in their effect e.g. high temperature causing death directly or ultimate e.g. sub-lethal temperature predisposing a weakened animal to predation which is then the proximate factor.

The systematics and zoogeography of sub-Antarctic molluscs are now well documented, but ecological data are mainly restricted to descriptive work (see section I(b), Review of Literature). Much more has been done on the molluscs of temperate zones. However, possible limiting factors are, with few exceptions assessed separately; the composite effect in nature of physico-chemical and biotic factors in limiting distribution still requires evaluation. Antarctic studies have dealt principally with the systematics and composition of communities. Eventual comparison of the ecology of the littoral zone over the full range of latitude requires sub-Antarctic studies to bridge the gap between existing temperate zone work and current studies on Antarctic benthos under the ice-shelf.

The opportunity to spend a year at the A.N.A.R.E. station adjacent to suitable study areas provided favourable conditions for both field and laboratory work. However, it was necessary to plan and provision the programme in advance while leaving room for manoeuvre in the event of unforeseen circumstances. Therefore, comparative study of several species, with emphasis on one (Patinigera macquariensis), was considered to be the most suitable approach. To commit this study to one species has obvious risks, and comparison of several has the added advantage that more use is made of analysis of environmental factors. In the event, one of the proposed species was not abundant enough for study, and though weather imposed restrictions, most of the field and experimental work proved practicable.

An aim, fundamental to this study, was to relate zonation at Macquarie Island to a universal zonation scheme. It was planned to measure the distribution and abundance of molluscs within this zonation scheme, and to relate these to aspects of possible significance, i.e. habitat structure and physico-chemical and biotic factors.

As so little is known about the life cycles and the type of reproductive development of marine invertebrates of sub-Antarctic shores, a further aim was to gather empirical data on these topics. Specimens of selected species (mainly molluscs and echinoderms) were collected and immediately preserved for later examination. Usually, these were taken at monthly intervals in order to follow the progression of the reproductive cycle.

(b) Review of Literature

(i) Mollusc collections and rocky shore ecology at Macquarie Island

Molluscs have been collected from Macquarie Island at intervals over a long period and these have been reported and classified. Many revisions of the taxonomy of these molluscs have been made.

Collections were made by Augustus Hamilton in 1894 and this material was described by Smith (1898) and Suter (1913). Harold Hamilton's collections of 1912-1914 were recorded by Hedley (1916). Iredale and Hull (1929-1932) revised the chitons as part of the New Zealand fauna. Part of the collections of the B.A.N.Z.A.R. Expedition were described by Cotton (1937) and Tomlin (1948). Powell (1957) revised Tomlin's work and reported on the whole of the material from the B.A.N.Z.A.R. Expedition.

Since the establishment of a base on Macquarie Island by the Australian National Antarctic Research Expeditions in 1948, collections of marine littoral fauna have been made by various people, notably Kenny and Haysom in 1948-1950, Bennett and Macpherson in 1959, and Vestjens in 1961-1962. This material has been deposited in the National Museum of Victoria. Dell (1964) examined the molluscs from this material and revised some of the common Macquarie species, making critical comparisons with the wide-ranging sub-Antarctic forms with which they had been grouped or from which they had been separated.

Littoral ecological studies on rocky shores were made in 1948-1950 and the results recorded by Haysom in the report on Macquarie Island by Law and Burstall (1956), and by Kenny and Haysom (1962). The ecology in these studies simply covered descriptions of distribution. Notes on littoral ecology were made in 1959 by Bennett and Macpherson (pers. comm.). A descriptive account of some of the organisms of the littoral zone of rocky shores has been given recently in a book by Bennett (1971).

(ii) Zoogeography of Macquarie Island

The distribution of Antarctic and sub-Antarctic molluscan fauna and the zoogeographical affinities of the Macquarie Island Mollusca have been discussed by Tomlin (1948); Powell (1957, 1965); Dell (1964); Kenny and Haysom (1962); and Knox (1960, 1963).

Tomlin (1948) suggested that Macquarie Island molluscs have a closer relationship with those of the Antarctic continent than with those of any other region. Powell (1957) rejected Tomlin's claim in support for a relationship with Kerguelen Island. He bracketed Macquarie Island and Kerguelen Island in a Kerguelenian Province stating that the Macquarie fauna has more in common with that of Kerguelen than with the New Zealand sub-Antarctic islands (which he placed in the Antipodean Province). Kenny and Haysom (1962) and Knox (1963) supported this view.

Dell (1964) listed three main sources for the derivation of Macquarie Island molluscs: (1) New Zealand, (2) circum-Antarctic element, and (3) Kerguelen. Dell noted that the fauna was also sufficiently isolated for a high degree of endemism to have developed and suggested that the fauna of Macquarie Island, with its very distinct elements and diverse origins, was misplaced when included within any zoogeographical province.

The West Wind Drift current is the dominating feature of the southern temperate and sub-Antarctic regions. It engulfs Macquarie Island and must be considered as a major distributing agent in the circum sub-Antarctic spread of marine organisms, particularly those species associated with algae. Powell (1965) suggested that drifting masses of algae are the means by which the herbivorous trochids (e.g. *Margarella*), certain patellids (e.g. *Nacella* and *Patinigera* of the *fuegiensis* group), and the byssiferous attached bivalves (e.g. *Hochstetteria*) have achieved their wide lateral dispersal.

(iii) Comparable ecological studies of littoral molluscs (and some other invertebrates) in the sub-Antarctic and other climatic regions

It is intended here to comment on the general scope of other, similar studies. The actual results and findings are discussed in detail in the later, relevant sub-sections, along with additional works which are more specific to the topic in question.

On sub-Antarctic shores, there has been little ecological work and this is generally confined to the recording of habitat and locality information during collections and observations. A descriptive account of zonation and abundance of organisms for Macquarie Island shores was given by Kenny and Haysom (1962). Fuller (1967) described the zonation pattern for Marion and Prince Edward Islands and noted the similarity of the zonation patterns of sub-Antarctic islands. Grua (1963, 1965) briefly reported on observations from SCUBA diving at Kerguelen Island with some reference to the effects of turbulence and light on marine organisms, particularly algae. Recently, Grua (1971) gave an account of the general ecology from diving studies at Kerguelen Island. The main features of this account were descriptions of (i) the structure and zonation pattern of submarine algae with relations to light and turbulence and (ii) the composition of biotic communities at diving stations with general observations on some invertebrates.

Studies have been made on the zonation of rocky shores of the temperate regions of the Southern Hemisphere: Guiler (1952), Bennett and Pope (1960) - Tasmania; Bennett and Pope (1953) - Victoria; Guiler (1959) - Chile. Morton and Miller (1968) summarized zonation studies in New Zealand. Knox (1960, 1968) reviewed littoral zonation studies in the Southern Ocean and the Antarctic.

In the Antarctic, surveys of benthic communities have been reported for both flora and fauna e.g. Dearborn (1963), Neushul (1963), Holme (1963), Wohlschlag (1963), Peckham (1964), Dearborn (1967). An important relation of faunal composition with substrate and ice formation was noted by Dearborn (1963). The gravel and sand of the shallows contained a paucity of organisms compared with the rich community structure of the volcanic debris of deeper water. Ice scouring effectively eliminated an intertidal fauna. Dearborn (1962) studied the food habits of the isopod, Glyptonotus antarcticus Eights, and noted that the diet frequently included gastropods and bivalves.

Hedgpeth (1969) briefly reported on the biotic composition of the littoral zone at Palmer Station (64° 45' S., 64° 05' W.). Shabica (1971) gave a preliminary report of recent ecological studies on the limpet, Patinigera polaris, at Palmer Station. Walker (pers. comm.) conducted an autecological study of the limpet, Patinigera polaris, at Signy Island. Migration down the shore was recorded in winter and this was attributed to ice action.

At Macquarie Island, the climate is actually a very equable one, and this constancy (different from other regions) raises the question as to whether or not factors which have been studied as the causes for limiting animal distribution in the littoral and sublittoral zones of other regions, have the same emphasis here. This has particular reference to the effects of the physical environment as increased physical stability could result in greater biological interaction. Because Macquarie Island shores are at the southerly end-point of ice-free littoral zones, they provide an interesting comparison with Antarctic and temperate regions. In the more accessible temperate and tropical regions (especially temperate) descriptive and experimental ecological studies of the littoral zone have been extensive. With the community composition and zonation described in detail, aspects of physiology, reproduction, behaviour, and competition have been investigated as possible causal mechanisms of distribution of organisms and the maintenance of zonation boundaries.

Temperature, desiccation, and salinity have been investigated for possible limiting effects on littoral molluscs in temperate regions. Broekhuysen (1940), Evans (1948), Southward (1958), Micallef (1966), Fraenkel (1966), and Sandison (1967) have looked at the influence of temperature. Although the sequence of temperature tolerance for different species was often found to correlate with the upper limits of their vertical distribution, the margin between the temperature tolerance of each species and environmental temperatures encountered was too high for temperature to have a direct influence as a limiting factor.

Broekhuysen (1940) also showed a correlation between the vertical order of the upper limits of distribution of a number of littoral prosobranch molluscs and their tolerances to desiccation and salinity. Again, physiological lethals were beyond the conditions imposed by the environment. Brown (1960) also showed a correlation between the desiccation resistance of gastropods and their zonational sequence. Other studies on desiccation as a factor limiting the distribution of littoral molluscs have been made by Micallef (1966) and Davies (1969). The relationships of tolerance to abnormal salinities of littoral molluscs to their distribution have been examined by Arnold (1957), Mayes (1962), and Arnold (1972).

There has been little investigation on the importance of combinations of environmental factors on the distribution of littoral molluscs. Sandison (1967) investigated the combined effects of respiratory responses, heat, and desiccation on limiting the vertical distribution of gastropods.

Meyer and O'Gower (1963) and O'Gower and Meyer (1965, 1971) studied the seasonal variation in numbers of six species of littoral gastropods, including relationships of various factors to abundance and distribution. They determined that the abundance and distribution of four was associated with wave action; one with the growth of the alga, Hormosira banksii; and the sixth was not affected by either of these factors. In three, seasonal variation in abundance was associated with temperature change. The density of one species was related to moist habitats and the density of another to dry habitats. In cool weather, a third species occurred in similar densities in habitats ranging from moist to dry but, during hot weather, tended to migrate to areas of intermediate humidity.

Biotic factors have been shown to be significant in affecting the abundance and distribution of littoral molluscs. Lodge (1948), Burrows and Lodge (1949), and Southward (1956) conducted experiments which showed an association between the abundance of the limpet, Patella vulgata, and algal growth. Species of the Californian limpet, genus Acmaea, exhibited food preferences in accordance with the algae present in their different habitats (Craig 1968; Eaton 1968).

Many autecological studies seek to explain distribution in the littoral zone e.g. Evans (1951) - chiton; Newell (1958a, 1958b) - littorinid; Connell (1961) - barnacles; Evans (1961, 1965) - periwinkles; Desai (1966) - gastropod; Frank (1965) - limpets. At Macquarie Island, more than one year was considered necessary to adequately and safely compile the life table of any species of mollusc. However, concentration on one species (Patinigera macquariensis) was warranted in order to draw comparisons - ecological, behavioural, and physiological - with work done on similar animals in other climatic regions. Extensive work has been done on various aspects of Patellid limpets in temperate regions e.g. reproduction (Orton et al, 1956); physiological ecology (Davies 1966, 1967, 1969); shell growth (Moore 1934);

glucose and glycogen levels (Barry and Munday 1959); population ecology and chemical composition (Blackmore 1969a, 1969b). Such studies cover areas that would be of comparative interest with Patinigera macquariensis.

(c) The Selected Species

Powell (1957) and Dell (1964) give the taxonomic authorities for the species of molluscs mentioned in this thesis. Those selected for detailed ecological studies were:

Cl. Amphineura
Sub-cl. Polyplacophora
  F. Plaxiphoridae

Plaxiphora aurata (Spalowsky, 1795)

Hemiarthrum setulosum (Dall, 1876)

Cl. Gastropoda
Sub-cl. Prosobranchia
  F. Patellidae

Patinigera macquariensis (Finlay, 1927)

F. Trochidae

Cantharidus (Plumbelenchus) coruscans (Hedley, 1916)

F. Littorinidae

Laevilitorina caliginosa (Gould, 1849)

Sub-cl. Pulmonata
  F. Siphonaridae

Kerguelenella lateralis (Gould, 1846)

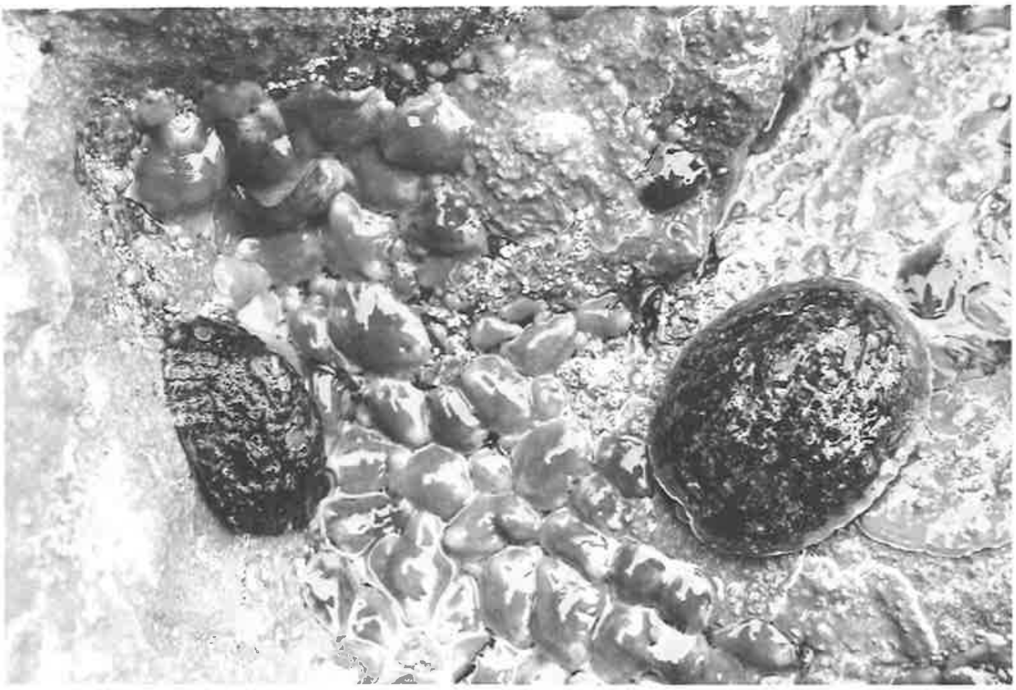
Plates 1 to 4 show the above molluscs on the shore except for Laevilitorina caliginosa which is depicted in the

Plate 1.

1A. A specimen of *Patinigera macquariensis* on a rock surface in the eulittoral zone.

1B. Two specimens of *Patinigera macquariensis* on a rock surface encrusted with coralline algae. A cluster of the holothuroids, *Pseudopsolus macquariensis*, is in the centre.

20 mm



20 mm

Plate 2.

2A. Cantharidus (P.) coruscans in a rock pool in the lower eulittoral zone.

2B. A specimen of Plaxiphora aurata on a rock surface in the lower eulittoral zone.


20 mm

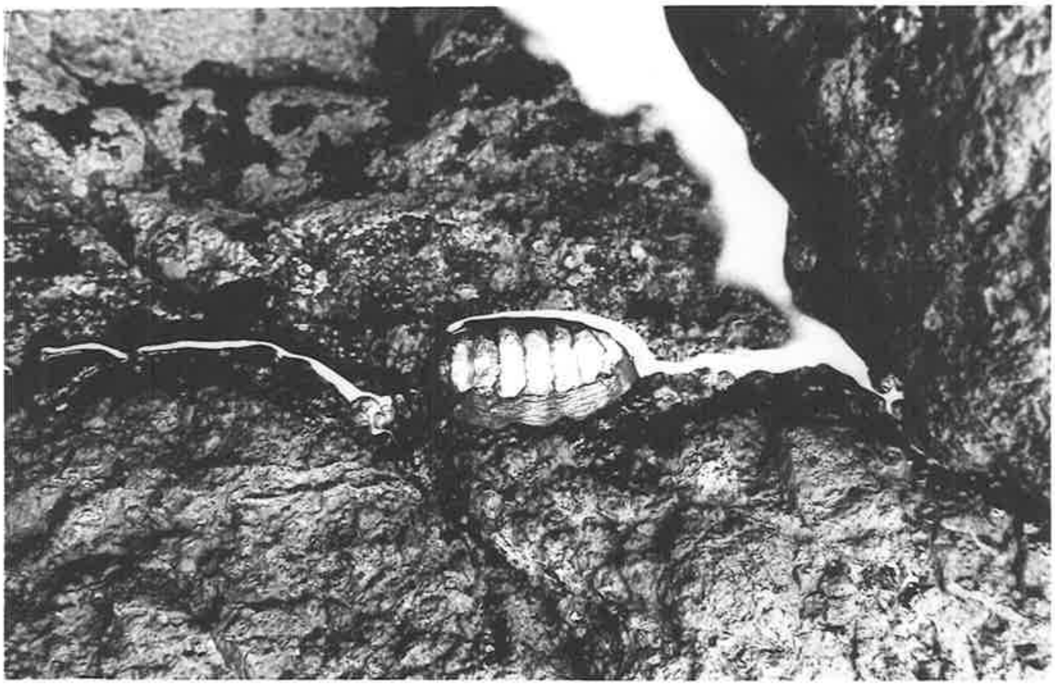

80 mm

Plate 3.

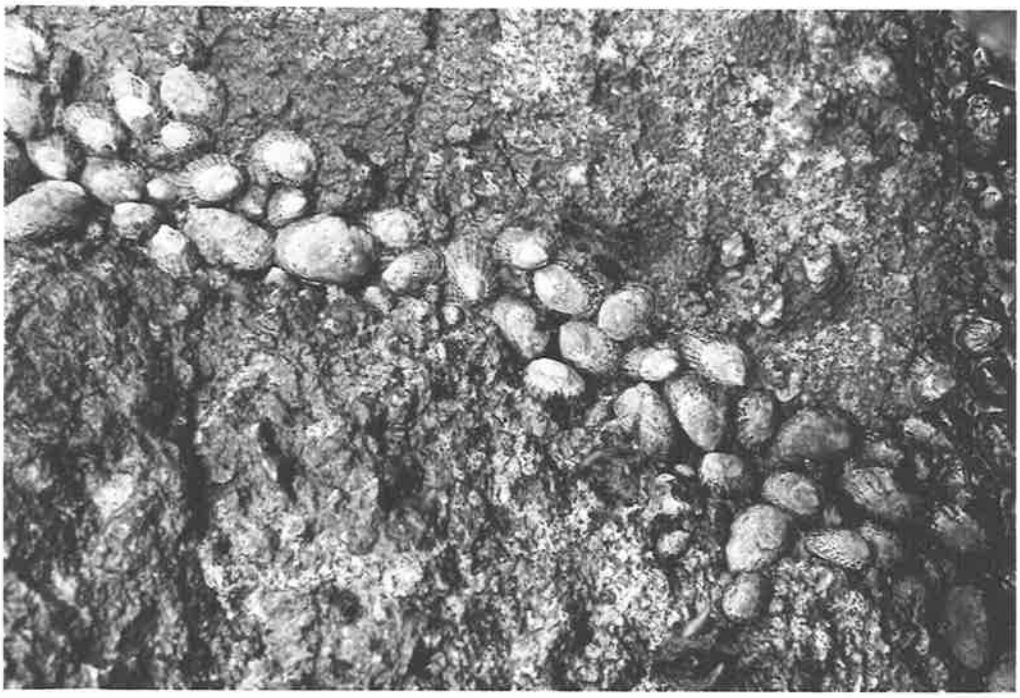
Hemiarthrum setulosum on a rock surface encrusted with coralline algae in the sublittoral zone.

10 mm

Plate 4.

4A. *Kerguelenella lateralis* in a rock crevice in the Bare Zone of the upper eulittoral.

4B. Rock crevices (in the Bare Zone of the upper eulittoral) lined with *Kerguelenella lateralis* during emerged dry conditions.



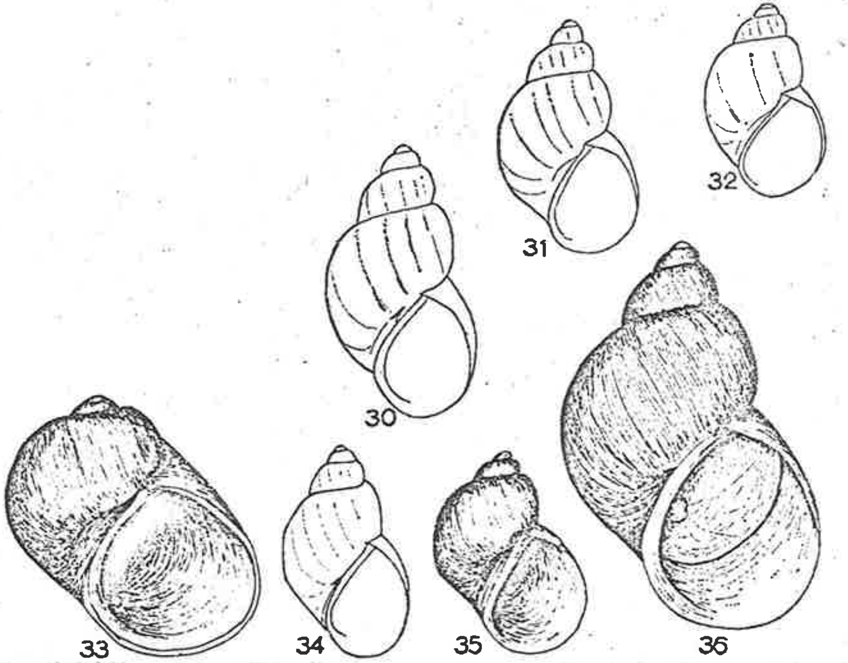
20 mm

illustrations of littorinids in Figure 1. The zones mentioned in the explanation of the Plates are taken from the results of the studies outlined and discussed in sections III(a) and III(b).

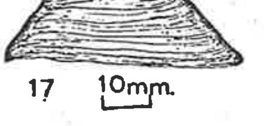
Specimens of *Patinigera macquariensis* were compared from two widely spaced habitats, i.e. eulittoral and from a depth of 3 to 6 metres. Care was taken to ensure that all were the same species, as four beach-worn shells of *Nacella kerguelenensis* (Smith, 1877) were collected by Hamilton (recorded by Hedley 1916) and different shell forms of *P. macquariensis* have been noted by Dell (1964). It was thus necessary to ensure that if *N. kerguelenensis* was present, it could be readily identified as such and not as another shell form of *P. macquariensis*. Dell (1964) suggested that sublittoral collecting would settle whether or not *N. kerguelenensis* was actually established on Macquarie Island shores. From the description of *N. kerguelenensis* by Smith (1877) and the subsequent comparison between *N. kerguelenensis* and *P. macquariensis* by Dell (1964), the two species can be separated on the basis of colouration of the head and cephalic tentacles, and by the shape of the shell. *N. kerguelenensis* has a grey to black head and black tentacles, while *P. macquariensis* has a white head and the tentacles are white on the ventral surface. In adult shells, the apex of *P. macquariensis* is in the form of a simple peak while that of

Figure 1. Littorinids of sub-Antarctic islands (from Dell, 1964).

Figure 2. Adult *Cantharidus* (*P.*) *coruscans* from Macquarie Island and juvenile *Nacella kerguelenensis* from Heard Island (from Dell, 1964).



Figs. 30, 32, 34: *Laevilitorina caliginosa* (Gould), Macquarie Island.
Fig. 31: *Laevilitorina caliginosa* (Gould), Kerguelen Island.
Fig. 33: *Macquariella hamiltoni* (Smith), Lectoype, 3·0 x 3.0 mm.
Fig. 35: *Macquariella macphersonae* n.sp., Holotype 3·3 x 3·0 mm.
Fig. 36: *Laevilitorina* (*Corneolitorina*) *heardensis* n.sp., Holotype, 7.· x 5·0 mm.



Figs. 11, 12: *Cantharidus* (*Plumbelenchhus*) *coruscans* (Hedley), Macquarie Island.

Figs. 13, 14, 15, 16, 17: *Nacella kerguelenensis* (Smith), Heard Island young shells showing transition from *"Nacella"* stage (all to same scale).

N. kerguelenensis has a slight overhang. In addition, juvenile *N. kerguelenensis* pass through a "Nacella" stage (see Figure 2.). No specimens of *N. kerguelenensis* were found at Macquarie Island though searches were made to a depth of 10 metres.

Three species of starfish (*Anasterias mawsoni* (Koehler), *Anasterias directa* (Koehler), and *Asterina hamiltoni* Koehler) are dealt with in this thesis in considering predator-prey relationships with molluscs. These same starfish also form part of a reproductive study (see Appendix 1). It is appropriate here to comment on the synonymy of the generic nomenclature of two of these starfish (*A. mawsoni* and *A. directa*) as other workers on littoral ecology have used *Sporasterias* as the generic name for these two species (Kenny and Haysom 1962; Bennett 1971).

Koehler (1920) named the three species as *Parastichaster mawsoni*, *Parastichaster directus*, and *Asterina hamiltoni* respectively. *Asterina hamiltoni*, as a nomenclature, has not been changed. Fisher (1930) merged the genus *Parastichaster* with the genus *Sporasterias*, renaming the first two species as *Sporasterias mawsoni* and *Sporasterias directa*. However, Clark (1962) placed these two species into the genus *Anasterias* and it is Clark's classification that is used here.

(d) General Methods

The materials and methods used are described in detail under the appropriate sub-sections. Generally, the method of approach was:

1. to record environmental factors (physico-chemical and biotic). When recording physical environmental factors, both macro- and microclimate were investigated;
2. to fully describe the distribution and habitats of the selected species;
3. to conduct experiments in the field and in the laboratory aimed at determining causal relations between distributional limits and environmental parameters and the nature of the habitat;
4. to study aspects of the biology and ecology of one species in further detail and to examine relationships of these aspects with the environment.

II. MACQUARIE ISLAND

(a) Geography and Geology

Macquarie Island is located at 54° 29' S., 158° 58' E. and is approximately 1,470 kilometres south-east of Tasmania and 1,440 kilometres from the nearest point of the Antarctic continent. Auckland and Campbell Islands, in the Antipodean group, are the nearest neighbours 640 kilometres to the north-east. The outlying "islands", Judge and Clerk (14 kilometres NNE) and Bishop and Clerk (32 kilometres south), are only large rock outcrops. Macquarie Island is 33 kilometres long and up to 5 kilometres wide. The axis along its length is approximately 15° east of north. Figure 3 positions Macquarie Island in the Antarctic region, Figure 4 showing the prominent features of the island.

Macquarie Island is possibly the only visible part of a disrupted submarine ridge or arc that might have provided a Cenozoic link between Antarctica and New Zealand (Harrington 1965). The island is separated from the Antipodean group by a narrow deep (3,700 to 5,500 metres in depth) and is separated from the Antarctic continent by another far broader deep.

The geology of Macquarie Island has been described by Mawson (1943) and a summary was made by Law and Burstall (1956) from both Mawson's account and subsequent observa-

Figure 3. Location of Macquarie Island and other islands in the sub-Antarctic and Antarctic regions.

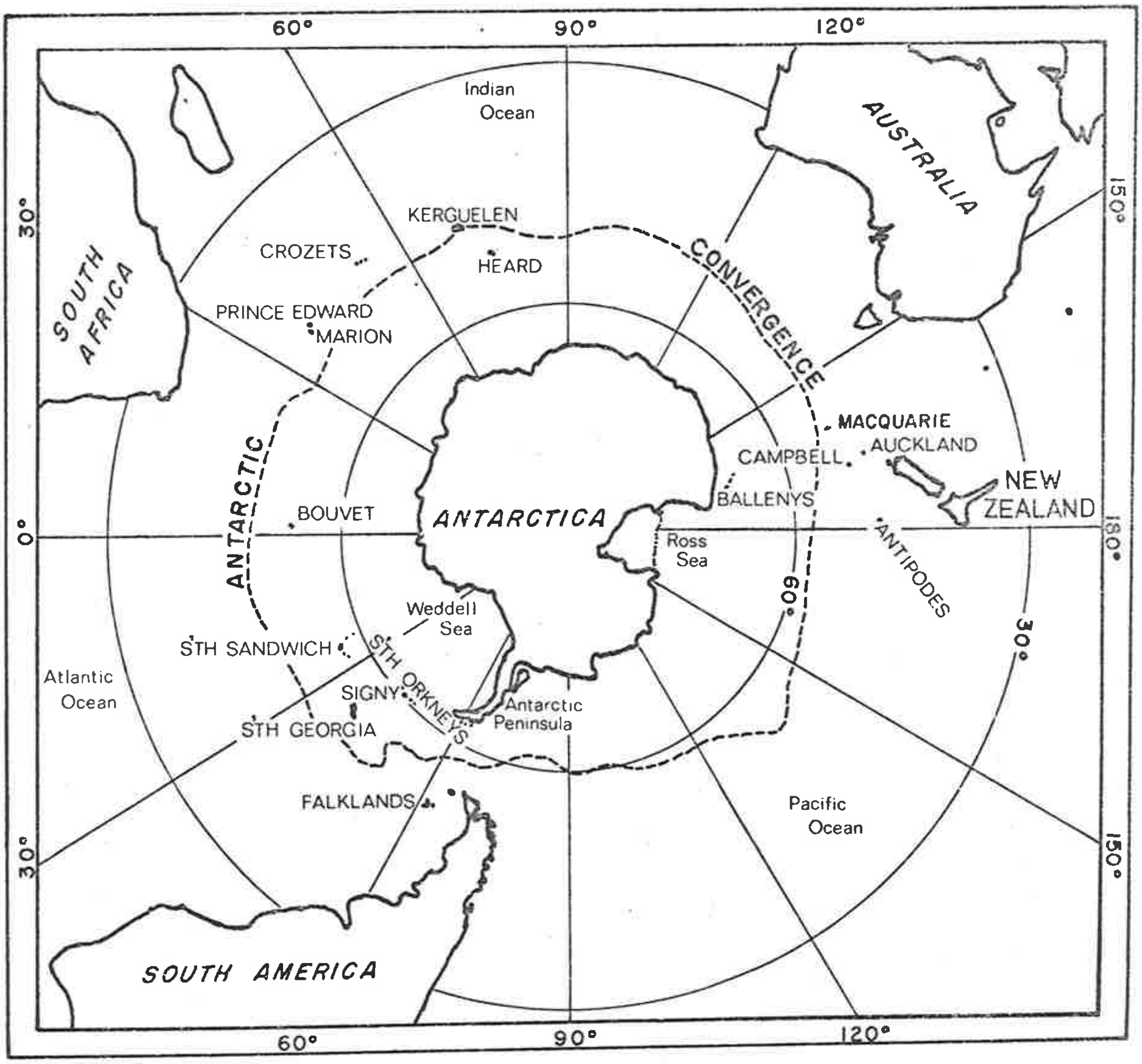
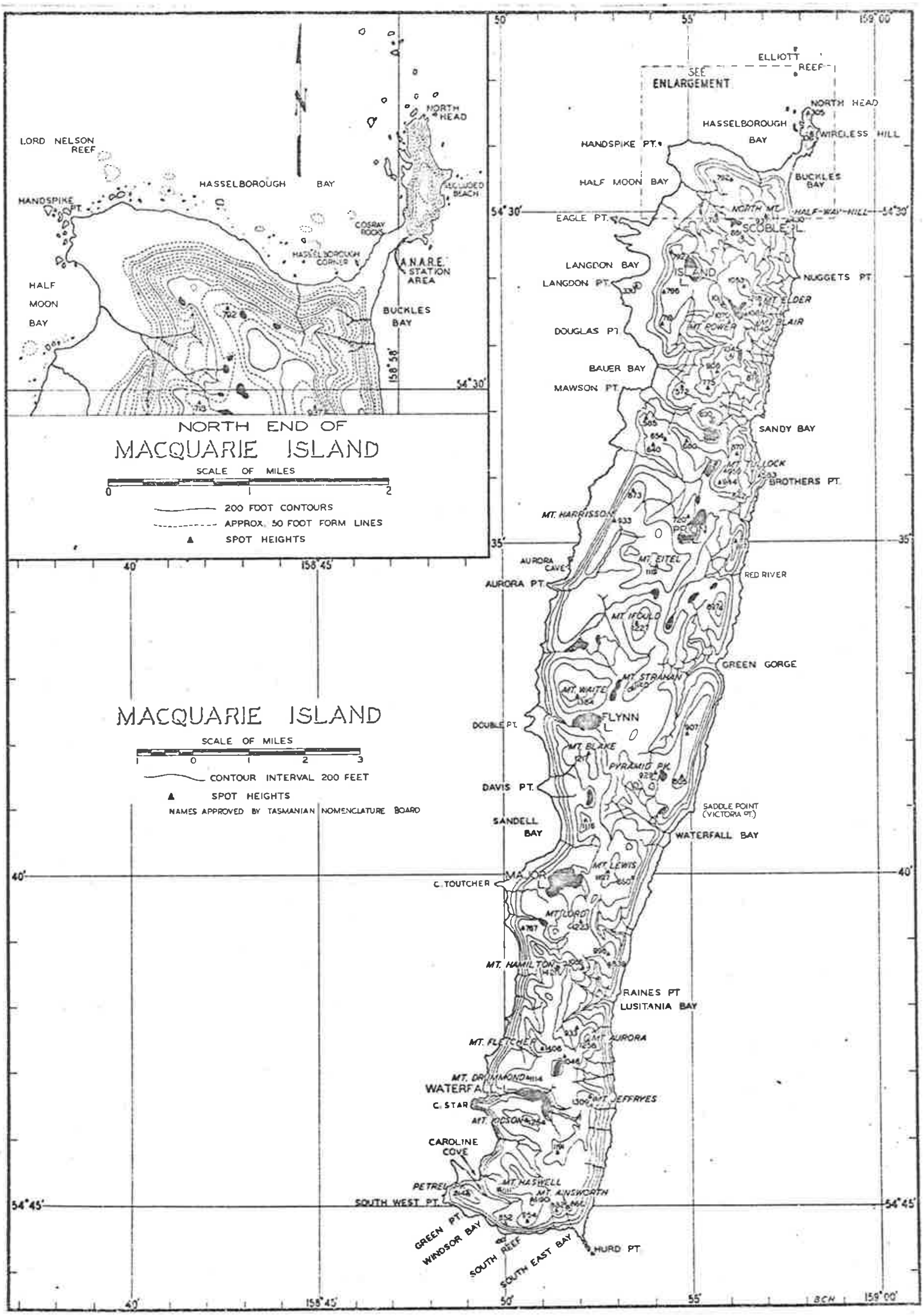

60°
90°
120°
Indian Ocean
AUSTRALIA
150°
30°
SOUTH AFRICA
KERGUELEN
CROZETS
HEARD
CONVERGENCE
PRINCE EDWARD
MARION
MACQUARIE
CAMPBELL
AUCKLAND
NEW ZEALAND
BALLENYS
ANTARCTIC
BOUVET
ANTARCTICA
0°
180°
Ross Sea
ANTIPODES
60°
Weddell Sea
STH SANDWICH
STH ORKNEYS
30°
Atlantic Ocean
SIGNY
Antarctic Peninsula
STH GEORGIA
FALKLANDS
Pacific Ocean
150°
30°
SOUTH AMERICA
60°
90°
120°

Figure 4. Macquarie Island, showing prominent geographical features.

(Map supplied by Antarctic Division, Department of Supply.)


NORTH END OF
MACQUARIE ISLAND
SCALE OF MILES
0
1
2
200 FOOT CONTOURS
APPROX. 50 FOOT FORM LINES
▲ SPOT HEIGHTS
LORD NELSON REEF
HANDSPIKE PT.
HASSELBOROUGH BAY
NORTH HEAD
SECLUDED BEACH
COSRAY ROCKS
HASSELBOROUGH CORNER
A.N.A.R.E. STATION AREA
HALF MOON BAY
BUCKLES BAY
158°58'
54°30'
40'
158°45'
50'
55'
159°00'
35'
54°45'
MACQUARIE ISLAND
SCALE OF MILES
1
0
1
2
3
CONTOUR INTERVAL 200 FEET
▲ SPOT HEIGHTS
NAMES APPROVED BY TASMANIAN NOMENCLATURE BOARD
SEE ENLARGEMENT
ELLIOTT REEF
NORTH HEAD
HASSELBOROUGH BAY
WIRELESS HILL
HANDSPIKE PT.
HALF MOON BAY
BUCKLES BAY
NORTH MT.
HALF-WAY-HILL
EAGLE PT.
SCOBLE L.
LANGDON BAY
LANGDON PT.
ISLAND L.
NUGGETS PT.
MT. ELDER
MT. BLAIR
MT. POWER
DOUGLAS PT.
BAUER BAY
MAWSON PT.
SANDY BAY
MT. TULLOCK
BROTHERS PT.
MT. HARRISSON
PRION L.
AURORA CAVE
AURORA PT.
MT. EITEL
RED RIVER
MT. IFOULD
GREEN GORGE
MT. STRAHAN
MT. WAITE
FLYNN L.
DOUBLE PT.
MT. BLAKE
PYRAMID PK.
DAVIS PT.
SADDLE POINT (VICTORIA PT.)
SANDELL BAY
WATERFALL BAY
MT. LEWIS
MAJOR L.
C. TOUTCHER
MT. LORD
MT. HAMILTON
RAINES PT
LUSITANIA BAY
MT. FLETCHER
MT. AURORA
MT. DRUMMOND
WATERFALL L.
MT. JEFFRYES
C. STAR
MT. DICSON
CAROLINE COVE
PETREL PT.
MT. HASWELL
MT. AINSWORTH
SOUTH WEST PT.
GREEN PT
WINDSOR BAY
SOUTH REEF
SOUTH EAST BAY
HURD PT.
BCH

tions by A.N.A.R.E. personnel. The rocks of the island are almost entirely of volcanic origin and the topography indicates that it has been heavily glaciated. There has been extensive marine erosion; off the east coast the sea floor drops steeply, but off the west coast, where most erosion has occurred, the slope is more gradual (Law and Burstall 1956).

Reefs are present on both the east and west coasts but extensive flat reefs are more predominant on the west. There are sand and shingle beaches on both sides of the island. An extensive reef area on the east coast in the vicinity of Garden Cove was used to carry out most of the work in this study.

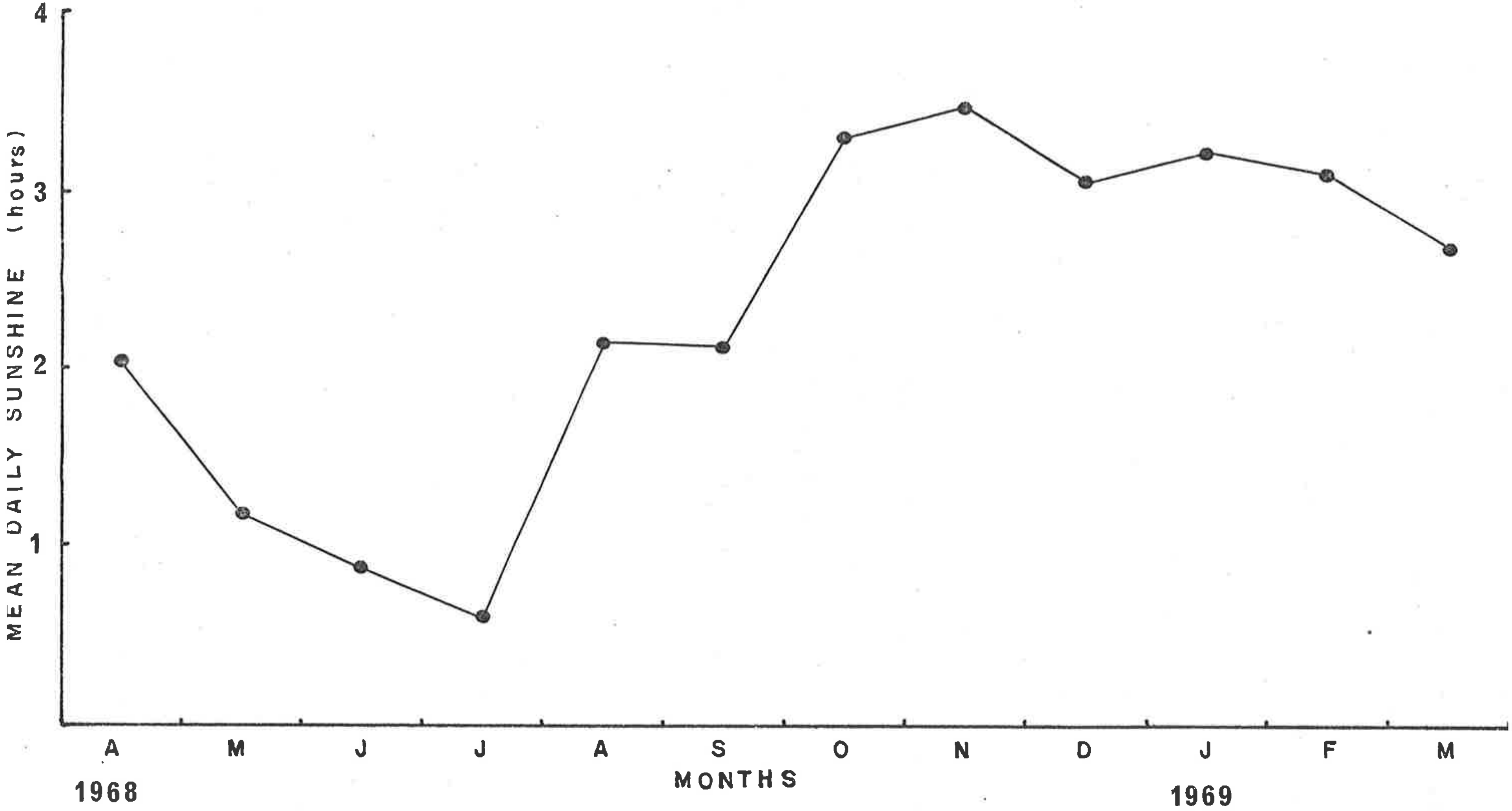
(b) Climate and Weather

The climate of Macquarie Island is representative of the sub-Antarctic. Taylor (1955) named the Macquarie climate as "cold temperate" or "sub-polar oceanic" which is characterized by a relatively even temperature (which is low), high humidity, and high wind velocities. In addition, cloudy and wet weather can be classed as typical for the island.

Data on the climate of Macquarie Island were obtained from records in "Meteorology" (A.N.A.R.E. Publications Series D), from the summary by Law and Burstall (1956), and from meteorological observations by A.N.A.R.E. personnel during the 1968 and 1969 expeditions.

The highest recorded temperature is 11.4°C and the lowest, -8.3°C. The range of mean temperatures is 3.0°C to 6.3°C. Precipitation is frequent but light, and the mean annual total is 40.5 inches, occurring over approximately 330 days of each year. The mean relative humidity is 88%. Approximately half of the observations show a relative humidity of 90% or greater, while approximately one tenth show a relative humidity of less than 70%. The annual average of bright sunshine is 800 hours, recorded on 264 days a year. On 101 days no sunshine is received. The average for the daily hours of sunshine varies from less than half an hour in June to just over three hours in February, the sunshine being concentrated in the period, October to March. Figure 5 graphs the mean daily sunshine (in hours) for the months April 1968 to March 1969, from readings taken by the A.N.A.R.E. meteorological section; a notable feature is the large increase in August over the preceding month. In six years of operation of a sunshine recorder, there were 35 days on which more than 10 hours of bright sunshine were recorded. Cloud cover is persistent; over 90% of the observations show that the sky is more than half covered with cloud. Completely cloudless skies are uncommon. Fogs and misty conditions occur frequently at all seasons. The pre-

Figure 5. Macquarie Island mean daily sunshine (in hours) for the months April, 1968 to March, 1969.


MEAN DAILY SUNSHINE (hours)
4
3
2
1
A
M
J
J
A
S
O
N
D
J
F
M
MONTHS
1968
1969

vailing winds are westerlies, two-thirds of all winds being in the sector 255° - 345°. The mean wind velocity is around 32 km p.h. and gusts of gale force are recorded for approximately 180 days each year. Heavy seas occur at all seasons and the coastline is very exposed with the western shores being subject to heavy wave action.

The Antarctic Convergence lies to the south of Macquarie Island (see Figure 3). This results in the general climate of Macquarie being milder than for an island of similar latitude but lying south of the convergence, e.g. Heard Island. There is no sea-ice formation at Macquarie Island. Ice may form at the edges of rock pools high in the littoral zone, during an exceptional cold spell.

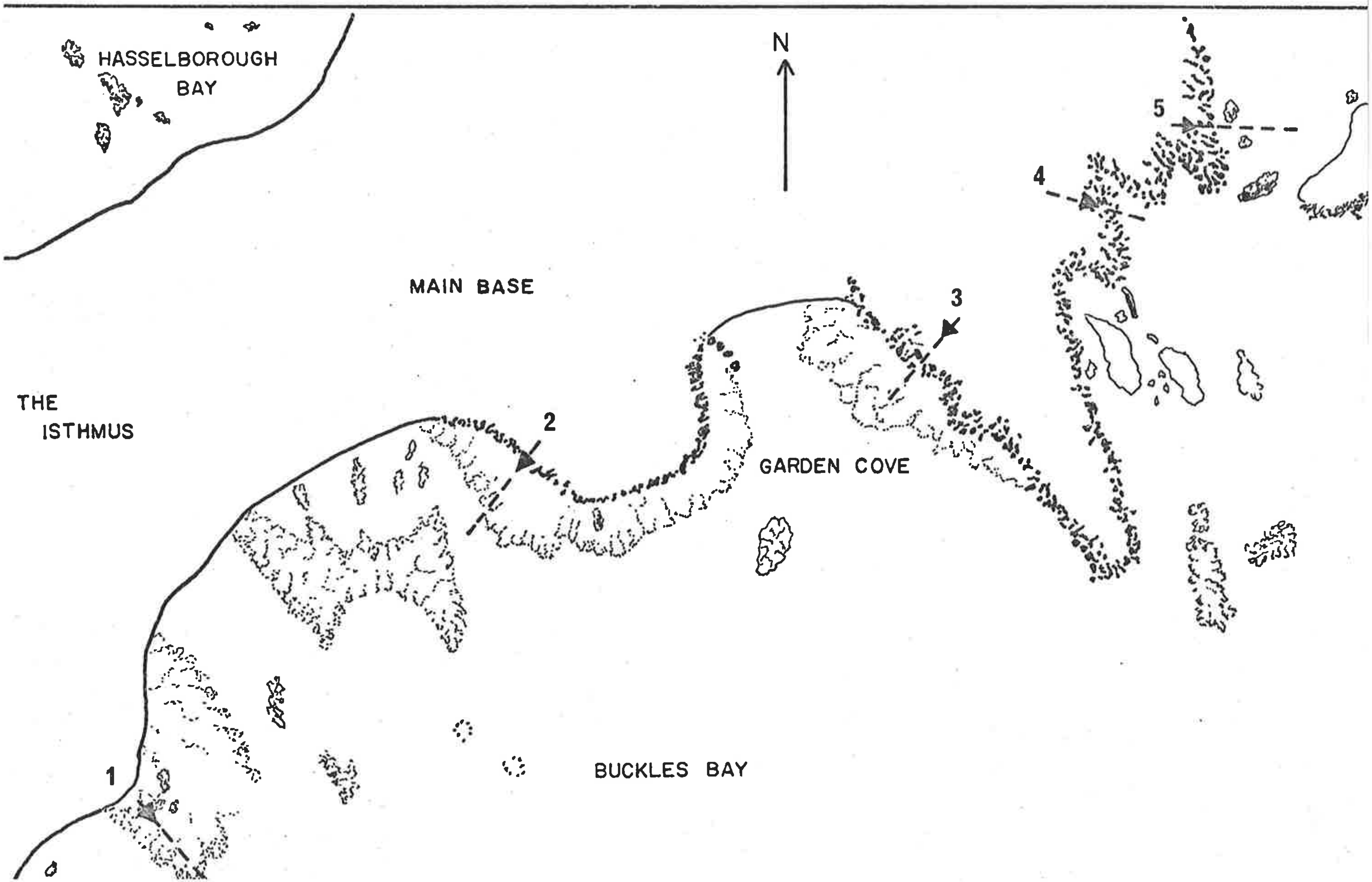
III. THE SHORE ENVIRONMENT

(a) Transects

(i) Materials and methods

Five transects of the shore-line were selected on the east coast of the isthmus area (Figure 6). These were used for determining (i) zones, as indicated by dominant organisms, (ii) the distribution and abundance of the molluscan species selected for study, and (iii) the common biota in each of the zones; during transect work, detailed descriptions of habitats were also made. In order to strengthen the data and to look for seasonal changes in any of the aspects of the transect studies, recordings along the transects were taken at bimonthly intervals over a one year period (May, July, September, November, January, March). The giant kelp, Durvillea antarctica, was cleared from Transect 5 in order to observe any effects (both short term and long term) on the zones and their composition and on the distribution and abundance of both the common organisms and the study molluscs. The kelp was removed by cutting the stipes close to the holdfasts. Because each transect was at right angles to the shore-line, the angle of orientation of each transect to the prevailing swells also indicated the orientation of the vertical aspect of the shore to the swells. Transect 1 faced directly on to ocean swells; the substrate

Figure 6. Location of transects on the Macquarie Island isthmus.


HASSELBOROUGH BAY
N
5
4
MAIN BASE
3
THE ISTHMUS
2
GARDEN COVE
1
BUCKLES BAY

was solid rock, and there was a sharp drop below the line of holdfasts of the giant kelp, *Durvillea antarctica*. Transect 2 was over a large rubble area where the shore was approximately 80° to the swell. Transect 3 traversed solid rock where the shore was at approximately 60° to the swell. Transects 4 and 5 had solid rock substrate and faced directly into sea swells. Transect 4 had a sharp drop at the level of the *Durvillea* holdfasts, whereas Transect 5 traversed a gentle slope.

Each transect was marked out with pegs, the highest being placed at about the upper limit of the *Porphyra* algae. This peg was used as a reference point for measurements along the transect line and for the vertical measurements needed for the construction of a profile.

A square metre, constructed of plastic tubing, was placed at or above the highest peg and was moved progressively down the transect line in conjunction with readings from a tape measure. In each square the presence of common algae and fauna and the density of the study molluscs were recorded. Plate 5A depicts the type of rocky coastline on which the transects were taken. Plates 5B to 7B give a view of each transect with the square and tape measure in use as described above.

The operation of a tide gauge resulted in the analysis of a year's tidal records by Easton (pers. comm.) and en-

Plate 5.

5A. Section of coastline on the eastern side of the isthmus where transects were taken.

5B. Transect 1.
The tape measure and square show the direction taken.

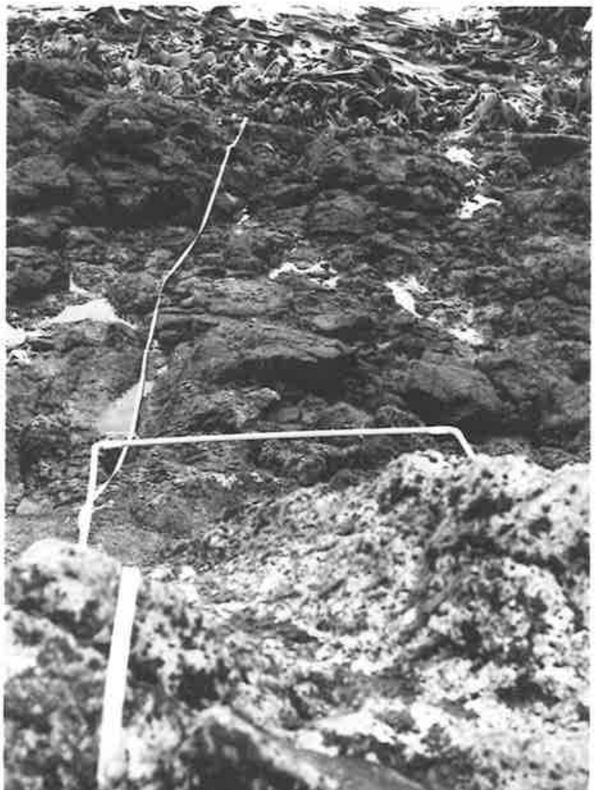


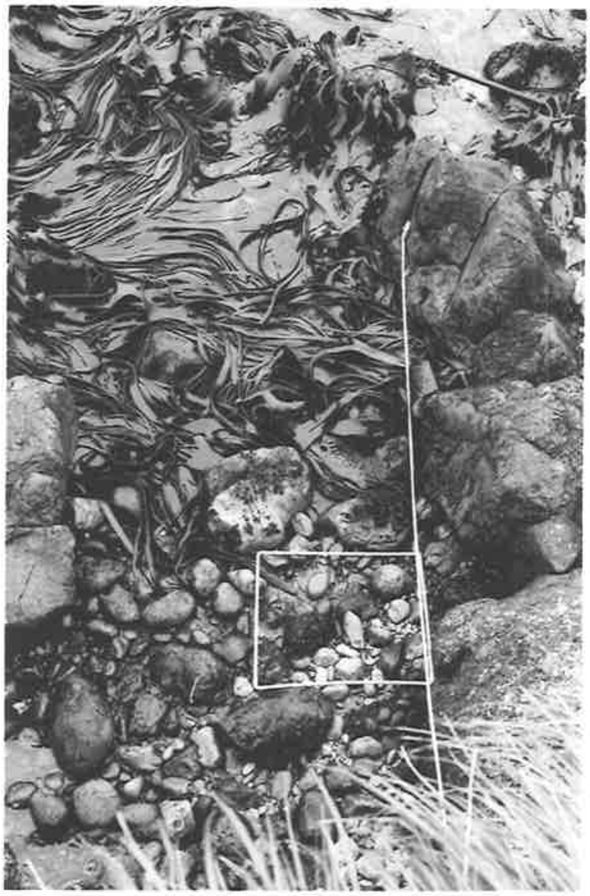
Plate 6.

6A. Transect 2.

The tape measure and square show the direction taken.

6B. Transect 3.

The tape measure and square show the direction taken.



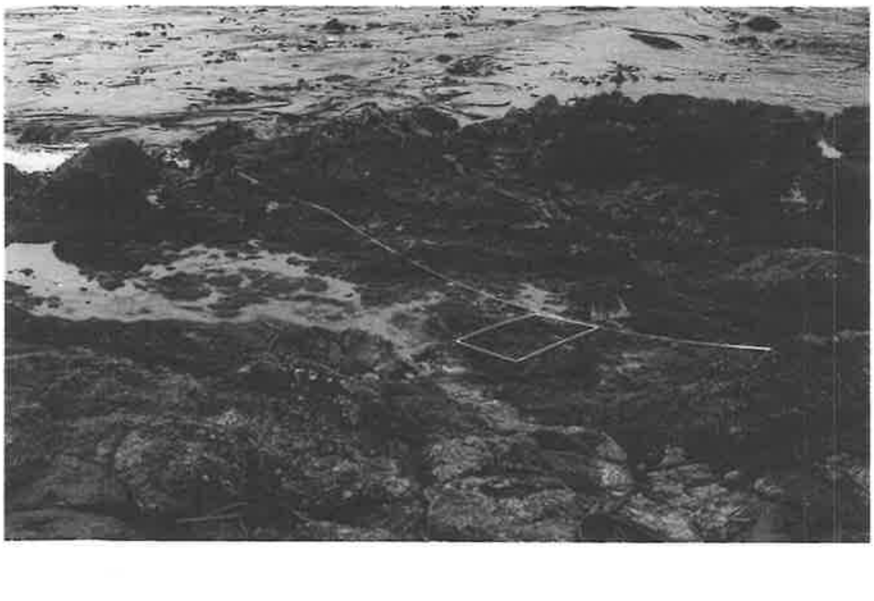
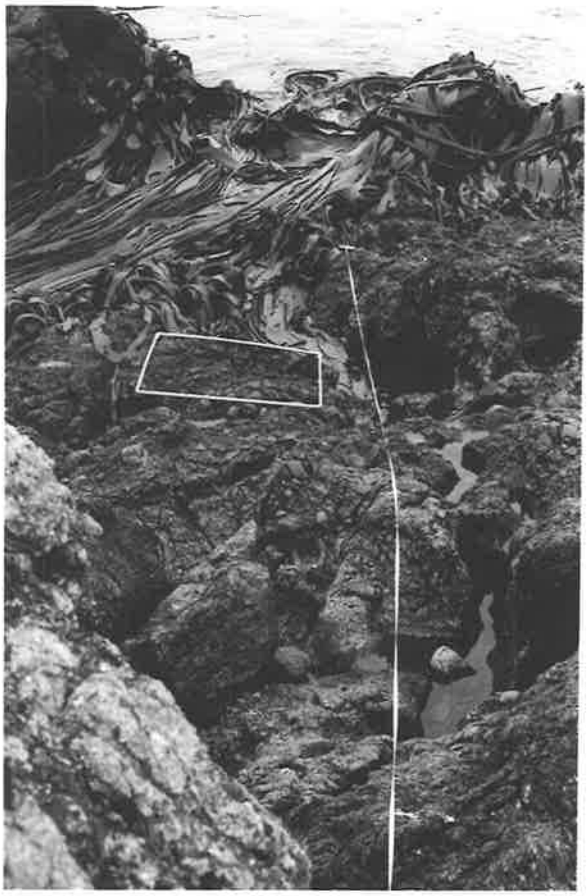
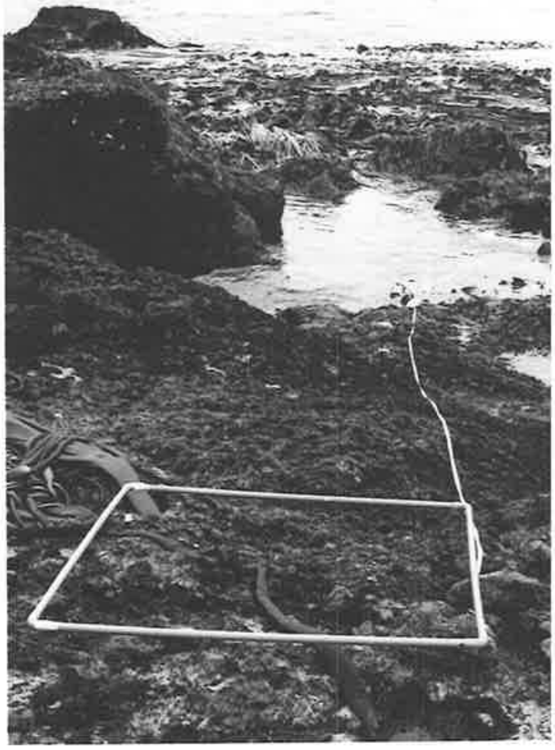


Plate 7.

7A. Transect 4.
The tape measure and square show the direction taken.

7B. Transect 5.
The tape measure and square show the direction taken.





abled the calculation of tidal constants. The following definitions and values from Easton are used:

M_2 = 0.912 ft. (0.278 m) = principal lunar constituent, moving at twice the speed of the mean moon.
O_1 = 0.245 ft. (0.075 m) { O_1 and part of K_1 allow for the
K_1 = 0.293 ft. (0.089 m) { effect of the moon's declination.
S_2 = 0.258 ft. (0.079 m) = principal solar constituent, moving at twice the speed of the mean sun.

O_1, K_1, M_2, and S_2 are amplitudes of the tidal components. The amplitudes plus their respective phases constitute the tidal constants. Tidal height can be calculated from the following formulae, where M.S.L. = the mean sea level and is calculated as 4.060 ft. (1.237 m):

M.H.W.S. (Mean high water spring) = M.S.L. + $(M_2 + S_2)$
M.H.W.N. (Mean high water neap) = M.S.L. + $(M_2 - S_2)$
M.L.W.N. (Mean low water neap) = M.S.L. − $(M_2 - S_2)$
M.L.W.S. (Mean low water spring) = M.S.L. − $(M_2 + S_2)$

The semi-diurnal range is $2(M_2 + S_2)$ and the diurnal range is $2(K_1 + O_1)$. These two ranges indicate the inequality of successive tidal heights in the one diurnal period.

During the 1911-1913 expedition, Blake surveyed Macquarie Island and established a bench mark which was 8.96 ft. (2.73 m) above mean sea level (Mawson 1943). A check of

Blake's figures showed that his M.S.L. determination gave the same surveying level as that used in the above study (Easton, pers. comm.).

For each transect a reference peg was surveyed for vertical height with respect to Blake's bench mark and the vertical heights of the tops of all the squares and some other prominent features were obtained in relation to the reference peg.

Therefore, the profile of each transect could be positionally related to mean sea level and hence to tidal levels using the previously explained formulae. E.H.W.S. (extreme high water spring) and E.L.W.S. (extreme low water spring) levels cannot be derived from the tidal constants and are set from field observations.

(ii) Results and discussion

The topography of the transects is shown in plane and profile views in Charts 1 to 5 and Figures 7 to 9 respectively. The location of prevalent algae and fauna is set out on the transect charts. The faunal lists indicate the distribution of the study molluscs and a number of other animals common on Macquarie Island rocky shores. The profile figures also include tidal levels and areas where the dominant organisms were (i) lichen, (ii) *Porphyra* - *Cladophora*, (iii) *Porphyra*, (iv) *Ulva* - *Chaetangium fastigiatum*, (v) *Ker-*

pp. 36 to 47.

Charts 1. to 5. Pages

Plane views of each, including location of prevalent algae and fauna.

(Each square = one square metre)

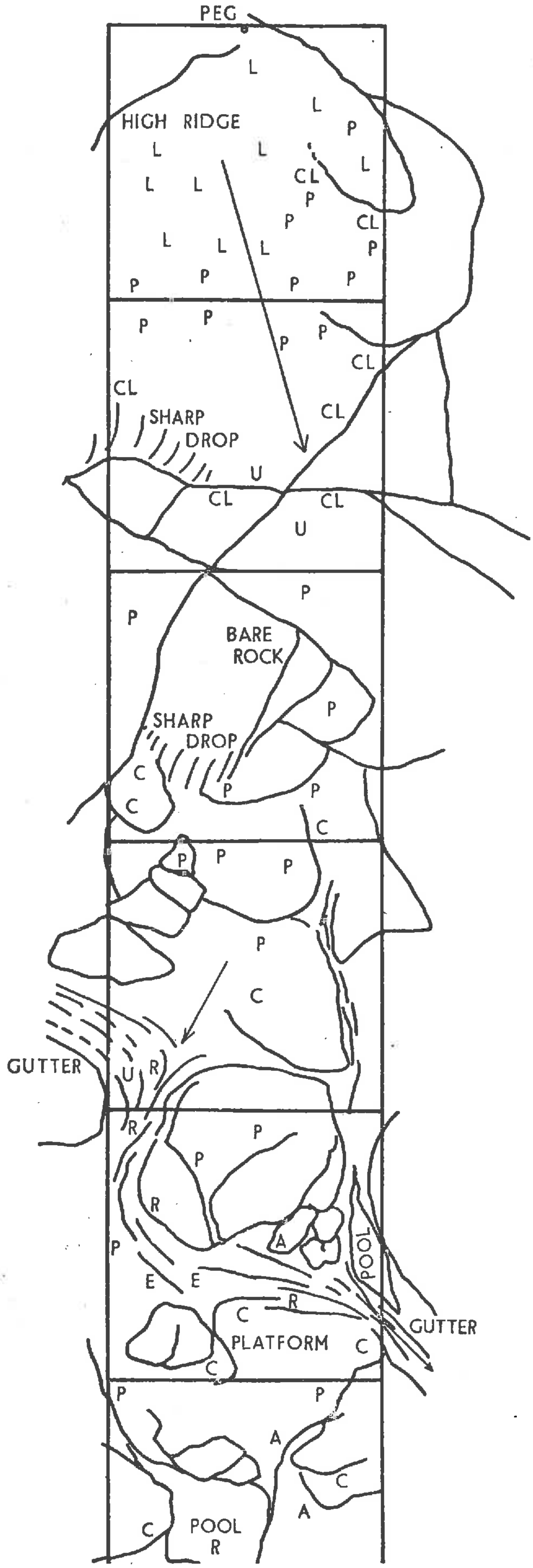
Key to symbols depicting flora on Charts 1 to 5.

L = Lichens

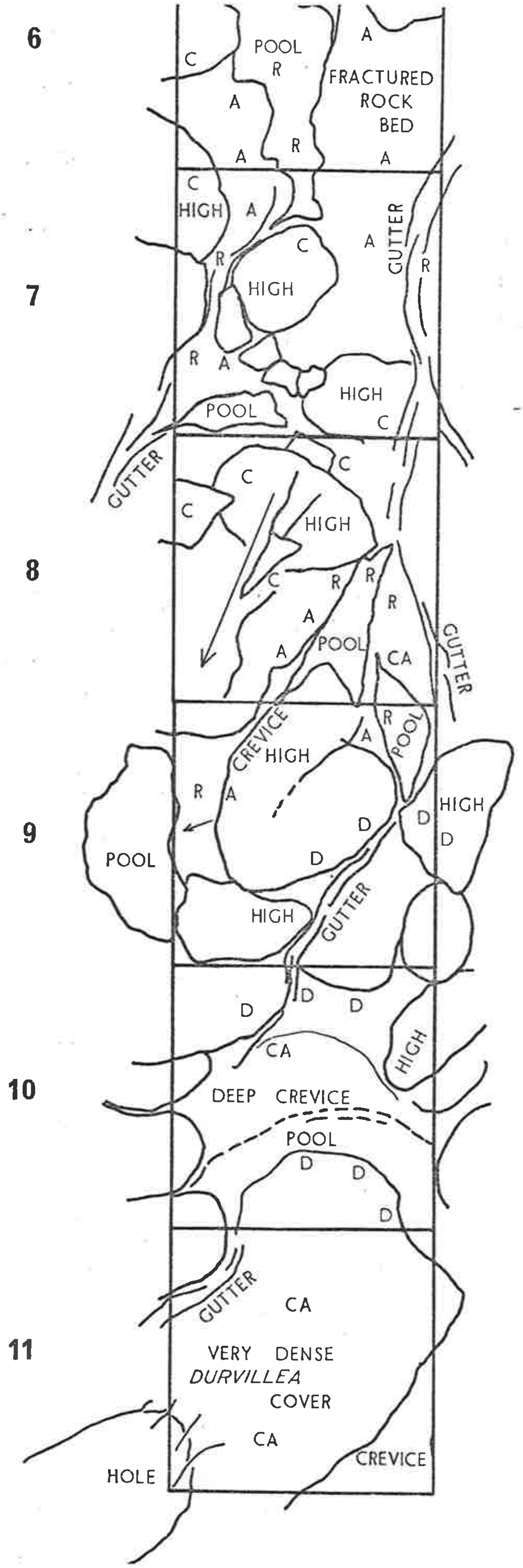
Algae:

P = *Porphyra umbilicus*
CL = *Cladophora* sp.
E = *Enteromorpha* sp.
C = *Chaetangium fastigiatum*
U = *Ulva* sp.
R = *Rhodymenia* sp.
A = *Adenocystis utricularis*
D = *Durvillea antarctica* holdfasts
CA = Encrusting coralline algae (lithothamnions)
RA = Red algae.

TRANSECT 1



1	MITES INSECTS INSECT LARVAE OLIGOCHAETES
2	MITES INSECTS INSECT LARVAE
3	MITES *K. LATERALIS*
4	MITES *K. LATERALIS* *L. CALIGINOSA* SMALL BIVALVES AMPHIPODS ISOPODS SEDENTARY POLYCHAETES
5	*K. LATERALIS* *L. CALIGINOSA* SMALL BIVALVES AMPHIPODS ISOPODS SEDENTARY POLYCHAETES
6	*K. LATERALIS* *L. CALIGINOSA* SMALL BIVALVES AMPHIPODS ISOPODS SEDENTARY POLYCHAETES



K. LATERALIS
L. CALIGINOSA
SMALL BIVALVES
AMPHIPODS
ISOPODS
SEDENTARY POLYCHAETES

K. LATERALIS
L. CALIGINOSA
SMALL BIVALVES
AMPHIPODS
ISOPODS
BRYOZOA

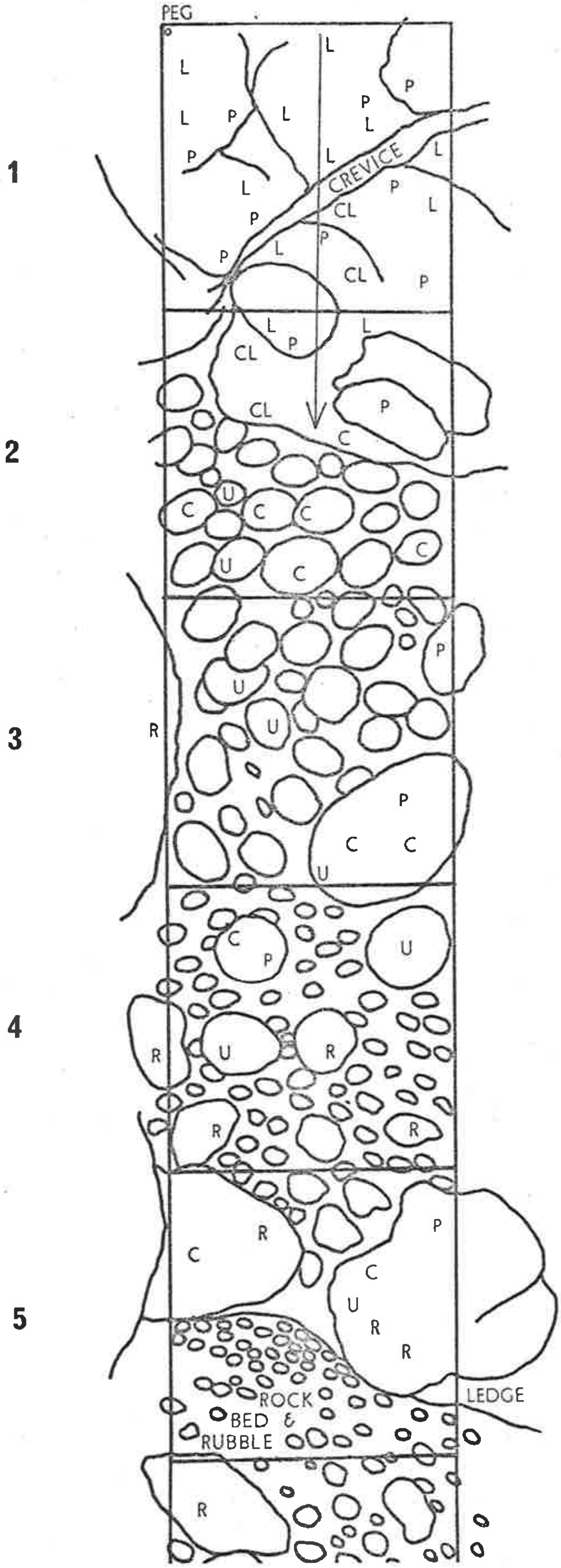
K. LATERALIS
L. CALIGINOSA
SMALL BIVALVES
P. MACQUARIENSIS
AMPHIPODS
ISOPODS

K. LATERALIS
SMALL BIVALVES
P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
AMPHIPODS
SPIRORBIS AGGREGATUS

P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
AMPHIPODS
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES

P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
HOLOTHUROIDS

TRANSECT 2



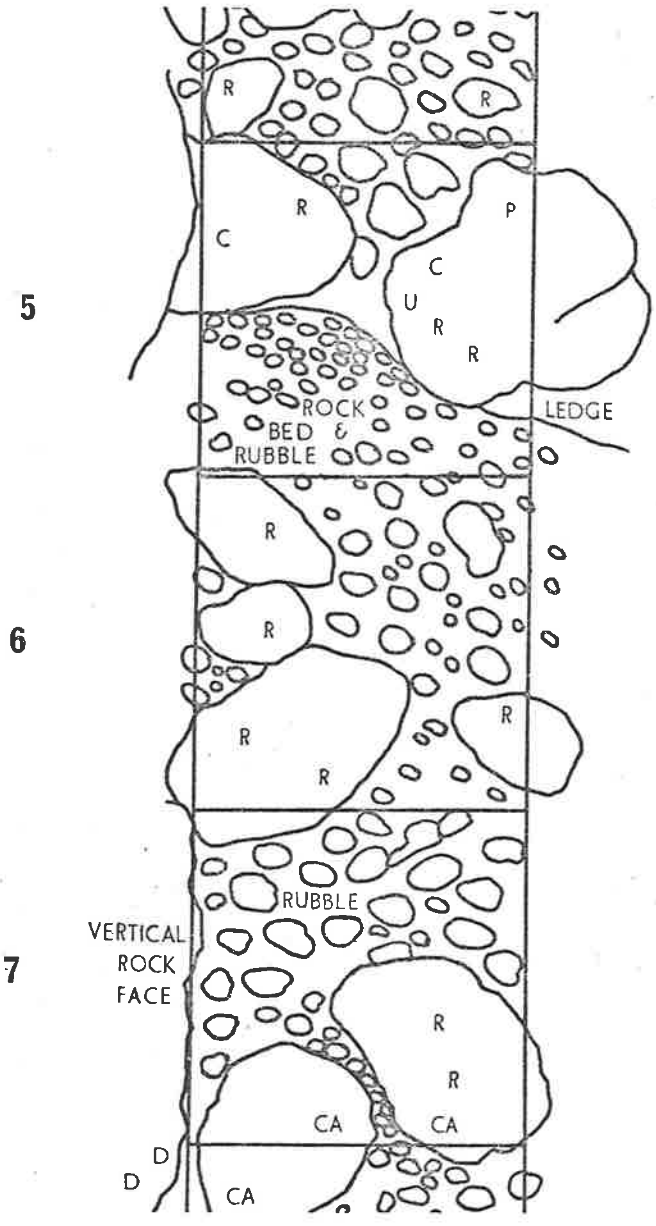
MITES
INSECTS
INSECT LARVAE
OLIGOCHAETES

MITES
INSECTS
K. LATERALIS
AMPHIPODS

L. CALIGINOSA
P. MACQUARIENSIS
AMPHIPODS
(*K. LATERALIS* IN RUBBLE
AREA OF SQUARES 3 AND 4
WERE SCARCE AND ONLY
FOUND ON THE TOPS OF
LARGE ROCKS)

L. CALIGINOSA
P. MACQUARIENSIS
AMPHIPODS

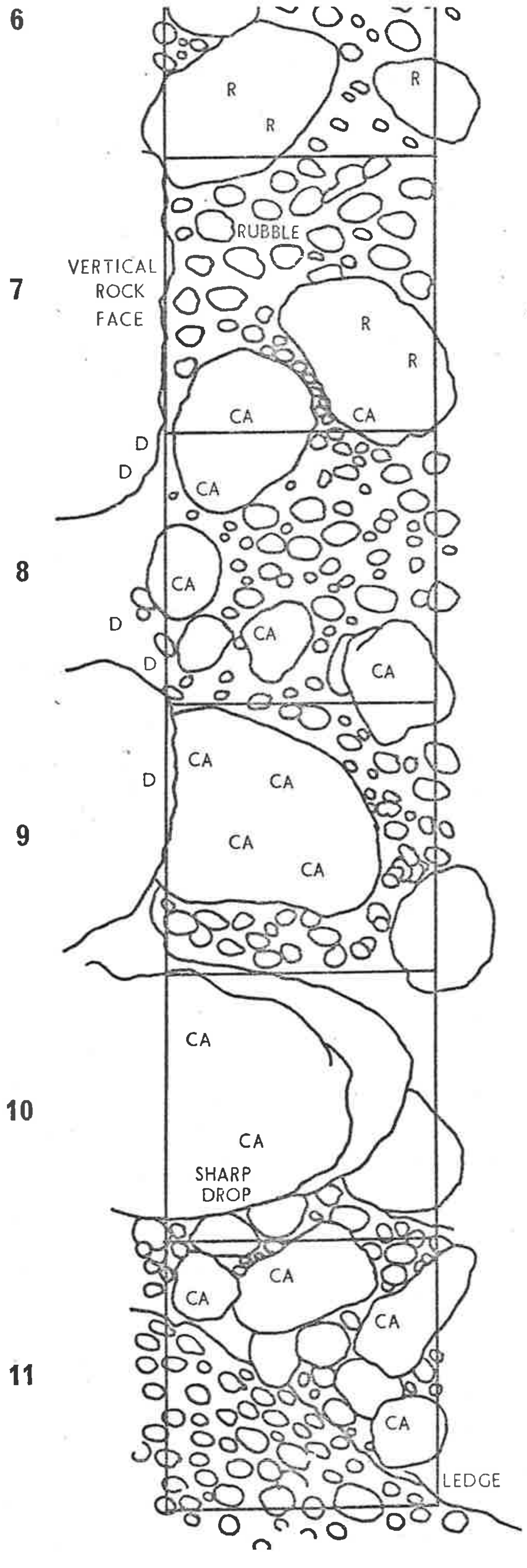
K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
AMPHIPODS
ISOPODS



K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
AMPHIPODS
ISOPODS

K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
AMPHIPODS
ISOPODS

K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
P. AURATA
AMPHIPODS
ISOPODS
SPIRORBIS AGGREGATUS



K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
P. AURATA
AMPHIPODS
ISOPODS
SPIRORBIS AGGREGATUS

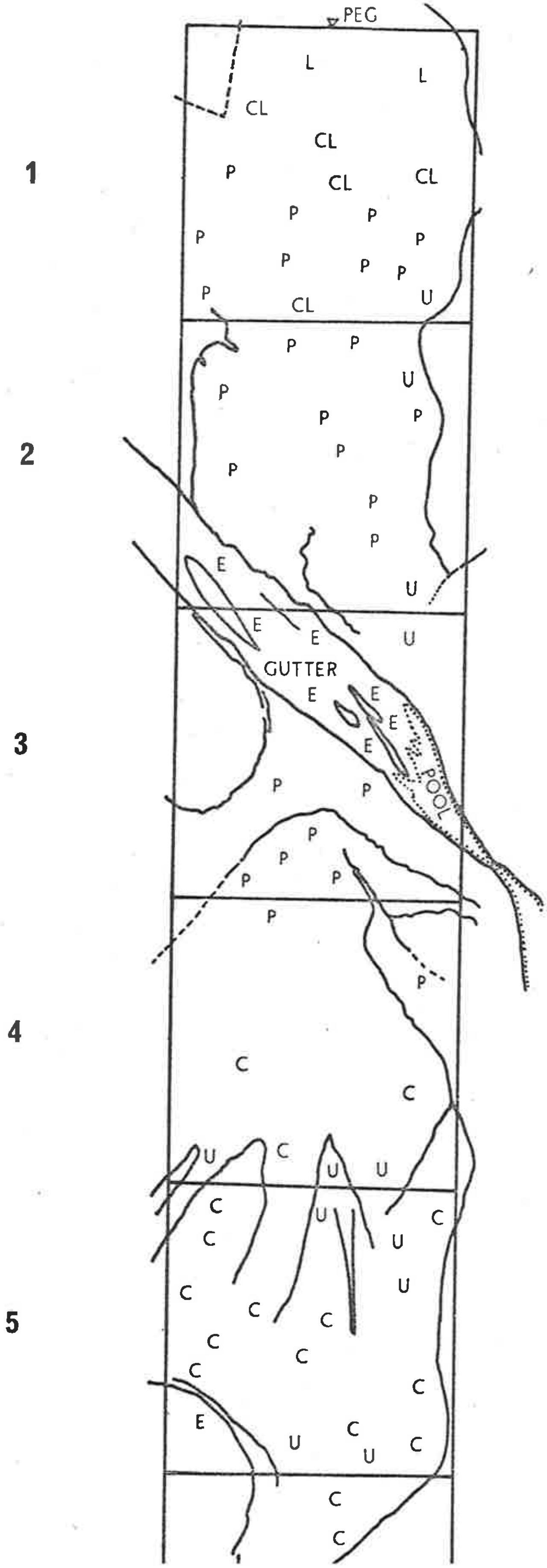
P. MACQUARIENSIS
P. AURATA
C. (*P.*) *CORUSCANS*
AMPHIPODS
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES
STARFISH

P. MACQUARIENSIS
P. AURATA
C. (*P.*) *CORUSCANS*
AMPHIPODS
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES
STARFISH

P. MACQUARIENSIS
P. AURATA
C. (*P.*) *CORUSCANS*
AMPHIPODS
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES
STARFISH

P. MACQUARIENSIS
P. AURATA
C. (*P.*) *CORUSCANS*
AMPHIPODS
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES
STARFISH

TRANSECT 3



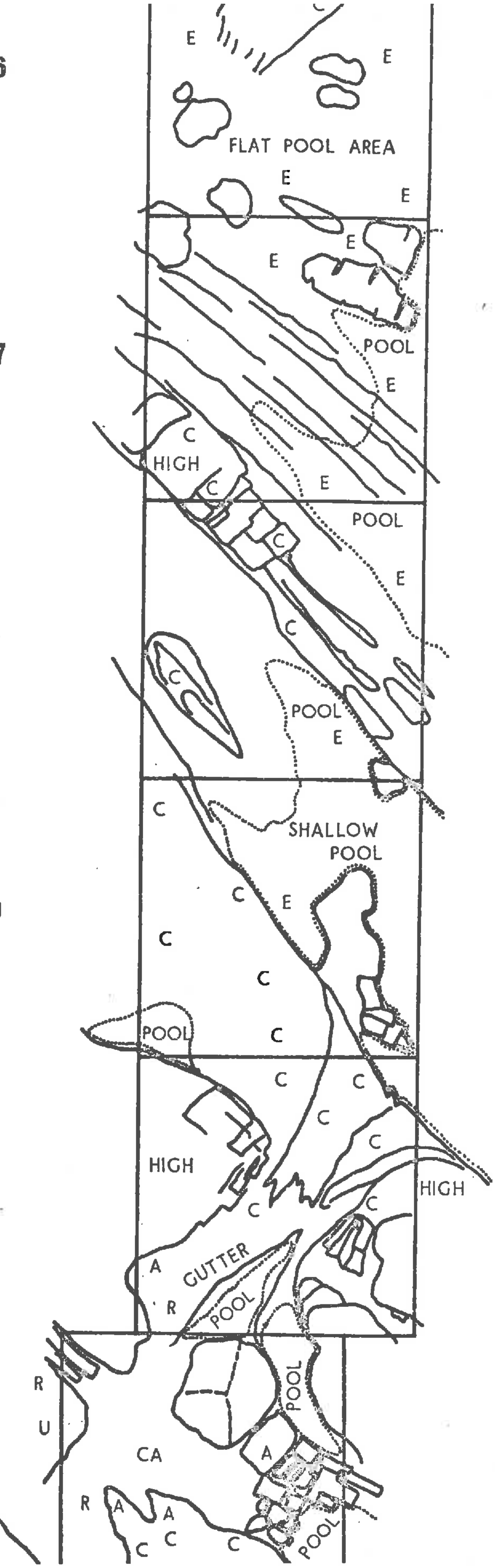
MITES
INSECTS
INSECT LARVAE
OLIGOCHAETES

MITES
INSECTS
INSECT LARVAE
OLIGOCHAETES

MITES
INSECTS
INSECT LARVAE
K. LATERALIS

MITES
INSECTS
INSECT LARVAE
K. LATERALIS

MITES
INSECTS
INSECT LARVAE
K. LATERALIS
L. CALIGINOSA



6

K. LATERALIS
L. CALIGINOSA
AMPHIPODS
ISOPODS
SEDENTARY POLYCHAETES

7

K. LATERALIS
L. CALIGINOSA
AMPHIPODS
ISOPODS
SEDENTARY POLYCHAETES

8

K. LATERALIS
L. CALIGINOSA
SMALL BIVALVES
AMPHIPODS
ISOPODS
SEDENTARY POLYCHAETES

9

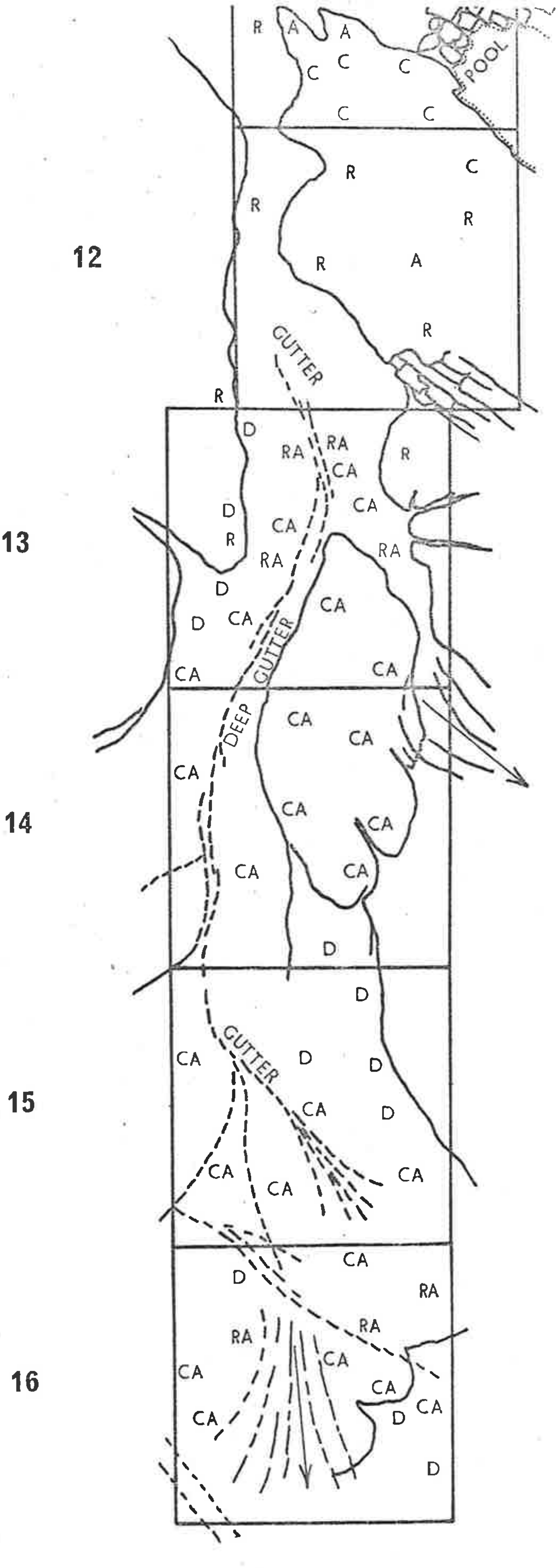
K. LATERALIS
L. CALIGINOSA
SMALL BIVALVES
AMPHIPODS
ISOPODS
SEDENTARY POLYCHAETES

10

K. LATERALIS
L. CALIGINOSA
SMALL BIVALVES
AMPHIPODS
ISOPODS

11

K. LATERALIS
L. CALIGINOSA
SMALL BIVAVLES
AMPHIPODS
ISOPODS



K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
AMPHIPODS
GUTTER (HOLOTHUROIDS
(ANEMONES
(*SPIRORBIS AGGREGATUS*

P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
AMPHIPODS
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES

P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
HOLOTHUROIDS
ANEMONES
SPIRORBIS AGGREGATUS
STARFISH

P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
C.(P.) CORUSCANS
HOLOTHUROIDS
ANEMONES
SPIRORBIS AGGREGATUS
STARFISH

P. MACQUARIENSIS
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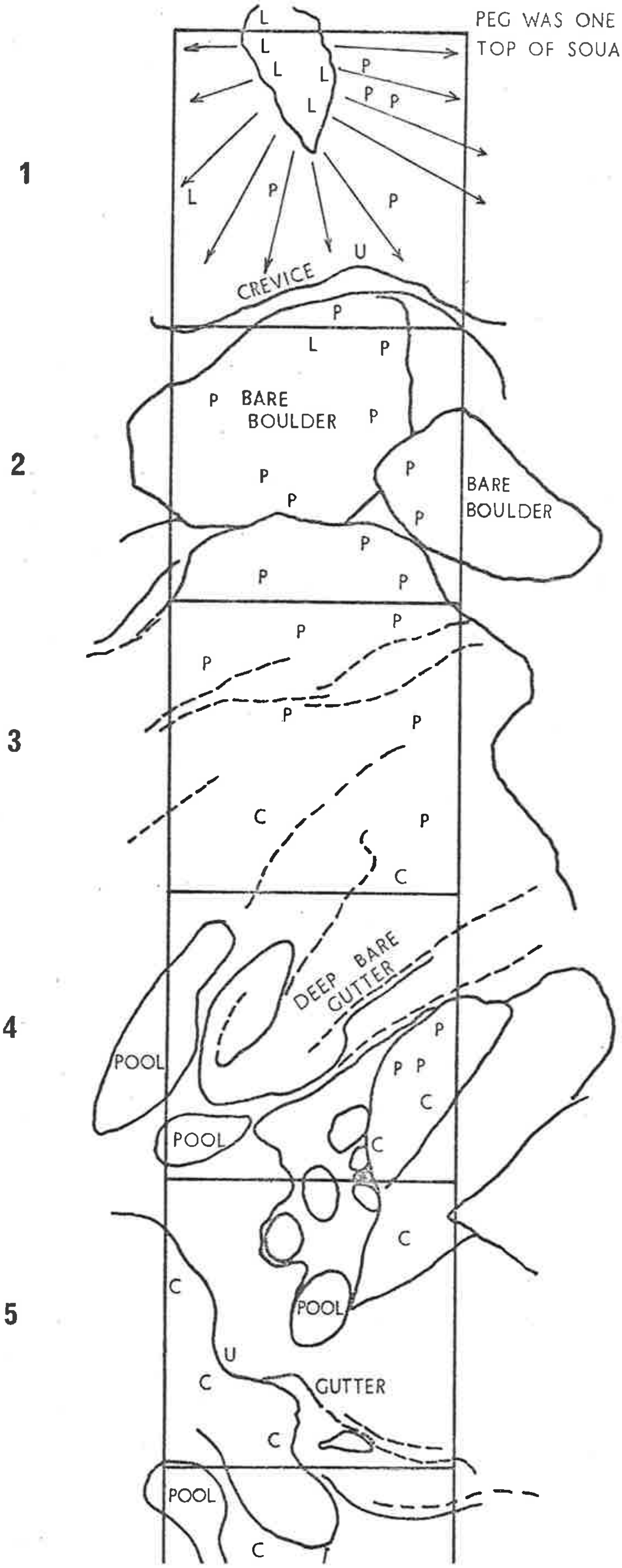
C.(P.) CORUSCANS
HOLOTHUROIDS
ANEMONES
SPIRORBIS AGGREGATUS
STARFISH

TRANSECT 4



PEG WAS ONE FOOT ABOVE
TOP OF SQUARE 1

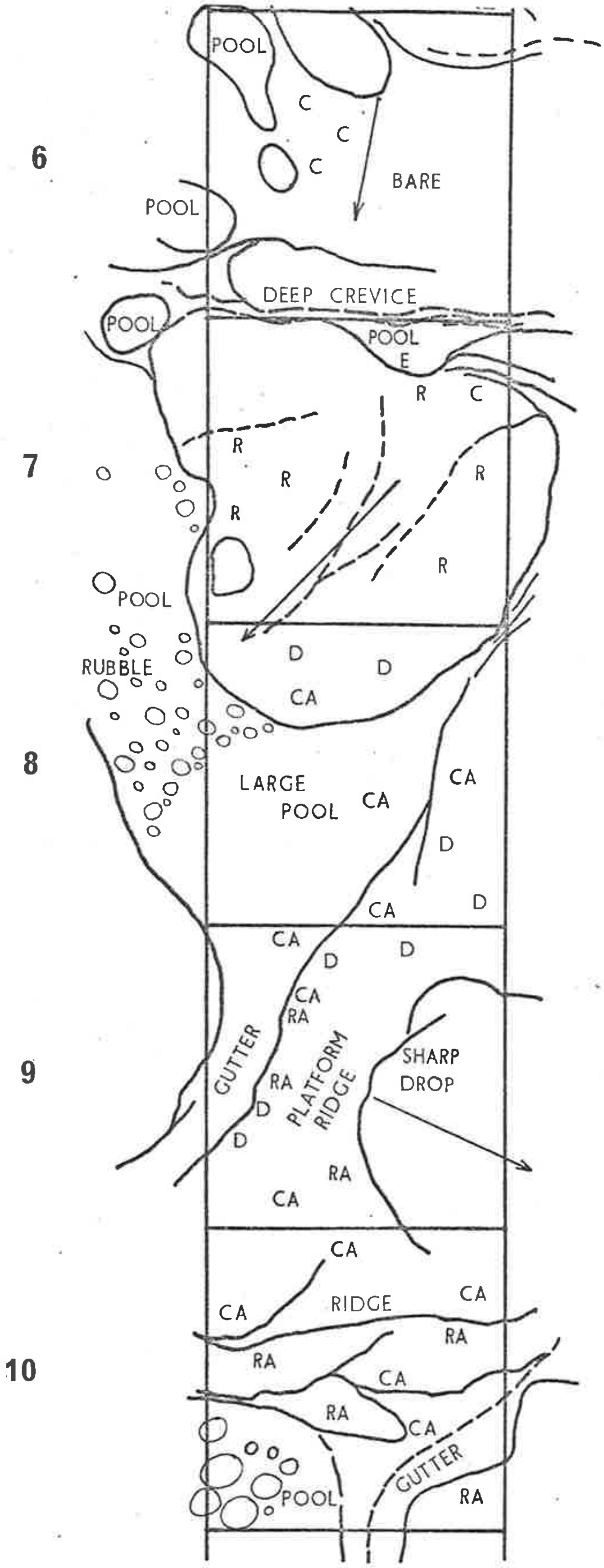
MITES
INSECTS
INSECT LARVAE

MITES
INSECTS

MITES
INSECTS
K. LATERALIS

K. LATERALIS
L. CALIGINOSA
AMPHIPODS
ISOPODS

K. LATERALIS
L. CALIGINOSA
AMPHIPODS
ISOPODS



K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
AMPHIPODS
ISOPODS

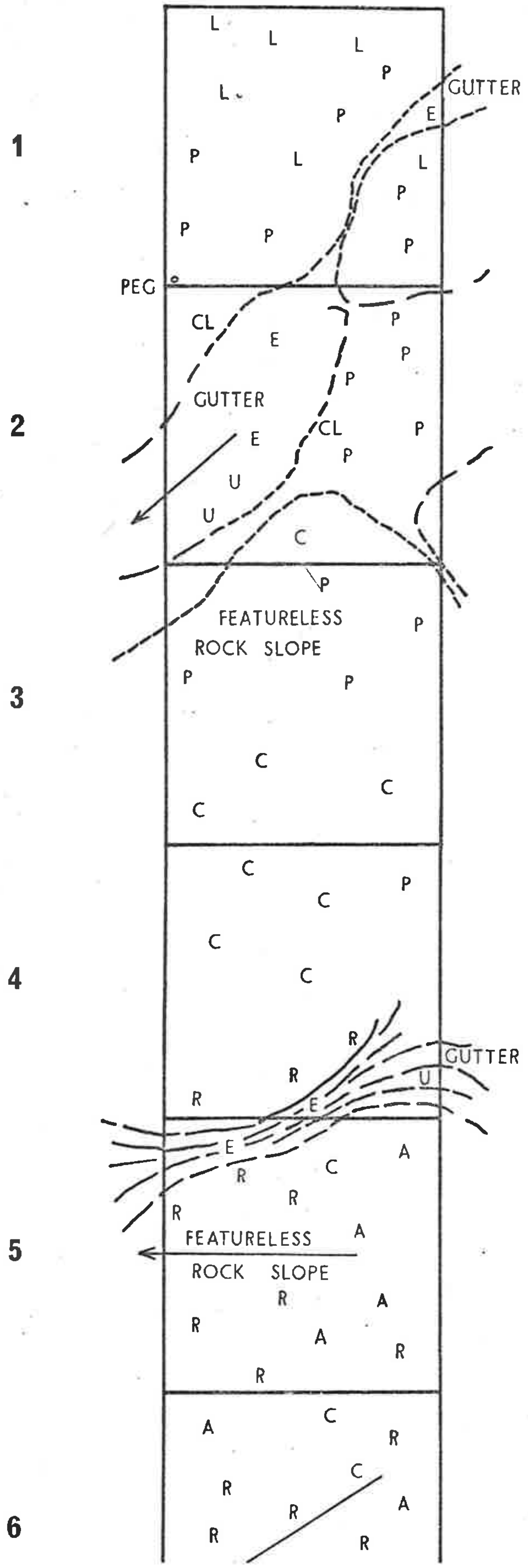
K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
SMALL BIVALVES
AMPHIPODS
ISOPODS

P. MACQUARIENSIS
L. CALIGINOSA
H. SETULOSUM
P. AURATA
C.(P.) CORUSCANS
AMPHIPODS
ISOPODS
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES
STARFISH

P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
C.(P.) CORUSCANS
AMPHIPODS
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES
STARFISH

P. MACQUARIENSIS
H. SETULOSUM
P. AURATA
C.(P.) CORUSCANS
M. HAMILTONI
SPIRORBIS AGGREGATUS
HOLOTHUROIDS
ANEMONES
STARFISH

TRANSECT 5



MITES
INSECTS
INSECT LARVAE
OLIGOCHAETES

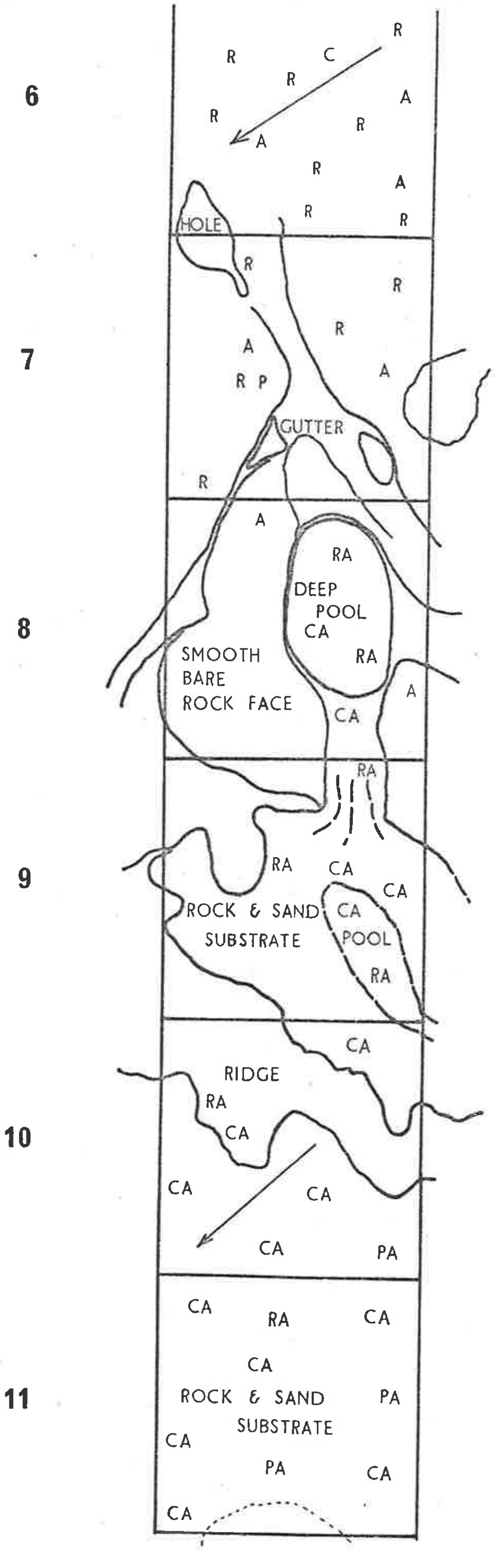
MITES
INSECTS
INSECT LARVAE

MITES
INSECTS

K. LATERALIS
L. CALIGINOSA
SMALL BIVALVES
AMPHIPODS

K. LATERALIS
L. CALIGINOSA
SMALL BIVALVES
AMPHIPODS

K. LATERALIS
L. CALIGINOSA
AMPHIPODS



K. LATERALIS
L. CALIGINOSA
AMPHIPODS

K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
SMALL BIVALVES
AMPHIPODS
ISOPODS

K. LATERALIS
L. CALIGINOSA
P. MACQUARIENSIS
AMPHIPODS
ISOPODS

L. CALIGINOSA
P. MACQUARIENSIS
P. AURATA
C.(P.) CORUSCANS
HOLOTHUROIDS
ANEMONES
AMPHIPODS

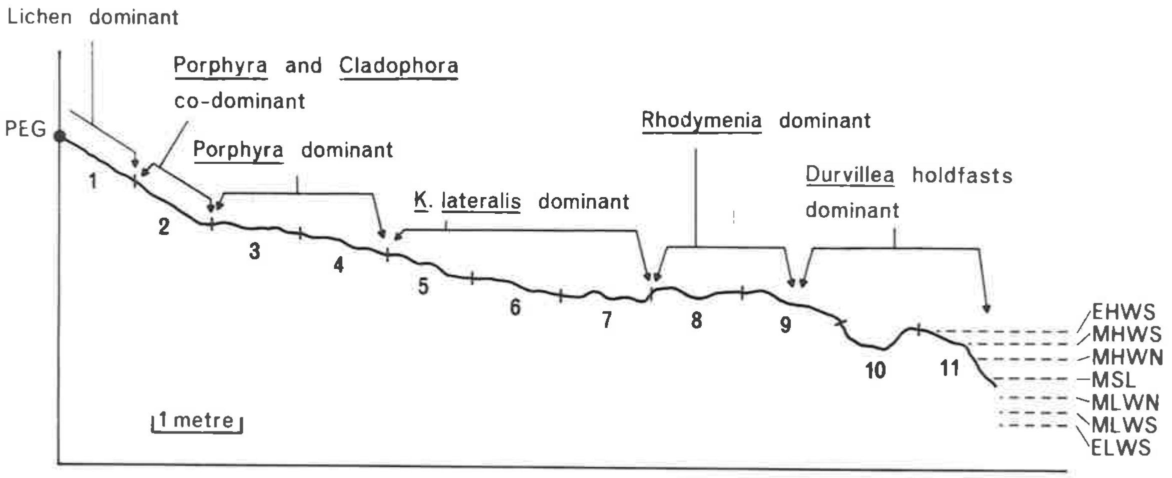
P. MACQUARIENSIS
P. AURATA
C.(P.) CORUSCANS
HOLOTHUROIDS
ANEMONES
STARFISH
SPIRORBIS AGGREGATUS

P. MACQUARIENSIS
P. AURATA
C.(P.) CORUSCANS
M. HAMILTONI
HOLOTHUROIDS
ANEMONES
STARFISH

pp. 48 to 50.

Figures 7. to 9. Page

TRANSECT 1.



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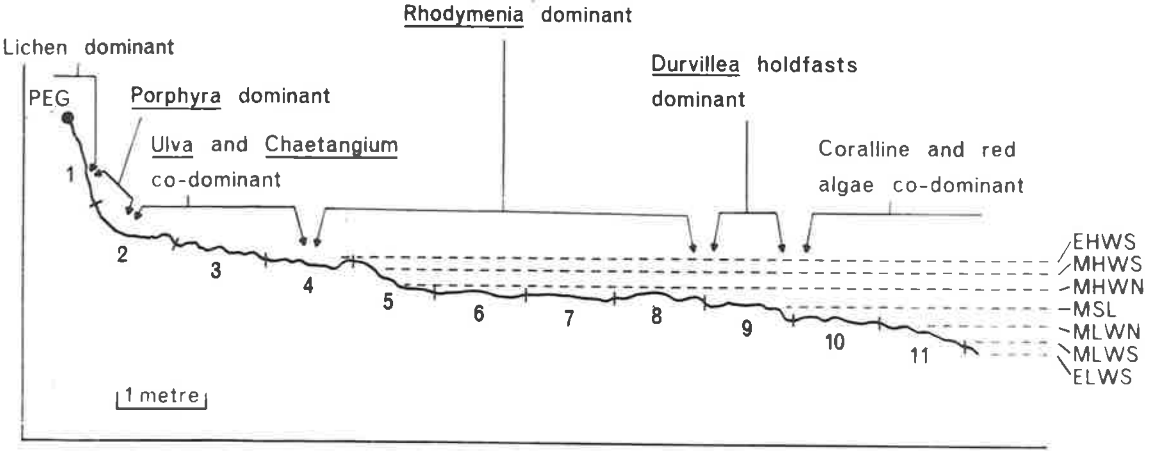

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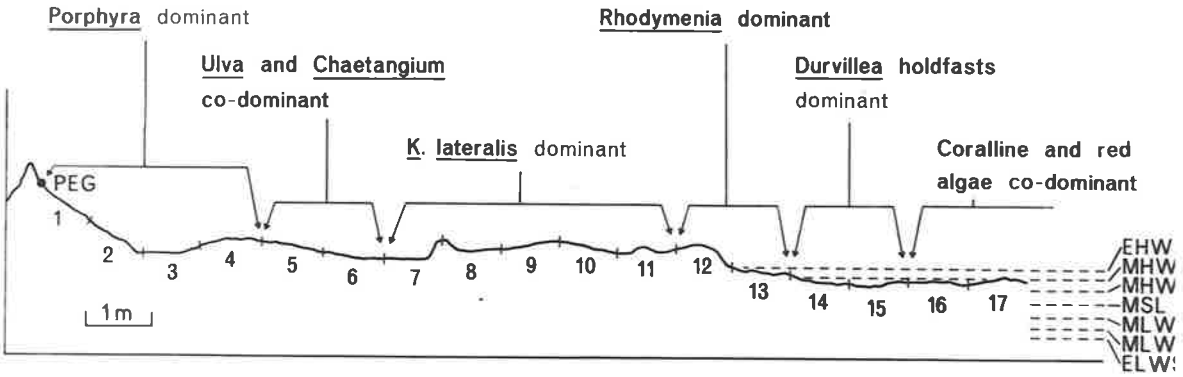
Porphyra dominant
Ulva and Chaetangium co-dominant
K. lateralis dominant
Rhodymenia dominant
Durvillea holdfasts dominant
Coralline and red algae co-dominant
PEG
1
2
3
4
5
6
7
8
9
10
11
12
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15
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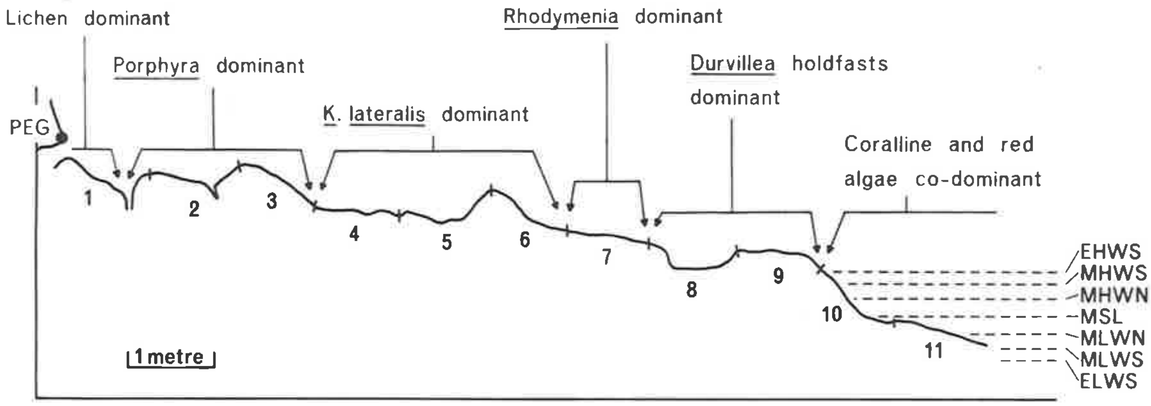
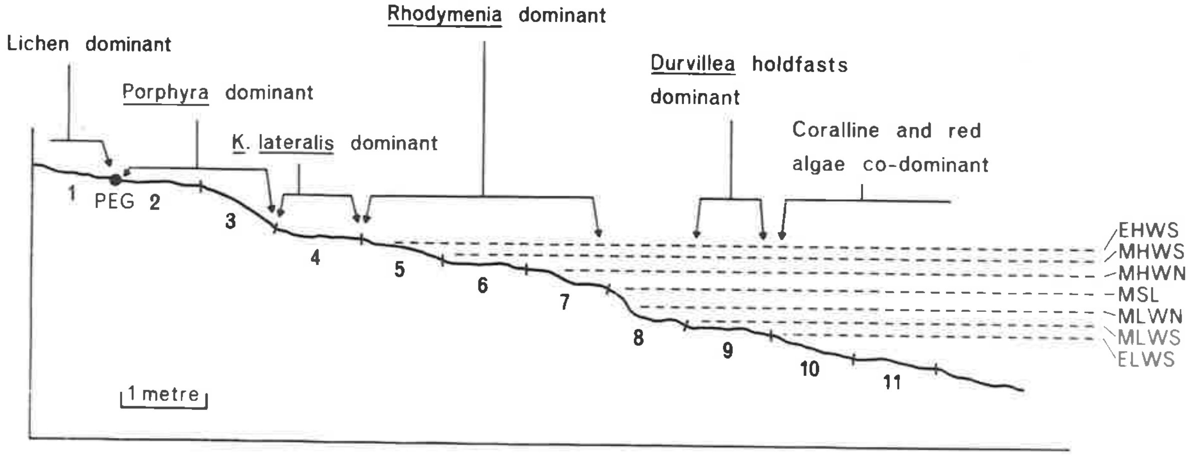
1m
EHW
MHW
MHW
MSL
MLW
MLW
ELW

TRANSECT 4.



TRANSECT 5.



guelenella lateralis, (vi) *Rhodymenia*, (vii) *Durvillea*, and (viii) coralline algae - red algae (*Cladophora*, *Ulva*, *Chaetangium*, *Rhodymenia* = algae, as yet unmentioned in this thesis). The tidal levels, calculated as described in the "Materials and methods", are theoretical levels which represent the extent of water rise and fall only during very calm seas.

As shown by Kenny and Haysom (1962) and Fuller (1967), the rocky shores of sub-Antarctic islands were dominated by algae. Except for one area where the siphonarid *K. lateralis* was dominant, algae were suitable as zone indicator organisms. The six zones described by Kenny and Haysom were evident here (see Table 1) though, with transects commencing at the upper limit of the *Porphyra*, the Lichen Zone was not studied in the same detail for both its extent and for the fauna in it. However, notes were made on the common organisms of the Lichen Zone.

Table 1. Macquarie Island Zonation described by Kenny and Haysom (1962)

Zone	Dominant organism
1. Lichen Zone	Lichens
2. *Porphyra* Zone	*Porphyra umbilicus* (alga)
3. Bare Zone	*Kerguelenella lateralis* (mollusc)
4. Upper Red Zone	*Rhodymenia* sp. (alga)
5. Kelp Zone	*Durvillea antarctica* (alga)
6. Lower Red Zone	Encrusting coralline algae, Red algae

Plates 8A to 10B show the dominant organisms for each of the above zones. The extent or, in some cases, the absence of any of the above zones in the present study differed according to slope, orientation to the prevailing swell, and substrate (see later description of the transects). The placing of these zones in a universal zonation scheme is discussed in section III (b).

A local sub-zone, additional to the zones described by Kenny and Haysom, was evident in Transects 2 and 3 where *Ulva* and *Chaetangium fastigiatum* were co-dominant. These algae were present in the same areas as *K. lateralis* and it was apparent that large rubble and the lack of creviced, rocky surfaces (see later description of the transects) caused the numbers of *K. lateralis* to decrease and *Ulva* - *Chaetangium fastigiatum* to be dominant, although these algae were still relatively sparse when compared to the dominant algal cover of *Porphyra* in the *Porphyra* Zone. In Transect 2, the zone of *Ulva* - *Chaetangium* replaced the zone of *K. lateralis* while in Transect 3, it was additional to the zone of *K. lateralis*. Because the ecological characteristics of both these sub-zones were very similar, for the purposes of this study, the term "Bare Zone", while mainly referring to the zone where *K. lateralis* were dominant, also included those areas dominated by *Ulva* and *Chaetangium fastigiatum*.

In Transect 1, another small additional sub-zone was

Plate 8.

8A. Lichen Zone.

Rocks encrusted with lichens interspersed with mosses.

8B. *Porphyra* Zone.

Dense covering of *Porphyra umbilicus*.

Plate 9.

9A. Bare Zone.

Bare rock on which *Kerguelenella lateralis* are very dense.

9B. Upper Red Zone.

Covering of *Rhodymenia* sp.

Plate 10.

10A. Kelp Zone.

Dense growth of Durvillea antarctica (at low tide and calm seas).

10B. Lower Red Zone.

Rock surfaces (below the Durvillea antarctica holdfasts) encrusted with coralline algae with isolated stands of red frond algae. The photograph was taken during low tide and calm seas.

evident where *Porphyra* and *Cladophora* algae were co-dominant. Again, for the purposes of this study, the *Porphyra* Zone, while mainly referring to the zone where *Porphyra* was dominant, also included those areas where such co-dominance existed.

Plate 11A shows a rocky area in Buckles Bay at E.L.W.S. and calm seas exposing the coralline algae below the *Durvillea* holdfasts. Plate 11B shows Transect 2 at E.H.W.S. and moderate seas when the water level was in the *Porphyra* Zone. E.H.W.S. and E.L.W.S. represent the tidal extremes (highest and lowest) which occur in accordance with particular positions of the moon and sun.

Observations at bimonthly intervals along Transects 1, 2, 3, and 4 showed no seasonal changes in the position of the zones or in their composition in terms of recording the presence of common organisms. More subtle changes may have occurred in more exactly defined communities.

The position and extent of each of the zones (local to Macquarie Island) on each of the five transects are described here with reference to orientation to the prevailing waves, shore topography, and tidal levels. The distribution of the study molluscs on each transect is also described. These molluscs together with other organisms found to be prevalent in each of these zones are listed after these descriptions in Table 2 (see later).

Plate 11.

11A. Reef in Buckles Bay uncovered at E.L.W.S. tide during calm seas.

11B. Transect 2 covered at E.H.W.S. tide during moderate seas.

In Transect 1 (Chart 1, Figure 7), the substrate was solid rock. The sharp drop of this transect at sea level and the aspect of the shore facing directly into the sea swells resulted in wetting by frequent surge. Tidal levels alone did not reach above square 11 even at E.H.W.S. The Lichen Zone was above square 1 and intersected with the *Porphyra* Zone at the bottom of square 1. *Porphyra* extended considerably down the transect and was dominant in squares 3 and 4 and co-dominant with *Cladophora* alga in square 2. The siphonarids (*K. lateralis*) were usually found in crevices in squares 3 to 7. The siphonarids were the dominant organisms from squares 5 to 7 (Bare Zone). *L. caliginosa* were found in pools and crevices as high as square 3. *Rhodymenia* alga extended up to square 7 and was dominant in square 8 and the top half of square 9, this dominance marking the Upper Red Zone. *Durvillea* holdfasts were found up to square 9 and were dominant in the lower half of square 9 and in squares 10 and 11.

P. macquariensis, *H. setulosum*, and *P. aurata* were part of the typical fauna of the Lower Red Zone below square 11, while *C.* (*P.*) *coruscans* were rare.

In Transect 2 (Chart 2, Figure 7), the substrate mainly consisted of large, firmly implanted rubble. Because the shore-line was at an obtuse angle to the prevailing swells, the impact of the waves was lessened. E.H.W.S. tidal level was at the top of square 5. The Lichen Zone was above square 1 and intersected with the Porphyra Zone which was very reduced, Porphyra umbilicus being dominant only in adjoining parts of squares 1 and 2. From the lower half of square 2 to the upper half of square 4, the algae, Ulva and Chaetangium fastigiatum, were co-dominant. K. lateralis were lacking in this area as it consisted solely of large rubble and, in such a habitat, the siphonarids were generally restricted to the tops of the large boulders. L. caliginosa were found under rocks high up on the shore. In Transect 2, the presence of the giant kelp, Durvillea antarctica, had to be considered in two ways: (i) the effect of fronds from nearby Durvillea holdfasts not in transect squares and (ii) the actual zone where Durvillea holdfasts were dominant. The transect was alongside large rock outcrops on which holdfasts were attached and the upper limit of these holdfasts was at the level of square 5. Although the fronds from these lay over the transect area from square 5 downwards during low tide and calm seas (see Plate 6A), Rhodymenia alga was dominant in the actual transect from the bottom half of square 4 to square 8. The Kelp Zone, where Durvillea holdfasts were dominant on the actual transect, was confined to square 9. Squares 10 and 11 were in the Lower Red Zone where coralline algae and red frond algae were dominant. P. macquariensis were found in all squares of the transect up to square 3 with the highest densities occurring in the Upper Red and Lower Red Zones. *P. aurata* were common in the Kelp and Lower Red Zones. *H. setulosum* and *C.* (*P.*) *coruscans* were rare in the Lower Red Zone.

In Transect 3, (Chart 4, Figure 8), the slope was very gentle along a solid rocky substrate. Because the shore-line was at approximately 60° to the prevailing swell, the impact of the waves was reduced. E.H.W.S. tidal level was in square 13. The Lichen Zone was above square 1 and intersected with the *Porphyra* Zone which extended from square 1 to square 4. The distribution of both *Chaetangium fastigiatum* alga and *K. lateralis* was greatly extended, i.e. from squares 4 to 11. From squares 7 to 11, the siphonarids were dominant. In squares 5 and 6, the rocky surfaces were smoother and lacked crevices. Although *K. lateralis* were present in these two squares, the algae, *Ulva* and *Chaetangium fastigiatum*, were co-dominant. *L. caliginosa* were found in pools and under stones from squares 5 to 12. *Rhodymenia* alga dominated squares 12 and 13 to mark the Upper Red Zone. The upper limit of *Durvillea* holdfasts was in square 13. Squares 14 and 15 had a dominant cover of *Durvillea* holdfasts (Kelp Zone) while squares 16 and 17 were in the Lower Red Zone. *P. macquariensis* had a distribution from just above the *Durvillea* holdfasts downwards. In the Kelp Zone, *H. setulosum* were common while *P. aurata* and *C.* (*P.*) *coruscans* were rare. In the Lower Red Zone, H. setulosum were rare while P. aurata and C. (P.) coruscans were common.

In Transect 4, (Chart 4, Figure 9), the substrate mainly consisted of solid rock. There was a sharp drop at sea level and wetting usually occurred by splash and surge from the sea with the shore line facing directly into the prevailing swells. The tidal level of E.H.W.S. was at the top of square 10. The Lichen Zone intersected with the Porphyra Zone in square 1 from which the Porphyra Zone extended down to square 3. K. lateralis were dominant through squares 4 to 6 with smaller numbers above and below this area. Again, L. caliginosa were found high on the shore in rock pools and crevices. Rhodymenia alga dominated square 7 to form the Upper Red Zone. The top of square 8 coincided with the upper limit of Durvillea holdfasts which dominated squares 8 and 9, forming the Kelp Zone. However, a large deep pool with a rubble bottom occupied parts of squares 8 and 9. There were no holdfasts in this pool which, because the kelp cover had little effect on it, could not be regarded as part of the Kelp Zone. This pool situation was apparently favourable to P. macquariensis as large numbers were found there, an atypical occurrence in the Kelp Zone. Coralline algae and red frond algae were dominant in squares 10 and 11, marking the Lower Red Zone. P. macquariensis, C. (P.) coruscans, and P. aurata were present in the Kelp Zone while H. setulosum were dense;

only P. macquariensis extended above this zone in large numbers. In the Lower Red Zone, P. macquariensis, C. (P.) coruscans, and P. aurata were common, while H. setulosum were rare.

In Transect 5 (Chart 5, Figure 9), the slope was gradual over a substrate of solid rock. Here, the shore faced directly into the prevailing swells. There was a fringing reef out to sea which greatly reduced the wave action. The tidal level of E.H.W.S. was at square 5. The removal of Durvillea had little effect on the zones or on their composition in terms of recording the presence of common organisms. Again, more subtle changes may have occurred in more exactly defined communities. In the first four months after the removal of Durvillea the only observed effect was on the Kelp and Lower Red Zones where some coralline algae died off and red algae increased; zones above the Kelp Zone were not affected. The study of the long-term effects of Durvillea removal on other zones in Transect 5 was hindered by the deposition of a moderate cover of dislodged kelp fronds after very large seas in October. The Lichen Zone intersected with the Porphyra Zone at the bottom of square 1. Porphyra umbilicus was dominant in squares 2 and 3. The Bare Zone here was very reduced, apparently by the encroachment of the Upper Red Zone. K. lateralis were found from squares 4 to 8 but their density was generally low and the siphonarids were dominant only in square 4. Rhodymenia alga was dominant from square 5 to square 7. L. caliginosa were found from squares 4 to 9 in pool pockets and crevices (the highest density being in the upper part of their distribution). Before removal, the upper limit of the Durvillea holdfasts was at square 8, but this square mainly comprised a rock surface with scattered stands of the alga, Adenocystis utricularis, and a pool containing coralline algae and red frond algae. Durvillea holdfasts had been dominant in square 9. Squares 10 and 11 were in the Lower Red Zone where coralline algae and red algae were dominant. P. aurata and C. (P.) coruscans were present in square 9 and common in squares 10 and 11. The removal of Durvillea increased lowered the overall numbers of P. macquariensis but did not alter the upper limit of their distribution, which was at square 7. (The results of Durvillea removal from Transect 5 on the numbers of P. macquariensis are given in section V(d).) The removal of kelp lowered the density estimate for H. setulosum from common to rare in squares 10 and 11. Further studies on the removal of Durvillea in other areas supported the changes in density shown for P. macquariensis and H. setulosum on Transect 5 (section IV 1. (c)).

As previously mentioned Table 2 lists the conspicuous biota common to each of the zones, with emphasis on the distribution of the molluscs under study. In all transects, the organisms of each zone were similar although their pro-

Table 2. Common biota of rocky shore zones of Macquarie Island.

ZONE	FAUNA	FLORA
LICHEN	Mites Beetles Insect larvae Collembola *Tigriopus angulatus* (copepod)	*Verrucaria* sp. lichen Other lichens *Hildenbrantia* sp. (alga) *Prasiola* sp. (alga) *Enteromorpha* sp. (alga) *Colobanthus muscoides* (vascular plant) *Cotula plumosa* Mosses
PORPHYRA	Mites Oligochaetes *Kerguelenella lateralis* (siphonarid) *Laevilitorina caliginosa* (littorinid) Small bivalves Amphipods *Exosphaeroma gigas* (isopod) Sedentary polychaetes	*Porphyra umbilicus* (alga) *Enteromorpha* sp. (alga) *Cladophora* sp. (alga) *Ulva* sp. (alga) *Prasiola* sp.
BARE	*Kerguelenella lateralis* *Laevilitorina caliginosa* Small bivalves Amphipods *Exosphaeroma gigas* Sedentary polychaetes	*Chaetangium fastigiatum* *Ulva* sp.

(cont.)

Table 2 (continued).

ZONE	FAUNA	FLORA
UPPER RED	Amphipods *Exosphaeroma gigas* *Kerguelenella lateralis* *Laevilitorina caliginosa* *Patinigera macquariensis* (limpet)	*Rhodymenia* sp. (alga) *Adenocystis utricularis* (alga)
KELP	*Hemiarthrum setulosum* (chiton) *Plaxiphora aurata* (chiton) *Patinigera macquariensis* *Spirorbis aggregatus* (tubicolous polychaete) *Pseudopsolus macquariensis* (holothuroid) Amphipods Anemones	*Durvillea antarctica* (giant kelp) Coralline algae
LOWER RED	*Patinigera macquariensis* *Plaxiphora aurata* *Cantharidus* (*P.*) *coruscans* (trochid) *Pseudopsolus macquariensis* *Spirorbis aggregatus* *Anasterias directa* (starfish) *Anasterias mawsoni* (starfish) Anemones	Coralline algae Red algae (several species)

portionate composition varied with the different transects. Plates 12A and 12B show some of the organisms under the dense *Durvillea* cover of the Kelp Zone, e.g. Plate 12A: encrusting coralline algae, sparse stands of red algae, *Hemiarthrum setulosum*, *Patinigera macquariensis*, a starfish (*Anasterias mawsoni*); Plate 12B: sea anemones, holothuroids (*Pseudopsolus macquariensis*).

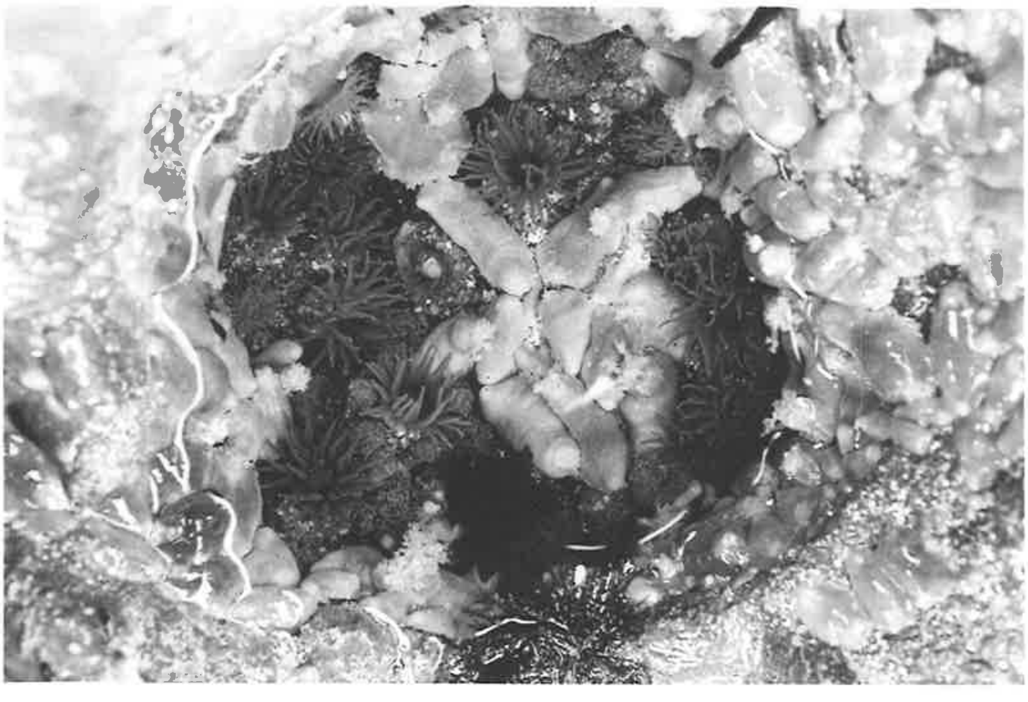
It was difficult to determine any seasonal changes in the distribution and abundance of the study molluscs. On some transects, catastrophic events such as kelp overlay from very large seas in October (Transects 4 and 5), unusually heavy predation from roosting Dominican gulls (Transect 2), and the movement of rubble in the Lower Red Zone (Transect 4), greatly altered the densities of the molluscs and, hence, hindered any study of the change in densities with seasons. (These catastrophic events are more fully described in sections IV 1.(c) and V (a).) In addition, the measures of abundance employed were apparently too gross to gauge any subtle changes for *K. lateralis*, *L. caliginosa*, *H. setulosum*, and *C.* (*P.*) *coruscans*. Numbers of *P. aurata* and *P. macquariensis* were counted in each square. *P. aurata* showed no seasonal changes in range or abundance. The data for *P. macquariensis* are presented and discussed in section V (d) from which the salient points are given here. The upper limit to the range of *P. macquariensis* did not change significantly

Plate 12.

12A. Fauna of the Lower Red Zone on rocks encrusted with coralline algae.

12B. Sea anemones and holothuroids in the Lower Red Zone.

40 mm



30 mm

throughout the year except in the case of kelp overlay after very heavy seas (Transect 4). There was no total migration of *P. macquariensis* out of the eulittoral zone at any season. There were two general trends: (1) the concentration of limpets at or just below the upper limit of *Durvillea* holdfasts increased in September; (2) the total number of limpets in each transect decreased in the summer months of January and March. However, because other factors altered limpet numbers on the transects (i.e. the so-called catastrophic events), any significance of these two trends to the overall limpet population was obscure.

There was no evidence to suggest that the lashing fronds of the *Durvillea* were the cause of the relatively barren nature of the Bare Zone, as postulated by Kenny and Haysom (1962). In Transect 5, the Bare Zone did not change in either position or composition of the conspicuous organisms after the removal of *Durvillea* fronds. However, Transect 5 was not a good study situation for the effects of *Durvillea* on the Bare Zone as the holdfasts were well away from it; the lower position of the Kelp Zone was probably brought about by the lesser wave action resulting from the fringing reef out to sea (see description of transects). In the other transects (1 to 4) much of the Bare Zone was well away from the influence of the kelp fronds. This was also observed on many parts of the shore-line. However, in other areas of the shore, the Bare Zone was closer to the Kelp Zone and was subjected to considerable contact by fronds thrown about by wave action. Durvillea was removed from a strip in five of these areas. (Three of these experimental areas were part of a study on the effects of algal growth on the abundance of the study molluscs, see section IV 1. (c).) Three of these areas were cleared in May, one in October, and one in February. Observations through to the following March showed that the Bare Zone did not change in position or composition of the conspicuous biota. The lashing of the Bare Zone by kelp fronds is regarded here as a coincidental rather than a causal occurrence. If anything, the Durvillea fronds should have had greater influence on the zone immediately above the Kelp Zone, i.e. the Upper Red Zone. The nature of the Bare Zone was apparently due to other factors. It is curious that on Marion and Prince Edward Islands, a Bare Zone occurred between the Lichen and the Porphyra Zones (Fuller 1967).

(b) Zonation Scheme

To describe the distribution of littoral molluscs it is important to note the zonation of typical shore organisms. This allows the grouping of animals into ecologically equivalent areas along the shore.

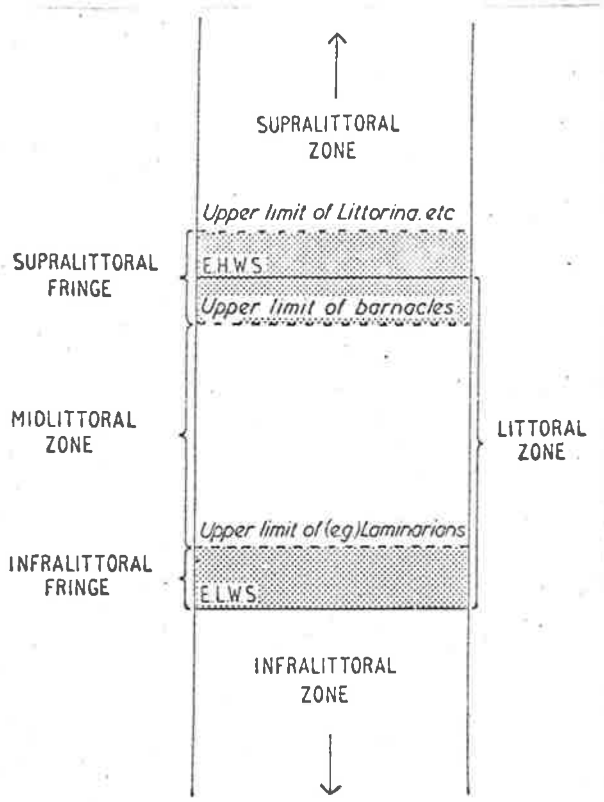
The use of zonation schemes to describe the shore environment has received attention from many workers. Various interpretations and terminologies have resulted and these have been reviewed by Doty (1957), Stephenson and Stephenson (1949), Southward (1958b), and Lewis (1961, 1964).

Attempts have been made to associate zonation schemes with average tidal levels. However, with the repeated lack of coincidence between observed distribution of organisms and tidal levels, allowances had to be made for other modifying factors, especially degree of exposure.

Stephenson and Stephenson (1949) proposed a universal system of classification (Figure 10). Using lichens, algae, and animals, they contended that certain "types" of organisms characterize approximately the same levels on all rocky shores. The Stephensons emphasized that the zones cannot be defined in terms of tidal levels, although related to these, but must be defined in terms of the distribution of organisms.

Lewis (1961) modified the Stephenson system and constructed a zonation scheme for universal application to rocky shores (Figure 11). The modifications by Lewis were different interpretations of a basic fact (the presence of three major biological zones on the shore) and fully rejected any physical definitions of zonation. In the scheme of Lewis, the zones were ecological entities completely defined by biological means. It is proposed (see later) that the Macquarie Island local zonation can be correlated with the scheme of Lewis. Therefore, it is appropriate to note the way in which

Figure 10. Zonation scheme of Stephenson and Stephenson (1949).


SUPRALITTORAL ZONE
Upper limit of Littorina. etc
SUPRALITTORAL FRINGE
E.H.W.S.
Upper limit of barnacles
MIDLITTORAL ZONE
LITTORAL ZONE
Upper limit of (eg) Laminarians
INFRALITTORAL FRINGE
E.L.W.S.
INFRALITTORAL ZONE

Lewis defined his zonation scheme and where his definitions primarily differed from those previously used, particularly from those of the Stephensons.

Lewis (1964) noted that Stephenson and Stephenson (1949) regarded "littoral" as the equivalent of "intertidal" and that E.L.W.S., an entirely physical boundary, was used to separate the infralittoral fringe from the infralittoral zone; Lewis suggested that such a boundary destroyed the natural unity of a population extending downwards to a considerable depth. The zonation scheme of Lewis embodied a changing pattern in accordance with degree of exposure whereas the Stephensons' scheme represented a standard, typical of an area where wave action was intermediate between maximal and minimal.

Lewis defined "littoral" as the zone occupied by marine organisms which were adaptable to or needed alternating exposure to air and wetting by submersion, splash or spray. The two subdivisions of the littoral (littoral fringe and eulittoral) respectively represented (1) an upper marginal zone in which the organisms were subjected to mainly terrestrial conditions but had greater littoral than terrestrial affinities and (2) a lower zone occupied by the majority of littoral organisms. The sublittoral zone denoted a region occupied in the main by fully marine organisms. These three divisions represented three basic ecologically distinct groupings in the shore environment.

The universality of zones defined by organisms stems not from the world-wide distribution of the same species at precisely the same levels, but from the recurrence of organisms of the same type in approximately the same positions relative to each other. When the typical indicators are absent, investigation of the shore reveals other biological indicators with which to set the boundaries of the three zones.

The indicator species used by Lewis to set the boundaries of zones have a wide geographical distribution. However, barnacles were not present on Macquarie shores and there were no littorinids in the littoral fringe where lichens, including Verrucaria sp., were present.

Kenny and Haysom (1962) noted the absence of "balanoid" and "littorinid" zones but unfortunately summarized this as an absence of barnacles and littorinids per se and this was repeated in the review of intertidal ecology of Australasian coasts by Knox (1963). While a littorinid zone in the area of the littoral fringe was certainly lacking, there were littorinid molluscs on Macquarie rocky shores in the eulittoral and sublittoral zones. However, there was no "littorinid sub-zone" within either of these zones. Barnacles were completely absent from rock surfaces in the littoral area. Live stalked barnacles were often found on drifting kelp and would have attached to the kelp in warmer waters. In a report on the littoral ecology of the Marion and Prince Edward Islands, Fuller (1967) stated that littorinids were absent. Identification in Fuller's faunal lists was incomplete and littorinids may yet be present. A comment was also made by Fuller on the absence of a "littorinid zone" and it would appear likely that there is similar confusion here between the absence of littorinids and the absence of a littorinid zone.

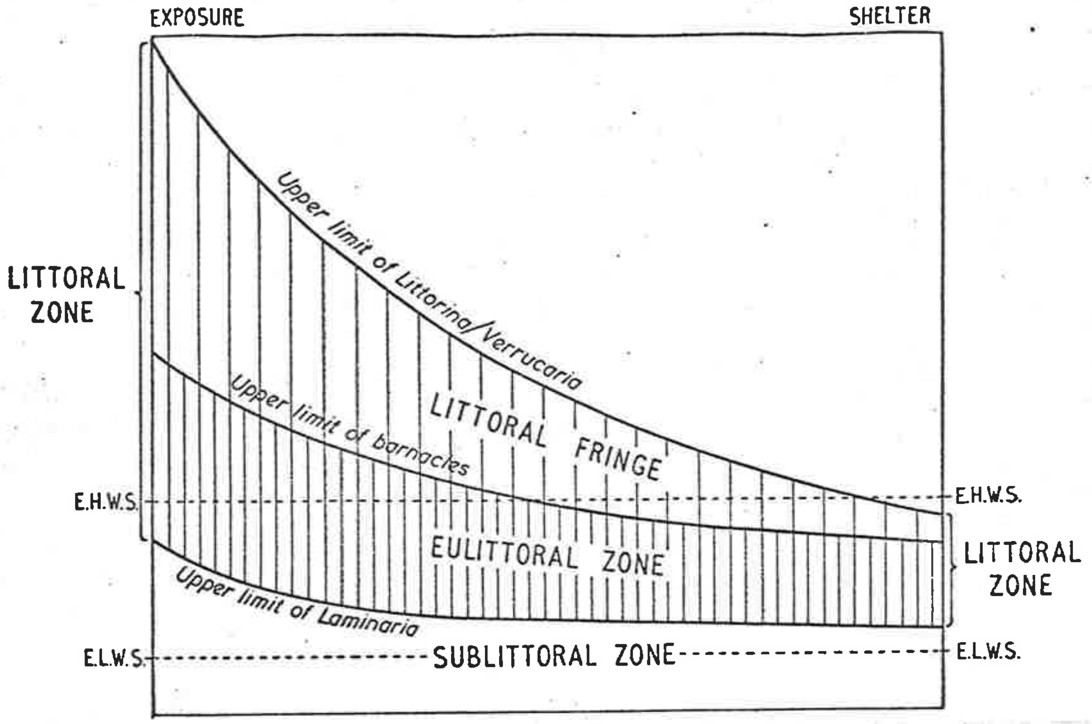
Owing to the absence of the "balanoid" and "littorinid" zones coupled with the high degree of wave action Kenny and Haysom (1962) stated that it was difficult to correlate the Macquarie zonation with the generalised plan of Stephenson and Stephenson (1949). They positioned the zones in relation to "effective tidal heights", following Endean et al (1956), where a subjective adjustment was made to the tidal level according to the tidal data, shore profile, degree of exposure, and the average conditions of wave action.

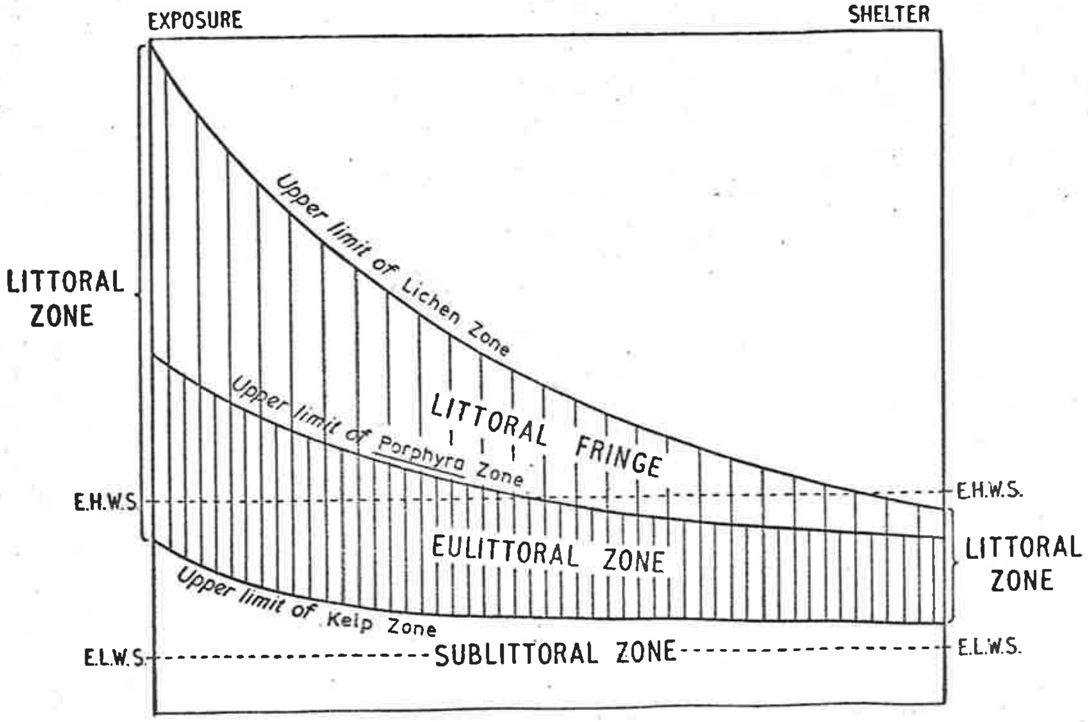
The transects down the shores (section III (a)) showed the lack of correspondence of zonal boundaries to pure tidal levels. Although the use of "effective tidal heights" would make allowances for other modifying factors, it was considered preferable to use the organisms to indicate the totality of impinging factors. The transects enabled the recording of the biotic composition in each of the "local" zones. It was possible to correlate this biotic composition with the definitions of ecological affinities that Lewis (1961, 1964) gave to his zones in a universal scheme. It appeared adequate to use the upper limit of the Lichen Zone to mark the top of the littoral fringe and the upper limit of the Kelp Zone to mark the top of the sublittoral. The upper limit of the Lichen Zone represented the upper boundary of an upper marginal zone with mainly terrestrial conditions but with many organisms having littoral affinities (see Table 2, section III (a)). The upper limit of the Kelp Zone represented the upper boundary of a region occupied in the main by fully marine organisms (see Table 2, section III (a)). The absence of barnacles required the substitution of an indicator species to denote the "littoral fringe - eulittoral" intersection.

Ballantine (1961) noted the prominence of Porphyra sp. on very exposed English coasts and Lewis (1964, p. 204) indicated the possible use of Porphyra sp. instead of barnacles as an equivalent indicator species. In the present study, the intersection of the Lichen and Porphyra Zones at Macquarie Island was taken as the upper limit of the eulittoral, as the organisms found on either side of this division represented groupings that exemplified littoral fringe and eulittoral classification. Figure 12 shows Macquarie Island rocky shore zonation imprinted on the Lewis scheme. In the future descriptions of habitats, small areas that were delineated

Figure 11. Zonation scheme of Lewis (1964).

Figure 12. Zonation of Macquarie Island rocky shores correlated with the universal zonation scheme of Lewis (1964).


EXPOSURE
SHELTER
LITTORAL ZONE
Upper limit of Littorina/Verrucaria
LITTORAL FRINGE
Upper limit of barnacles
E.H.W.S.
E.H.W.S.
EULITTORAL ZONE
LITTORAL ZONE
Upper limit of Laminaria
E.L.W.S.
SUBLITTORAL ZONE
E.L.W.S.


EXPOSURE
SHELTER
LITTORAL ZONE
Upper limit of Lichen Zone
LITTORAL FRINGE
Upper limit of Porphyra Zone
E.H.W.S.
E.H.W.S.
EULITTORAL ZONE
LITTORAL ZONE
Upper limit of Kelp Zone
E.L.W.S.
SUBLITTORAL ZONE
E.L.W.S.

in terms of organisms used in defining local zones could be positioned in relation to the broader, ecological zones of the universal scheme by using Figure 12.

In the universal scheme proposed by Lewis (1964), the boundaries of the zones were marked by the upper limit of actual organisms which dominated particular sub-zones. However, in the present study, it was found that this did not implicitly account for the occasional occurrences of a few of the indicator organisms at a higher level than normal, immediately below which the biota belonged to a different ecological area. Therefore the upper limits of the sub-zones as entities have been used as marking the boundaries of the littoral fringe and the eulittoral and sublittoral zones. Because it is ecological areas that are being grouped in a universal zonation scheme, it is suggested here that this choice is more exact.

(c) Environmental Factors

(i) Materials and methods

Wave action, sea temperatures, salinity, pH, phosphate content in sea-water, and chlorophyll estimations in sea-water were recorded throughout the year. This was in addition to the general weather records outlined in section II (b).

Daily wave action recordings covered estimations of vertical height of waves and time for a set number of waves to break, the number in this case being 19.

Sea temperatures were taken each day with an accurately calibrated mercury thermometer placed in sea-water scooped up in a bucket. Though water was taken from the shallows the influence of local heating was minimal, owing to the continuous wave action.

Salinity measurements were taken with a portable chlorinity - temperature bridge. Chlorinity values were converted to salinity using the equation, salinity = 0.03 + chlorinity x 1.805, Hamon (1956). This meter was also used to record water temperatures in the field. The description and working capabilities of this meter are dealt with in section IV 2. (c).

Measurements of pH were taken with a portable Metrohm pH meter (Model E 300). The pH range of this meter was 0 to 14 and its accuracy of reading was 0.01 pH. The scale length was 220 mm. The meter was calibrated with standard solutions prior to each use, and temperature compensation was possible by the use of a built-in adjust. The electrodes used were Metrohm, model numbers EA 120T and EA 132X.

Phosphate analysis of sea-water was undertaken at intervals of approximately one month from June to February. The method used is that outlined by Strickland and Parsons (1960, p. 41-46). This uses the combination of phosphate and a molybdate reagent to form a phosphomolybdate complex and the reduction of this complex to a highly coloured blue compound. An EEL colorimeter and red filter were used to measure the absorption of the solutions. A standard curve was drawn up using known solutions of potassium di-hydrogen orthophosphate and this curve was used to equate the absorption values of unknown samples with phosphate values. At each analysis, standards were also compared with readings for sea-water.

Estimations of chlorophyll content in sea-water were used to gauge the amount of phytoplankton pigment which, in turn, gave a correlation with phytoplankton present. Again, the readings were taken at approximately monthly intervals from June to February. The general method used was adapted from those outlined in Barnes (1959, p. 240-42) and Strickland and Parsons (1960, p. 107-112). A sample of sea-water (0.5 to 5 litres) was first filtered through a metal gauze with a mesh opening of 0.4 mm to remove detritus and large zooplankton. 0.1 ml magnesium carbonate suspension for each litre of sea-water was added to prevent development of acidity. The water was then run through a Millipore vacuum filter apparatus after which the residue closely adhered to the Millipore filter paper. This was transferred to a desiccator kept in the dark for approximately 1½ hours to remove superficial moisture. The darkness prevented deterioration of pigments. The filter paper was then added to 90% v/v acetone in a graduated centrifuge tube and shaken during which time the Millipore filter paper dissolved. The extraction of pigments by the acetone was allowed to proceed for 20-24 hours in a dark cool place. Acetone volume was then made up to 10 ml, centrifuged, and the supernatant decanted into a cuvette for measuring the absorption of the colouration caused by pigment extraction. A pure acetone solution was used as a blank.

Absorptions of solutions were measured with an EEL colorimeter and purple filter. Readings for sea-water were compared with those for a standard solution which was designated in terms of "Harvey units", one "Harvey unit" being equivalent to 1 ml of a solution of 25 mg K_2CrO_4 and 430 mg of $NiSO_4.6H_2O$ in one litre of distilled water. Comparisons between "Harvey units" and chlorophyll solutions have shown that 1 unit is equivalent to 0.3 µg chlorophyll as the best estimate (Barnes 1959).

(ii) Results and discussion

Figure 13 shows mean wave heights for each month of the year on the east and west coasts. Figure 14 shows the time for a set number (nineteen) of waves to break on the west and east coasts. In each case, the range, mean, and 2 standard errors either side of the mean are shown.

The mean heights of the waves on the west coast were

Figure 13. Monthly mean wave heights (March 1968 - March 1969).

█ = east coast.

▨ = west coast.

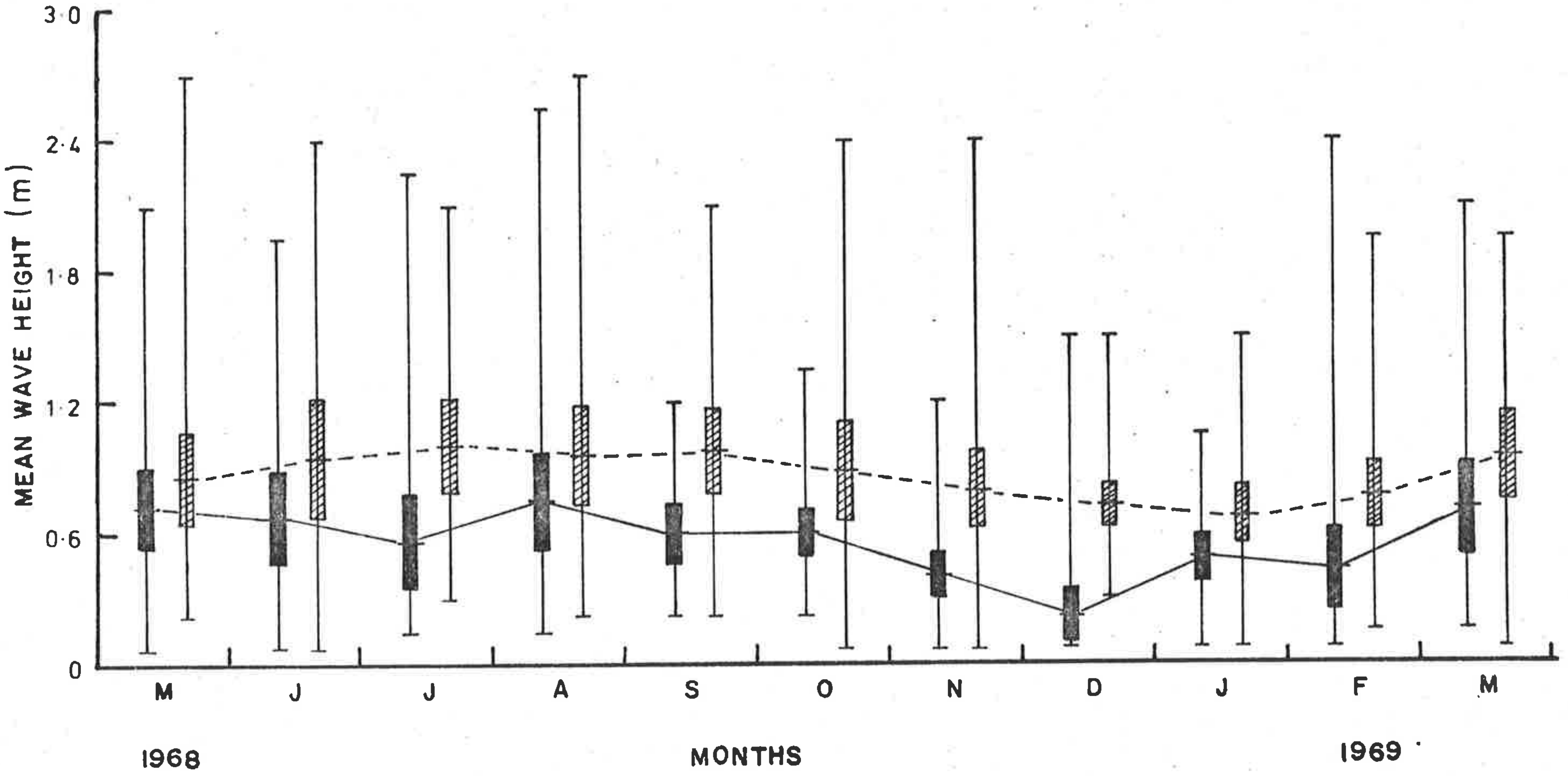
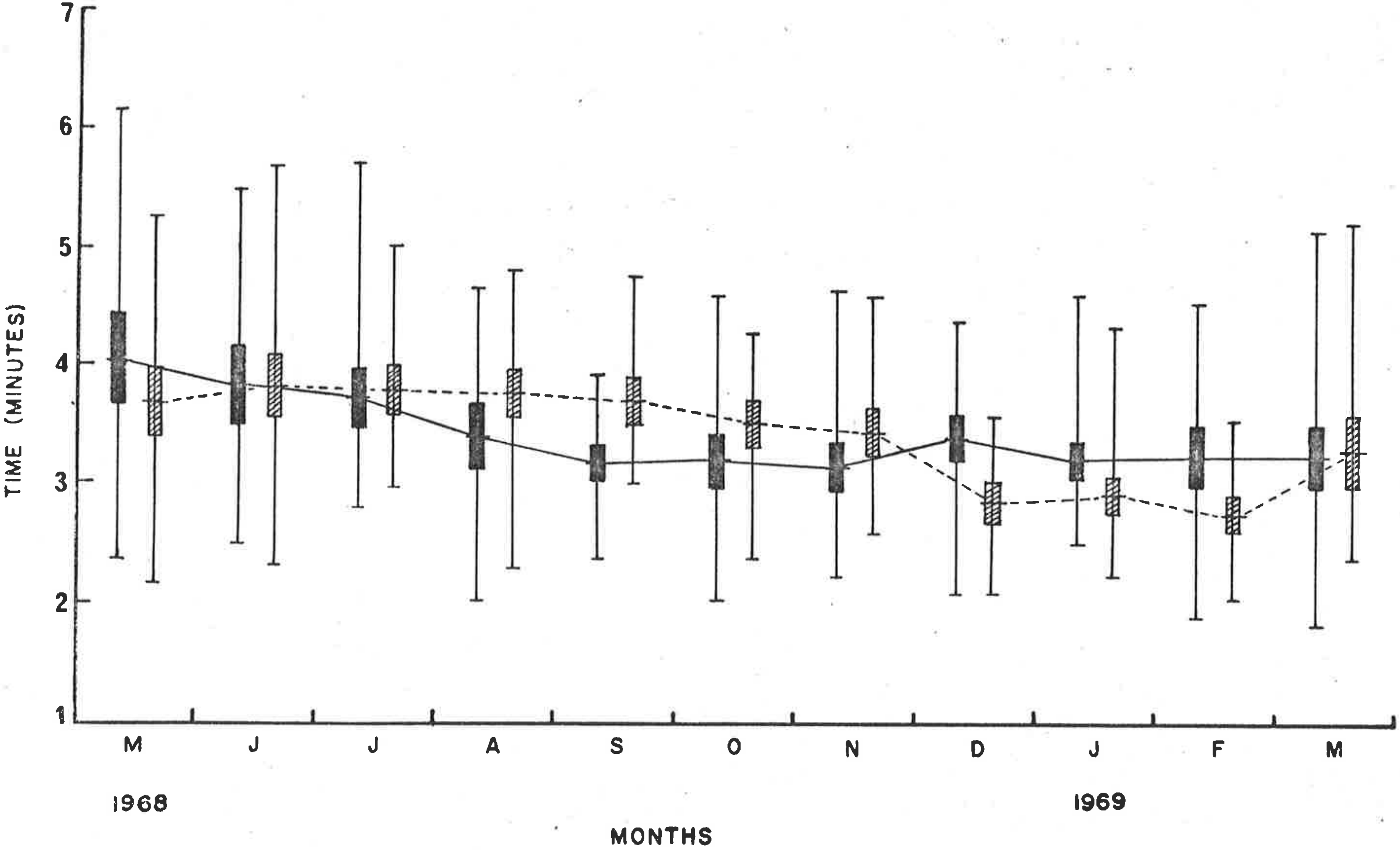

3·0
2·4
1·8
1·2
0·6
0
MEAN WAVE HEIGHT (m)
M
J
J
A
S
O
N
D
J
F
M
1968
MONTHS
1969

Figure 14. Monthly mean times for nineteen waves to break on the shore (March 1968 - March 1969).

■ = east coast.

▨ = west coast.


7
6
5
4
3
2
1
TIME (MINUTES)
M
J
J
A
S
O
N
D
J
F
M
1968
1969
MONTHS

consistently greater than those for the east coast. In considering individual months, the difference could be taken as significant in July, September, November, December, and February in relation to overlap of the standard error margin. The frequency of wave action can be gauged as the reciprocal of the time taken for a set number of waves. Thus, waves generally broke more frequently on the east coast from August to November, more frequently on the west coast from December to February and in May, while other months gave equable figures for both coasts. Significant differences with respect to the standard error were shown for the December to February period and in September.

The frequency of wave action coupled with the height of the waves is postulated here as pointing to the total effect of turbulence caused by wave action. Thus, on the east coast, water turbulence was much less in the summer period (December to February) in relation both to the west coast and to wave action on the east coast itself in other months. The higher frequency of wave action on the east during August to November would bring the overall turbulence comparison between east and west to a more equable level. In the other months, the west generally has greater turbulence but the differences were not so marked. Plate 13A shows wave action in June 1968 on the west coast on an average day of westerly wind while plate 13B shows simultaneous wave action on the

Plate 13.

13A.* Wave action in Hasselborough Bay (west coast of Macquarie Island).

13B.* Wave action in Buckles Bay (east coast of Macquarie Island).

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* Photograph 13A was taken immediately after 13B.

east. On the west the waves were 1.0-1.5 metres in height and on the east, the waves were 0.5-1.0 metres in height.

Table 3 gives the monthly averages for sea temperatures recorded through 1968-1969 compared with records of sea temperatures from other periods, from Loewe (1957). Loewe noted that the period, 1951-54, had appreciably higher temperatures than the period 1912-14, particularly during the summer. The temperature measurements from these two periods listed in Table 3 were taken at the same time of day and at the same place i.e. the A.N.A.R.E. station at the northern end of the island. The sea temperature records of the present study provided an interesting comparison with the records of the periods listed by Loewe. In 1968-69, the mean sea temperatures did not show such wide variations between winter and summer averages as noted in 1951-54. The temperatures during the colder months of 1968 (May to October) were appreciably higher than those in the corresponding months of both the periods listed by Loewe. As, in 1968-69, the place and time of recording were the same as that for 1912-14 and 1951-54, it appeared as though Macquarie Island was subjected to sea temperatures more equable than usual in 1968-69.

As expected for an oceanic climate, Loewe showed that there was a close connection between the simultaneous temperatures of the water and the air. This was again evident in this study. For 1968-1969, sea temperatures for August and

Table 3. Macquarie Island mean sea temperatures.

Mean monthly sea temperatures (^{o}C.) for Macquarie Island - converted into ^{o}C. from Loewe (1957). Time of recording was 9 a.m.

Period	Months											
	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
1912-14	4.72	3.83	3.44	3.28	3.44	3.67	3.89	4.83	4.50	6.33	5.50	5.06
1951-54	5.78	4.72	3.78	3.61	3.50	3.78	3.83	5.44	6.72	7.28	7.22	6.72

Mean monthly sea temperatures (^{o}C.) for Macquarie Island - from records for 1968-69. Time of recording was approx. 9-11 a.m.

Period	Months											
	1968									1969		
	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
1968-69	5.61	5.72	5.28	4.28	4.67	4.50	4.33	4.56	5.72	6.78	6.67	6.28

Mean annual sea temperatures (^{o}C.)

Period	
1912-14	4.50
1951-54	5.22
1968-69	5.39

Maximum and minimum sea temperatures (^{o}C.) for the period 1968-69.

Max. - 8.22 (Jan.)
Min. - 3.33 (Jul. Aug. Oct.)

October were out of the general trend, August being too high and October too low. Air temperatures recorded by the meteorological section on the island also showed an increase in August. This can be seen in Figure 15 which combines the air and sea temperature means. This unusual temperature rise may have been due to a temporary southward movement of the Antarctic convergence, thereby causing warmer water to circulate further south to Macquarie Island.

Figure 16 shows phosphate and chlorophyll values obtained from the open sea. Phosphate level in the sea was generally low, mostly around the 20-30 µg/litre mark except for late November when the level rose sharply to 65 µg/litre. What caused this was unknown. The amount of wave action certainly did not increase in November to suggest the stirring up of deposits. The increase in phosphate showed a close connection with the upsurge in phytoplankton in December as indicated by the chlorophyll curve. The higher phosphate level would provide extra nutriment favourable for the increasing numbers of phytoplankton. The high phytoplankton level continued on the increase through to January but fell back to the usual level in February.

Salinity and pH readings for the sea were taken at various times throughout the year, and as expected, were quite consistent. The salinity readings were found to be between 33‰ and 35‰ and the pH between 7.9 and 8.1. There was no

Figure 15. Mean maximum and mean minimum air temperatures and mean sea temperature (monthly, from April 1968 to March 1969).

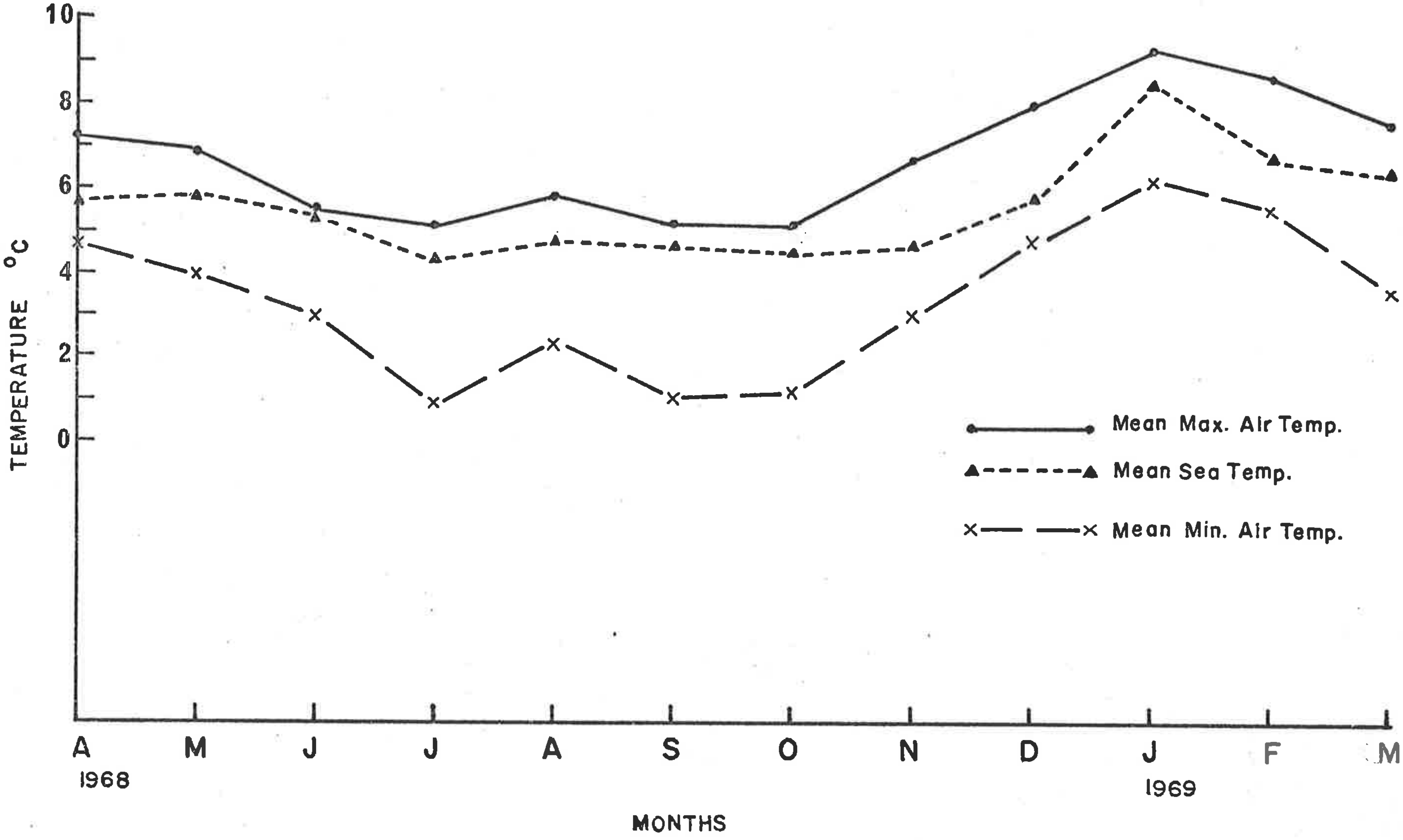
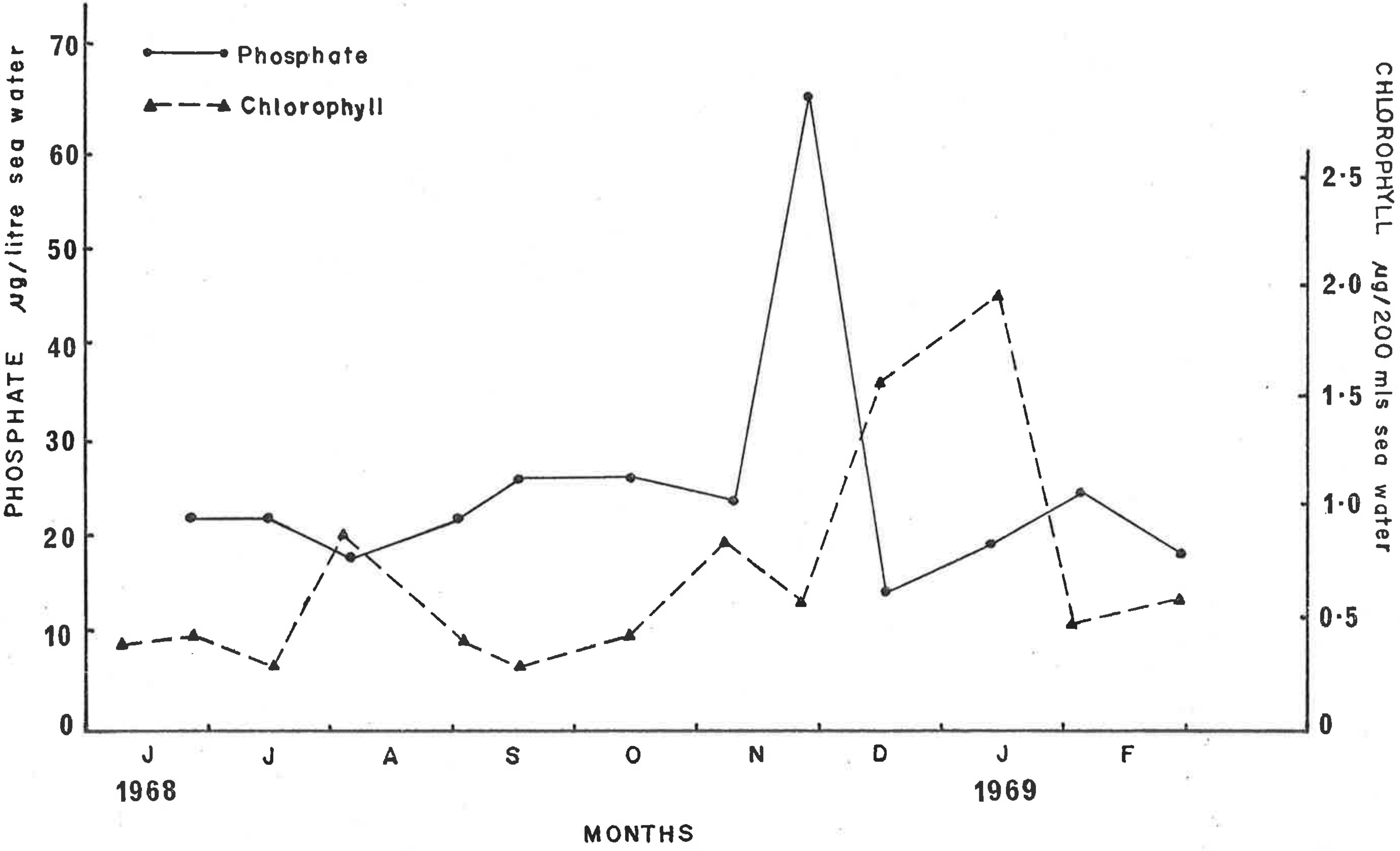

10
8
6
4
2
0
TEMPERATURE °C
A
M
J
J
A
S
O
N
D
J
F
M
1968
1969
MONTHS
Mean Max. Air Temp.
Mean Sea Temp.
Mean Min. Air Temp.

Figure 16. Phosphate and chlorophyll levels in the sea, (June 1968 - February 1969).


Phosphate
Chlorophyll
PHOSPHATE µg/litre sea water
CHLOROPHYLL µg/200 mls sea water
70
60
50
40
30
20
10
0
2·5
2·0
1·5
1·0
0·5
0
J
J
A
S
O
N
D
J
F
1968
1969
MONTHS

trend in any variation in the small range of these values and variations obtained were probably due to errors in instrument usage in the field.

The results of further measurements of salinity, pH, and temperature in rock pools are set out in section III (d).

(d) Analysis of Rock Pools

(i) Materials and methods

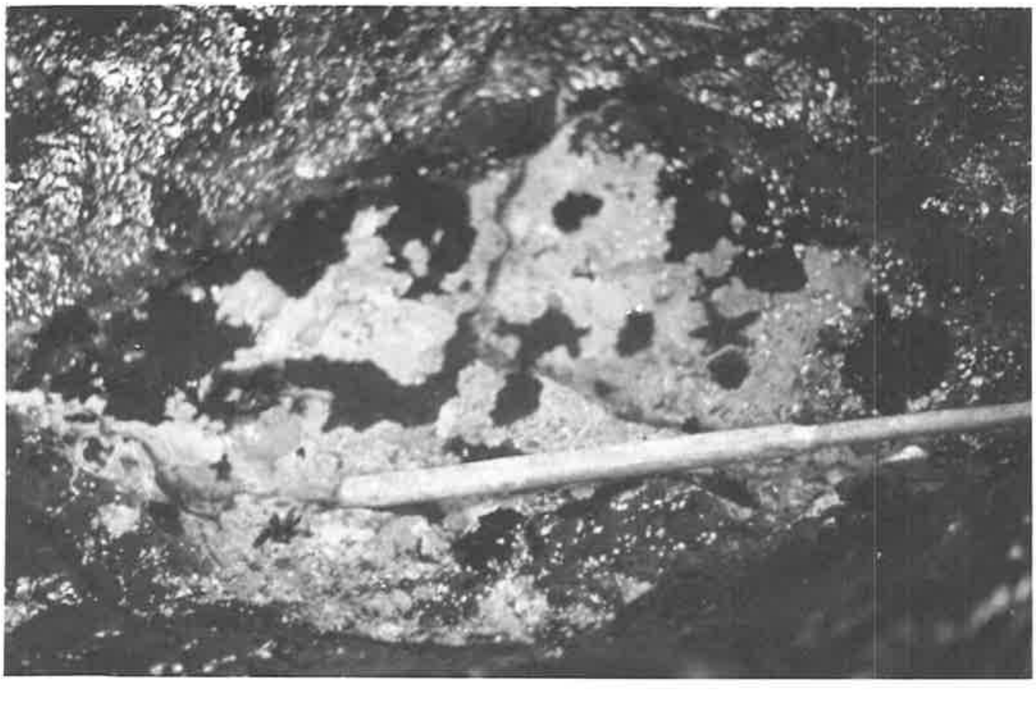
Rock pools in the littoral zone were analysed for changes in temperature, salinity, and pH. Pools were selected for differential occupancy in reference to the range of molluscs under study i.e. some species were not to be found in a pool, depending on its position on the shore, while others were present. The pools chosen gave a gradation through this exclusion.

Temperatures in rock pools were taken in two ways: (1) continuous temperature recording and (2) spot checks with thermometers. Clockwork circular chart-recorders as described below were used for continuous temperature measurements. The thermometers were mercury-in-steel type and were connected to the recorders through steel capillary tubing which enabled the sensing head to be placed in a rock pool and the recorder to be bolted to a nearby rock face. The connecting tubing was secured to rock pitons. One "Cambridge" and two "Negretti and Zambra" recorders were used. Plate 14A shows

Plate 14.

14A. Temperature chart-recorders being secured to a rock face.

14B. Mercury-in-steel sensing head (of a temperature recorder) positioned in a pool.



two recorders bolted in position on a rock face while Plate 14B shows a sensing head in a pool.

The pH and salinity of rock pools were measured using the portable meters which have been described in section III (c).

(ii) Results and discussion

Table 4 shows the change of species composition of molluscs in the pools and lists pool locations, algae present, and the range encountered for temperature, pH, and salinity from May 1968 to March 1969. The temperatures listed combine records from both continuous recording and spot checks. The time periods, for which the temperature of a pool was maintained in particular temperature ranges, were measured from the continuous recordings. These measurements are given in section IV 2(a) where the tolerances of molluscs, kept in these temperature ranges in the laboratory, are investigated. High pools that did not have mollusc populations are also included in Table 4. These pools were situated in the Lichen Zone (the littoral fringe). Sea-water flowed into these pools only during heavy seas or during moderate seas and high tide. The foreground of Plate 15B shows rock pools in the littoral fringe awash during heavy seas. For the pools in the Lichen Zone, high alkaline conditions (pH = 10) existed if the pool had not received sea-water flow for about three

Table 4. The biota and physical conditions in rock pools in the littoral fringe and eulittoral zones

Pool Dimensions LxBxDepth (cm)	Mollusc Occupants (when molluscs not present, main fauna is listed)	Zonal Position	Common Algae	*Ranges of physical conditions recorded from May 1968 to March 1969		
				Salinity ‰	pH	Temp. °C
58x30x27	*Tigriopus angulatus* (copepod) Amphipods	Lichen Zone	*Enteromorpha* sp. Green algal film	8 - 35	8.0 - 10.5	-4.0 - 24.2
64x53x33	*Tigriopus angulatus* Amphipods	Lichen Zone	*Enteromorpha* sp. Green algal film	9 - 35	8.0 - 10.3	-4.3 - 23.5
66x28x18	*K. lateralis* *L. caliginosa*	*Porphyra* Zone	Green algal film	18 - 35	8.0 - 8.3	-2.5 - 17.1
51x33x23	*K. lateralis* *L. caliginosa* *P. macquariensis* (one specimen)	Bare Zone	Green algal film	22 - 35	7.9 - 8.2	-1.7 - 15.3
56x38x25	*K. lateralis* *L. caliginosa* *P. macquariensis*	Bare Zone	Green algal film Coralline algae (gnarled)	26 - 35	8.0 - 8.1	-1.9 - 11.0
53x33x20	*P. macquariensis*	Upper Red Zone	Green algal film Coralline algae	30 - 35	7.9 - 8.1	-0.9 - 11.3
51x38x30	*P. macquariensis* *C.* (*P.*) *coruscans*	Upper Red Zone	Coralline algae Red algae	31 - 35	7.9 - 8.1	-0.5 - 9.5

* See "Materials and methods".

Plate 15.

15A. Moulting elephant seals lying on rotting kelp in the littoral fringe.

15B. Rock pools in the littoral fringe awash during heavy seas.

days. Such periods occurred frequently; for example, one pool in the Lichen Zone had 10 periods of at least three consecutive days free of sea-water flow in 13 weeks. This was shown on continuous temperature recordings during which a flow of sea-water into the pool registered as a sharp bump on the chart. The pH of the pools below the Lichen Zone did not vary significantly from pH = 8. The ranges of temperatures and salinity were wider in accordance with increasing distance of the pool up the shore.

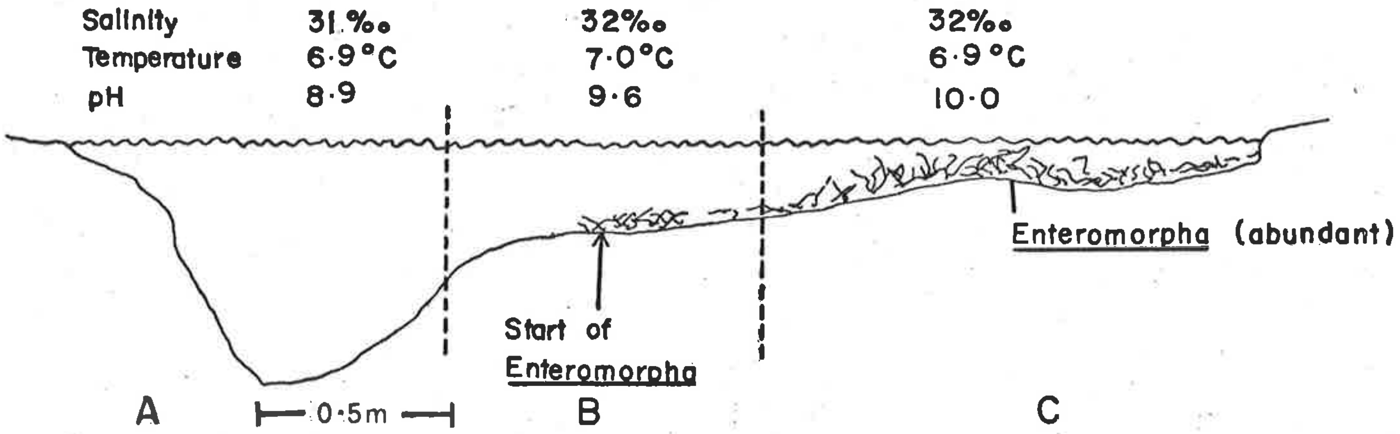
By association, it appeared as though *K. lateralis* and *L. caliginosa* could tolerate a wider range of salinity and water temperature than *P. macquariensis* while *C. (P.) coruscans* showed very little tolerance to variations in these two factors. The chitons, *P. aurata* and *H. setulosum*, were rarely found in small rock pools. They were often present in large rock pools that would be more stable in physico-chemical factors and this suggested that fluctuation in one or more of these may be contributing strongly to the exclusion of chitons from higher pools. Other factors might be limiting e.g. food, competition, predation. A study of physiological tolerances would provide further evidence on the former suggestion. Experimental investigation of physiological tolerances of the molluscs was undertaken to test this association between occupancy and absence with varying physical factors.

In the pools, there were gradations of decreasing green algal film and increasing coralline algae with progressive proximity of the pools to the sublittoral zone. Experiments were conducted on food preferences of molluscs (section IV 1. (b)), indicating any possible association between food types and occupancy by different molluscs.

Figure 17 depicts a pool high in the Porphyra Zone which often showed differential pH along its length, the pool being frequently without splash. Salinity, temperature, and pH shown on Figure 17 were typical of values when the pool had been emerged for some time e.g. three days. All readings were taken 7 cm below the water surface. Temperature and salinity proved comparable along the length of the pool. The decreasing number of K. lateralis corresponded to the increasing pH although the increasing growth of Enteromorpha may have acted as an actual physical restriction on the density of K. lateralis.

There were additional hazards to be faced by biota in littoral rock pools besides fluctuations in physico-chemical factors. Kelp thrown up by heavy seas often formed a heavy layer over pools in the littoral zone, frequently resulting in the death of all occupants. Elephant seals, especially during their moulting periods in summer, often formed groups in the littoral fringe. The seals were particularly attracted to areas of washed-up kelp. Plate 15A shows such a group.

Figure 17. Physical conditions and biota of a rock pool in the <u>Porphyra</u> Zone.



K. lateralis Numbers

Area A = 92
B = 41
C = 9

Occupants

Molluscs = *K. lateralis*

Flora = *Enteromorpha*

Green algal film

The overlay of seals, their excrement, and the rotting kelp quickly killed off any rock pool biota in such areas.

IV. COMPARISON OF SELECTED SPECIES

1. ECOLOGY AND BIOLOGY

(a) Distribution and Abundance

(i) Materials and methods

The distribution and abundance of molluscs studied were determined from transects and separate counts in selected habitats. The densities of molluscs were determined during the bimonthly recordings down Transects 1, 2, 3, and 4 over a one year period (for the methods involved in taking these transects, see section III (a)). The densities at a depth of six metres were averaged from ten counts (in summer) of areas, one metre square, on relatively even rocky substrate. Abundance ratings were made for *K. lateralis*, *L. caliginosa*, *H. setulosum*, and *C.* (*P.*) *coruscans* while, for *P. macquariensis* and *P. aurata*, actual numbers were recorded.

Some additional notes on the abundance, distribution, and habitat of the littorinid, *Macquariella hamiltoni*, were also taken. Although not part of the overall study, these observations together with those on the food preferences of *M. hamiltoni* (section IV 1. (b)) are relevant to the discussion on the reproduction of this species (see Appendix I).

The use of a square metre to delineate an area for counting molluscs could not be employed in all cases e.g. *C.* (*P.*) *coruscans* on algae and *L. caliginosa* in pools. Here, numbers were more closely allied with a particular habitat than a zonal position.

The distribution of molluscs could only be determined to a depth of approximately 10 metres. The lack of any sea-craft prevented SCUBA diving to any greater depths. Molluscs have been dredged from greater depths e.g. *Patinigera macquariensis* from 69 metres (Tomlin 1948). Diving was undertaken either from rock ledges or from a diving platform. This platform was constructed on the island from 44 gallon drums, angle iron, and timber. The platform did not have any means of propulsion. Its main benefit was as a depot for close inshore work. Plate 16A shows the diving platform being loaded prior to a SCUBA dive while Plate 16B was taken during a dive from a rock ledge. The *Durvillea* fronds were no problem during actual diving and collecting but proved a hindrance to coming and going from any shore depot.

Plate 16.

16A. Loading the diving platform.

16B. *Durvillea antarctica* fronds from holdfasts attached to a rock ledge used for a diving depot.

(ii) Results and discussion

Table 5 outlines the abundance classification applied to molluscs. The usefulness of such a classification was in determining different abundances peculiar to certain habitats in the distributional ranges. Further counting and experimentation to gain insight into this differential density was based on such notes e.g. in the study of influence of algal cover (section IV 1. (c)).

Table 6 gives the densities of molluscs in their distributions over the vertical zonal divisions. In the transect counts, Transect 5 was not included as it was subjected to the removal of kelp as an experimental study. Attempts to gauge any differences of density with different seasons were hindered by short term events which altered the numbers of molluscs. For example, the heavy overlay of *Durvillea* fronds after very large seas affected the density of all molluscs on Transect 4; the unusual heavy predation by Dominican gulls decreased the numbers of *P. macquariensis* and *P. aurata* on Transect 2 in December. (The density of *P. macquariensis* at different seasons along the transects is dealt with in detail in section V (d).) After such events, no further data on the densities of molluscs on Transects 2 and 4 were used in compiling Table 6. Also, the Kelp Zone of Transect 4 contained a large pool which was free of *Durvillea* holdfasts and was little affected by the movement of adjacent *Durvillea*

* Table 5. Abundance classification of molluscs

Definition of Abundance	Density of Species (per sq. metre)			
	K. lateralis	*L. caliginosa*	*H. setulosum*	*C. (P.) coruscans*
Rare	→10	→10	→10	→2
Present	10-50	10-50	10-50	2-10
Common	50-100	50-80	50-80	10-50
Dense	Over 100	Over 80	Over 80	Culsters of over 50
Dominant	- Organism present in greater numbers than any other -			

* Comparison of densities for *P. macquariensis* and *P. aurata* in different localities were made by actual counts and not by abundance estimates as used above.

Table 6. Densities of molluscs in relation to their vertical distribution.

Location	Average Abundance Ratings per sq. metre				Mean number per sq. metre	
	K. lateralis	**L. caliginosa*	*H. setulosum*	**C.* (*P.*) *coruscans*	*P. macquariensis*	*P. aurata*
Porphyra Zone	Rare	Rare	None	None	None	None
Bare Zone	Dense	Common	None	None	1	None
Upper Red Zone	Common	Dense	Rare	Rare	19	1
Kelp Zone	Rare	Rare	Dense	Present	13	2
Lower Red Zone	None	None	Present	Dense	38	4
Depth of 6 metres	None	None	Rare	Dense	41	5

* High numbers dependent on suitable habitats, i.e. pools and crevices (*L. caliginosa*), algal fronds (*C.* (*P.*) *coruscans*).

fronds. The molluscs in this pool (which were mainly limpets) were not regarded as part of the population of the Kelp Zone. The data from other recordings were averaged for each zone. Zonal abundance ratings were averaged by taking the most common abundance rating per square metre. In any transect, these did not show any variations with time; the subjective notation of the abundance ratings would have been too gross for small variations. For P. macquariensis and P. aurata, the mean number per square metre was calculated for each zone. In any transect, variations with time were slight and the figures in Table 6 are the averages of the mean number per square metre for each zone recorded at each bimonthly count. Because no great alterations in numbers took place with time and the same trend in numbers was shown for each transect, no further statistical treatment was warranted as the object was to show the general differences in density over the vertical zonal divisions. Figure 18 shows the distribution of the molluscs in relation to the zonation scheme. For all species, abundances were noted to differ with certain changes in habitat within the ranges of distribution. Table 7 shows actual numbers in particular habitats, thereby indicating possible advantages or disadvantages to each species.

Patinigera macquariensis and Plaxiphora aurata were always found on rocky substrate, except for rare occurrences on the outside of Durvillea holdfasts. The density of

Figure 18. Distribution of molluscs in relation to zonation.

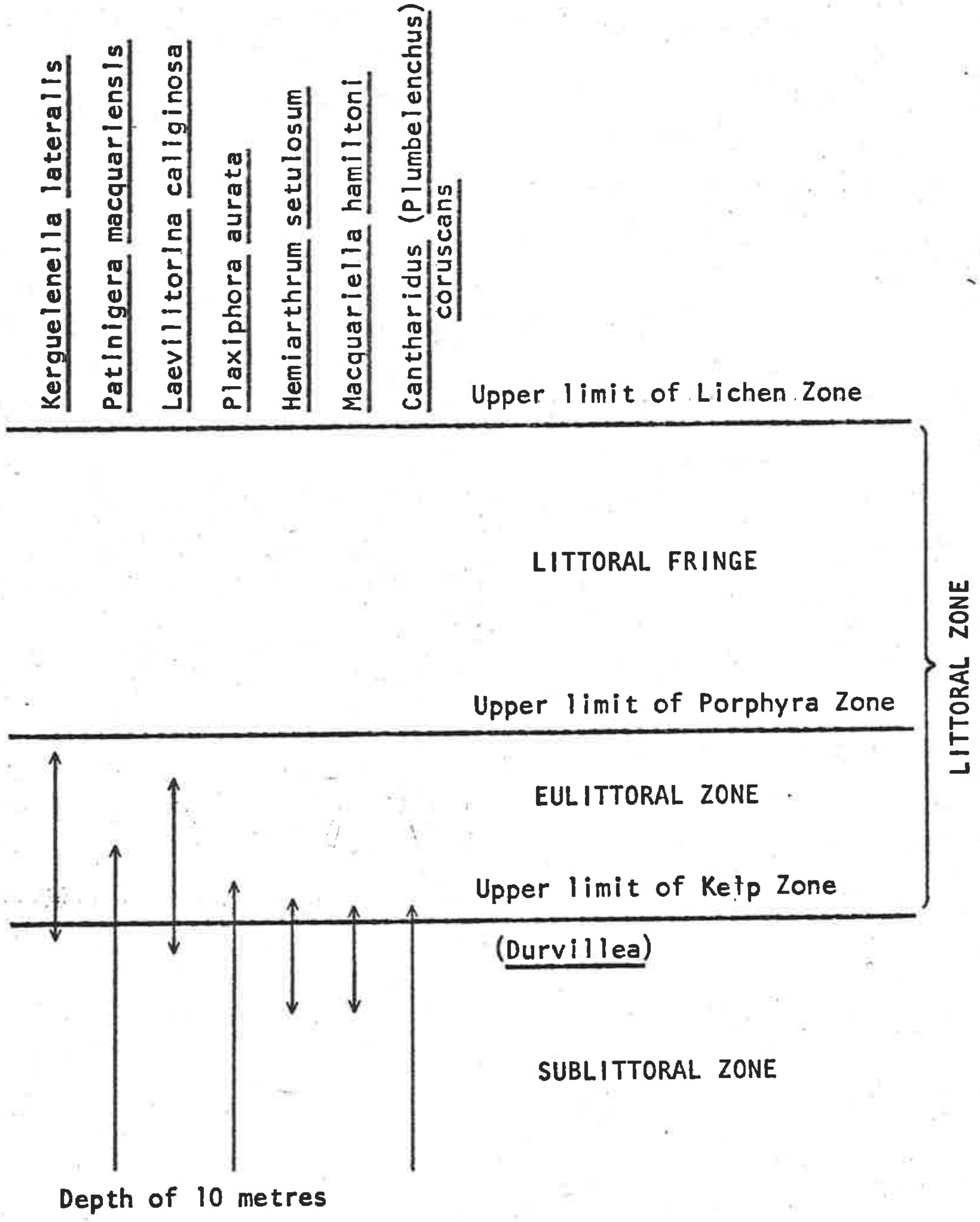

Kerguelenella lateralis
Patinigera macquariensis
Laevilitorina caliginosa
Plaxiphora aurata
Hemiarthrum setulosum
Macquariella hamiltoni
Cantharidus (Plumbelenchus) coruscans
Upper limit of Lichen Zone
LITTORAL FRINGE
LITTORAL ZONE
Upper limit of Porphyra Zone
EULITTORAL ZONE
Upper limit of Kelp Zone
(Durvillea)
SUBLITTORAL ZONE
Depth of 10 metres

Table 7. Densities of molluscs in particular habitats

Habitat	Species	Numbers
Kelp Zone:		
Heavy *Durvillea* cover	*H. setulosum*	194, 162, 170 /sq.metre
	P. macquariensis	11, 3, 6, /sq.metre
Light *Durvillea* cover	*H. setulosum*	35, 42, 19 /sq.metre
	P. macquariensis	22, 17, 25 /sq.metre
Eulittoral pools: (LxBxDepth, cm)		
38 x 58 x 18	*L. caliginosa*	56
61 x 53 x 23 (with rubble)	*L. caliginosa*	147
On dislodged *Durvillea*: stipe (24 x 4 cm), from a depth of approx. 5 metres	*C.* (*P.*) *coruscans*	124
On dislodged *Macrocystis*: frond (approx. 60 x 10 cm)	*C.* (*P.*) *coruscans*	63
On fronds of red algae: (collectively measuring 0.5 sq.metres in surface area), from Lower Red Zone	*M. hamiltoni*	95
Large rock pools in the high eulittoral: (LxBxDepth, m)		
0.9 x 0.6 x 0.3	*P. macquariensis*	8
0.8 x 0.8 x 0.8	*P. macquariensis*	30
0.4 x 0.6 x 0.5	*P. macquariensis*	6
Small rock pools in the lower eulittoral: (LxBxDepth, cm)		
33 x 53 x 8	*P. macquariensis*	10
51 x 33 x 20	*P. macquariensis*	6
58 x 33 x 10	*P. macquariensis*	8
69 x 35 x 6	*P. macquariensis*	5
Large, deep rock pools in the lower eulittoral: (LxBxDepth, m)		
1.4 x 1.2 x 1.0	*P. aurata*	37
	P. macquariensis	226
1.8 x 0.8 x 1.2	*P. aurata*	45
	P. macquariensis	267
Bare Zone:		
Smooth rock surfaces	*K. lateralis*	48, 72, 59 /sq.metre
Fragmented rock surfaces with crevices	*K. lateralis*	275, 301, 251 /sq.metre
Upper Red Zone:		
Smooth rock surfaces	*P. macquariensis*	24, 16, 27 /sq.metre
Large rubble, secured to the substrate	*P. macquariensis*	44, 55, 39 /sq.metre

P. macquariensis increased in areas consisting of large, firmly implanted rubble. This was further supported by counts along Transect 2 (section V (d)). The rubble formation provided (i) simply more space and (ii) a protection from lashing kelp fronds at low tides. The range of both P. macquariensis and P. aurata extended from the eulittoral down to the maximum depth investigated - 10 metres. However, the limpets were found further up in the eulittoral than the large chitons; it was evident that the eulittoral was a marginal area for P. aurata. Large rock pools in the eulittoral contained both P. macquariensis and P. aurata. These pools were obvious reflections of conditions at lower levels. P. aurata were rarely found in small rock pools (section III (a)). In the sublittoral, the abundance of P. macquariensis decreased in areas of heavy Durvillea cover. The densities of both P. macquariensis and P. aurata were greater well down in the sublittoral (Lower Red Zone) and at diving stations than in the Kelp Zone (top of the sublittoral) and in the eulittoral. Although the actual numbers of P. macquariensis were far higher than those for P. aurata in any area, the increase in density at the lower levels described above was greater for P. aurata.

The range of Kerguelenella lateralis extended over the eulittoral with the greatest abundance being the Bare Zone in the middle of the eulittoral. The siphonarids were found on solid, rocky substrate. The numbers greatly increased in areas where the substrate was fragmented and creviced. During dry conditions, especially during sunny weather, *K. lateralis* inhabited these crevices during periods of emergence (see Plate 4B).

Hemiarthrum setulosum had a narrow range of distribution from the lower eulittoral to the Lower Red Zone, beyond which, specimens were rare. The greatest abundance of *H. setulosum* was on rock surfaces covered with pink coralline algae among the *Durvillea* holdfasts. These small chitons were also found on and/or in the *Durvillea* holdfasts.

The range of *Laevilitorina caliginosa* extended from high in the eulittoral to the *Durvillea* holdfasts. *L. caliginosa* were often found in small pools where there was either a film of green algae or encrustations of pink coralline algae. They were rarely found on algal fronds. This was in contrast to the littorinids, *Macquariella hamiltoni*, which were typically found on the fronds of red algae in the lower eulittoral and the sublittoral zones.

The eulittoral-sublittoral junction was the upper limit for *Cantharidus* (*P.*) *coruscans* which extended down to the maximum depth investigated (10 metres), excepting those found in large rock pools in the eulittoral. There was an uneven distribution within this range and this was related to their food preference (see section IV 1. (b)). For example, they were often found in large clusters on dislodged fronds of *Durvillea* and *Macrocystis* and were commonly found on the fronds of red algae. They were scarce on rock surfaces where no frond algae were present. In pools, they often formed static clusters on rocky surfaces, usually under rocky overhangs.

During heavy storms, molluscs and other invertebrates were often thrown up to levels that they would not normally occupy. A count of animals and notes on their condition in a measured area on a *Porphyra* rock flat was taken at the first low tide after one such storm (Table 8). After heavy seas, molluscs were frequently found in high level pools, especially in areas where eddy currents were formed during the retreat of wave surge. For example, eleven trochids and seven limpets were found in the fourth pool (dimensions = 51 x 33 x depth 23 cm) of Table 3 (section III (d)) after a storm. After one week, the new occupants had gone. During this period, isopods (*Exosphaeroma gigas*) were observed gnawing at the mantle, foot, and tentacles of enfeebled animals.

The primary aim of recording the distribution and abundance of molluscs was to draw relationships with environmental factors, both physical and biotic, that may determine the limits of distribution and abundance in particular areas. Relationships could be further tested in the laboratory.

Table 8. Animals deposited in *Porphyra* Zone by wave action of storm.

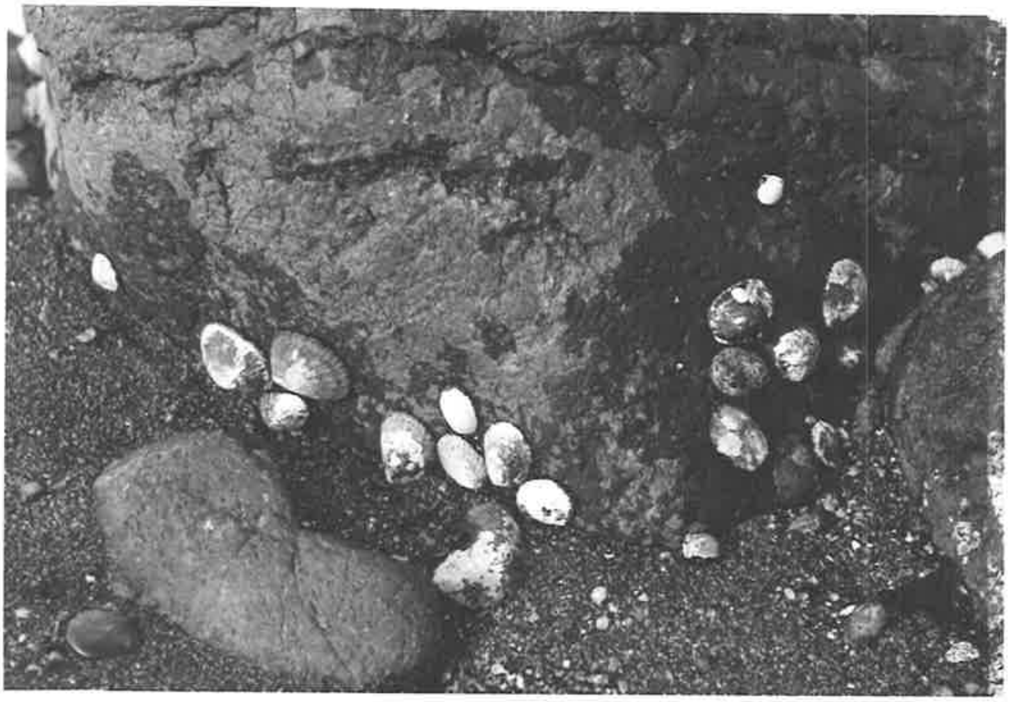
(Area = 10 metres x 10 metres on rock flat		
Animal	Number	Condition
Patinigera macquariensis	27	2 eaten 2 overturned, alive 23 attached to rocks
Plaxiphora aurata	10	All eaten
Cantharidus (*Plumbelenchus*) *coruscans*	103	35 alive, poor condition, mainly in pools 46 eaten (usually grouped into small piles) 22 dead, overturned, foot extruding
Anasterias mawsoni (starfish)	5	Dead

There were local hazards to the molluscs in particular areas, but these were not considered to be limiting on the whole population. For example, sand in certain areas was built up by the seas so that it sometimes covered limpets (see Plate 17A). Chance settling of the kelp, *Durvillea antarctica*, on the shells of molluscs could easily result in the molluscs being dislodged and killed. Plate 17B shows a

Plate 17.

17A. Sand build-up encroaching on specimens of *Patinigera macquariensis* in the eulittoral.

17B. Small holdfast (*Durvillea antarctica*) attached to a specimen of *Patinigera macquariensis*.



holdfast attached to a limpet shell.

(b) Food Preferences

(i) Materials and methods

Observation in the field, laboratory experiments, and dissections were used to determine food preferences of the study molluscs. Additional notes were also made on the food preferences of the littorinid, *Macquariella hamiltoni*. As previously mentioned, although not part of the overall study, these observations on *M. hamiltoni* are relevant to the discussion on the reproduction of this species (see Appendix I).

In the field, the types of algae on which the molluscs were found were noted. To substantiate these observations, molluscs were placed in aquarium tanks with different types of algae which were in two states: (1) taken directly from the field and (2) scrubbed. The cleaning was to ensure that no epiphytic growth remained and comparison of the two sets of results would ascertain whether the molluscs were eating the alga itself.

Further experiments in aquaria were conducted on the two chitons, *Plaxiphora aurata* and *Hemiarthrum setulosum*, and on the limpet, *Patinigera macquariensis*. Each of these species was found on rocks covered with (1) a film of green algae and diatoms and (2) coralline algae. The following combination of experiments were set up to determine whether there were any differences in survival capabilities of each species from different zones on the two types of algae. Two samples of twenty specimens of each species were taken from both the eulittoral and sublittoral zones. One sample was placed in aquaria with rocks covered with a film of green algae and diatoms while the other sample was placed in aquaria with rocks encrusted with coralline algae. The numbers of molluscs were divided up among the aquaria so that there was no overcrowding. The sea-water in the aquaria was well-aerated and changed regularly and the rocks were replaced with ones bearing fresh algae each week. Deaths were recorded over a three month period.

Dissections were used to determine general types of algae present in the gut. In particular, coralline algae were readily distinguishable in the gut and their presence also showed that feeding had taken place in the sublittoral zone or in eulittoral rock pools, the coralline algae being unable to grow in other areas. No detailed identification of algal species found in the guts was attempted.

(ii) Results and discussion

Table 9 lists the algae eaten by molluscs as shown by field and laboratory results. This table indicates whether particular algae were eaten or not. Further observations on the extent and/or frequency of grazing of different algae

Table 9. Field and laboratory observations of algae eaten by molluscs.

Species	Habitat	Algae eaten (from observations in the field)	*Feeding trials in laboratory aquaria										
			Green algal film	*Enteromorpha* sp.	*Porphyra* sp.	*Chaetangium fastigiatum*	*Ulva* sp.	*Rhodymenia* sp.	*Durvillea antarctica*	*Codium* sp.	Coralline algae	Red algae	*Macrocystis* sp.
K. lateralis	Rock surfaces and crevices	Green algal film	/	x	x	x	x	x	x	x	x	x	x
L. caliginosa	Rock pools Under rocks Algal fronds - (rare)	Green algal film	/	x	x	x	x	/	/	x	/	x	x
P. macquariensis													
- eulittoral	Rock surfaces	Green algal film	/	x	x	x	x	x	x	x	/	x	x
- depth of 6 m	Rock surfaces	Coralline algae	/	x	x	x	x	x	x	x	/	x	x
P. aurata	Rock surfaces	Green algal film Coralline algae	/	x	x	x	x	x	x	x	/	x	x
H. setulosum	Rock surfaces	Coralline algae Green algal film	/	x	x	x	x	x	x	x	/	x	x
M. hamiltoni	Algal fronds Holdfasts of *Durvillea*	*Rhodymenia* sp. Red algae	x	x	x	x	x	/	/	x	x	/	x
C. (*P.*) *coruscans*	Algal fronds Rock surfaces	*Durvillea* sp. *Macrocystis* sp. Red algae *Rhodymenia* sp.	/	x	x	x	x	/	/	x	x	/	/

* / = eaten
x = not eaten

served to determine food preferences. In all feeding experiments, the same results were obtained whether the algae had been cleaned or not, indicating that no incidences of grazing were due to the cropping of epiphytic growth.

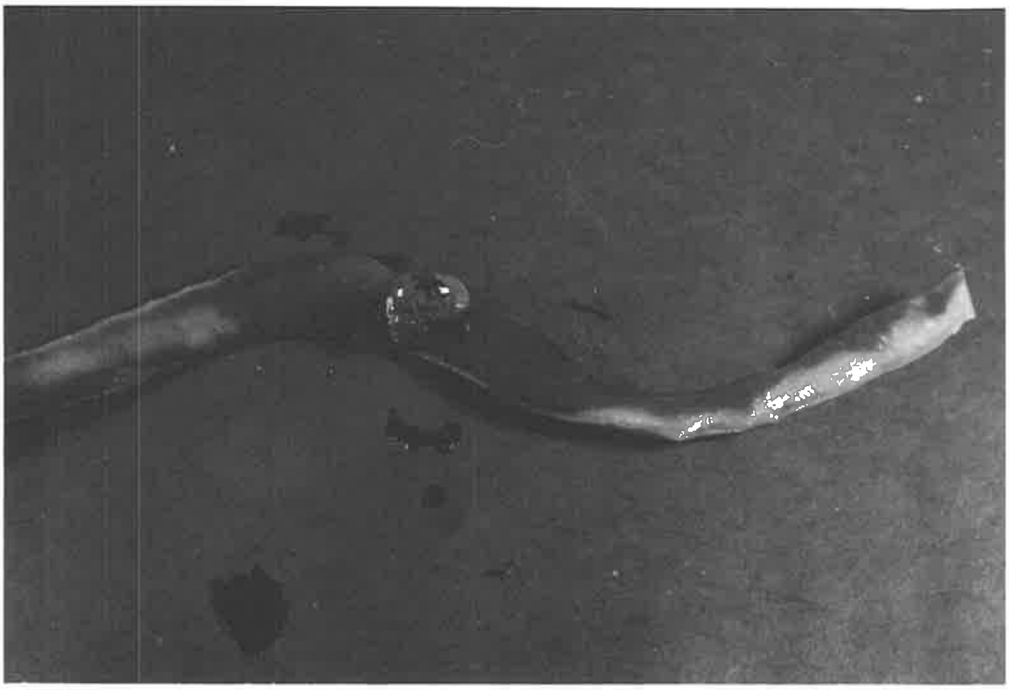
The habitats of the molluscs indicated the types of algae available. C. (P.) coruscans and M. hamiltoni were commonly found on algal fronds. L. caliginosa was occasionally found on algal fronds, but usually on rock surfaces. Both M. hamiltoni and L. caliginosa were found in the hollows of Durvillea antarctica holdfasts. The other molluscs were located exclusively on rock surfaces.

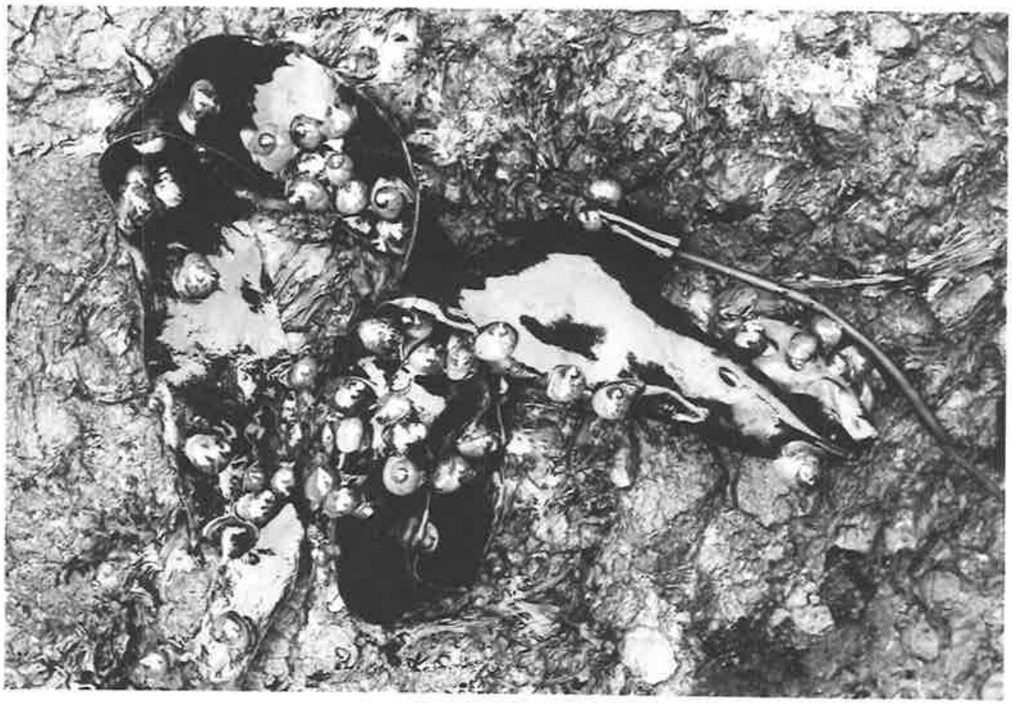
The frond algae - Durvillea, Macrocystis, Rhodymenia, and various red algae - were readily eaten in the laboratory by C. (P.) coruscans, which could be found grazing on Rhodymenia and other red algae still attached and growing. However, C. (P.) coruscans were rarely found on Durvillea or Macrocystis attached to the substrate. When fronds of these kelps were dislodged, they would sink if still joined to the holdfast attachment. Trochids were found in great numbers swarming over and feeding on the dislodged kelp. For example, on a small piece of dislodged Durvillea, 24 x 4 cm, there were 124 trochids clustered in a grape-like bunch (Table 7, section IV 1. (a)) and the kelp was scored by extensive feeding tracks. Plate 18A shows trochids attached to kelp which had been lying at the bottom of a large rock pool in the low-

Plate 18.

18A. *Cantharidus* (*P.*) *coruscans* feeding on a dislodged *Macrocystis* frond.

18B. Feeding tracks made by *Cantharidus* (*P.*) *coruscans* on a frond of *Durvillea*, kept in an aquarium.





er eulittoral. Apparently, the violent movement of the kelps prevented the trochids from attaching securely but, once the fronds were dislodged and on the bottom, movement was greatly minimized, particularly if the kelp lodged between boulders etc. Thus, these two kelps were a prime food for *C.* (*P.*) *coruscans* but were not always available. Plate 18B shows feeding tracks made by trochids on a *Durvillea* frond kept in an aquarium. Although available in the sublittoral, coralline algae were not found amongst their gut contents.

The littorinids, *M. hamiltoni*, readily ate *Rhodymenia* and other red algae in the laboratory. Whether feeding or not, they remained attached to the algal fronds. Only an occasional specimen of the littorinids, *L. caliginosa*, was found on such algal fronds in the aquaria. They showed a tendency to attach to the sides of the aquaria or on rocks placed in the tanks and instances of feeding on the frond algae were rare. Both these littorinids were not found on living or dislodged *Durvillea* and *Macrocystis* and did not eat these kelps in aquaria.

K. lateralis, *P. macquariensis*, *P. aurata*, and *H. setulosum* were not found on frond algae in the field and did not eat them in the aquaria. *K. lateralis* were rarely found in areas where there were encrustations of coralline algae although dissections did show some traces in gut contents. *P. macquariensis* were located (1) in eulittoral areas where only a covering film of greenish algae and diatoms was available, (2) in sublittoral areas where coralline algae encrusted all available rock surfaces, and (3) in areas with both coralline algae and a film of algae and diatoms. P. aurata and H. setulosum were predominantly located in area type 2 above (e.g. H. setulosum in Plate 3) and were occasionally found in area type 3. These distributions and abundances of the limpet and the two chitons defined in relation to algal cover in effect corresponded to those determined from the vertical transects (section IV 1. (a)). That is, P. macquariensis were abundant in the sublittoral (coralline algae) and extended through the sublittoral-eulittoral intersection (coralline algae, film of green algae and diatoms) well into the eulittoral (film of green algae and diatoms). P. aurata and H. setulosum were abundant in the sublittoral (coralline algae) but did not extend as far as, nor were abundant as, P. macquariensis in the eulittoral.

This suggested the hypothesis that a preference for coralline algae as a food by the two species of chiton might be a controlling factor in their distribution, whereas a capability of the limpets to adjust to a more varied diet provided them with more scope for spatial expansion. This was tested by field observations and dissections of specimens from specific areas and by survival experiments on different algae, as previously described. Naturally, in the situations where limpets were well into the eulittoral and where limpets and chitons were well into the sublittoral only one type of algal cover was available in each case (film of green algae and coralline algae, respectively). Dissections showed that these algae formed the staple diet of the molluscs in these areas. In the sublittoral-eulittoral intersection, areas were selected where coverings of both green algal film and coralline algae were both accessible and approximately equal. These areas included pools and rock surfaces under virtually continuous splash. Fifty specimens of each of the three species of molluscs were dissected and classified as to whether the gut predominantly held coralline algae or greenish algae and diatoms. The results are listed in Table 10. The greater frequency of coralline algae in the guts of both species of chitons was significantly different from the occurrence of greenish algae and diatoms but limpets showed no differentiation (chi-squared tests).

The results of the survival experiments for the three species of molluscs on the two forms of algae are recorded in Table 11. It was intended to determine whether there was any difference in survival among species when given the opportunity to graze only one of the algal forms. This was applied to molluscs that, at their collecting site in the field, had access to the algal cover being tested (i.e. molluscs from eulittoral put with green algae in aquaria; molluscs from sublittoral put with coralline algae in aquaria) and

Table 10. Main algae in the intestine of limpets and chitons collected in the field.

Location of all molluscs:
Areas in the lower eulittoral and upper sublittoral zones where coverings of green algal film and coralline algae were both accessible and equal.

Type of algae mainly present in intestine	<u>H. setulosum</u> (N = 50)	<u>P. aurata</u> (N = 50)	<u>P. macquariensis</u> (N = 50)
Green algae (and diatoms)	18	15	29
Coralline algae	32	35	21
χ^2	3.92	8	1.28
Probability	$0.05>P>0.01$	$0.01>P>0.001$	$P>0.05$
Significant difference at the 5% level	✓	✓	-

Table 11. Survival of limpets and chitons on green algae and coralline algae in the laboratory.

Location of molluscs when collected	Algae provided in aquaria	*Deaths after 3 months		
		<u>H. setulosum</u>	<u>P. aurata</u>	<u>P. macquariensis</u>
Eulittoral zone	Coralline	3	2	2
	Green	2	3	4
Sublittoral zone	Coralline	2	3	2
	Green	4	2	3

* 20 of each species were used in each of the four experiments.

also to molluscs that had little or no such access (i.e. molluscs from eulittoral put with coralline algae in aquaria; molluscs from sublittoral put with green algae in aquaria). It was obvious that there were no significant differences in survival between any experimental combinations.

The dissections of molluscs from the sublittoral-eulittoral intersection and the survival experiments indicated that all three species can survive equally on the two types of algae but coralline algae were preferred by the chitons. Although all precautions were taken, other adverse factors, inherent in maintaining tank populations, could have masked any trends showing different survival capabilities owing to the algal food available.

The alga, *Codium* sp., formed flattened cushions in sublittoral areas but, though appearing to be ideal formations for herbivorous molluscs, were not grazed by any species under study. No molluscs of any other type were found on *Codium* in the field.

(c) Influence of Algal Cover and Recolonisation

(i) Materials and methods

Within the distributional ranges of some of the species of molluscs, their abundances differed markedly with a change of habitat, particularly with the onset of *Durvillea* cover (section IV 1. (a)). Consequently, areas were selected for removal of *Durvillea* to determine any possible influence on the distribution of the molluscs. The kelp was removed by cutting the fronds close to the holdfasts which remained attached to the rocky substrate. The numbers of molluscs counted immediately after removal of kelp gave the initial abundance. Subsequent counts were made at pre-determined intervals.

These experiments were particularly directed at *P. macquariensis* and *H. setulosum* whose numbers were found to vary with *Durvillea* cover during field work undertaken to plot their range and record their abundance (see section IV 1. (a)).

One particular species of *Rhodymenia* was also removed from an area when it was noted that its cover varied during the year.

Molluscs were completely cleared from a shallow pool, approximately one square metre in area, in the Kelp Zone to observe recolonisation - for its extent, composition, and timing. Algae were not removed and comprised encrusting coralline, one *Durvillea* holdfast, and scattered clumps of red algae.

(ii) Results and discussion

Tables 12, 13, and 14 show the changes in the densities of *P. macquariensis* and *H. setulosum* on removing *Durvillea*.

*
Table 12. Changes in the density of molluscs after Durvillea removal. (Each square = 1 sq. metre)

Date - September to October 1968						
Time Interval	Numbers					
	Square 1		Square 2		Square 3	
	P. macquariensis	H. setulosum	P. macquariensis	H. setulosum	P. macquariensis	H. setulosum
Start - Removal of kelp	7	203	2	175	4	181
1 week	14	176	8	151	19	129
4 weeks	16	92	10	81	23	83

* Durvillea holdfasts were not removed.
Rock surfaces between the holdfasts were encrusted with coralline algae.

*
Table 13. Changes in the density of molluscs after the removal of Durvillea (Each square = 1 sq. metre)

Date - February to March 1969															
Time Interval	Numbers														
	Square 1			Square 2			Square 3			Square 4			Square 5		
	P. macquariensis	H. setulosum	P. aurata	P. macquariensis	H. setulosum	P. aurata	P. macquariensis	H. setulosum	P. aurata	P. macquariensis	H. setulosum	P. aurata	P. macquariensis	H. setulosum	P. aurata
Start - Removal of kelp	18	VD	1	42	C	0	22	D	0	21	D	1	2	VD	0
1 week	25	D	1	46	P	0	27	C	0	28	R	1	8	C	0
3 weeks	29	P	1	47	R	0	31	P	0	30	R	0	6	P	0

* Durvillea holdfasts were not removed. Rock surfaces between the holdfasts were encrusted with coralline algae. Most of the coralline algae (90% of the cover) was dead at the 3 weeks time interval.

Abundance symbols for H. setulosum:

VD = very dense - over 150
D = dense - 80 to 150
C = common - 50 to 80
P = present - 10 to 50
R = rare - 0 to 10

Table 14. Changes in the density of *Patinigera macquariensis* after *Durvillea* removal.

Month	Time Interval	Limpet numbers on boulder surface which was divided into 4 areas with respect to compass direction -			
		North	South	East	West
May	Start - Removal of kelp	10	14	13	17
May	1 day	10	16	19	16
May	3 days	11	21	24	18
May	1 week	11	22	37	15
May	2 weeks	11	28	51	17
June	4 weeks	16	27	69	21
July	2 months	17	32	98	18
September	4 months	87	51	121	35
November	6 months	57	57	69	40
*December	7 months	0	2	1	0
*January	8 months	3	7	4	3

* December and January figures were catastrophically reduced owing to concentrated predation by Dominican gulls. The boulder was in the roosting area of gulls that were attracted to the December relief ship.

Clearly, the numbers of limpets increased while the numbers of chitons decreased.

In the experiment depicted by Table 14, the holdfasts were only on the eastern and south-eastern sides of the boulder. The holdfasts were in a single line about three-quarters of the distance up the boulder and, before removal, the fronds lashed at the surrounding areas of the eastern and southern sections of the boulder. After kelp removal, there was a marked increase in the number of limpets on the southern and eastern sides of the boulder in the initial time intervals up to two months, while the number of limpets on the northern and western sides remained steady. This result suggested that the lashing Durvillea fronds reduced the numbers of limpets. The lashing probably hindered movement with safe attachment, thereby preventing limpets from grazing these areas. Although a limpet's hold in a clamped-down attitude would appear to be sufficient to withstand a blow from a Durvillea frond, a grazing limpet's hold would be less. If blows from Durvillea fronds did not actually dislodge a grazing limpet, they would cause the limpet to be continually clamping down in order to secure a hold. This would be fatiguing and would lessen the amount of grazing time for the limpet. The underlying algal film was rich. Because the removal of the kelp enabled the limpets to move freely into the areas, the numbers increased not because of new algal growth but because of new access to existing growth. This was further suggested by the sharp increase in the numbers of limpets shortly after *Durvillea* removal. If the density of limpets was regulated here by the amount of algal food, it was not likely that any increase in algal growth after *Durvillea* removal would have been sufficient to cause such a large and quick increase in the numbers of limpets. Further counts at bimonthly intervals showed that the numbers of limpets in all sectors had increased on the original numbers at the four and six month time intervals (in September and November). These increases were apparently due to causes other than effects from *Durvillea* removal. Studies on the seasonal variation in the numbers of limpets along transect lines running down the shore (section V (d)) also showed that the density of limpets at or just below the *Durvillea* holdfast line increased in September. The large decrease in numbers in December and January were due to unusual heavy predation by Dominican gulls, the boulder being in the roosting area of gulls that were attracted to the December relief ship.

In the experiment depicted by Table 13, the combination of calm seas and sunny weather had killed off most of the underlying coralline algae (90 percent of the cover was whitened) shortly after the removal of *Durvillea*. Thus, although the food source for limpets (coralline algae were prime food for limpets, see section IV 1. (b)) was reduced in the areas of Durvillea removal, the numbers of limpets still increased. This emphasized that the increase in the density of limpets after kelp removal was not due to new algal growth.

In the experiment depicted by Table 12, the underlying coralline algae did not die off after the removal of Durvillea. The experimental areas, depicted by Tables 12 and 13, were thickly covered with holdfasts and the situation was simply one of dense cover and not lashing frond cover as for the study area depicted by Table 14.

If the limpets were highly mobile, kelp cover could have prevented their progress and, hence, on removal of the Durvillea, the limpet density may increase owing to their normal course of movement and exploration. However, experiments with marked limpets (section V (c)), showed that limpets in stable populations tended to remain in small fixed areas. Thus, increases in limpet numbers after Durvillea removal would be long term in considering the normal movement patterns of limpets. The sharp, short term increases, as shown by these experiments, suggested the creation of an unstable situation in the population with increased degree of movement bringing limpets into the areas of Durvillea removal.

In summary, whether the kelp overlay was one of just dense cover or of lashing fronds, the physical effects on the limpets by the presence of the kelp was apparently decreasing the density of limpets by (1) a reduction of available space, (2) the lashing of the fronds having an adverse effect on the attachment of limpets to the substrate, resulting in possible dislodgement or hindrance of free movement. Other factors may have been involved e.g. reduction of light, lack of ventilation during conditions of low tide and calm seas.

H. setulosum preferred areas thickly covered with holdfasts and encrusted with coralline algae, see Tables 12 and 13. They were not found where fronds freely lashed the rock surface, see Table 14. Their small size and flat body aspect were ideal for inhabiting the restricted areas between the holdfasts under the kelp overlay. For *H. setulosum*, such a habitat would be relatively sheltered. The sharp decrease in density after removal of *Durvillea antarctica* suggested a physical causal factor (e.g. dislodgement by wave action) rather than deterioration of a food source.

Table 15 lists the density of limpets during both sparse and heavy cover of *Rhodymenia*. The sparse cover occurred naturally and was also induced artificially by clearing.

No significant change in limpet density took place after either natural or artificial changes in the cover of *Rhodymenia*. Thus, not only did the extent of algal cover not affect the limpet density but also the fluctuation in the algal cover was not due to increased grazing from an influx of limpets. It was unlikely that the feeding rate of the existing population changed. The alteration in algal cover was probably due to effects of climatic changes on the alga itself or part of its life cycle.

Table 15. Density of *Patinigera macquariensis* in relation to *Rhodymenia* cover.

Month	Extent of *Rhodymenia* sp. cover	Limpet numbers in an area of 2 sq. metres	
May	Sparse	93	
September	Heavy	87	
September	*Rhodymenia* sp. removed from the 2 sq. metre area	Time after removal	Limpet nos.
		1 day	83
		1 week	90
		2 weeks	86

Table 16 shows how molluscs re-entered areas cleared of all species. The short re-entry times of the trochids (*C.* (*P.*) *coruscans*) reflected their high mobility. Initially, their numbers were greater than originally but they decreased in number when other species became re-established, suggesting some form of competitive exclusion. The non-return of *H. setulosum* could be associated with its cryptic habitat under dense kelp cover, a fact suggesting very slow exploration into new territory. The original proportion of numbers for the other species was approached after 6 weeks. The lesser

*Table 16. Recolonisation by molluscs. (Molluscs originally in the experimental area were completely removed from the site)

Date - April to May 1968						
	Numbers					
		Time interval after removal of molluscs.				
Species	Original	2 days	1 week	2 weeks	4 weeks	6 weeks
P. macquariensis	125	13	41	65	93	114
P. aurata	11	0	1	1	4	7
H. setulosum	6	0	0	0	0	0
C. (P.) coruscans	8	10	30	32	15	11

* Experimental area was a rock surface of 3 sq. metres in a slight depression in the Kelp Zone. Molluscs listed above were also on adjacent rock surfaces and had access to the experimental area.

mobility of P. aurata could have explained their slow re-entry.

Thus, although re-entry numbers after 6 weeks approached the original figures in three of the four species, only in the case of the trochids were the numbers quickly restored to the original. The recolonisation suggested constant exploration by the mobile trochids for favourable areas in contrast to the constancy of location shown by the other species. The results could be indicative of two possible factors: differences in (1) mobility or (2) population pressures.

(d) Predation

(i) Materials and methods

Predation of the study molluscs was investigated in both the field and the laboratory. After predators were determined from field observations, predator-prey relationships were examined. The predators of the molluscs comprised birds, starfish, and an isopod; the actual species are listed in the results.

With the materials available, it was difficult to establish enclosed areas in the field for a study of predator-prey relationships between starfish and molluscs. As an alternative, small rock pools (containing both starfish and molluscs) in the lower eulittoral were used to record frequencies of predation. The occupants were regularly observed and counted at approximately three day intervals for four months. However, disturbances from wave action and associated effects greatly reduced the data. Attempts to quantify bird predation also met with little success. Counts of the shells of molluscs left at Dominican roosting sites were undertaken but it was difficult to determine both the feeding area and the number of birds using the site. In addition, other smaller molluscs would have been swallowed whole and the shell regurgitated later.

In the laboratory, the starfish - Anasterias directa and Anasterias mawsoni - were placed in aquaria (size: 35 x 18 x 25 cm) with all species of the study molluscs in the following combinations: (a) 3 specimens of each starfish with 6 specimens of each mollusc, (b) 3 specimens of each starfish with 20 specimens of each mollusc (except for Plaxiphora aurata when only 10 were used because of their large size), (c) 6 specimens of one starfish with the two combinations of molluscs in (a) and (b). The sea-water in the aquaria was well aerated, constantly stirred at a moderate speed, and changed regularly.

Generally, the studies on predation consisted of the determination of 1) the actual predators of each mollusc, 2) what part of the diet of predators was formed by molluscan prey, and 3) the conditions and the habitats in which predation occurred. Emphasis was placed on the effects of predation at the upper limits of distribution of the molluscs, although subsidiary studies were undertaken. The effect of predation on the internal population structure of molluscs was not an aim of the overall study.

In addition, experiments were conducted with the study molluscs and the starfish - *Anasterias directa*, *Anasterias mawsoni*, and *Asterina hamiltoni* - in aquaria and in the field to ascertain whether or not the molluscs showed any escape responses. In the laboratory, the molluscs were touched with a number of objects both animate and inanimate besides the starfish e.g. glass rod, rock, the isopod - *Exosphaeroma gigas*, the crab - *Helicarcinus planatus*, other molluscs, and human fingers. Contact was made with starfish in three ways: (1) allowing the mollusc and starfish to approach each other without prompting, (2) bringing the starfish in contact with the mollusc, and (3) bringing a tube foot of the starfish in contact with the mollusc. The starfish were brought up to the molluscs from the front, sides, and rear. In the field, the contact experiments were repeated and, in addition, damaged starfish and starfish body fluids were introduced into small rock pools with mollusc populations.

(ii) Results and discussion

Table 17 lists the observed predators of the study molluscs. Table 18 lists the prey of starfish as found during

Table 17. Predators of molluscs

Species	Predators:			
	Starfish	Avoidance reaction to starfish	Bird	Isopod
K. lateralis				
P. macquariensis	*Anasterias directa* *Anasterias mawsoni*	✓ ✓	*Larus dominicanus* (Dominican Gull) *Gallirallus australis scotti* (Weka) *Sterna vittata* (Antarctic Tern)	**Exosphaeroma gigas*
L. caliginosa	*Anasterias directa*			
P. aurata	---		Dominican Gull Weka	
H. setulosum	---		---	
C. (*P.*) *coruscans*	*Anasterias directa* *Anasterias mawsoni*	✓ ✓	Dominican Gull Weka Antarctic Tern	**Exosphaeroma gigas*

* *E. gigas* preyed on molluscs that were overturned owing to injury or weakened condition

Table 18. Prey of starfish

	Starfish Predator:	
	Anasterias directa	_Anasterias mawsoni_
Prey	*Frequency of prey being eaten by starfish (recorded during field collections)	
P. macquariensis	9	7
_C._ (_P._) _coruscans_	4	5
L. caliginosa	2	-
Helicarcinus planatus (crab)	1	1
Exosphaeroma gigas (isopod)	-	1
Pseudopsolus macquariensis (holothuroid)	2	3
Spirorbis aggregatus (tube dwelling) (polychaete)	1	3

*The frequency of prey is taken from observations of 120 of each species of starfish over a one year period.

observations of 120 of each species of starfish collected over a one year period. (These starfish formed part of the collection for reproductive studies (Appendix I).)

The main bird predators of littoral molluscs were the Dominican gull, _Larus dominicanus_, and the weka, _Gallirallus australis scotti_. Dominicans and wekas were observed walking over rocks preying on molluscs at low tide. Dominicans rode on the water amongst rocks and picked off molluscs. A catastrophic predation by Dominicans on limpets occurred in early December 1968. The birds were attracted to the relief ship and chose to roost on a small area of rocks in Buckles Bay near the main camp (see Plate 19A). Seventy to eighty birds were often present. During this time, the seas were calm and a later investigation showed that the birds had removed every limpet in the roosting area. Limpet shells were scattered over the rocks with the flesh picked out (see Plate 19B).

The food of Dominican gulls was listed in a study by Merilees (pers. comm.) who found that molluscs formed 39% of the diet as a percentage of the total number of items identified, see Table 19. Seasonal differences of the percentage of molluscs in the food of gulls were slight, there being a small increase in summer and this was attributed to availability of food sources. The severity of Macquarie's climate combined with the short day length in winter was suggested as the explanation for the seasonal difference in the frequency

Plate 19.

19A. Dominican gulls (Larus dominicanus) roosting on an area of rocky shore in Buckles Bay.

19B. Limpet shells (Patinigera macquariensis) from specimens which had been picked off and eaten by Dominican gulls.

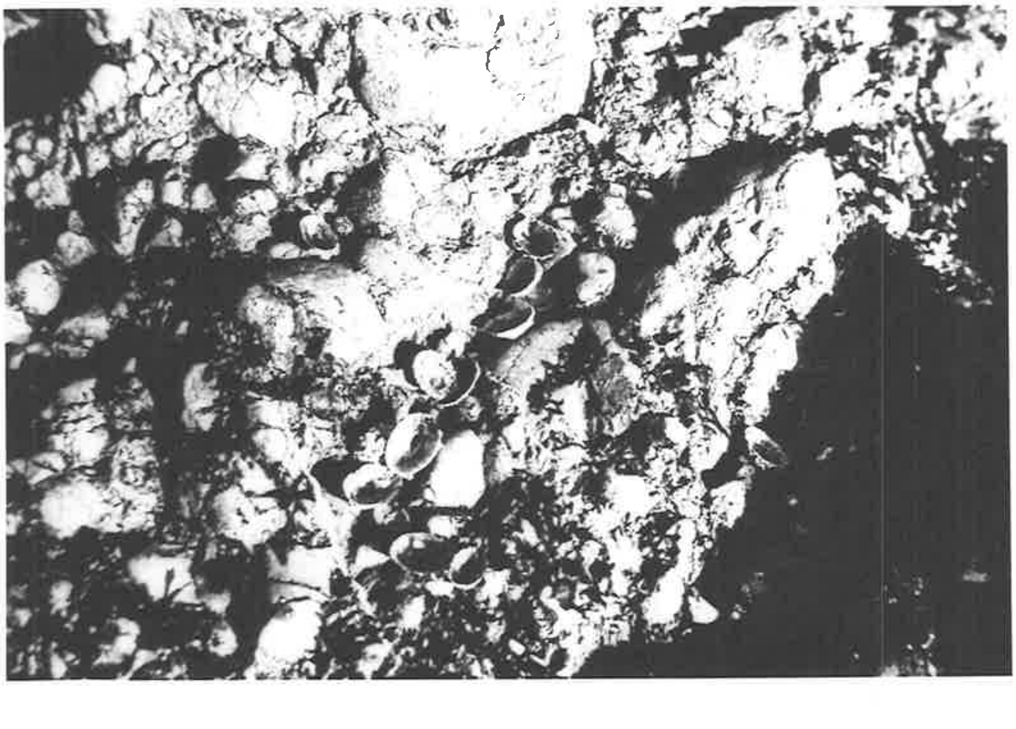


*Table 19. Molluscan food of Dominican gulls

Species Composition - Combined Stomach and Regurgitation Analysis	
Mollusca:	Percentage of Total
Amphineura	
Plaxiphora aurata	8.0%
Gastropoda	
Cantharidus (P.) coruscans	15.7%
Patinigera macquariensis	11.2%
Margarella macquariensis	0.6%
Macquariella hamiltoni	0.2%
Lamellibranchiata	
Gaimardia t. coccinea	0.9%
Kidderia bicolor	0.2%
Cephalopoda	
unidentified beaks	2.7%

* Data from Merilees (pers. comm.)

of mollusc and fish species taken. Although the percentages of the molluscs in the diet did not increase greatly in the summer, the volume of total food could well have increased owing to greater feeding requirements associated with chick rearing. In addition, Merilees obtained his data from stomach and regurgitation analyses. Specimens of P. aurata and P. macquariensis which had been eaten by Dominicans at shore feeding sites, not by swallowing and later regurgitating but by picking out the flesh after dislodging the mollusc, would not be accounted for in regurgitation samples and would often escape frequency counts from stomach contents owing to digestion. This suggested a greater frequency of P. aurata and P. macquariensis taken when assessing data from stomach contents and regurgitations. C. (P.) coruscans were almost invariably swallowed whole and later regurgitated. This would explain the higher percentage for C. (P.) coruscans in Table 16.

In the starfish predation experiments, molluscs did not show any specific avoidance reactions to objects other than starfish. In all tests with such objects, the responses were to clamp down (P. macquariensis), remain immobile (all), move uninterruptedly around the object (all), or close the operculum when touched (C. (P.) coruscans and L. caliginosa).

Avoidance reactions of molluscs to starfish have been studied by a number of workers and reviews have been made by

Bullock (1953), Kohn (1961), Feder (1963), and Feder and Christensen (1966). The last compiled a comprehensive table of organisms responding to the presence or contact of starfish as reported in the literature. No such studies have been previously conducted on sub-Antarctic starfish.

Specific escape responses to *Anasterias directa* and *Anasterias mawsoni* were exhibited by *P. macquariensis* and *C.* (*P.*) *coruscans* but not to *Asterina hamiltoni*. A single tube foot from either species of starfish was enough to elicit a response. The other molluscs did not show escape responses to starfish. Avoidance reactions of *P. macquariensis* to starfish were very similar to those shown by *Acmaea* sp. (Bullock 1953; Feder 1963; Margolin 1964). Responses were immediate when the limpet was submerged and active with the pallial and cephalic tentacles out. If the limpet was clamped down with the tentacles withdrawn, the response was often delayed. Times for this delay were recorded between 3 and 70 seconds. When the limpets were clamped down and out of the water, contact of the starfish body with the shell did not invoke a response. In the field, the tube foot of a starfish was placed under the shell of a limpet attached to an emerged rock substrate. Contact was maintained for three minutes. Forty such trials were conducted and only two limpets were induced to respond but the reaction was sluggish.

Typically, in an avoidance reaction, *P. macquariensis* elevated its shell and the tentacles elongated and waved about. Elevation of the shell was aptly termed "mushrooming" for *Acmaea* limpets by Bullock (1953). The extent of this elevation varied from slight to very high in initial contacts with different specimens of *P. macquariensis*. Plate 20A shows the mushrooming reaction of one such limpet gripped by the arm of the starfish, *Anasterias mawsoni*. When touched directly from the front, limpets reacted in three ways: (1) the front of the shell was lowered and the animal retreated; (2) the limpet reared the front of the shell and turned with the anterior part of the foot off the substrate. The foot was placed down and the limpet moved away rapidly. This rearing was often so violent as to cause the limpet to fall off if on the side of a rock or aquarium; (3) the limpet turned in an arc until contact was lost and moved away rapidly. When touched from the side, the limpet rapidly turned through 90^o away from the contact and moved off quickly. Contact from the side rarely invoked rearing of the foot during the turn. When contacted from the rear, the limpet moved away rapidly and the foot would be trailing behind the shell.

When contacted by the appropriate starfish, *C.* (*P.*) *coruscans* were immediately geared into a hyperactive state. The tentacles elongated and waved about. The agitated state climaxed in a violent twisting of the shell. The twisting occurred in both clockwise and anticlockwise directions. On

Plate 20.

20A. A limpet (*Patinigera macquariensis*) showing the "mushroom" reaction while gripped by a starfish (*Anasterias mawsoni*).

20B. *Anasterias mawsoni* ingesting a trochid (*Cantharidus* (*P.*) *coruscans*). The starfish was overturned for display.

30 mm

30 mm

coming in contact with a starfish, a trochid abruptly moved off in this state. If touched from behind or from the side, the trochid moved away from the point of contact. Often when confronted head-on, the trochid reared and turned while twisting and this frequently resulted in loss of adherence to the substrate by the foot muscle.

Despite these avoidance reactions, both limpets and trochids were eaten by starfish in the field. Plate 20B shows a trochid being ingested by a specimen of *Anasterias mawsoni*. In the field, molluscs were found with a number of starfish upon them. For example, one limpet was found in a cluster of eleven *Anasterias directa* in a sublittoral rock pool, only two having their stomachs out. This suggested that the capture of food by starfish attracted other starfish, most likely by the release of a chemical. (Such occurrences were not used in the compiling of Table 18.)

Though starfish and molluscs were kept together in aquaria for six weeks, no molluscs were eaten. Limpets were often gripped by the starfish but either the starfish moved on or the limpet broke the grip. Trochids were also cornered and gripped by the starfish with the same result. The starfish were probably affected by the unnatural conditions of the aquaria. The placing of a starfish on top of a mollusc in the field always resulted in the escape of the mollusc.

Only two of the rock pool populations observed for predation frequencies were not affected by extraneous conditions (shifting rubble, kelp overlay, storms). The population of starfish and molluscs in these pools together with occurrences of predation are listed in Table 20. From the transect studies (section III (a)), adult predatory starfish were rare in the lower eulittoral zone and had an average density of one per sq. metre in the upper sublittoral zone. At diving stations (at depths of 6 to 10 metres), their average density was two per sq. metre. The limited data left little scope for interpretation but suggested a low predation pressure by starfish.

Predation by the isopods, _Exosphaeroma gigas_, was restricted to animals either in a damaged or enfeebled condition. The latter frequently occurred when _P_. _macquariensis_ and _C_. (_P_.) _coruscans_ were subjected to unfavourable physical conditions in rock pools in the eulittoral (e.g. high temperatures). This took place either at the upper limit of the distributions of the molluscs (particularly for limpets) or, _en masse_, after they were transported to higher levels by heavy wave action (particularly for trochids).

(e) Reproduction

(i) Materials and methods

From March 1968 to March 1969, specimens of the six species of molluscs in this study were collected at approxi-

Table 20. Predation by starfish on molluscs in rock pools over a period of four months.

	Numbers in pool (Ranges from counts) (at different times)	Number eaten over 4 months	Eaten by
POOL 1.			
Prey:			
P. macquariensis	13 to 16	1	*A. directa* (a)
C. (P.) coruscans	3 to 7	1	*A. directa* (b)
Predators:			
A. directa (a) *A. directa* (b)	2		
POOL 2.			
Prey:			
P. macquariensis	39 to 47	3	*A. directa* (a) *A. directa* (b) *A. mawsoni* (b)
C. (P.) coruscans	17 to 25	1	*A. mawsoni* (a)
Predators:			
A. directa (a) *A. directa* (b)	2		
A. mawsoni (a) *A. mawsoni* (b)	2		

mately monthly intervals. The number taken at each collection depended on the relative abundance of each species. A sample of at least ten specimens of each sex was obtained for L. caliginosa, P. macquariensis, H. setulosum, and C. (P.) coruscans; five of each sex for P. aurata; and ten for the hermaphroditic K. lateralis.

All the species were found either in the eulittoral and/or sublittoral zones and some spread from these zones to deeper waters (section IV 1. (a)). However, eulittoral and sublittoral areas were always used as sites for the monthly collections. Some specimens were taken from a depth of approximately 6 metres during SCUBA dives but only in the case of Patinigera macquariensis was this done regularly.

For each species, the positioning of the collecting site was kept to narrow limits by the use of the smaller, local sub-zones (e.g. Bare Zone, Upper Red, Kelp Zone) which, in turn, could be related to the broader eulittoral and sublittoral classifications of a universal zonation scheme (see section III (b)).

K. lateralis were found in the eulittoral zone and were the dominant indicator organisms of the Bare Zone (section III (a)). They were always found attached to rocky substrate and retreated to crevices when emerged in dry weather. Although their distribution did extend into the algal cover of the Porphyra and Upper Red Zones, specimens were collected from the Bare Zone.

L. caliginosa were confined to the eulittoral zone and to the upper part of the sublittoral zone. They were common in pools and under stones in the eulittoral zone and uncommon on algal fronds in any area. Specimens were collected from shallow pools in the Upper Red Zone.

The reproduction of *P. macquariensis* was studied in detail and is described in section V (f) as part of a study of the biology of this species. The areas of collection of *P. macquariensis* are outlined in section V (f).

The distribution of *P. aurata* extended from the bottom of the eulittoral zone to a depth of at least 10 metres. Specimens were collected from pools at the top of the sublittoral zone. During the summer months, specimens were also collected during SCUBA dives at depths of approximately 6 metres.

H. setulosum were abundant in the Kelp Zone on rocky substrate encrusted with coralline algae. Usually, *Durvillea* holdfasts were prevalent in these areas which, at low tides with calm seas, were covered by the *Durvillea* fronds. Collections of specimens for reproductive study were made in these areas.

The distribution of *C. (P.) coruscans* extended from the top of the sublittoral zone to a depth of at least 10 metres. Specimens were collected at the top of the sublittoral zone in channels and pools where they were found either in clusters on rock surfaces and dislodged kelp or on the fronds of red algae.

Immediately after they were collected, all specimens were preserved and bottled for later examination. Preservatives used were: Baker's formol calcium (37% formaldehyde : 10% aqueous solution of anhydrous calcium chloride : distilled water = 1:1:8), Baker's formol cobalt calcium (37% formaldehyde : 10% aqueous solution of anhydrous calcium chloride : 10% aqueous solution of cobalt chloride : distilled water = 1:1:1:7), and a glycerol-alcohol mixture consisting of 95% = 70% ethyl alcohol and 5% = glycerol. Bennett (pers. comm.) recommended the use of the Baker's formaldehyde solutions for good preservation of lipids which are likely to be abundant in the gonads and storage sites of sub-Antarctic invertebrates. Specimens were first placed in Baker's formol calcium for at least 24 hours. Preservative was also injected through the body wall of the four larger species (_K_. _lateralis_, _P_. _macquariensis_, _P_. _aurata_, and _C_. (_P_.) _coruscans_). All species were then transferred to Baker's formol cobalt calcium for storage. This solution also contained powdered calcium carbonate to act as a buffer against the preservative becoming strongly acidic. Acidity in formaldehyde-based preservatives causes the deterioration of molluscan shells. The animals were stored in Baker's formol cobalt calcium for at least a year. Before the specimens were dissected, they were transferred to and subsequently stored in the glycerol-alcohol mixture.

Descriptions of reproduction employed (1) egg sizes; (2) the state of gonads and of broods; (3) observations of egg cases laid in the field; and (4) gametogenic activity (particularly spermatogenesis) determined by microscopical examination of smears of gonadial tissue.

(ii) Results and discussion

(1) *K. lateralis*

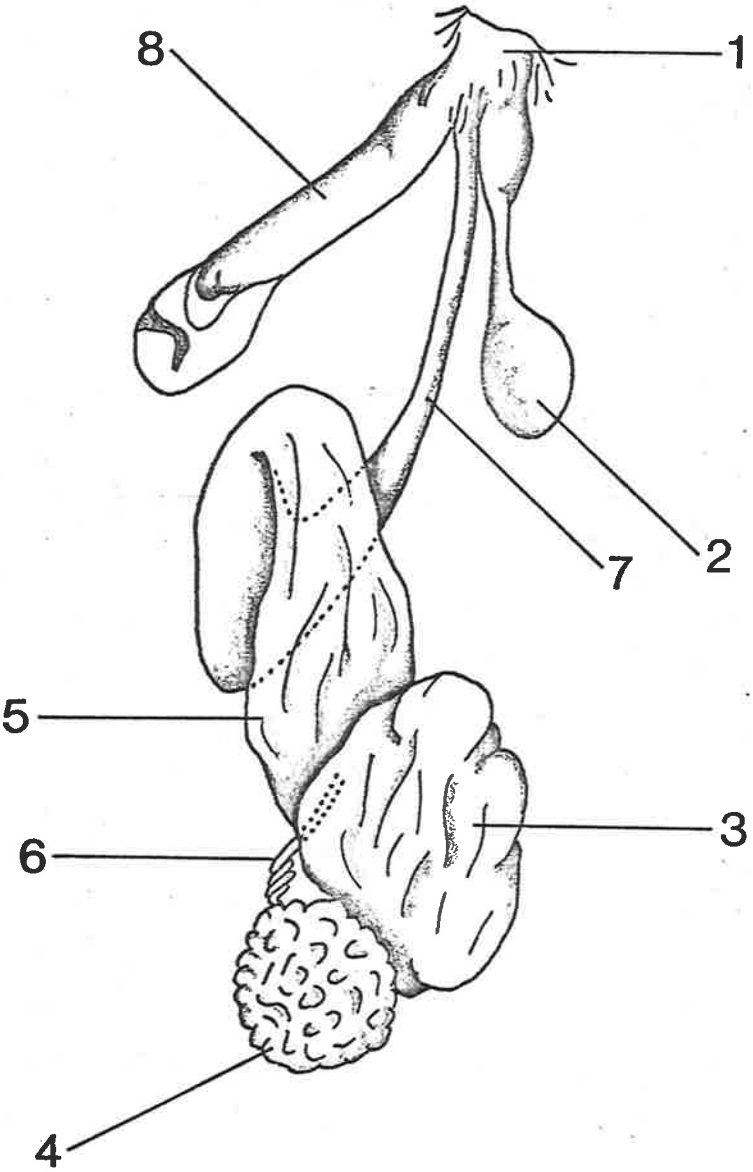
Preliminary dissections showed that specimens of *K. lateralis* of 10 to 11 mm in length were immature, the organs of the reproductive system being noticeably smaller. Therefore, individuals 14 mm in shell length or greater were used for these studies. The abundance of *K. lateralis* ensured ease of collecting sufficient specimens of this size.

K. lateralis, like most pulmonates, were hermaphroditic. The reproductive system extended down the right-hand side of the body, the penial apparatus being displaced to the left. The relationship of the parts of this complex system was determined as far as possible from dissection and slide smears. Figure 19 shows the reproductive system of *K. lateralis*.

Reproductive organs were not embedded in other parts of the viscera. The ovotestis was readily distinguishable and

Figure 19. Reproductive system of *Kerguelenella lateralis*.

1 = common genital atrium
2 = gland
3 = gland
4 = ovotestis
5 = gland
6 = hermaphroditic duct
7 = spermoviduct
8 = penial apparatus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3
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4

from this, a hermaphroditic duct ran into a large glandular structure "3". There were two distinct glandular structures in this region ("3" and "5"). Slide smears of these showed that the tissue contained many oil-like droplets; there was no evidence of any storage of spermatozoa or ova. The spermoviduct continued from these glands on to a common genital atrium. The spermoviduct was joined by the duct from structure "2". This structure was in a position normally occupied by the spermatheca in pulmonates, and more specifically, in siphonarids (Marcus and Marcus 1960; Hyman 1967). Yet no spermatozoa or spermatophores were found in structure "2" during the dissections of specimens from each monthly sample. The structure was not a hollow sac but was filled with a compact gland-like tissue. Regions of the penial apparatus and the spermoviduct were teased out and examined for spermatophores but none were found.

The ovotestis contained sites of both spermatogenesis and ovogenesis without any apparent order of arrangement into specific areas for either male or female function. At each month, the ovotestis contained mature spermatozoa which were clumped together. They were attached at the head regions which appeared to be embedded in gonadial tissue, the tails projecting out in sheaths. Ova were embedded throughout the ovotestis, their diameter being 160 to 180 µm.

K. lateralis laid a spherical egg mass which was firmly attached to the rock substrate. The eggs were usually laid in crevices and small channels. Each egg was contained in its own compartment made of a tough gelatinous material and each compartment was cemented together to form a spherical mass, the innermost eggs being completely enclosed. Although the number of eggs in each mass varied, the average was twenty-four. Eggs developed to fully formed juveniles in these cases. The phase of development was the same for all embryos in any one egg mass. The structure and capacity of the egg-case and the development of larvae within this case to a crawling, juvenile stage were very similar to that described for Kerguelenella stewartiana by Knox (1955). It appears likely that such reproductive development is a feature of the Kerguelenella group of siphonarids all of which have a circum-Antarctic distribution.

Insect larvae and oligochaetes were found in egg masses which still had early embryos in other compartments, indicating that they actively invaded the spheres and did not occupy ones vacated by juveniles. The outer covering remained largely intact and still attached to the substrate. The larvae and oligochaetes most likely preyed on the eggs, though they may have used the gelatinous sphere as a form of sanctuary against unfavourable environmental conditions, particularly wave action.

Egg masses were found throughout a period of one year.

There appeared to be an increase in their frequency in summer but no quantitative survey was undertaken. The dissections of the gonads suggested that the production of gametes was constant throughout the year. Any reproductive cycle period was indeterminate.

(2) *L. caliginosa*

L. caliginosa is a small species. In this study, the length from the apex to the outer lip of the mouth of the shell of the largest adult was 4.5 mm. The abundance of these littorinids enabled sufficient specimens measuring 3 to 4 mm in this dimension to be taken, hence ensuring sexual maturity.

The sexes were separate. The males were easily distinguishable from the female by the relatively large penis behind the right tentacle. The gonads were closely applied to the digestive gland and occupied the apical portion of the viscera.

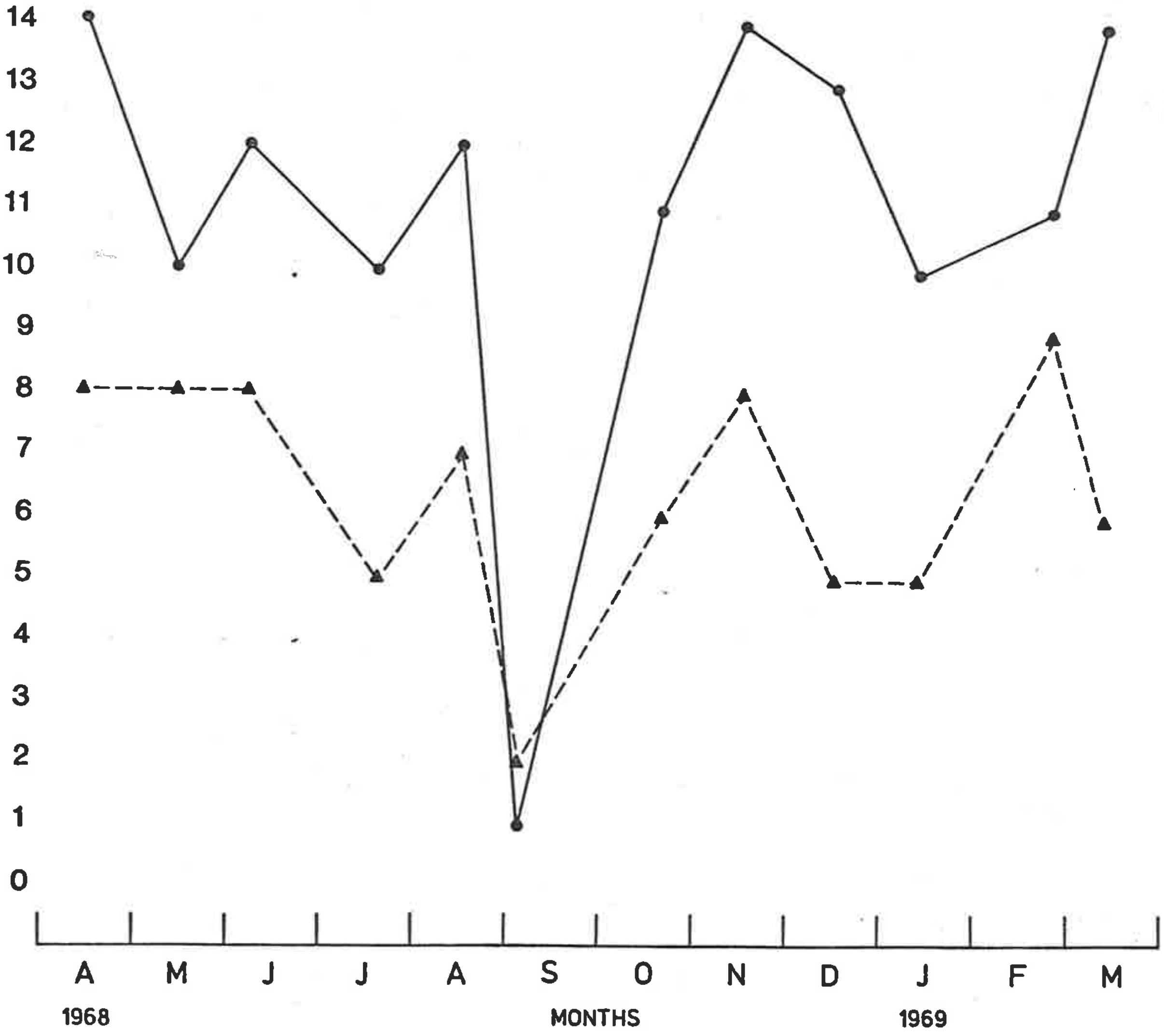
Figure 20 shows the general reproductive condition of the gonads of *L. caliginosa* as indicated by the monthly state of two particular features: (1) the average number of mature eggs in the ovaries per individual female and (2) the number of males with an abundance of mature spermatozoa in the testes.

In females the ovary contained a small number of mature

Figure 20. Monthly reproductive condition of *Laevilitorina caliginosa*.

Females: ●———● average number of mature eggs per individual.
(N = 10, each month)

Males: ▲-----▲ number with an abundance of mature spermatozoa in the testis.
(N = 10, each month)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eggs at each month except for September. The number of eggs per individual varied from nine to sixteen and their size range varied from 100 to 200 µm. No brooding was discovered. The ovary was small and the restricted number of eggs suggested that the eggs were laid in cases although this was not observed in the field.

In males, mature spermatozoa were found in the testes in any month and were packed into separate clumps. From slide smears, there was no appreciable seasonal difference in either spermatogenic activity or the amount of mature spermatozoa. However, the number of males with an abundance of mature spermatozoa in the testes decreased sharply in September.

It appeared that the production of eggs and spermatozoa was constant throughout the year. In September, the females lacked mature eggs and there was a corresponding decrease in the number of males with an abundance of mature spermatozoa in the testes. This could have been due to the existence of particularly favourable conditions for spawning just prior to collecting the littorinids.

(3) P. macquariensis

As previously mentioned, the reproduction of P. macquariensis was studied in detail and is described in section V (f) as part of a study of the biology of this species.

(4) *P. aurata*

P. aurata is a large species, the largest specimen in this study being 11.5 cm in length. The minimum size examined was 6 cm in length, in order to ensure sexual maturity.

On dissecting specimens of *P. aurata*, it was apparent that this species did not brood but built up large gonads to release gametes for external fertilization. Though a graph of reproductive condition using a gonad index formula could have been constructed to describe such a reproductive type (see section V (f) for *Patinigera macquariensis*), this was not done, because on preservation (the chitons were injected with preservative) the muscular tissues tended to become inflated. This would introduce errors into the ratio of gonad to other tissue.

Figure 21 shows the reproductive cycle for *P. aurata*. Symbols were used to designate particular reproductive conditions of the gonads in both males and females. The sets of each symbol were separated horizontally on the figure. The cycle was an annual one with the end points of the records indicating similar synchronizations in both 1968 and 1969.

P. aurata developed large gonads. The ovary contained a very large number of small eggs (diameter at maturity = 270 μm), indicating that gametes were released to the sea for external fertilization and subsequent larval development. There was no evidence of brooding. The gonad was unpaired

Figure 21. *Reproductive cycle of <u>Plaxiphora aurata</u>.

A. Females:

(N = 5, each month)

X = spawning
● = ripe
○ = oogenesis
□ = regressed
▲ = resorbing

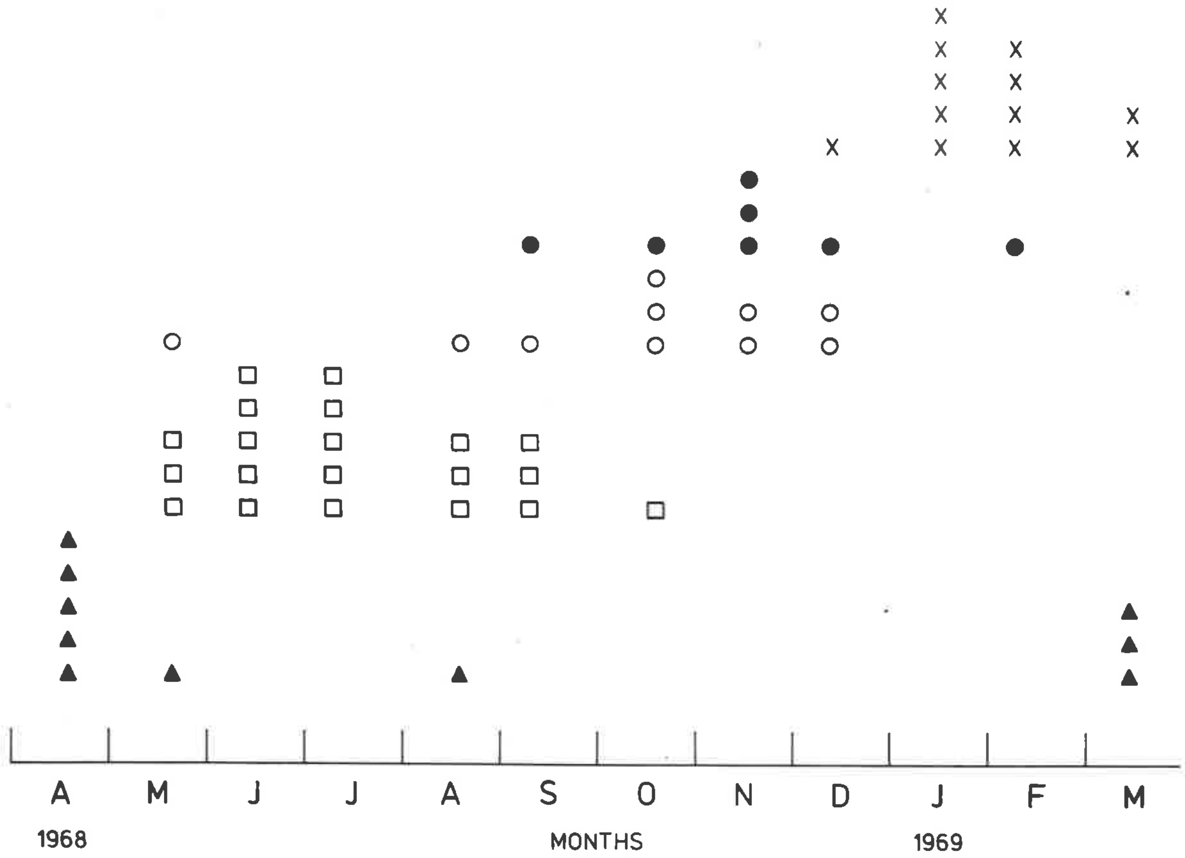
B. Males:

(N = 5, each month)

X = spawning
● = ripe
○ = abundance of spermatids
■ = early spermatogenesis
□ = regressed
▲ = resorbing

---

*A symbol is used to classify the predominant reproductive state of the gonad of each specimen. Sets of symbols are separated horizontally on the figure.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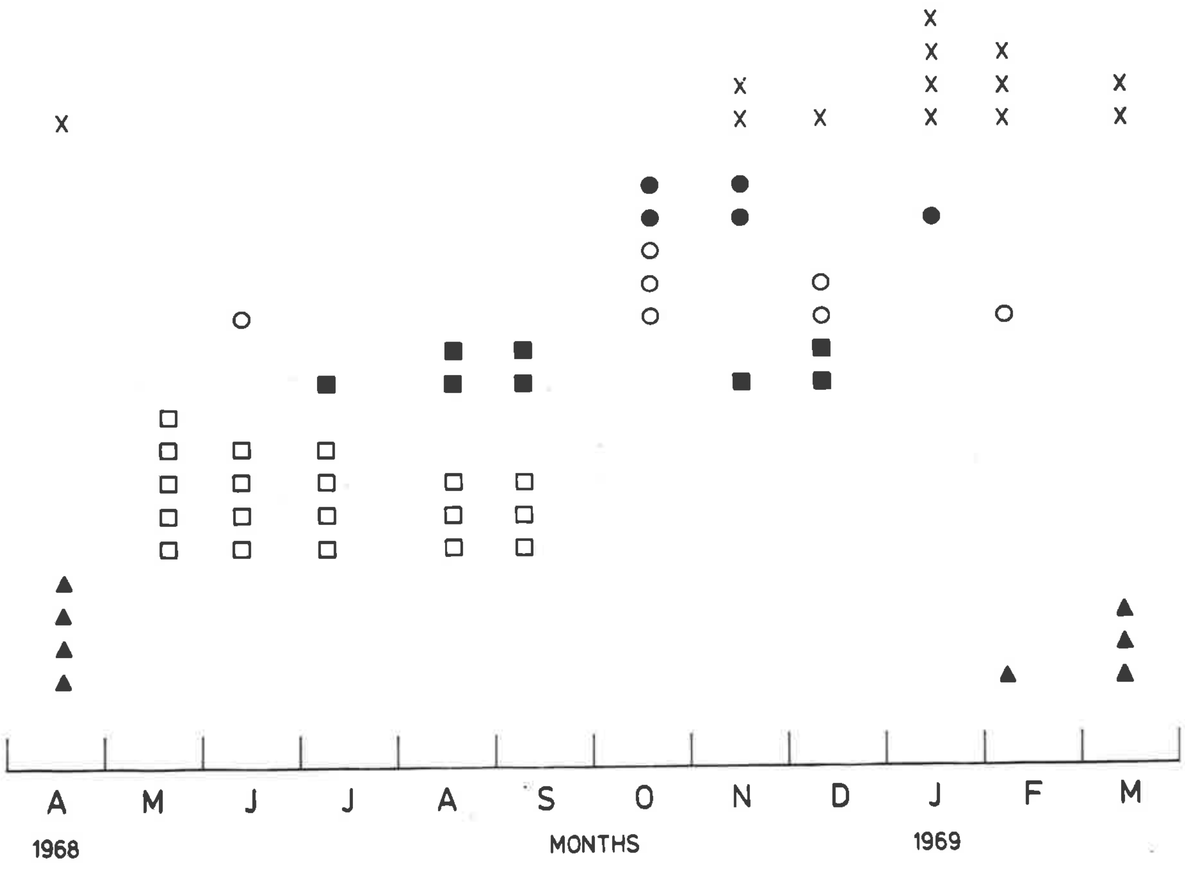
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1969

and was posterio-dorsal to the visceral mass.

In both males and females, the cycle followed a similar pattern. The gonads were predominantly in a resting condition during May, June, and July. Gametogenic activity was observed in both sexes in August. The gonads progressively increased in the following months, both in size and in stages of development of gametes. In November, the gonads were very large and were predominantly in a ripe condition; in males, spawning was observed. In December, there was evidence of spawning and gametogenic growth in gonads of both sexes. In January, the condition of the gonads showed that spawning had occurred in most animals. The ovaries were reduced in size, had lost their firmness, and the eggs in them were easily loosened; the testes were reduced in size, had lost their firmness, and showed sunken discoloured patches. After January, there were little signs of gametogenesis. March to May was the apparent period of resorption. Thus the breeding season spread from December to March with a spawning peak in January, although the males appeared to be in a breeding condition over a wider period than the females.

Plaxiphora aurata were not collected as regularly as Patinigera macquariensis (section V (f)) during SCUBA dives and a reproductive cycle of a population in deeper water could not be plotted. However, collections were taken during dives from December to February and the gonads of the specimens were either in a mature or spawning condition.

(5) H. setulosum

The minimum size at which H. setulosum was able to reproduce was found to be 4 mm in length. Only specimens over 6 mm long were used in this study.

Figure 22 shows the reproductive cycle for both male and female chitons. For males, the plot of the number of specimens with ripe testes for each month indicates the general reproductive state. The females brooded their young to a juvenile stage under the girdle in the mantle cavity along each side of the animal. Plate 21 shows two female chitons, with broods at the egg stage (A) and at the juvenile stage just prior to release (B). Although Dell (1962) reported the occurrence of brooding in H. setulosum, the time periods for developmental stages within the reproductive cycle were unknown prior to the present study. In order to illustrate these stages, a symbol was used to designate particular reproductive conditions of the gonad, brood, and of juvenile release. The sets of each symbol were separated horizontally on the figure.

The reproductive cycle of H. setulosum was annual and both males and females were shown to be at the same reproductive state in March 1968 and March 1969. In March of both years, the majority of males had testes which were reduced

Figure 22. Reproductive cycle of *Hemiarthrum setulosum*.

A. *Females:

(N = 10, each month)

X = release of juveniles

▲ = juveniles in brood

△ = embryos in brood

● = eggs (showing embryonic differentiation) in brood

○ = eggs (non-differentiated) in brood

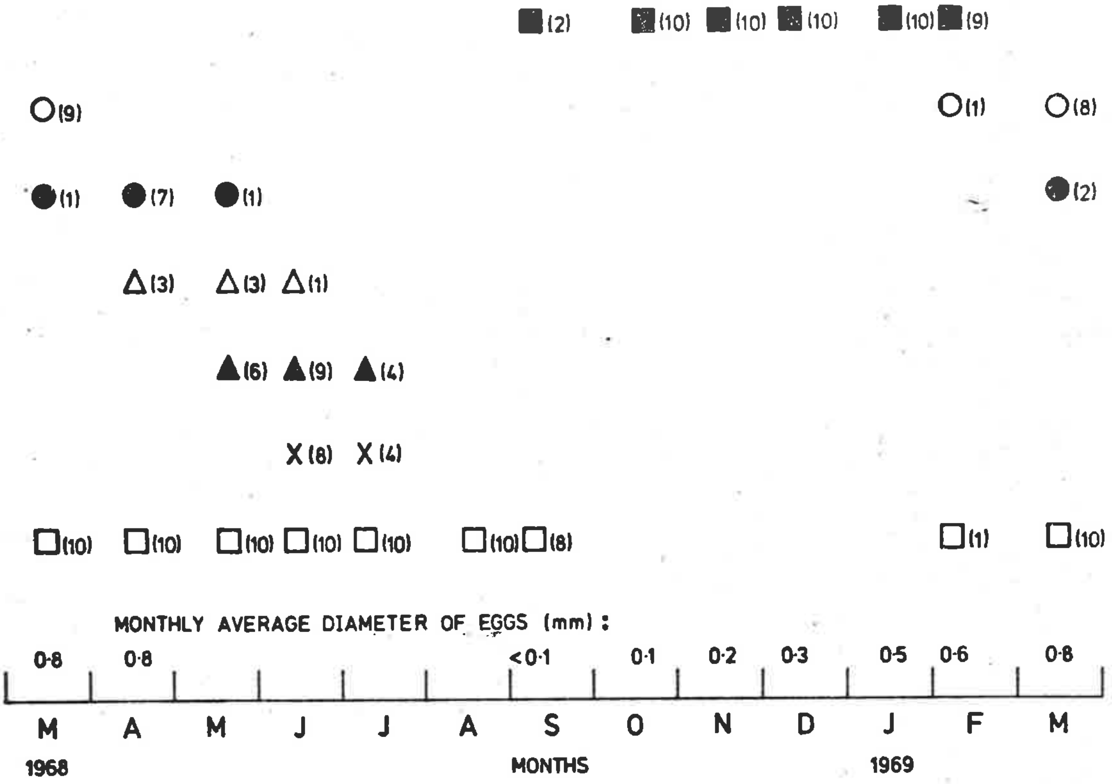
■ = ovary with eggs

□ = ovary with no eggs

B. Males: ●———● Number with ripe testes

(N = 10, each month)

*Each reproductive state is designated by a symbol. More than one state was sometimes found in an individual and the number in brackets alongside the symbol shows the number of specimens with that ovarian condition. Sets of each symbol are separated horizontally on the figure.


(2)
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(1)
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MONTHLY AVERAGE DIAMETER OF EGGS (mm) :
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0·8
<0·1
0·1
0·2
0·3
0·5
0·6
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1968
MONTHS
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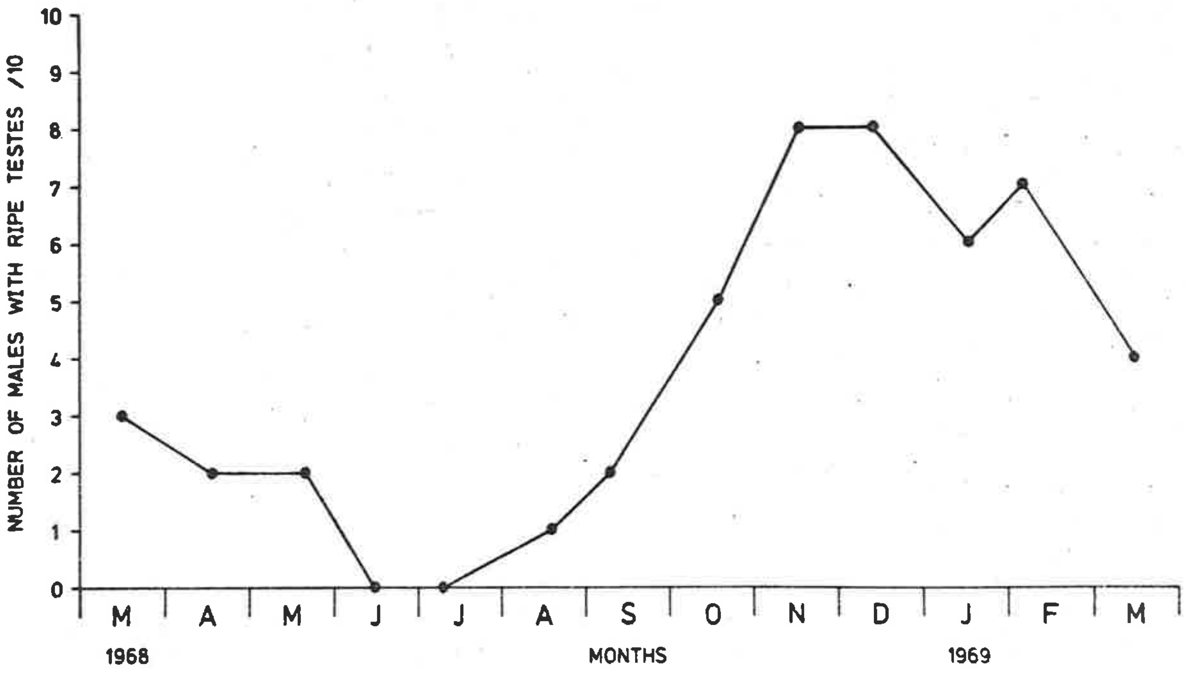
NUMBER OF MALES WITH RIPE TESTES /10
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6
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MONTHS
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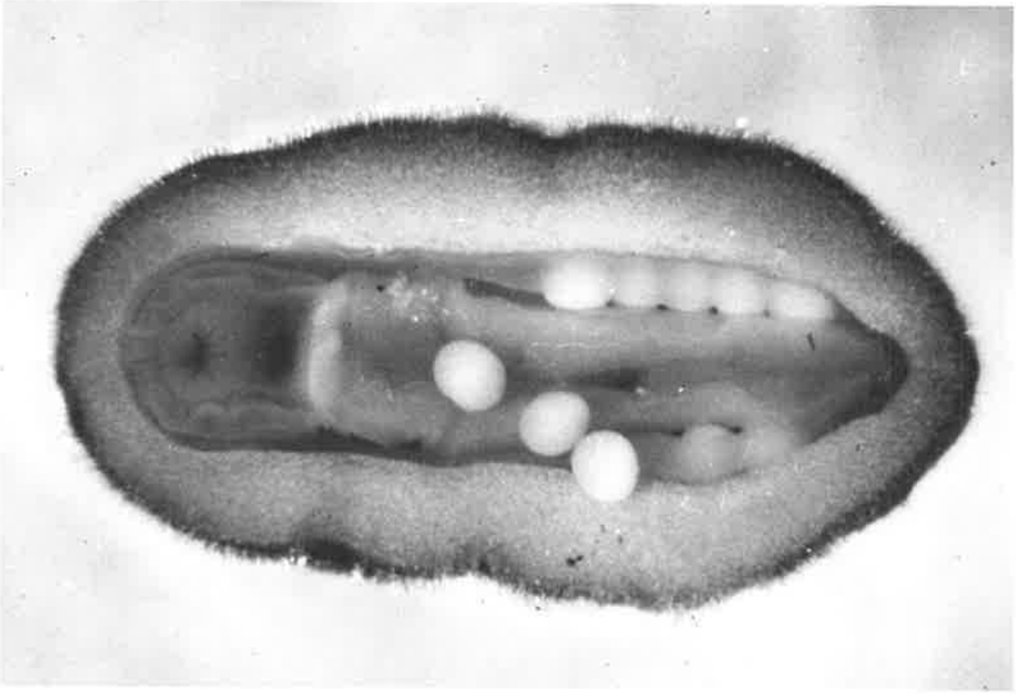
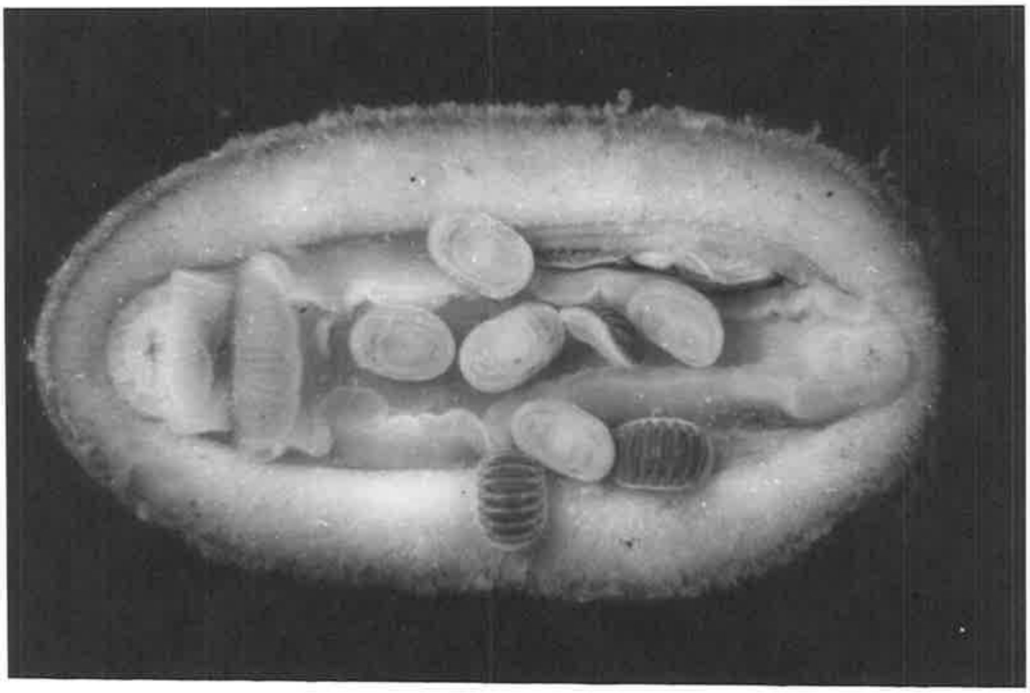
Plate 21.

21A. Specimen of Hemiarthrum setulosum with a brood at the egg stage.

21B. Specimen of Hemiarthrum setulosum with a brood at the juvenile stage just prior to release.





2 mm

and consisted of mature spermatozoa, indicating an advanced spawning condition. Although this condition in the males could be assigned to any point over a three-month period, the females in the two March samples were at a very similar reproductive state which could be assigned to a more precise period. In March of both years, the eggs were in the mantle cavity and generally showed no visible sign of embryonic differentiation. There were distinctly different stages for the eggs at a period of approximately one month either side of the above condition. That is, in February, the eggs were predominantly found in the gonad while in April, they showed either embryonic differentiation or had developed into an embryonic chiton.

In H. setulosum, as in other Amphineura, the gonad of both males and females was unpaired and lay posterio-dorsal to the visceral mass. In females, the ovary was in the resting state in the months of July and August. In September, eggs with a diameter of less than 0.1 mm were distinguishable. They were retained in the ovary until February, their size gradually and progressively increasing up to 0.6 mm in early February. In March, eggs appeared in the mantle cavity and, in the majority of females, showed no sign of embryonic differentiation. In the mantle cavity, the eggs averaged 0.8 mm in diameter. They began to show signs of differentiation in April. In May, young in two stages of development were found in broods: (a) some having an embryonic body with the foot and the head not fully formed, (b) others, juveniles, possessing all the external features of a chiton. Juveniles were larger in June and July and were released in those months, principally in June.

In the males, the testes were resting over June and July. In late August there were some signs of spermatogenesis. After September, both the size of the testis and the spermatogenic activity increased. Mature spermatozoa were abundant in late November and in December; slide smears showed that almost all of the testis consisted of spermatozoa in 8 out of the 10 specimens examined in each of these two months. There was a resurgence of spermatogenic activity in January although mature spermatozoa were still plentiful. The testes decreased in size through February to April. After February there were only slight signs of spermatogenesis. April to June was a period of resorption.

As indicated by the male reproductive cycle, the breeding season of H. setulosum extended from December to March with peak spawnings around December and February. In the females, transfer of the eggs to the mantle cavity did not begin until February. Thus, it appeared that fertilization occurred just prior to or during this transfer of the eggs. Although H. setulosum had a summer breeding season, the direct development of its eggs in a brood resulted in the absence of a summer planktonic larval stage and the winter release of juveniles. This restricted method of recruitment may be correlated with the cryptic habitat of *H. setulosum* (under heavy cover of *Durvillea antarctica*). However, the brooding habit of *Hemiarthrum* has not prevented their wide distribution in the Southern Hemisphere (Dell 1962). The brooding habit of marine invertebrates of the littoral zone is further discussed in Appendix I.

(6) *C.* (*P.*) *coruscans*

Only large specimens of *C.* (*P.*) *coruscans* were dissected in order to ensure sexual maturity, i.e. specimens whose greatest length from apex to the outer lip of the mouth was at least 18 mm. *C.* (*P.*) *coruscans* were very common and there was no problem in obtaining sufficient specimens of this size.

In *C.* (*P.*) *coruscans* the sexes were separate. The mature gonad was large, spreading over the surface of the digestive gland and extending into and solely occupying the apical position of the viscera.

The ovary contained a large number of small eggs (diameter at maturity = 170 µm, each egg being enclosed in a narrow gelatinous sheath). The production of eggs in this manner suggested that gametes were shed into the sea and that fertilization was external. As further evidence, no brooding or laying of egg cases were observed.

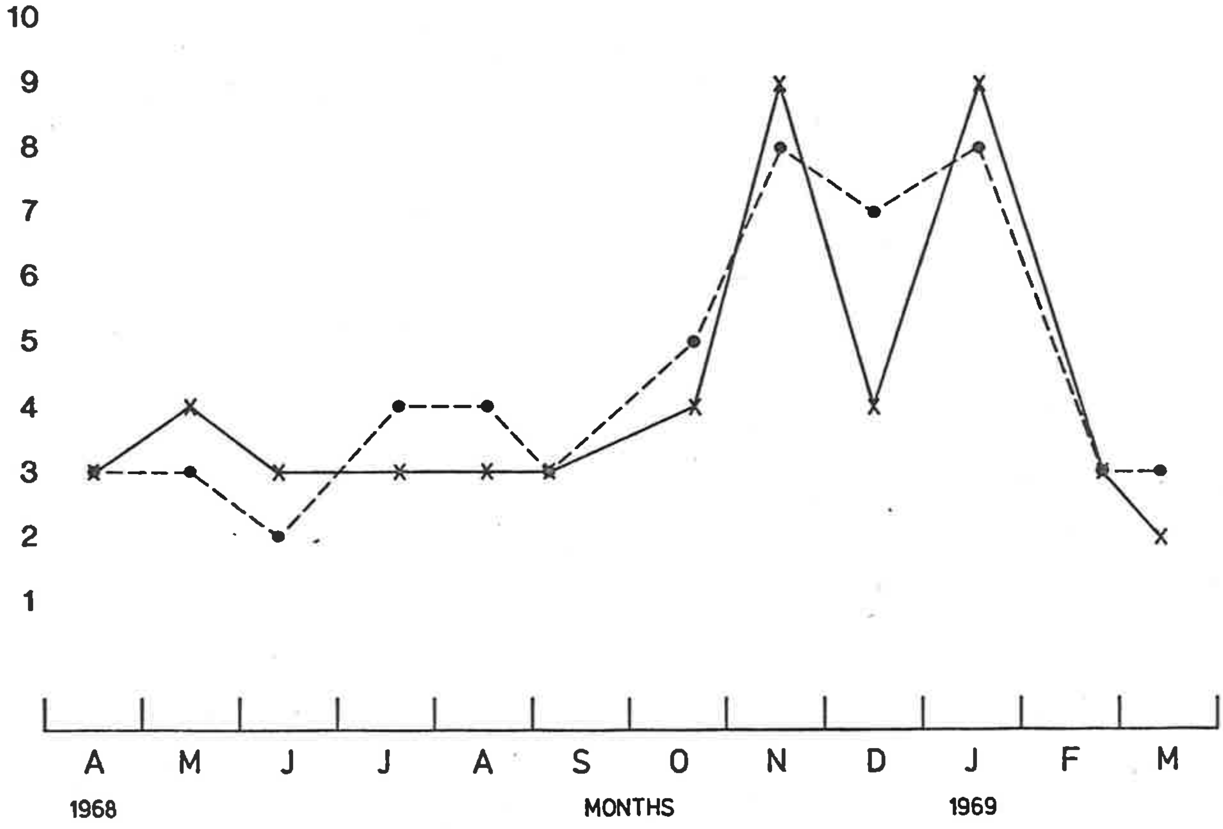
Figure 23 shows the monthly reproductive conditions of both males and females over a one year period. For both sexes, the number of specimens with ripe gonads for each month is plotted to indicate the general reproductive state. A reproductive cycle was indistinct with a considerable percentage of individuals with ripe gonads being present throughout the year. However, there was an evident increase of reproductive activity in the summer months.

At any monthly collection there were always some females with ripe ovaries containing a predominance of mature ova with well-formed gelatinous sheaths. These specimens formed about 30% of each sample, except in November and January when the figure increased to 90%. A similar situation existed for the males. At any one month's collection 20-50% of the specimens had ripe testes which contained predominantly mature spermatozoa, except in November to January when the figure increased to 70-80%. In February, almost all of the specimens not having ripe gonads showed a spawned condition. (In males, the testis was reduced, had lost its firmness, and consisted mainly of mature spermatozoa. In females, the ovary was reduced and the eggs were loosely packed and easily dislodged.) In other months when the number with ripe gonads was lower (i.e. March to October), a spawned condition was not predominant; during this period resting, growth, ripe, spawned, and resorbing stages were found and there was no

Figure 23. Monthly reproductive condition of *Cantharidus* (*P.*) *coruscans*.

Females: ×———× number with
(N = 10, each month) ripe ovaries.

Males: ●----● number with
(N = 10, each month) ripe testes.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MONTHS
1969

formation of an overall cycle.

Thus, over an annual period the reproduction of C. (P.) coruscans collected from the top of the sublittoral zone appeared to be divisible into two parts: (1) a period of low-level breeding activity (autumn-winter), (2) a period of high-level breeding activity (late spring-summer). From the monthly reproductive conditions, it was difficult to decide between two conclusions: (1) that the upsurge in the number of ripe individuals in summer indicated an annual reproductive cycle with a breeding season in late spring-summer; (2) the duration of a reproductive cycle was shorter than one year and individuals were not in phase, thus resulting in a constant production of gametes by the population; favourable conditions in summer stimulated animals to maintain a breeding condition. The relatively high and consistent number of specimens with ripe gonads in the autumn and winter months favoured the second conclusion.

IV. COMPARISON OF SELECTED SPECIES

2. PHYSIOLOGY

(a) Temperature

(i) Materials and methods

Investigations were conducted on six molluscs: *Kerguelenella lateralis*, *Laevilitorina caliginosa*, *Patinigera macquariensis*, *Plaxiphora aurata*, *Hemiarthrum setulosum*, and *Cantharidus* (*P*.) *coruscans*. The distributional ranges of these six molluscs are outlined in section IV 1. (a). For the experiments, adult molluscs were collected from the upper regions of their distribution, each species being taken from a specific habitat and level on the shore, i.e. *K. lateralis* and *P. macquariensis* from rock platforms of the Bare Zone and the Upper Red Zone respectively, *L. caliginosa* from mid-eulittoral rock pools (i.e. in the Bare Zone), *P. aurata* from lower eulittoral and upper sublittoral rock platforms, and *C.* (*P*.) *coruscans* and *H. setulosum* from rock platforms in the upper sublittoral. The same habitats and levels were also used for collecting specimens for desiccation and salinity studies. In addition, limpets from a depth of approximately 6 metres were collected for experiments on tolerance to increased temperatures.

The procedure during temperature experiments covered three categories: (1) the recording of death temperatures and the establishment of a lethal temperature (50% mortality) for each species, (2) recording the temperatures at which specimens lost their adherence to the substrate, and (3) the effect of prolonged heating at a sub-lethal temperature attained in the environment. Molluscs were placed in holding tanks immediately after collection, and experiments were conducted within 24 hours of collection. For each determination of lethal temperature, ten or more individuals were placed on the sides of an aquarium containing sea-water. This aquarium was inside a large electrically heated water bath. The sea-water in the aquarium was constantly stirred and aerated. The temperature of the sea-water was increased by 0.8°C to 1.0°C per 4 minutes. This allowed the body temperatures to equilibrate with the water temperature. To test the rate of increase of body temperature against increasing water temperature, specimens of _K. lateralis_, _P. macquariensis_, _C. (P.) coruscans_, and _P. aurata_ were removed from the water and body temperatures taken by immediately inserting a thermistor probe through the body wall above the foot. The thermistors used were S.T.C. type (No. F23). They were connected to a wheatstone bridge incorporating a galvanometer with a full scale deflection of 40 divisions. The unit was battery operated and portable. Settings of the bridge resistors would give a suitable range with an accuracy of 0.1°C. Calibrations were made at each usage to check on range settings and reading stability. For the first three of the species tested, the greatest lag of body temperature behind water temperature was 0.2°C and this was considered insignificant. However, the large chiton, P. aurata, showed a temperature lag of 0.4°C to 0.7°C. Consequently, the results for P. aurata were adjusted by 0.5°C. L. caliginosa and H. setulosum were of such small body size that temperature equilibration was assumed.

Successive trial and error runs were employed to approximate the lethal temperature of each species. Then, the exact lethal was determined by removing a suitable number (usually five) from the aquarium at temperature intervals of 0.5°C on either side of the approximate lethal and testing for recovery in sea-water kept at 5.0°C to 8.0°C. Those that failed to respond to pricking with a needle within forty-eight hours were considered dead. The response to touch as a death criterion for chitons was often difficult to employ but could be determined in marginal cases by placing the chiton against the jaws of vernier calipers in order to gauge responsive movement of the foot. Besides lethal temperature determination, the temperature range over which all deaths occurred was recorded.

Loss of adherence to the substrate by the foot muscle with temperature increase was investigated using the same heating equipment. Both the range of temperatures over which all specimens lost adherence and the temperature at which 50% had done so were recorded. During the heating process, some had moved to the bottom of the tank and these were tested for loss of grip by pressing gently with a glass stirring rod. This was considered equivalent to the fall-off condition of those at the sides. All specimens that lost adherence were transferred to recovery tanks which contained sea-water at a temperature of 5.0°C to 8.0°C.

For four species - *K. lateralis*, *P. macquariensis*, *P. aurata*, and *C.* (*P.*) *coruscans* - these heating experiments were carried out at two different seasons, July 1968 and February 1969.

For the sub-lethal exposure experiments, twenty specimens of one species of mollusc were placed in aquaria in which the sea-water was kept in a selected range by the use of aquarium heating elements coupled with thermostats. Two temperature ranges were used: 12.0°C - 15.9°C and 16.0°C - 20.0°C. Again, the water was constantly stirred and aerated. The loss of adherence of specimens was recorded at time intervals of 1, 6, 10, and 16 hours (12.0°C to 15.9°C range) and ½, 2, 8, 15 hours (16.0°C to 20.0°C range). At the last time interval, the specimens were transferred to sea-water at 5.0°C to 8.0°C to test for recovery after 48 hours. This procedure was carried out for each species. The temperatures were not prolonged beyond 16 hours as this would have exceeded their duration in nature (see environmental data, section III (c)).

Molluscs were also exposed to low air temperature. They were placed on trays in a "deep-freeze" room where the temperature was kept at -7.8°C. After time intervals of 2, 3½, and 4½ hours, ten specimens of each species of mollusc were transferred to sea-water at 5.0°C to 8.0°C to test for recovery after 48 hours. The temperature of -7.8°C was just within the low point (-8.3°C) of Macquarie Island's temperature range (see section II (b)), and is thus representative of extreme low temperature conditions. There were no facilities for gradually decreasing the temperature to such a point, nor for maintaining a slightly higher temperature.

Environmental temperatures were taken in two ways: (1) continuous temperature recording in rock pools containing molluscs and (2) spot checks with thermometers and the portable thermistor apparatus previously described. Clockwork circular chart-recorders, as described in section III (d), were used for the continuous temperature measurements. The thermistor apparatus was also used in the field to record body temperatures of molluscs and the adjacent microclimatic temperatures. Body temperatures were taken in the same way as during the laboratory heating experiments, i.e. the thermistor probe was inserted through the body wall above the foot. Spot checks were taken on a number of animals during sunny weather conditions in the summer. Rock substrate temperatures alongside molluscs were recorded by placing the thermistor tip on the substrate with a covering of masking tape for insulation. Adjacent air temperatures were taken with the thermistor tip dry and shaded.

(ii) Results and discussion

Studies have been made on the importance of high temperatures on the distribution of littoral molluscs in the cool and warm temperate climatic regions by Broekhuysen (1940); Evans (1948); Southward (1958); Fraenkel (1966, 1968); Sandison (1967); and in tropical regions by Lewis (1963) and Fraenkel (1968). The results obtained have shown that temperature *per se* does not limit vertical distribution of the animals, as environmental temperatures were well within their tolerance limits. Strong correlations were found between heat resistance and the position of species in the littoral zone, the higher the position, the higher the temperature tolerance. However, Evans (1948) found no such correlation and demonstrated a correlation between thermal resistance and habitat temperature. The correlations between thermal resistance and zonational sequence may have been masked by the broken nature of the shore used by Evans as a study area. The resistance of molluscs to low temperatures and freezing has also been shown to be related to zonal position (Kanwisher 1955, 1959).

The measuring of body temperatures of littoral molluscs in the field is important for the analysis of the significance of the relationship between the temperature tolerance of the animal and environmental temperature. Such measurements were made on a chiton by Kenny (1958) and on gastropods by Southward (1958), Lewis (1963), Blasini de Austin (1968), and Davies (1970). Generally, these studies showed that during insolation, the body temperatures of molluscs were considerably higher than air temperatures (both ambient and microclimatic). The body temperatures closely followed those of the rocky substrate although there was some variation among the studies on this point. Kenny (1958), in warm temperate Western Australia, and Blasini de Austin (1968), in tropical West Indies, showed a close correlation between body temperature and rock temperature; Blasini de Austin suggested a thigmothermic relationship for the three species of Nerita under study. Davies (1970), working on Patella limpets in Scotland, found that rock temperatures were consistently above the body temperatures of the animals. In England, Southward (1958) attributed the rise in body temperatures of molluscs above sea and air temperatures to warming by sunlight. Lewis (1963) reasoned that such an effect of insolation would be more pronounced in the tropics. However, he found that body temperatures of Nerita in the tropical West Indies were below that of the rock surface while those of limpets were above. The lower body temperatures of Nerita were due to evaporative cooling and Lewis suggested that the ability of littoral molluscs to regulate their body temperatures by evaporation was related to their littoral zonation.

Southward (1958) suggested that a causal relation between temperature and distribution must be sought in non-lethal terms such as debilitating effects, indirectly through competition between species, or in combination with other factors. Micallef (1966, 1968) and Sandison (1967) have shown that stresses owing to temperatures of less than lethal values may play an important part in controlling the distribution of gastropods on the shore. As high or low temperatures were approached, the activity of trochids was reduced and finally ceased; further thermal stress led to loss of attachment from the substratum (Micallef 1966, 1968). Sandison (1967) found that temperatures causing heat coma were below lethal values, with the coma temperature in air being greater than that in water. Heat coma in air limited vertical distribution by subjecting the animal to further desiccation after the resultant relaxation. No further harm was postulated for molluscs that suffered heat coma while submerged. Temperatures experienced on the shore approached those causing the above disabilities (Newell 1970).

The thermal tolerance of littoral invertebrates (including molluscs) at the subindividual level and its relationship to ecological factors are receiving increasing attention. Prosser (1967), Rose (1967), and Kinne (1970) have comprehensively reviewed such studies, from which a general understanding of the organic basis of thermal resistance of invertebrates is developing. However, such work was not an aim of the present study which centred on the response of the living mollusc to environmental variation of temperature.

Climatic temperatures at Macquarie Island are low and have a small range. The aims of this investigation were to see if temperature tolerances of littoral molluscs differed markedly from those in other climatic regions, whether lethal temperatures were to be found in the environment during exceptionally high temperature conditions, and to evaluate the effects of temperature, in non-lethal terms, as a causal relationship with vertical distribution.

For each species, Table 21 shows the temperature ranges for loss of adherence and death, temperature at which 50% lost adherence, and lethal temperature (50% dead); localities of specimens collected for the above determinations are also listed. Duplicate experiments on death temperatures and loss of adherence at different times of the year gave the same result, the maximum difference being 0.5°C, the limit of accuracy of the technique.

The range of death temperatures was closely grouped around the lethal temperature. The range of "loss of adherence"

Table 21. Tolerance limits and enfeebling effects with increasing water temperature.

Species	Locality	Range of death temps.	Lethal temps. (50% mortality)	Temp. range for loss of adherence	Temp. at which 50% lost adherence
K. lateralis	Eulittoral	38.0-41.5°C	40.0°C	28.0-36.0°C	32.5°C
L. caliginosa	Eulittoral (pools)	33.0-36.5°C	34.5°C	20.5-28.0°C	24.0°C
P. macquariensis	Eulittoral	30.0-33.0°C	31.0°C	16.0-27.0°C	21.0°C
	From depth of 6 metres	30.0-32.5°C	31.0°C	17.0-26.0°C	21.5°C
P. aurata	Sublittoral	34.5-37.5°C	36.0°C	22.0-27.5°C	25.5°C
H. setulosum	Sublittoral	33.0-36.5°C	34.5°C	19.5-26.0°C	23.5°C
C. (*P.*) *coruscans*	Sublittoral	30.0-32.0°C	31.0°C	15.5-23.5°C	19.5°C

temperatures was wide, although the 50% point was reasonably constant. All specimens that lost adherence recovered in sea-water (temperature 5.0°C to 8.0°C) within twenty-four hours.

Table 22 records the effects of sustained water temperatures in the ranges: 12°C to 15.9°C and 16°C to 20°C. In Table 23, body temperatures and corresponding adjacent microclimatic ones are outlined. For rock pools in which temperature was continuously recorded, Table 24 shows the fauna of each pool together with the periods for the temperature ranges of 12°C to 15.9°C, 16°C to 20°C, and >20°C; these periods are further illustrated in Figure 24.

Lethal temperatures provide an indication of the degree of tolerance of animals (Prosser and Brown 1965, p. 241). This is borne out by the results here, where lethal temperatures for the six species show a gradation corresponding to the temperatures causing loss of adherence (see Table 21). The temperature tolerances of all developmental stages of an animal are needed to formulate a complete picture of the effects of temperature on distribution. However, while recruitment of young may be restricted to narrow limits, mobile littoral animals, such as molluscs, may tolerate a wider range of temperatures as adults and thus be able to invade areas away from a recruitment zone and still contribute to reproduction (e.g. spawning during high tide, deposition of

Table 22. Effects of prolonged exposure to high water temperatures (sub-lethal).

Temperature Range = 12°C - 15.9°C

Species	N	Time of submersion in hours				*Recovery
		1	6	10	16	
K. lateralis	20	A	A	A	A	-
L. caliginosa	20	A	A	A	20%LA	100%
P. macquariensis	20	A	45%LA	100%LA	100%LA	100%
P. aurata	20	A	A	A	A	-
H. setulosum	20	A	A	A	30%LA	100%
C. (P.) coruscans	20	A	55%LA	100%LA	100%LA	100%

Temperature Range = 16°C - 20°C

Species	N	Time of submersion in hours				*Recovery
		½	2	8	15	
K. lateralis	20	A	A	A	A	-
L. caliginosa	20	A	A	25%LA	45%LA	100%
P. macquariensis	20	50%LA	100%LA	100%LA	100%LA	80%
P. aurata	20	A	A	A	A	-
H. setulosum	20	A	A	30%LA	55%LA	100%
C. (P.) coruscans	20	60%LA	100%LA	100%LA	100%LA	60%

LA = Lost adherence
A = Attached

* Refers to specimens that fully recovered and reattached after 48 hrs.

Table 23. *Field measurements: body and microclimatic temperatures, water loss (sunny weather).

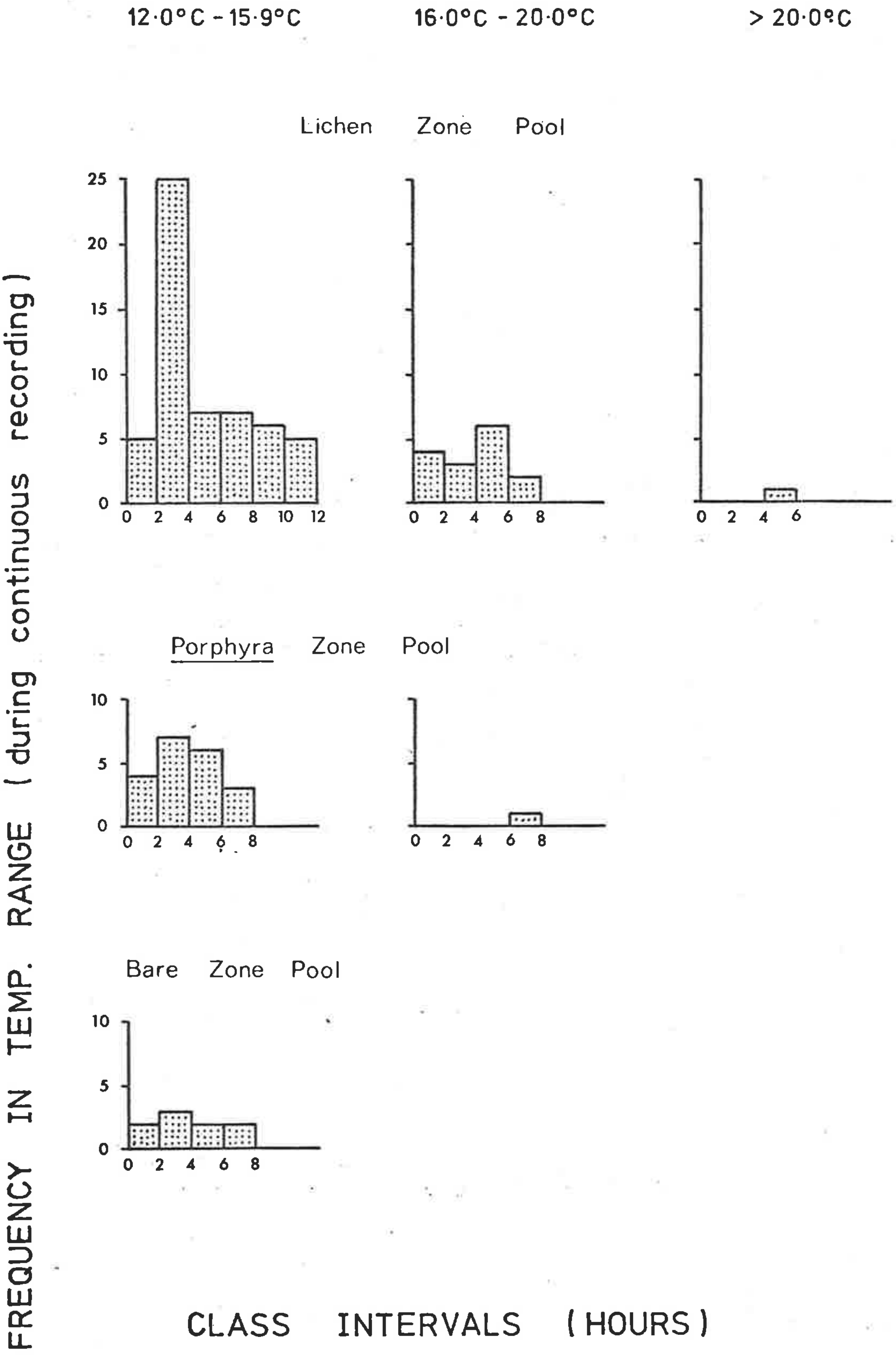
Species	N	Zonal Position Habitat Conditions	Range of Body Temps. (°C)	Microclimatic Temps. (°C)			State of Specimens	Water Loss (when studied)
				Air	Rock Substrate	Pool		
K. lateralis	12	Upper Eulittoral. Emerged, on rock surfaces. Sunny.	23.3-25.8	10.7-12.1	17.0-20.3	-	Attached (alive)	
"	8	"	29.2 26.7-[redacted]	11.5-12.4	19.7-21.9	-	Unattached (dead)	Bodies severely desiccated
"	11	Upper Eulittoral. Emerged, in shaded crevices. Sunny.	15.0-18.8	8.9-10.0	15.5-20.9	-	Attached (alive)	
P. macquariensis	13	Eulittoral. Emerged, on rock surfaces. Sunny.	12.0-22.7	9.3-11.0	12.1-13.8	-	Attached (alive)	6%-12%
"	6	"	20.8-24.1	11.7-12.4	15.2-16.1	-	Unattached (dead)	18%-21%
"	7	Eulittoral. Rock Pool. Sunny	17.5-19.0	-	-	18.0	Unattached (4 dead) (3 alive)	
P. aurata	6	Lower Eulittoral. Emerged, on rock surfaces. Sunny	8.9-11.5	8.5-9.6	8.8-11.0	-	Attached (alive)	
H. setulosum	6	Upper Sublittoral. Emerged, on rock surfaces. Sunny	8.5-10.8	9.4-9.5	8.6-10.5	-	Attached (alive)	
C. (P.) coruscans	7	Lower Eulittoral. Rock Pools. Sunny	11.0-12.0	-	-	11.5	Attached (alive)	
"	8	Lower Eulittoral. Emerged, in shaded crevices. Sunny.	7.6-8.9	7.9-9.3	8.1-8.6	-	Attached (alive)	

* Dates of recordings were in the period, Nov. 1968 to Jan. 1969.

Table 24. Continuous temperature recording in rock pools.

Zonal Position of Pool	Pool Occupants	Period of Continuous Temp. Recording	Class Intervals (hours)	0-1.9	2-3.9	4-5.9	6-7.9	8-9.9	10-11.9
Lichen Zone	No molluscs *Tigriopus* sp. Amphipods	10/10/1968-16/1/1969	Frequency in Temp. Range:						
			12°C-15.9°C	5	25	7	7	6	5
			16°C-20.0°C	4	3	6	2		
			>20.0°C			1			
Porphyra Zone	*K. lateralis* *L. caliginosa*	18/9/1968-23/1/1969	Frequency in Temp. Range:						
			12°C-15.9°C	4	7	6	3		
			16°C-20.0°C				1		
Bare Zone	*K. lateralis* *L. caliginosa* *P. macquariensis* (one specimen)	30/1/1969-21/3/1969	Frequency in Temp. Range:						
			12°C-15.9°C	2	3	2	2		
Upper Red Zone	*P. macquariensis*	17/9/1968-14/2/1969	Pool Temp. did not rise above 12°C Maximum Temp. recorded was 11.3°C						

Figure 24. Duration in high temperature ranges for rock pools during continuous recording.


12·0°C - 15·9°C
16·0°C - 20·0°C
> 20·0°C
Lichen Zone Pool
25
20
15
10
5
0
0 2 4 6 8 10 12
0 2 4 6 8
0 2 4 6
Porphyra Zone Pool
10
5
0
0 2 4 6 8
0 2 4 6 8
Bare Zone Pool
10
5
0
0 2 4 6 8
FREQUENCY IN TEMP. RANGE (during continuous recording)
CLASS INTERVALS (HOURS)

eggs in sheltered crevices).

At high temperatures, the tolerance of Macquarie molluscs was low in comparison to that for those from temperate regions (Broekhuysen 1940; Evans 1948; Southward 1958). Lethal levels for the Macquarie littoral molluscs studied here were well above environmental temperatures as has also been found in temperate regions. Thus, the low, equable temperature range of the sub-Antarctic did not appear to accentuate the importance of temperature in regard to direct lethal considerations.

From other studies in both temperate and tropical regions, the temperature tolerances of littoral molluscs increased in proportion to relative capacity to withstand exposure out of water, as indicated by the zonal position of the animal (Broekhuysen 1940; Southward 1958; Fraenkel 1968). All molluscs in the above studies were gastropods. With the selected Macquarie Island molluscs this correlation did not occur. *K. lateralis* had the highest vertical distribution and exhibited the greatest tolerance. However, the remaining species did not follow in order. The two chitons, *P. aurata* and *H. setulosum*, had comparatively high tolerances. The four gastropods exhibited temperature tolerances in proportion to their upper vertical limits of distribution. It would appear that Amphineura have greater temperature tolerance than Gastropoda from the equivalent vertical position.

Temperature tolerances for P. macquariensis taken from two locations widely separate in the vertical aspect (i.e. eulittoral and from a depth of 6 metres) were found to be the same, see Table 21.

While environmental temperatures were well within the lethal temperature range for the six molluscs, this was not so for the temperatures which induced loss of adherence. An air temperature of 11.5°C was recorded during the summer of 1968-1969 and this was equivalent to the highest ever for Macquarie Island. Mean maximum was 6.3°C; the highest sea temperature recorded was 8.2°C and the summer average (December to March) was 6.9°C (from section III (c)). Temperatures of rock pools and body temperatures of molluscs in the field higher than 12°C were caused by radiation from the sun, see Table 23.

Molluscs (siphonarids and limpets) high up in the eulittoral zone and exposed to the sun had body temperatures considerably higher than adjacent substrate temperatures. The body temperatures of molluscs low in the eulittoral zone and in the sublittoral zone were similar to air and substrate temperatures; the sun's radiation had little chance to effectively heat up such animals. The results for molluscs high on the shore showed a marked difference to those from other studies where the body temperatures generally followed the substrate during insolation (Kenny 1958, Lewis 1963, Blasini de Austin 1968, Davies 1970). Comparisons between the measurements of substrate temperature from different studies require standardization of the measuring technique. Although not stated, Kenny and Lewis apparently placed a probe against the rock surface while Davies inserted a probe into a small piece of plasticene mixed with powdered copper that was sealed to the substrate with tape. In the present study, it was found that the substrate temperature readings varied considerably during measuring if the probe was exposed, hence the use of a covering of masking tape. This could have resulted in lower readings than if an exposed probe were used. However, as the body temperatures were considerably higher than the substrate temperatures, the difference from the body-substrate temperature relationships recorded in other climatic regions is regarded as real. Thus, regulation of body temperatures during insolation was apparently lacking in those molluscs likely to be exposed to the sun in the sub-Antarctic climate.

The determination of lethal levels and the debilitating effects at high temperatures were made during immersion. Emerged molluscs on the shore in sunny weather would be expected to suffer the effects of high temperature and desiccation combined. This could set a tolerance gradation for a range of species that would be different if each of the two factors were considered independently.

Environmental deaths through physical factors alone were observed for *K. lateralis* and the body temperatures were well below tolerance limits, see Table 23. The state of the bodies (see section IV 2. (b)) indicated that desiccation brought about the deaths although temperature may have caused the initial loss of grip thereby allowing desiccation to be accentuated, especially if the mollusc overturned. No predation was ever observed on overturned *K. lateralis*. Environmental deaths were also observed for *P. macquariensis* both emerged and submerged, see Table 23. Temperatures in both cases were within the range that would have caused loss of grip if sustained and, for limpets in the pool, the temperature was in the range that could prove lethal if prolonged. These environmental deaths were under extreme climatic conditions at the upper limit of their distribution.

Body temperatures for unaffected *K. lateralis* in the Bare Zone have been recorded in a range that would result in loss of adherence for *P. macquariensis* and *C.* (*P.*) *coruscans*. Once weakened by increased temperature and overturned, the limpets and trochids were under heavy predation pressure from Dominican gulls and wekas. This was especially applicable to *P. macquariensis* as the adaptations of shell shape and the strong holding power of the foot were suitable for living on rock surfaces of the Bare Zone; *C.* (*P.*) *coruscans*, once out of water, could not properly support themselves and were normally only found out of the sublittoral under rocks, in rock pools, and in crevices. At E.L.W.S. tides with calm seas or after a heavy storm that transported them to higher levels, the trochids had difficulty both in attaching properly and in moving freely on rock surfaces and algae that were not covered by water. Gulls and wekas were observed preying on them at these times, see section IV 1. (d)).

Environmental temperatures recorded in rock pools (Table 24) show durations in a range that would frequently have debilitating effects on *P. macquariensis* and *C.* (*P.*) *coruscans* (cf. Table 22). In Table 24, the duration in the temperature range of 16.0°C to 20.0°C (and above) has to be considered as having the additional effect of the pool temperature rising and falling through the 12.0°C to 15.9°C range. Whilst these periods of high temperature might not be lethal, they would certainly induce loss of adherence in *P. macquariensis* and *C.* (*P.*) *coruscans* if they were to occupy a pool normally inhabited by *K. lateralis* and *L. caliginosa*. When limpets or trochids overturned because of weakness from high temperatures in a shallow pool, just as in emerged situations, they were prone to predation from Dominican gulls and wekas. A third predator was the large isopod, *Exosphaeroma gigas*, which was active in water at these temperatures. Overturned limpets and trochids in pools have been observed with a swarm of *E. gigas* over them, the isopods gnawing away at the tissues. If a limpet or trochid lost its adherence and fell into deeper water, it would have to re-establish itself quickly, or could otherwise be susceptible to starfish predation.

Head and tail body temperatures of emerged limpets attached to rock surfaces exposed to the sun, differed consistently by 0.3°C to 0.4°C, the head temperature usually being higher. Orientation to the sun appeared to be the causal factor. Head and tail temperature readings were alternated in sequence with different limpets in order to guard against any artefact causing a higher or lower temperature to occur shortly after insertion of the thermistor probe.

The siphonarids, *K. lateralis*, exhibited a temperature tolerance indicating a suitability for high vertical distribution. However, by the same reasoning, the chitons - *P. aurata* and *H. setulosum* - would be expected to have a higher distribution and it appeared that other factors could be operating more strongly with respect to limiting the distribution of these two species.

In high rock pools, environmental temperatures that would cause loss of adherence by *L. caliginosa* and *H. setulosum*, occurred frequently and were often prolonged. Such pools usually contained no molluscs except for occasional siphonarids whose temperature tolerances would ably accommodate the pool temperatures (refer to Tables 22 and 24). Although temperature would be limiting for L. caliginosa and H. setulosum in these situations, pH and salinity also varied considerably and could have been involved in their exclusion.

Table 25 shows the recovery of molluscs after being kept at a low air temperature (-7.8°C) for brief periods. Few conclusions can be drawn from the limited experimentation at -7.8°C. P. macquariensis showed a great cold resistance in comparison with their tolerance to high temperature. In contrast to high temperature tolerances, there was a correlation between cold resistance and the upper limits of vertical distribution. Further experimentation would require equipment capable of reducing body temperatures of molluscs to -10.0°C at a constant rate and maintaining them at a number of selected low temperatures.

Frequently, at both high temperatures (in water) and low temperatures (in air) P. macquariensis raised their shells ("mushrooming reaction") and C. (P.) coruscans twisted violently. This was particularly so just prior to the animals' losing adherence in the experiments with increasing water temperatures.

(b) Desiccation

(i) Materials and methods

The same six species of molluscs were used for these experiments, all of which were conducted in the months of

Table 25. Recovery of molluscs after exposure to low air temperature.

Trial 1. = Specimens (out of water) at air temperature of -7.8°C for 2 hours.
Trial 2. = Specimens (out of water) at air temperature of -7.8°C for 3½ hours.
Trial 3. = Specimens (out of water) at air temperature of -7.8°C for 4½ hours.

	*Recovery (After 48 hours in sea-water) (at 7°C)		
Species	Trial 1. (N=10)	Trial 2. (N=10)	Trial 3. (N=10)
K. lateralis	100%R	100%R	100%R
L. caliginosa	100%R	100%R	100%R
P. macquariensis	100%R	100%R	20%R, 80%E
P. aurata	100%R	50%R, 50%E	80%E, 20%D
H. setulosum	100%E	100%E	70%E, 30%D
C. (P.) coruscans	100%E	100%D	100%D

* R = recovered and attached

E = responded to mechanical agitation but did not reattach

D = dead

August and September. Adult molluscs were collected from the same specific habitat and level on the shore for each species as previously described in the studies on temperature (see section IV 2. (a), Materials and methods). Limpets, collected from a depth of approximately 6 metres, were also subjected to these experiments.

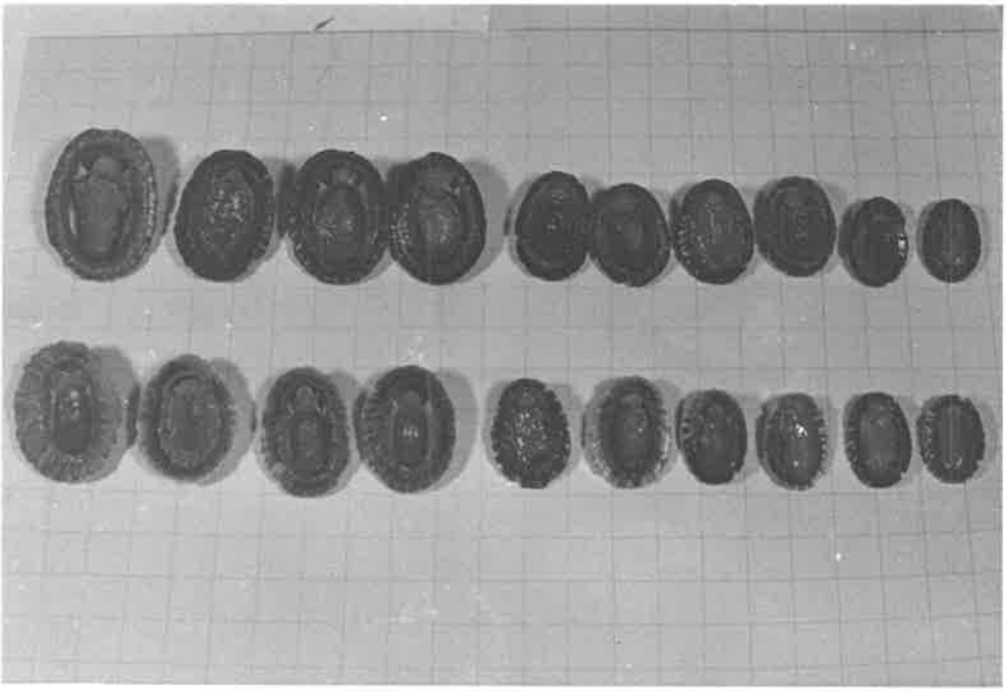
After collection from the field, the molluscs were placed in an aquarium for 12 hours, after which they were dried with blotting paper and placed in small petri dishes and weighed; the dishes were placed in a desiccator over calcium chloride. The desiccators were placed outdoors in a shaded position and were maintained at a temperature of 5.0°C to 7.0°C. The effect of desiccation at high temperature was investigated by keeping the desiccators at room temperature of 17.0°C to 19.0°C.

Preliminary trials were used to estimate survival time and vital limit (water loss at which death occurred). Near the critical periods, molluscs (usually five) were removed, weighed in the small dishes, and placed in recovery tanks containing sea-water at 5.0°C to 7.0°C. Death was assessed by the animal's failure to recover after forty-eight hours. Using response to mechanical prodding as a criterion for death was extremely difficult for animals in the desiccated state. Plate 22A shows limpets in a desiccated condition during an experiment. The mantle and foot retracted back

Plate 22.

22A. Specimens of _Patinigera macquariensis_ after desiccation over calcium chloride.

22B. _Kerguelenella lateralis_ (some dead, overturned, and in an advanced state of desiccation) during sunny, calm weather.



into the shell, and the mantle became dry and hard. The desiccation in the head and tentacles made them unresponsive to mechanical pricking even though recovery might have later occurred.

The loss of weight as a percentage of the fully hydrated weight of the soft body parts was used to indicate water loss. To obtain such figures, shells were removed from soft parts by placing the animals in boiling water. The shells were subsequently weighed and the weights subtracted from the initial total body weights. Girdle weights of chitons were also subtracted from total hydrated weights as, though not strictly shell, girdles were considered inert in terms of water loss.

In the field, water loss from P. macquariensis was estimated by the determination of blood osmotic concentration using a highly sensitive thermistor apparatus to measure freezing point depression (see section V (e) for method). This method is dependent on whether or not salts are excreted, and although it seemed unlikely that P. macquariensis would osmoregulate by salt excretion, experiments were conducted to test this (see section V (e)).

The distribution of K. lateralis and P. macquariensis was such that they were subjected to potential desiccation during emergence. The distribution and habitats of the other four molluscs lessened desiccation danger.

As the use of the thermistor apparatus for determining osmotic concentration required a fairly large sample of blood (0.2 ml), experimentation on *K. lateralis* was not practicable. Blood from limpets was withdrawn from the heart into a hypodermic syringe.

Davies (1969) used a capillary method to determine freezing point depression in the blood of *Patella vulgata* and *Patella aspersa*, expressing water loss as a percentage of the weight of the soft body parts. A similar notation is used here for *P. macquariensis*:

Water loss as % of total body water = $100 \frac{(b)\ 100}{(w)}$

where (b) is the concentration of a blood sample in milliosmols and (w) is the concentration of sea-water in milliosmols.

Water loss as a % of the weight of soft parts =

$\frac{\text{Mean water content}}{100}$ x water loss as % total body water.

In *P. macquariensis*, mean water content at full hydration, which was determined by drying the soft parts of 50 adult limpets in an oven at 110°C for forty-eight hours, was found to be 82.4% (standard error ± 0.7%). Therefore water loss as % soft parts = $\frac{82.4}{100} \times \left(100 - \frac{(b) \times 100}{(w)}\right)$.

This expression then enables a direct comparison with water loss determinations made by weighing an animal before and after water loss, the shell weight being subsequently subtracted.

(ii) Results and discussion

Desiccation is widely regarded as one of the main factors determining the vertical distribution of molluscs in the littoral and sublittoral zones. Broekhuysen (1940) and Brown (1960) found a correlation between the vertical order of the upper limits of distribution of a number of gastropods and their tolerances to desiccation. In a study of the desiccation resistances of four species of trochids, Micallef (1966) showed a correspondence between zonational sequence of three of the species and desiccation resistance; the fourth had a high resistance but a lower position on the shore, suggesting that some other factor was important in controlling the upper limit of distribution.

Davies (1969) studied the desiccation resistances of Patella limpets (P. vulgata and P. aspera) using the criteria of rate of water loss and lethal water loss. Field measurements showed that water loss was well below the lethal level although the greater rate of water loss of small limpets suggested that desiccation is likely to be a limiting factor for them at high levels on the shore. Davies concluded that the upper level of distribution of limpets may be set by an interplay between loss of water, and the time required to regain this when the limpet is covered by the tide.

From the present study, the vital limit and the water loss causing 50% mortality for the two temperature ranges, 5°C to 7°C and 17°C to 19°C, are outlined in Table 26.

Interspecific differences in tolerances were marked. The range of water loss causing death in a given species was narrow, the greatest variation being for the species with the greatest tolerance, i.e. K. lateralis. There was a slight yet distinguishable difference between the tolerances of limpets from the eulittoral and from a depth of 6 metres. This was most likely a phenotypic adaptation.

In other studies, correlations have been found between resistance to desiccation and the level in the littoral zone occupied by individuals of the same species of mollusc i.e. the higher the level, the higher the resistance (Davies 1969 (limpet); Kensler 1967 (bivalve)).

Except for L. caliginosa, tolerance limits corresponded to the order of upper distributional limits. L. caliginosa was typically found in rock pools or under stones. Its relatively low desiccation tolerance was indicative of its microhabitat rather than vertical distribution. The results obtained here show a similar pattern to that found by Broekhuysen (1940) in six South African littoral prosobranchs.

Dead K. lateralis and P. macquariensis were found in exposed situations during very sunny and calm weather. Plate 22B shows K. lateralis during such conditions. Three specimens in the centre of the plate were found overturned and severely desiccated. Estimation of water loss for P. macqua-

Table 26. The tolerance limits of molluscs to water loss at two temperature ranges.

Temperature = 5°C - 7°C

Species	Locality	Range of % water loss spanning 100% survival to 100% mortality	% water loss causing 50% mortality
K. lateralis	Eulittoral	51-59	55
L. caliginosa	Eulittoral (pools)	27-33	30
P. macquariensis	Eulittoral	39-44	42
	From depth of 6 metres	36-42	39
P. aurata	Sublittoral	29-35	32
H. setulosum	Sublittoral	25-30	27
C. (P.) coruscans	Sublittoral	23-29	26

Temperature = 17°C - 19°C

Species	Locality	Range of % water loss spanning 100% survival to 100% mortality	% water loss causing 50% mortality
K. lateralis	Eulittoral	47-55	51
L. caliginosa	Eulittoral (pools)	23-29	25
P. macquariensis	Eulittoral	33-40	37
	From depth of 6 metres	29-36	33
P. aurata	Sublittoral	25-31	28
H. setulosum	Sublittoral	20-25	22
C. (P.) coruscans	Sublittoral	18-22	20

riensis in the field indicated that death occurred through a combination of desiccation and high temperature, each factor in itself being sub-lethal. Side effects may also have contributed e.g. desiccation of gills causing detrimental reduction in oxygen intake. Sandison (1967) noted the consequences of heat coma on exposed molluscs. As relaxation increased susceptibility to desiccation increased; this was also apparent for *K. lateralis* and *P. macquariensis*.

The chitons and the trochid were rarely found in situations where death by desiccation was likely. Frequently, heavy wave action transported *P. aurata* and *C.* (*P.*) *coruscans* to higher levels where desiccation would prevent successful settlement. Other factors (e.g. predation) also operated at this time and could well have assumed greater importance in limiting distribution under more normal circumstances. *H. setulosum* was not evident in mollusc samples transported to higher levels by wave action.

(c) Salinity

(i) Materials and methods

Two types of investigation were made: (1) measurement of the salinities at which loss of adherence occurred and (2) evaluation of the effects of prolonged submersion in water of different salinities.

Again, adult molluscs were collected for the experiments from the same specific habitat and level on the shore for each species as previously described in the studies on temperature (see section IV 2. (a), Materials and methods).

A portable chlorinity-temperature meter was used to determine salinities in the laboratory and in the field. Chlorinity readings were converted to salinity values using the equation, Salinity = 0.03 + 1.805 x chlorinity (Hamon 1956).

The temperature-chlorinity meter used was designed by C.S.I.R.O. Australia, and its specifications and capabilities are fully outlined by Hamon (1956). The sensing head consisted of a thermistor and an electrical conductivity cell with platinum electrodes. Both were supported in epoxy resin casting and enclosed by metal guard rails. The sensing head was connected to the meter by approximately 10 metres of twin core shielded cable. The instrument gave direct readings with ranges of 0 to 30°C for temperature and 0 to 20‰ for chlorinity. The instrument had an accuracy of ± 0.1°C and ± 0.05‰ which was more than sufficient for the requirements of this study. Highly saline samples were diluted with distilled water to give a direct reading on the scale. In such cases, applying a dilution correction factor was not considered necessary.

To investigate loss of adherence, molluscs were placed in a large plastic container which held 20 litres of constantly aerated sea-water. Fifteen to twenty of each species were allowed to attach to immersed glass plates supported at an angle of approximately 40° by glass bottles. Initially, some molluscs moved off the plates to the sides and bottom of the container. Determinations could still be made on them using the criteria of fall-off for those on vertical surfaces and loss of grip for those on horizontal ones.

Salinity of the water was altered at intervals of fifteen minutes. It was raised by adding salt mixtures approximating the composition of sea-water (as tabulated in Prosser and Brown 1965, p. 60) and of a strength calculated to raise the salinity by approximately 6‰ each time.

The dissolving of the salt was effected by using an intermediary conical flask reservoir. A small water pump maintained a flow of water from the plastic container into the reservoir and thence back to the plastic container. Dissolving time varied from two to five minutes.

To lower salinity, a volume of water was removed and replaced with fresh water while stirring constantly. The volume removed was calculated to lower the salinity in steps of approximately 5‰.

During salinity decrease, the temperature of the water remained steady at 7.0°C to 8.0°C in an unheated room. During salinity increase, the temperature rose to 10.0°C owing to heat generated by dissolving and pump circulation; such temperature was only reached during the latter salt additions. There was no concern here as, at this point, the experimental salinity values were far beyond relation to the environment and results obtained were only in terms of laboratory tolerance.

For experiments on prolonged submersion at different salinities, twenty of each species were placed in glass aquaria containing water of 75% and 50% sea-water concentration. The water was constantly aerated and circulated with an aquarium pump. Controls were first undertaken to determine whether prolonged submersion in normal sea-water had any adverse effect. After submergence for two weeks in normal sea-water, no species showed ill effects.

During experiments at different salinities and the control submersions, molluscs were prevented from leaving the water by placing cardboard at the tops of the tanks. The cardboard pieces were cut to fit exactly and were positioned about one centimetre below the water-line by allowing water to flow out through a small hole which was later used as a passage for the aerator hose.

At the completion of both types of salinity tolerance investigation, the molluscs were removed to recovery tanks for subsequent observation. Each tank contained normal sea-water (temperature = 6.0°C to 7.0°C) aerated by aquarium pumps.

When determining loss of adherence, the time was too short to enable molluscs to crawl out of the water via the glass plates and the sides of the container and, in addition, once the alteration of salinity commenced, activity generally decreased. Occasionally, a mollusc did come near the water surface but was blocked by a glass stirring rod from proceeding any further.

(ii) Results and discussion

The determination of salinities limiting the activities of molluscs of the littoral zone has been undertaken by Gowanloch and Hayes (1926) and Broekhuysen (1940). Although Broekhuysen found a correlation between tolerance to abnormal salinities and position on the shore (the higher on the shore, the greater the tolerance), he concluded that salinity was of secondary importance as a limiting factor. However, one species which often inhabited rock pools showed a better adaptation to variations in salinity than its zonation level suggested. Mayes (1962) investigated interspecific differences of salinity tolerance in littorinids and also found relationships between resistance to changing salinity and the position of the animal in the littoral zone.

The tolerance to abnormal salinities has been shown to differ for different stages in the life cycle of the one species. Hayes (1927) found that the eggs of <u>Littorina lit-</u>

torea had a minimum salinity limit of 20‰ while the adults could live in much lower salinities. Arnold (1957) showed that limpets (Patella vulgata) from the high-water mark had a greater tolerance to lowered salinities than those from a lower position on the shore. Recently, Arnold (1972) found that this difference in tolerances was not inherent in the limpets but developed as they aged. A broad tolerance was possessed when animals were young, regardless of tidal levels, but the tolerance decreased if the animal aged on a part of the shore little affected by fresh-water influx. Arnold (1972) found different patterns of adaptation to reduced salinities in molluscs of other families. Littorina spp. and Nucella showed a wide tolerance to reduced salinity but this was not modified as the animals aged and differences between high and low tide samples were not marked. Gibbula, characteristically an inhabitant of the lower shore, had a narrow tolerance.

In the present study, differences in tolerance to abnormal salinity were measured in adults of the six species concerned. Collections for experimental purposes were always made from the same level in the littoral zone in the upper regions of their distribution, as previously described in the studies on temperature (see section IV 2. (a), Materials and methods).

Tables 27 and 28 give the percentages of molluscs which

Table 27.* Effects of salinity increase.

Species (N = 20)	Progressive % Loss of Adherence for Steps of Salinity Increase:									
	34‰	40‰	47‰	52‰	58‰	65‰	73‰	79‰	86‰	Recovery
K. lateralis	A	A	5%	5%	10%	25%	25%	25%	30%	80%R 20%E
L. caliginosa	A	A	55%A 40%M 5%C	15%A 80%M 5%C	85%M 15%C	80%M 20%C	→			75%R 25%E
P. macquariensis	A	5%	10%	10%	20%	20%	20%	30%	30%	20%R 80%E
P. aurata	A	5%	15%	15%	25%	50%	60%	65%	70%	10%R 90%E
H. setulosum	A	10%	15%	25%	50%	95%	95%	100%	100%	100%E
C. (P.) coruscans	A	90%	100%	→						5%R 65%E 30%D

* 34‰ = salinity of normal sea-water which was used to start the experiment
A = attached
M = *L. caliginosa* attached by mucous thread with the operculum closed
C = *L. caliginosa* lost adherence and the operculum was closed
R = recovered and attached
E = responded to mechanical agitation but did not reattach
D = dead

Table 28.* Effects of salinity decrease.

Species (N = 20)	Progressive % Loss of Adherence for Steps of Salinity Decrease:							
	34‰	28‰	23‰	18‰	13‰	7‰	1‰	Recovery
K. lateralis	A	A	A	5%	5%	10%	15%	100%R
L. caliginosa	A	A	A	A	30%A 60%M 10%C	90%M 10%C	90%M 10%C	100%R
P. macquariensis	A	A	A	A	A	5%	10%	100%R
P. aurata	A	A	A	15%	15%	20%	30%	95%R 5%E
H. setulosum	A	A	A	20%	30%	50%	90%	90%R 10%E
C. (P.) coruscans	A	5%	40%	80%	100%	→	→	95%R 5%E

* 34‰ = salinity of normal sea-water which was used to start the experiment
A = attached
M = L. caliginosa attached by mucous thread with the operculum closed
C = L. caliginosa lost adherence and the operculum was closed
R = recovered and attached
E = responded to mechanical agitation but did not reattach

had lost their adherence at each salinity change. Table 29 shows the condition of molluscs after prolonged submersion at reduced salinities.

Results of salinity determinations in the environment have been outlined in sections III (c) and III (d). Salinity of inshore waters showed little change. From Table 4 (section III (d)) it is clear that the climate of Macquarie Island did not bring about greatly increased salinities in pool waters on the shore. However, salinities were often lowered by fresh water run-off.

The possible effects on upper limits of distribution for individual species imposed by differing environmental salinities are also examined here. On the shore, a gradation of reduced salinities was evident in rock pools. High pools often contained water with low salinities. Both the occurrence of low salinities and the duration of time at low salinity were progressively reduced from the littoral fringe to the sea.

H. setulosum and *C.* (*P.*) *coruscans* clearly demonstrated poor salinity tolerances, both in terms of lethal limits and loss of adherence. Low salinities of high rock pools containing *K. lateralis* and *L. caliginosa* would exclude *H. setulosum* and *C.* (*P.*) *coruscans* from successfully inhabiting such areas. Absence of the food of *C.* (*P.*) *coruscans* in such high pools would also be limiting. *H. setulosum* survived well on

Table 29. Recovery of molluscs after prolonged exposure to reduced salinities.

Trial 1. = Specimens kept for 7 days in 75% sea-water (Salinity = 25.5‰).

Trial 2. = Specimens kept for 3½ days in 50% sea-water (Salinity = 17.0‰).

Species	* Recovery after 48 hours in normal sea-water (Salinity = 34.0‰).	
	Trial 1. (N=20)	Trial 2. (N=20)
K. lateralis	85% R, 15% E	90% R, 10% E
L. caliginosa	100% R	100% R
P. macquariensis	100% R	100% R
P. aurata	45% R, 55% E	40% R, 60% E
H. setulosum	100% D	100% D
C. (P.) coruscans	100% D	100% D

* R = recovered and attached

E = responded to mechanical agitation but did not reattach

D = dead

algal film on eulittoral rocks and reduced salinity would be more important in limiting their distribution.

L. caliginosa, *P. macquariensis*, and *K. lateralis* had greater salinity tolerances. *P. macquariensis* had the physiological capacity of withstanding more reduced salinities than found within their distributional range and salinity appeared to be of little importance as a limiting factor on the limpets' distribution. Further experimentation (see section V (e)) showed that *P. macquariensis* did not excrete or lose salts to counteract reduced environmental salinities. The blood soon matched the concentrations of external water and thus, there was simply a high tolerance to an increase in body water. *L. caliginosa* and *K. lateralis* were not found in pools well into the Lichen Zone. These pools often had greatly reduced salinities but there were also other variable factors (e.g. pH). Algal growth was often restricted to *Enteromorpha* which was not a food for these two molluscs, see section IV 1. (b). Although salinities were reduced markedly in these high pools, the physiological capacity of *K. lateralis* could have adequately coped with them, and other factors must be determinants of distribution. *L. caliginosa* also proved able to withstand the reduced salinities of high pools of the Lichen Zone; however, more than physiological tolerance was involved. The littorinids avoided unfavourable external salinities by tightly closing their opercula. In both short term (step-wise salinity changes) and long term (prolonged submersion in reduced salinities) experiments, the littorinids fared well, see Tables 28 and 29. This may not indicate a physiological resistance of the tissues but rather a behavioural adaptation (closing the operculum) which prevents subjection of sensitive tissues to a harsh environment.

For *P. aurata*, salinity tolerance was low and would restrict its invasion of high pools which were occupied by other molluscs.

During both salinity increase and decrease, limpets and trochids again exhibited distinctive reactions just prior to losing their adherence. Limpets showed the "mushrooming reaction" and trochids twisted violently. These reactions were evident on a number of occasions e.g. during contact with starfish as parts of the sequence of avoidance reactions, at high and low temperatures, and at high and low salinities. Limpets were also observed "mushrooming" in pools when apparent unfavourable conditions prevailed e.g. with rotting kelp in the pool. The raising of shells by acmaeid limpets has been suggested as a mechanism to aid cooling by the use of evaporation (Segal and Dehnel 1962). However, mushrooming by *P. macquariensis* and the twisting of *C.* (*P.*) *coruscans* in the above situations suggested that they were responses to stress in general and the reaction may or may not assist in alleviating particular unfavourable conditions. Further investigation would be required to ascertain any adaptive advantages.

V. THE LIMPET, PATINIGERA MACQUARIENSIS

(a) Introduction

The following sections (V (b) to V (h)) deal with various aspects of one species of mollusc and its environmental relationships. The conclusions and discussion on each aspect are dealt with in the respective sections.

Further information was obtained on factors limiting distribution and this has been included where appropriate in section VI, DISCUSSION: FACTORS LIMITING DISTRIBUTION, which mainly refers to results of investigations outlined in sections II (b) to IV (c) inclusive.

(b) Activity and Feeding

(i) Materials and methods

Macquarie Island weather does not favour the monitoring of activity of individual molluscs in or below the eulittoral zone. Instead, a quantitative record of the activities of a large number of individuals at different times and in different situations was more practical. Even then, observations were restricted to relatively calm conditions.

Four habitats were selected to examine the activity and feeding behaviour of limpets:

1. Rock faces in the eulittoral zone,
2. Pools in the eulittoral zone,
3. Immediately below the Durvillea antarctica holdfast line,
4. At a depth of 6 metres.

In one of the pools in the eulittoral zone, the limpet population was artificially increased (= category 2.(a)).

1. Rock faces in the eulittoral zone:

Five boulders and a vertical rock face were used. There were small stands of Chaetangium fastigiatum and Rhodymenia sp. but algal film provided the predominant cover (approximately 90%). Each of the five boulders was separated from other rock areas by sand and the limpets on each boulder did not have crawling access to adjacent rock. The limpets on the vertical rock face did have access to other areas and a section 1.5 metres in width was arbitrarily selected. The boulders varied from 0.45 to 0.75 metres in diameter. The six study situations were in a compact group inside a fringing reef where wave surge was reduced. For investigating vertical movements, the boulders were designated as Areas 1 to 5 and the vertical rock face as Area 6. Three vertical divisions, each of 20 cm in height, were marked out from a datum line which corresponded with the bottom of the boulders or below. The sand was quite level and there was little discrepancy in defining a common bottom to each of the boulders during the study period. The datum line was projected on to the nearby rock face where it also corresponded to the sandy bottom.

2. Pools in the eulittoral zone:

These were completely cut off from the water during low tide and/or when there were calm seas. Even during moderate wave action, no wash reached a number of the pools owing to intermediate rock formations. Encrusting coralline algae were interspersed with small patches of green algal film.

3. Immediately below the *Durvillea antarctica* holdfast line:

This area was in a large channel in approximately 1 metre of water at low tide. Encrusting coralline algae were predominant, being interspersed with patches of *Codium* alga and stands of various red algae.

4. At a depth of 6 metres:

Again, the predominant algae were encrusting corallines. There were stands of various red algae but less frequently than in category 3.

2.(a) Population-increased area in the eulittoral zone:

This area was a shallow pool, 0.3 by 0.75 metres, cut off from the sea at low tide. It supported a limpet population and was predominantly covered with a film of greenish algae. There were isolated patches of encrusting corallines. The existing population of thirty-four was increased to seventy-two by adding limpets taken from similar areas. The first activity and feeding observations were undertaken nine hours after increasing the population, i.e. after one high tide.

In the laboratory, specimens of P. macquariensis were observed feeding on the glass sides of aquaria which were coated with an algal film. When feeding, they moved slowly forward grazing algae in small arcs as the head moved from side to side. Incidence of feeding in the field was determined by counting limpets showing sideways movements of the head and cephalic tentacles.

Phototactic and geotactic responses of limpets were investigated in the laboratory. A light gradient was set up in an aquarium by placing a light bulb opposite one end of the tank and shielding all other sides with black cardboard.

The length of the tank was measured into four equal sections of 10 cm each and four limpets were placed in each section. Distribution of the limpets after 24 hours was recorded. The experiment was repeated 4 times. A control tank with no light gradient was also set up to ensure that limpets were not induced to move by some other factor. For the experiments on geotaxis, a vertical tank was measured into four equal lengths (13 cm each) and four limpets were placed in each section. Distribution of the limpets after 24 hours was recorded. The vertical tank was evenly illuminated. Separate trials were conducted under both still and turbulent conditions; four trials being conducted in each case. Turbulence was induced simultaneously by violent aeration from an air pump outlet placed at the bottom of the tank and by a propellor-type water stirrer.

(ii) Results and discussion

The degree of movement of limpets in the littoral zones has been shown to be dependent on whether they are splashed or submerged. At other times they are inactive (Orton 1929; Eaton 1968; Craig 1968; Rogers 1968). Arnold (1957) showed that limpets living high on the shore have a greater and more immediate response to splash.

The vertical distribution of P. macquariensis extended from the lower eulittoral zone to deep water (section IV 1.

(a)). Their activity and feeding behaviour were investigated in part of this range i.e. from the eulittoral to a depth of 6 metres.

In each of the five situations general activity and feeding were observed; the results are shown in Figure 25. Where the limpets were continuously submerged (in pools, below the kelp holdfast line, or at a depth of 6 metres), activity and feeding showed a constancy reflecting the comparative equability of these three habitats. Phase of the tide did not appear to affect the behaviour pattern in these limpets.

In the eulittoral zone, the activity and feeding rates were dependent on existing conditions of wetting and submergence. When exposed, they did not feed and movement was slight, being restricted to moist situations; when awash they exhibited the same rate of feeding as for continuously submerged populations; when submerged they showed both greater movement and feeding rates.

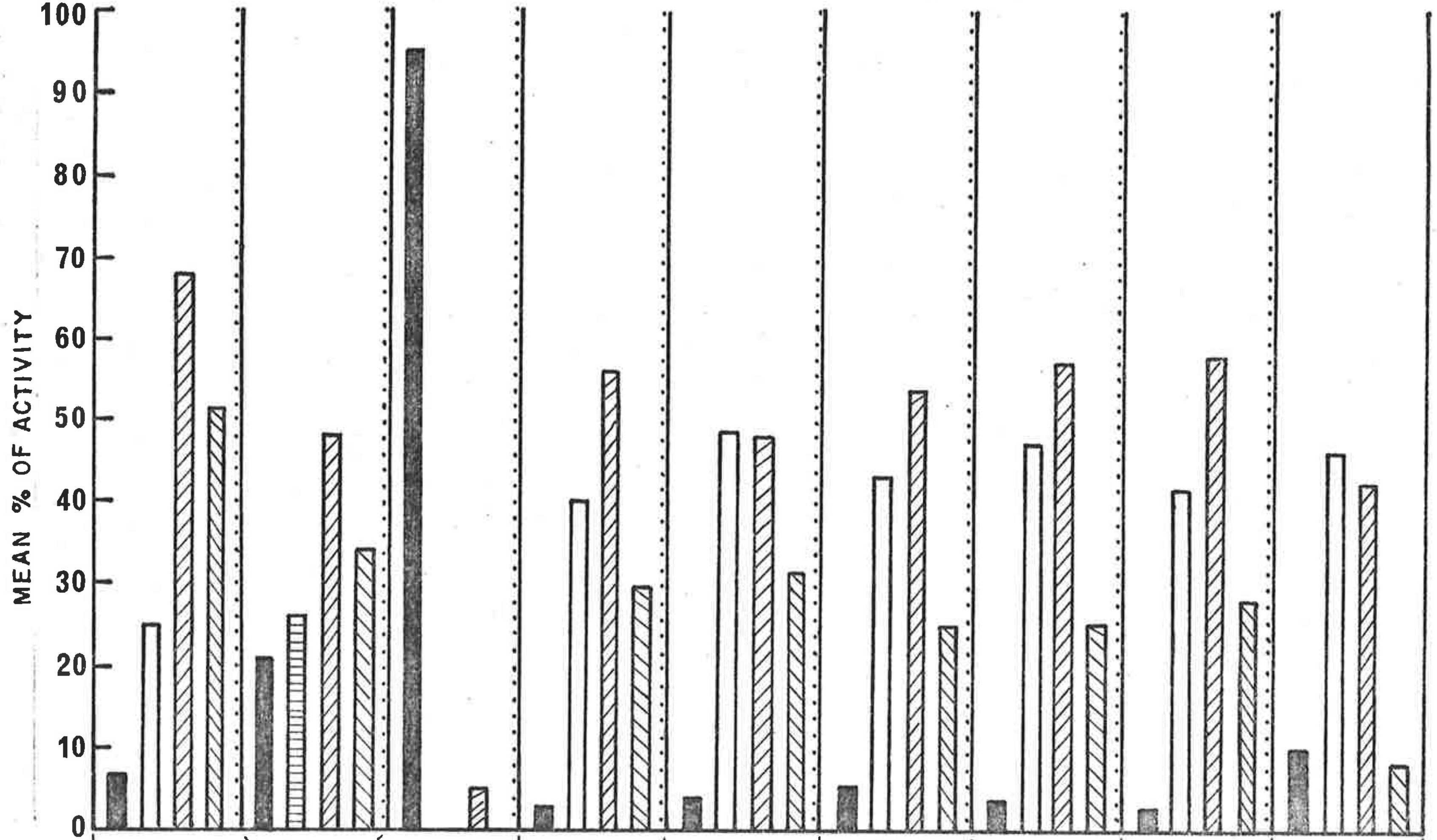
Thus, this one species occupied habitats which can be grouped into two categories: (1) periodic emersion and (2) continuous submersion. The prime importance of the environment on the feeding of limpets in the eulittoral zone was evident. Comparison of feeding activity of limpets in the submerged and eulittoral habitats indicated a physiological need for a certain food intake which can be met in these two

Figure 25.

Activity and Feeding of *Patinigera macquariensis*.

Key:

▮	Stationary and clamped down.
▯	Stationary, shell raised and pallial tentacles out.
▤	Stationary, shell raised and pallial tentacles retracted.
▨	Moving.
▧	Feeding.



Tidal State	High Water Submerged	Ebb Awash	Low Water Emerged	High Water	Low Water	High Water	Low Water	Low Water	Low Water
Location	Eulittoral Rock Surfaces			Eulittoral Pools		1.2 metres below Durvillea holdfast line		Depth of 6 metres	Population Increase Pool
No. of Counts	4	4	4	4	4	3	3	2	3

different situations by a flexible adaptation to activity and feeding times; i.e. a submerged habitat presented constant, favourable conditions for both movement and feeding and these activities were conducted at a steady rate regardless of the state of the tide. The eulittoral habitat presented periods of emergence which caused both movement and feeding to cease but this necessary cessation of activities was compensated for by increased rates during the favourable conditions of submergence. Some molluscs have been found to exhibit rhythmic activity in correlation with tidal cycles (Stephens *et al*. 1953; Zann 1971). In the present study, the lack of rhythmic activity in continuously submerged limpets suggested that the activity and feeding behaviour of those in the eulittoral zone were determined by environmental stimuli and not rigid predetermined patterns. If a study following individuals over a long continuous period were possible, the actual times spent while stationary, moving, and feeding could have been summed to see if these parts of the energy budget equalized in both eulittoral and continuously submerged habitats.

Figures 26 and 27 clearly show vertical movement by *P. macquariensis* in the eulittoral zone. The limpets move up with the incoming tide and down with the outgoing tide.

The boulders (Areas 1 to 5) were situations where the population density could not be influenced by an influx of limpets from adjacent horizontal areas and/or the sublittoral pp. 220 and 221.

Figures 26 and 27.

Vertical movements of *Patinigera macquariensis*.

Key:

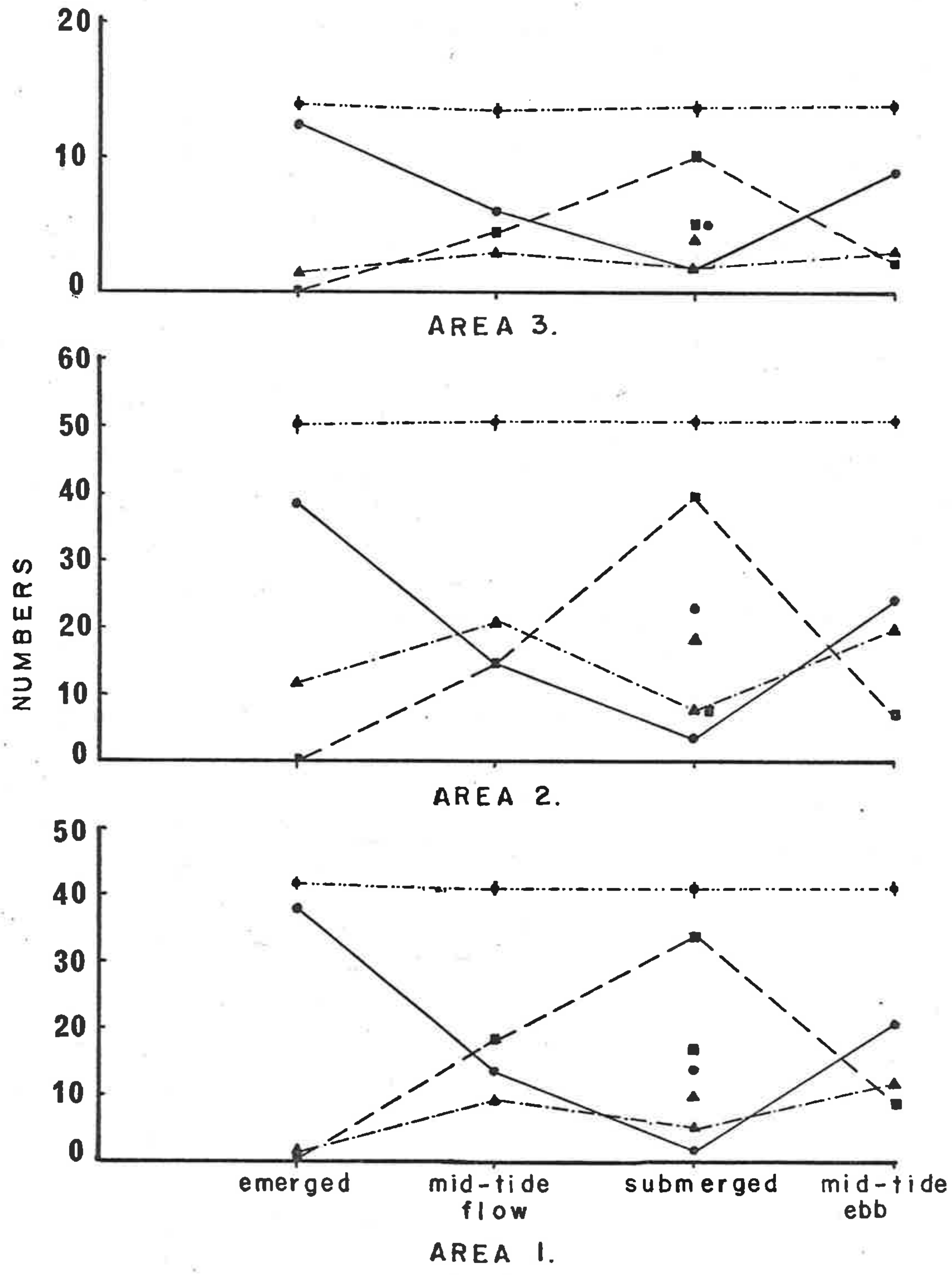
■– – – – –■ Numbers in top 20 cm division.

▲·–·–·–·▲ Numbers in middle 20 cm division.

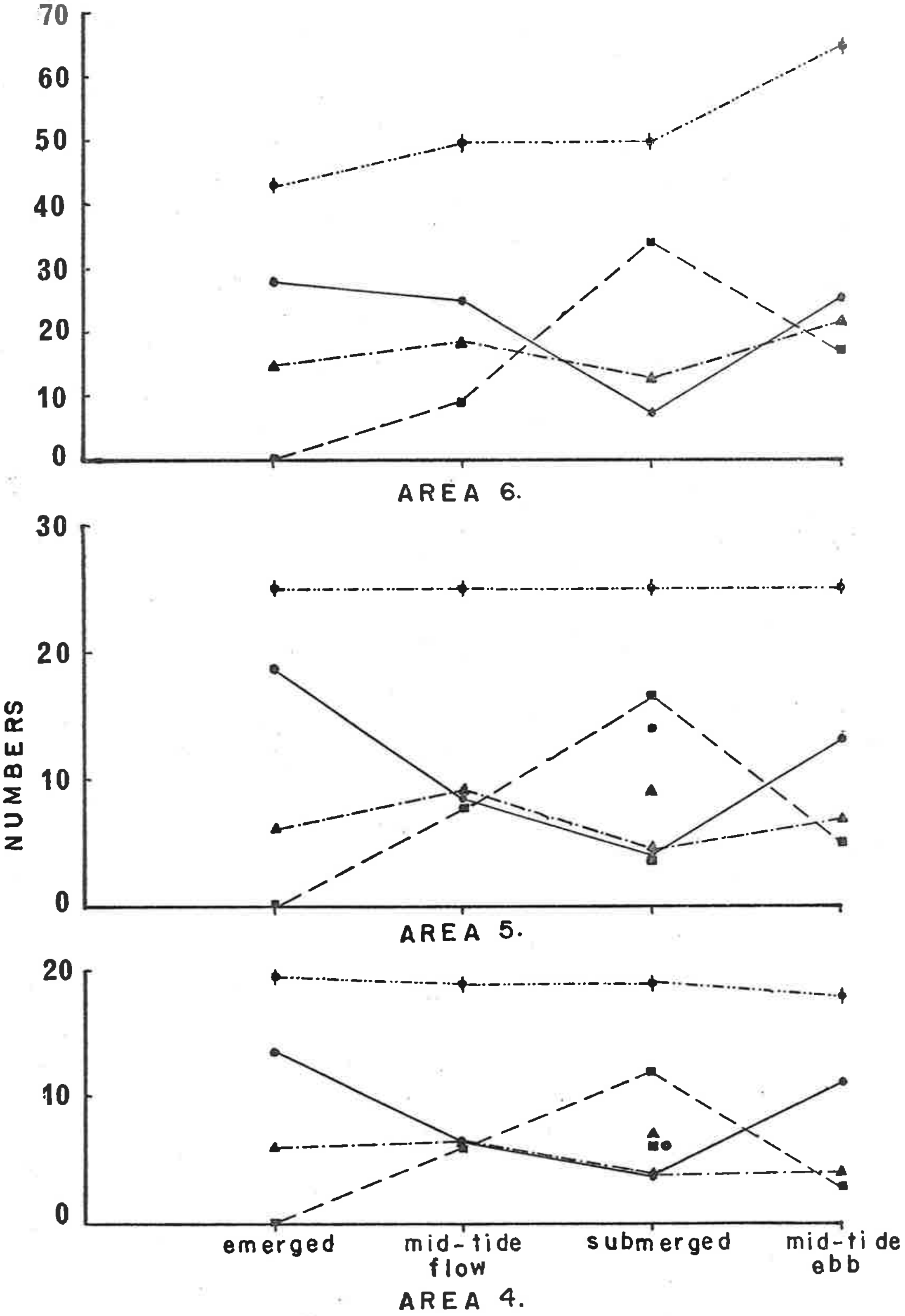
●———● Numbers in bottom 20 cm division.

⊕··–··–··⊕ Totals for the three divisions.

■ ▲ ● Numbers in the respective divisions during sustained sunshine.



20
10
0
AREA 3.
60
50
40
30
20
10
0
NUMBERS
AREA 2.
50
40
30
20
10
0
emerged
mid-tide flow
submerged
mid-tide ebb
AREA 1.


70
60
50
40
30
20
10
0
AREA 6.
30
20
10
0
NUMBERS
AREA 5.
20
10
0
emerged
mid-tide flow
submerged
mid-tide ebb
AREA 4.

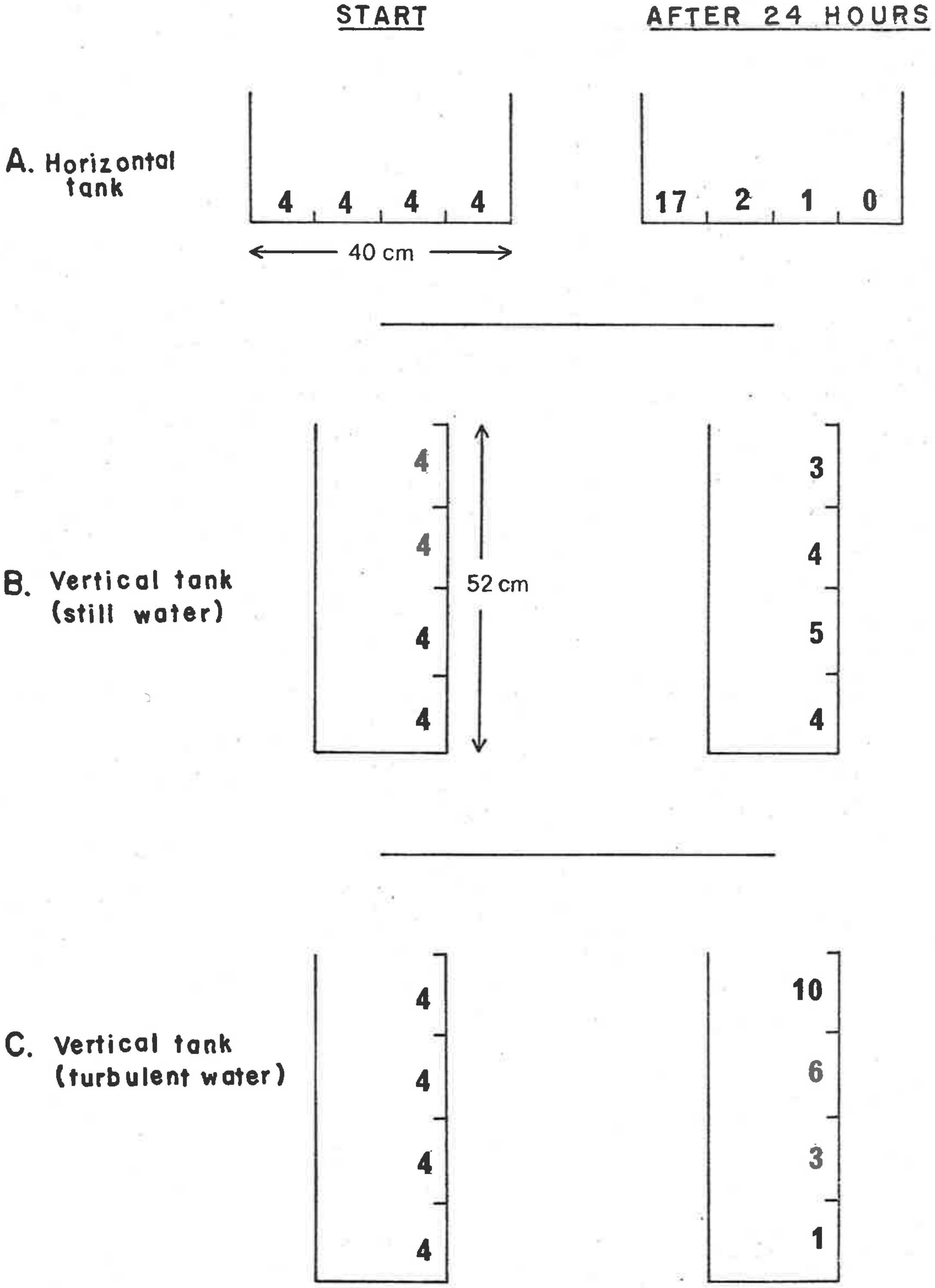
zone. The limpet population on the vertical rock face (Area 6) was subject to immigration from horizontally adjacent areas and the density increased during the study period.

The figures for the six study areas show a clear vertical displacement by limpets in accordance with tides. If limpets had responded to the incoming tide by dispersing to effectively cover the whole available area, a more even distribution would have been expected during submergence. At mid-tide flow the limpets were moving upwards and at mid-tide ebb, they were moving downwards.

The distribution of limpets on the boulders (Areas 1 to 5) during sustained sunshine and submergence was also plotted in Figures 26 and 27 using the same symbols as before. It was evident that the limpets showed a lesser degree of upward movement under such conditions. Limpets in aquaria in the laboratory demonstrated negative phototaxis as shown by Figure 28A which averages the distribution over the four trials. This tactic response elicited in the laboratory corresponded to the reduction of upward movement in the field during sunny conditions.

Figures 28B and C show the average distributions for the four trials in the two investigations of geotaxis. The limpets did not show any movement trend in still water yet were induced to move upward when the water was turbulent. The turbulence during an incoming tide and submergence could in-

Figure 28. Phototactic and Geotactic responses of *Patinigera macquariensis*.


START
AFTER 24 HOURS
A. Horizontal tank
4 4 4 4
40 cm
17 2 1 0
B. Vertical tank (still water)
4 4 4 4
52 cm
3 4 5 4
C. Vertical tank (turbulent water)
4 4 4 4
10 6 3 1

duce upward movement in limpets in the littoral zone as suggested by the laboratory response and by the upward movement of limpets during mid-tide flow and submergence (Figures 26 and 27). However, if turbulence alone resulted in this upward movement, the downward movement as seen during mid-tide ebb, when there was also considerable turbulence, is left unexplained. If the limpets did not have some form of rhythm controlling such movement, another environmental stimulus must have been inducing this downward movement. Lesser duration of wetting was shown by Miller (1968) to be a stimulus for invoking downward movement in *Acmaea* sp. and such may well have been operative on *P. macquariensis*.

The upward movement of limpets in the eulittoral with rising water enabled a greater area to be occupied during favourable conditions. The downward movement brought the limpets back to areas where there was less danger from environmental stress. Thus this movement increased the amount of grazing area and hence the availability of food. As previously discussed, the increased feeding activity reflected the shorter time that limpets could use these areas for grazing. By the combination of this movement and increased feeding activity during submergence more effective usage was made of the habitat at the upper range of distribution.

It was noticed that pool populations remained within the pool area even when covered by high tide. At high tide, there were very few limpets in the eulittoral zone with a heavy covering of coralline algae on their shells such as is typical of limpets that are continuously submerged. These pose interesting lines of investigation for both population and behavioural studies. If the vertical movements of a eulittoral population of limpets were artificially halted, what would the effect on the population be? Do the limpets require periodic emersion to initiate a vertical displacement pattern? Are there any differences in taxes between eulittoral and submerged limpets?

After limpets were added to the population in a pool (approximately doubling the existing number), they showed a slight decrease in movement and a marked decrease in feeding compared to that for limpets in other pools. Whether this was brought about directly by crowding, or indirectly by some form of chemical detection, was not known. It was unlikely that lack of oxygen and/or accumulation of carbon dioxide in the water had any effect, as observations were made at low tide while occasional surge was still reaching the pool. Further experiments have shown that, on doubling limpet numbers, emigration was induced in populations on rock surfaces in the eulittoral and sublittoral as well as in rock pools (section V (c)). Unfortunately, no feeding activity studies were conducted on the increased populations of rock surfaces. With the absence of possible chemical inhibition, decreased feeding activity of rock surface populations would have suggested direct influence from overcrowding (if immediate) or result of decreasing food supply (if not immediate).

The reduction in feeding in an artificially increased population of a pool indicated a clear detrimental effect that would be encountered if emigration did not take place. It could be reasoned that other factors, determining both distribution and abundance, would not allow such an overcrowded situation to develop. However, acute density increase was brought about naturally by storms. Limpets were dislodged and collected in eddying waters around certain rock formations where there were pools supporting already existing limpet populations (see section IV 1. (a)). Later experiments on adding limpets to existing pool populations showed that the original numbers were soon re-established indicating an optimum population number (see section V (c)).

(c) Movement within populations

(i) Materials and methods

To gauge the amount of both short term and long term movements of Patinigera macquariensis and the stability of existing populations, limpets were marked and their population density artificially altered in specific locations. For short term studies, orange "Dayglo" paint was placed on a filed section of the shell. For the long term studies a number, pressed in "Dynotape", was affixed to a filed section of shell with "Pliobond" cement. During alteration of density, limpets were marked with paint spots in such a way as to enable recognition of original inhabitants. Populations were altered in pools and on eulittoral and sublittoral rock surfaces.

In order to investigate homing, 20 limpets in the eulittoral were individually marked with bright orange paint. Different parts of each shell were filed and painted. The limpets were marked during low tide while they were attached to rock surfaces in the eulittoral zone. A corresponding paint code was placed alongside a limpet's position. The positions of the limpets at low tide (daylight tide) were noted each day for four weeks.

(ii) Results and discussion

Table 30 shows the adjustment in limpet numbers for both pool and eulittoral rock surface populations when the original population was artificially doubled. The numbers soon reverted close to the original even though the former inhabitants, both for pools and rock surfaces, did not necessarily remain. This alteration of the densities of limpets showed that there was an optimum population level which was re-established after alteration, both in pool populations and in those on regularly emerged rock surfaces. Thus, both in the eulittoral and the

*
Table 30. The doubling of existing populations of *P. macquariensis*

POOLS IN THE EULITTORAL ZONE

LIMPET NUMBERS

Original, Added	After the following time periods					R	M
	1 day	3 days	1 week	4 weeks	6 weeks		
(a) 6 + 6	6, 5	5, 7	5, 4	6, 3	4, 3	4	-
(b) 7 + 7	5, 6	6, 4	4, 4	3, 5	1, 7	2	0.6 m
(c) 10 +10	10,10	10, 9	7, 5	6, 5	7, 3	7	-
(d) 11 +11	11, 9	10, 7	9, 6	9, 6	9, 4	10	0.9 m
(e) 25 +25	22,21	20, 18	18, 15	18, 14	16, 10	18	1.5 m

ROCK SURFACE AREA OF 2 SQ. METRES IN THE EULITTORAL ZONE

LIMPET NUMBERS

Original, Added	After the following time periods					R	M
	1 day	3 days	1 week	4 weeks			
53 + 53	50,49	51, 45	34, 29	30, 27		49	3.4 m

ROCK SURFACE AREA OF 2 SQ. METRES IN THE SUBLITTORAL ZONE

LIMPET NUMBERS

Original, Added	After the following time periods					R	M
	1 day	3 days	1 week	4 weeks			
47 + 47	45,48	40, 49	29, 25	19, 27		44	4.0 m

* The first number in each set of limpet numbers designates the original inhabitants.

R = Total resighting of original inhabitants, both in the prescribed location and away, at the end of the observation period.

M = Maximum distance (metres) travelled by any one original inhabitant on moving away.

sublittoral, artificial doubling of populations induced the original occupants of rock surfaces to move considerable distances, sometimes into different habitats. The high number of re-sightings after movement indicated that mortality was low. Original occupants of eulittoral rock pools were also induced to move away by overcrowding although to a lesser degree. The number of re-sightings after movement was low, suggesting greater mortality for such populations on leaving their established habitat.

As discussed in section V (b), pool populations may have gauged stress directly through overcrowding or by chemical means. On rock surfaces, factors other than chemical ones must be sought e.g. contact between limpets, reduced food supply.

Table 31 shows the location of marked limpets after a nine months period (June 1968 to March 1969) in three different habitats - eulittoral rock surfaces, sublittoral rock surfaces, and eulittoral rock pools. In each the limpets showed a very high degree of constancy of location. In the eulittoral zone, limpets on rock surfaces were in the same general area after nine months. Movements over great distances by individual limpets were rare and even then the limpets were still to be found in the same vertical zone and habitat situation. Limpets in rock pools in the eulittoral showed a remarkably high degree of constancy of location, all specimens

Table 31. Location of Marked Limpets

Habitat	No. marked	After 9 months (June 1968 - Mar. 1969)			
		No. found	Number that moved as follows:		
			More than 3 metres in any direction	Out of pool	Into an adjacent zone
Eulittoral rock surfaces	41	36	2	-	0
Sublittoral rock surfaces	36	29	7	-	5 (into the eulittoral)
Rock pools in the eulittoral	35	32	0	1	0

except one remaining within these pools during the entire nine months. Limpets on rock surfaces in the sublittoral zone showed the greatest amount of movement. After nine months, the majority were still in the same general area but some were more than 3 metres from their original location and often into the adjacent eulittoral zone above the *Durvillea* holdfast line.

Of the 20 limpets marked for homing, two were lost. No homing was evident in the remaining 18 during the four-week observation period. Although the limpets did not return to a fixed spot, again, they tended to live in a fixed area as has been borne out in more detail by the other experiments in this section.

In stable populations, only limpets in the sublittoral showed any movement into a new habitat but, even then, these limpets formed only a small part of the total sample. Greater movement away from a fixed area and hence more chance of changing habitats, was induced by doubling the existing populations of limpets in specific areas. However, such alterations created immediate unstable population levels which only occurred naturally in special situations (e.g. in some areas where dislodged, alive limpets were deposited after a heavy storm).

If limpets changed their habitats, there would be an accompanying change of any phenotypic effects resulting from environmental factors peculiar to individual habitats. If these phenotypic effects can be gauged by measuring some feature of the animal, variations in such a measurement would be greatly increased by the amount of interchange between habitats. However, from the above studies, variation resulting from migration of ecotypes to new habitats was small.

The extent of movement in populations has application to other studies. For example, section V (d) and section IV 1. (c) examine changes in the density of limpets with seasons and with alteration in algal cover, respectively; in section V (h), differences in shell morphology are related to the maintenance of position in distinct habitats. If limpets normally and frequently moved over appreciable distances and between habitats (regarded as containing separate, stable populations) the interpretation of any results found in the investigations in these other sections would have been adversely affected.

(d) Seasonal Variation in Numbers

(i) Materials and methods

The number of limpets per square metre were recorded along the five transect lines described in section III (a), the counts being at bimonthly intervals (May, July, September, November, January, March). The distribution of the limpet populations along these transects extended from the lower eulittoral to the sublittoral. Recordings were always done at low tides. Because of the surge of waves, the person counting the limpets in the sublittoral often had to wear a diving suit and mask.

(ii) Results and discussion

Many studies have used traverse counting to follow seasonal and vertical distributions of molluscs, and findings have been reviewed: Moore (1958), Fretter and Graham (1962), Lewis (1964).

In counting Patinigera macquariensis along transect lines, the objective was not part of a population dynamics study. Unfortunately, population structure of P. macquariensis could not be adequately covered in the time available. Transect counts of limpets and the artificial alteration of populations and habitats were to assess (a) seasonal vertical migration of limpets in the topmost section of the range, i.e. in the eulittoral, and (b) relationships of limpet distribution and abundance with differing habitats.

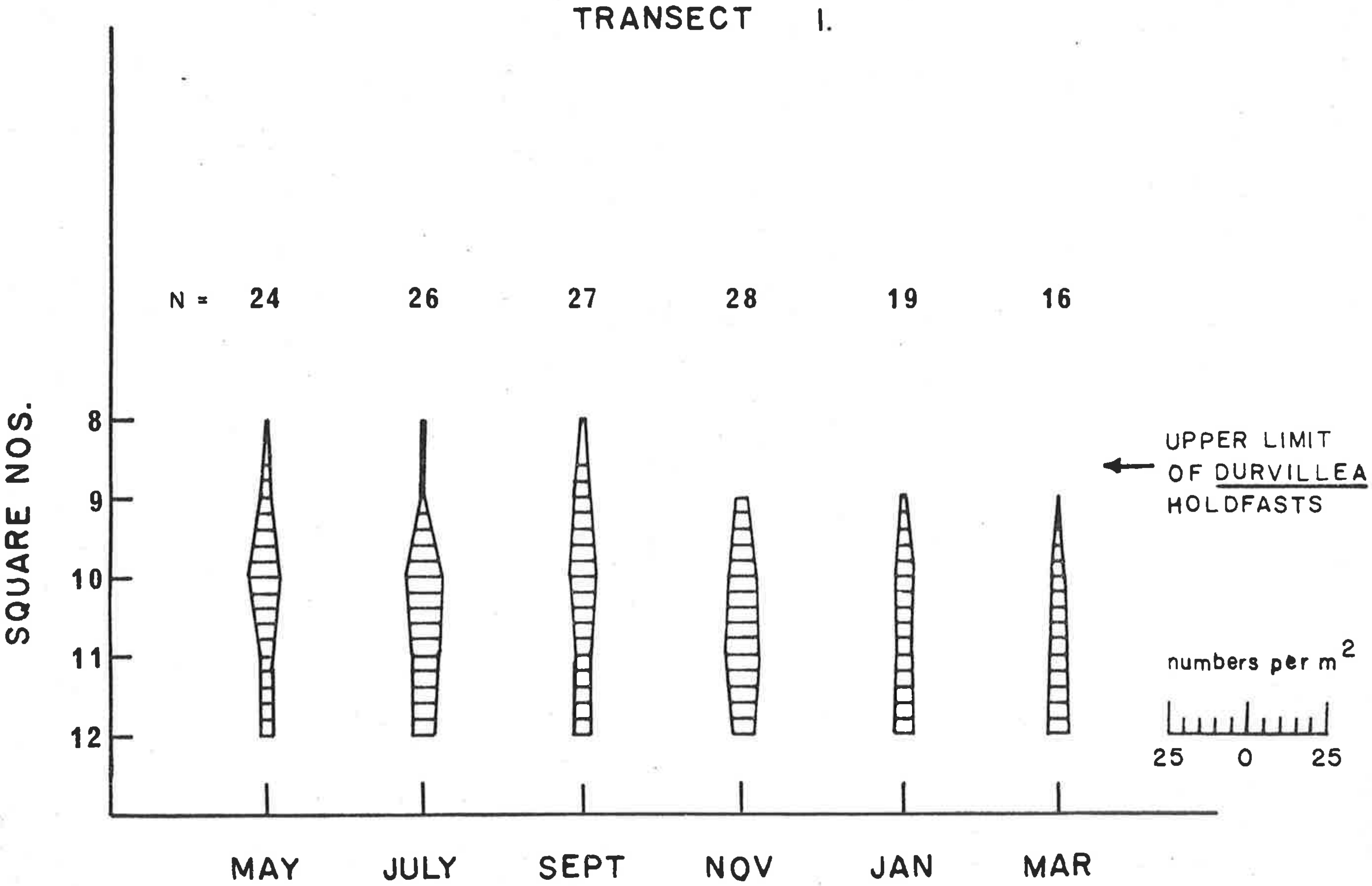
Figures 29, 30, 31, 32 and 33 illustrate the limpet density per square metre from eulittoral to the upper part of the sublittoral at bimonthly intervals, over a one year period and at the five different transect localities.

Transect 5 was cleared of kelp. A census before and after kelp removal was taken and Figure 33 shows the marked

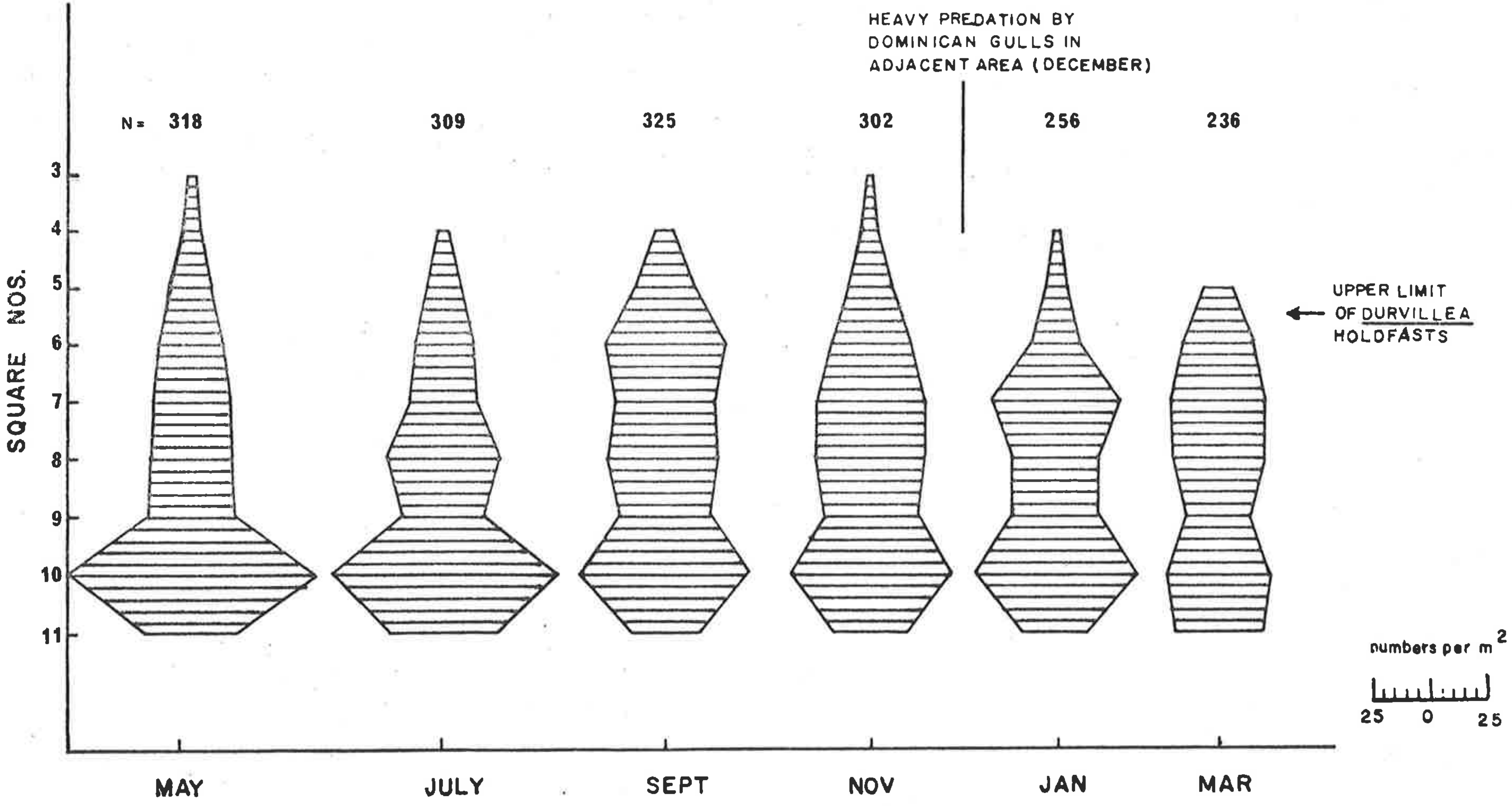
pp. 234 to 238.

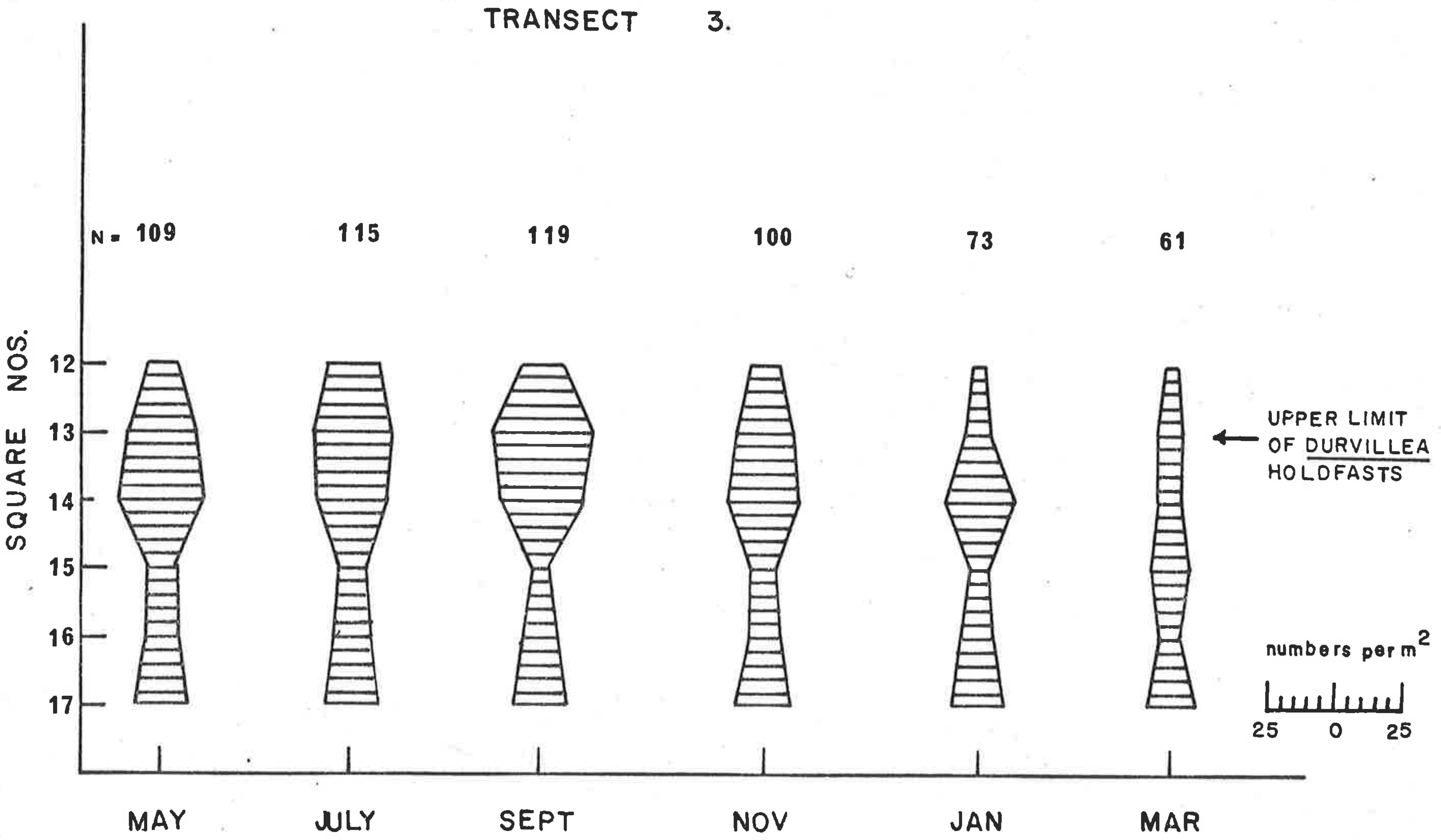
Figures 29 to 33.

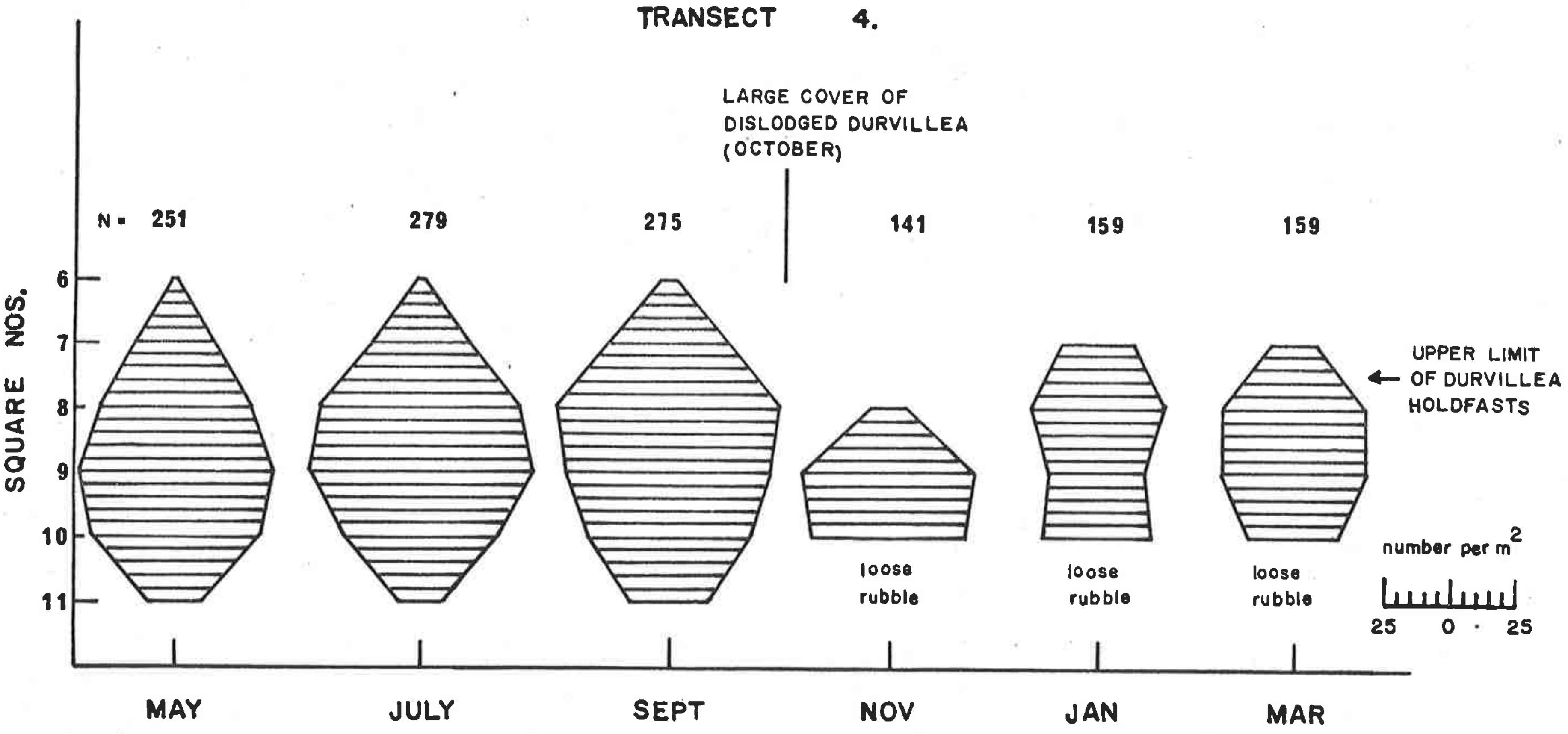
Density of Patinigera macquariensis taken at bimonthly intervals for one year on five transects.

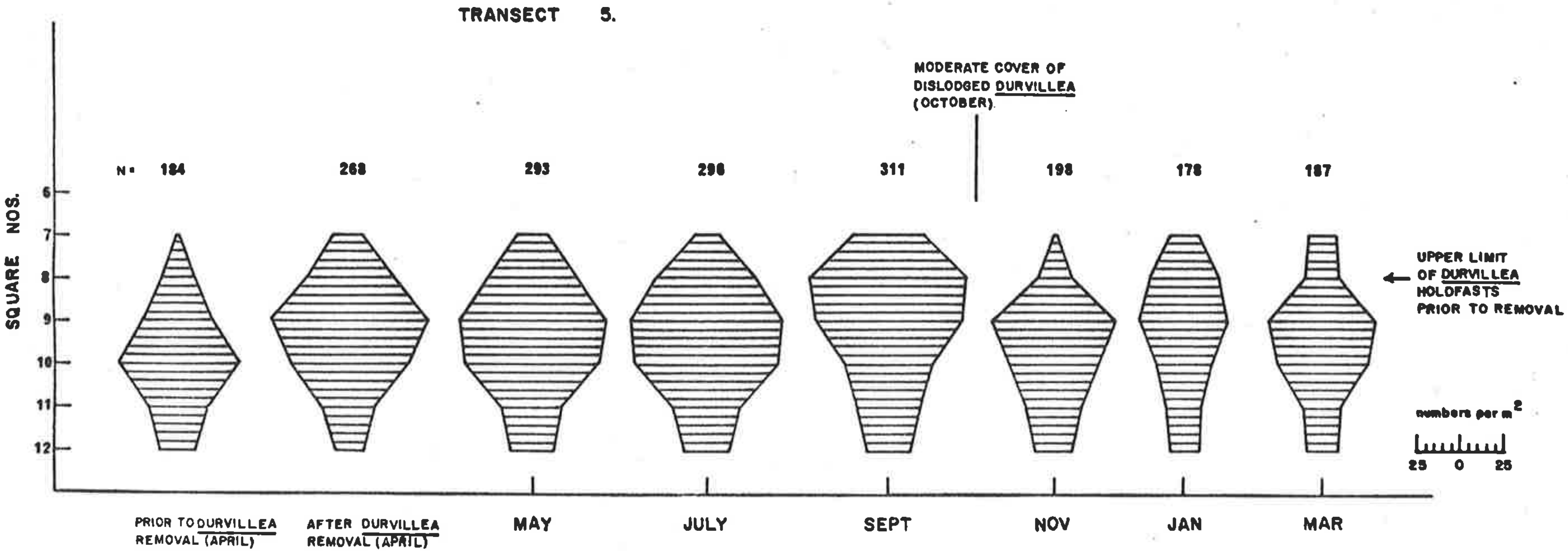

TRANSECT I.
N = 24
26
27
28
19
16
SQUARE NOS.
8
9
10
11
12
UPPER LIMIT OF DURVILLEA HOLDFASTS
numbers per m²
25
0
25
MAY
JULY
SEPT
NOV
JAN
MAR

TRANSECT 2.


HEAVY PREDATION BY DOMINICAN GULLS IN ADJACENT AREA (DECEMBER)
N= 318
309
325
302
256
236
SQUARE NOS.
3
4
5
6
7
8
9
10
11
UPPER LIMIT OF DURVILLEA HOLDFASTS
numbers per m^2
25
0
25
MAY
JULY
SEPT
NOV
JAN
MAR


TRANSECT 3.
N = 109
115
119
100
73
61
SQUARE NOS.
12
13
14
15
16
17
UPPER LIMIT OF DURVILLEA HOLDFASTS
numbers per m^2
25
0
25
MAY
JULY
SEPT
NOV
JAN
MAR


TRANSECT 4.
LARGE COVER OF
DISLODGED DURVILLEA
(OCTOBER)
N = 251
279
275
141
159
159
SQUARE NOS.
6
7
8
9
10
11
UPPER LIMIT
OF DURVILLEA
HOLDFASTS
number per m²
25 0 25
loose rubble
loose rubble
loose rubble
MAY
JULY
SEPT
NOV
JAN
MAR


TRANSECT 5.
MODERATE COVER OF DISLODGED DURVILLEA (OCTOBER)
N = 184
268
293
296
311
198
178
187
SQUARE NOS.
6
7
8
9
10
11
12
UPPER LIMIT OF DURVILLEA HOLOFASTS PRIOR TO REMOVAL
numbers per m²
25 0 25
PRIOR TO DURVILLEA REMOVAL (APRIL)
AFTER DURVILLEA REMOVAL (APRIL)
MAY
JULY
SEPT
NOV
JAN
MAR

increase in limpet numbers and an upward shift in the maximum concentration. All censuses were taken during low tide which thus standardized limpet movements with respect to tides (see section V (b)).

A total migration of *Patinigera macquariensis* out of the eulittoral zone did not occur. This was in contrast to *Patinigera polaris* on Signy Island which moved into the sublittoral in autumn, the downward migration apparently initiated by ice on the shore (Walker, pers. comm.). However, *P. macquariensis* does not have to cope with shore ice on Macquarie Island.

The upper limit to the range of *P. macquariensis* did not change significantly throughout the year except in the case of catastrophic events such as kelp overlay after high swells (Transect 4). There were two general trends: (1) the concentration of limpets at or just below the upper limit of *Durvillea* holdfasts increased in September; (2) the total number of limpets in each transect decreased in the summer months of January and March. However, this latter trend was somewhat masked by other effects in Transects 2, 4, and 5. Heavy eastern swells in early October had deposited a heavy cover of dislodged kelp on the upper squares of Transect 4. Plate 23A shows this kelp deposit in the area of Transect 4 while Plate 23B shows the same area after the kelp had been cleared by seas. Algae below were killed. Kelp was also strewn on

Plate 23.

23A. *Durvillea antarctica* deposited on Transect 4 after a severe storm.

23B. Dead algae, having been under *Durvillea antarctica* deposits as shown in plate 23A.

Transect 5 but not as severely as on Transect 4. A later count showed that loose rubble had also been deposited in square 11 of Transect 4 and had persisted there. The kelp overlay remained on Transect 4 for three weeks before being removed by seas; underlying *Porphyra*, *Chaetangium*, and *Rhodymenia* algae had been killed. The kelp on Transect 5 was removed gradually by seas over a weekly period and underlying algae were not unduly affected. The difference in kelp deposition and removal between these two transects was attributed to their profiles, 5 having a gradual slope and 4 an abrupt one. The effect of this kelp overlay in reducing limpet numbers can be seen in the figures for November (Figures 32 and 33). The November figures for the other transects were stable. These were not strewn with dislodged kelp at that time owing to their different aspect to the swells. January and March figures in Transects 4 and 5 suggested that the limpet numbers had stabilized after the kelp overlay interference and the lower density indicated that they were following the trend of decrease as found in the other transects. A heavy concentration of Dominican gulls followed the relief ship in early December and during calm weather, roosted on rocks near Transect 2 (see section IV 1. (d)). The concentrated feeding of the Dominican gulls removed every exposed limpet in the roosting area. The gulls ventured into the area of Transect 2 as well. Although this could have accounted for the decrease in numbers in the January count, the further decrease in March indicated a downward trend in numbers independent of the action of the gulls.

Without information on age structure, growth, mortality, and recruitment, explanation of other phenomena, such as general trends (1) and (2) would be largely speculative.

Absence of a total migration from the upper areas of the limpets' distribution correlated with the relative equability of the climate. The environment did not set the complete vacating of the eulittoral as a necessity at any season.

The different habitats encountered along the transects provided an insight into factors affecting the limpets' abundance. Heavy kelp cover reduced limpet numbers. In Transect 1 mere space was at a premium as the squares were densely covered with holdfasts. In Transect 5 the squares were lashed by kelp fronds whose subsequent removal brought about an increase in limpet numbers. This aspect is more fully treated in section IV 1. (c). Transect 3 was intermediate in kelp holdfast density. Transect 2 provided large rubble which was favourable to high limpet density. Although such a substrate provides more surface area upon which limpets can graze, there are two other considerations: (1) kelp holdfasts can only establish themselves on the largest boulders. and (2) at low tide the limpets move down the sides of the rocks and thereby avoid lashing by kelp fronds. The figures for Transect 4 at first appear as a contradiction to the foregoing, i.e. solid rock substrate with kelp cover and high limpet density. However, squares 8, 9 and 10 covered pools, gutters, and sharp ridges in which limpets were congregated. These structures probably protected limpets from lashing by kelp.

It appeared as though a cover of Durvillea reduced limpet numbers in two ways: (a) through a reduction of available space and, (b) through an adverse effect on the attachment of the limpets to the substrate. These conclusions were also suggested from the studies in section IV 1. (c).

(e) Osmotic Control

(i) Materials and methods

The osmotic behaviour of limpets was investigated by measuring the change, with time, of osmotic concentration of the blood of animals in different concentrations of sea-water.

It is appropriate here to outline what is actually measured by osmotic concentration. Potts and Parry (1964) and Prosser and Brown (1965) deal with the definition of osmotic concentration and the considerations of its use as a measure. The osmotic concentration of a solution and its other colligative properties, such as the freezing point depression, are functions of the total number of solute particles independent of size or chemical nature of the dissolved material.

In the present study, the osmotic concentrations of both the external medium (different sea-water concentrations) and the blood of limpets are expressed in milliosmols per kg water in reference to a standard solution of sodium chloride. Osmotic concentration is equivalent to the molal concentration of a solution of an ideal non-electrolyte. Because solutes do not behave exactly as ideal non-electrolytes and because some electrolytes in biological solutions only partially dissociate, a discrepancy will exist between the real and the ideal osmotic concentrations. This discrepancy can be expressed as an osmotic coefficient. The calculation of osmotic coefficients was not in the scope of the present study. However, the osmotic coefficient for the external medium was not expected to be equal to that for the blood of limpets; the difference was considered here to have little effect on the comparisons of the osmotic concentrations of external medium and blood.

The freezing point depression was measured by a thermistor apparatus with an absolute accuracy of ± 0.001°C. Full accuracy depended on standardization of technique during measurements. The circuit of this apparatus is shown in Figure 34 (A and B). It was constructed by the scientific section of the Antarctic Division, Australia, and was based on the circuit of the commercial Fiske Osmometer. It is

Figure 34

A. Circuit of Osmometer (Amplifier).

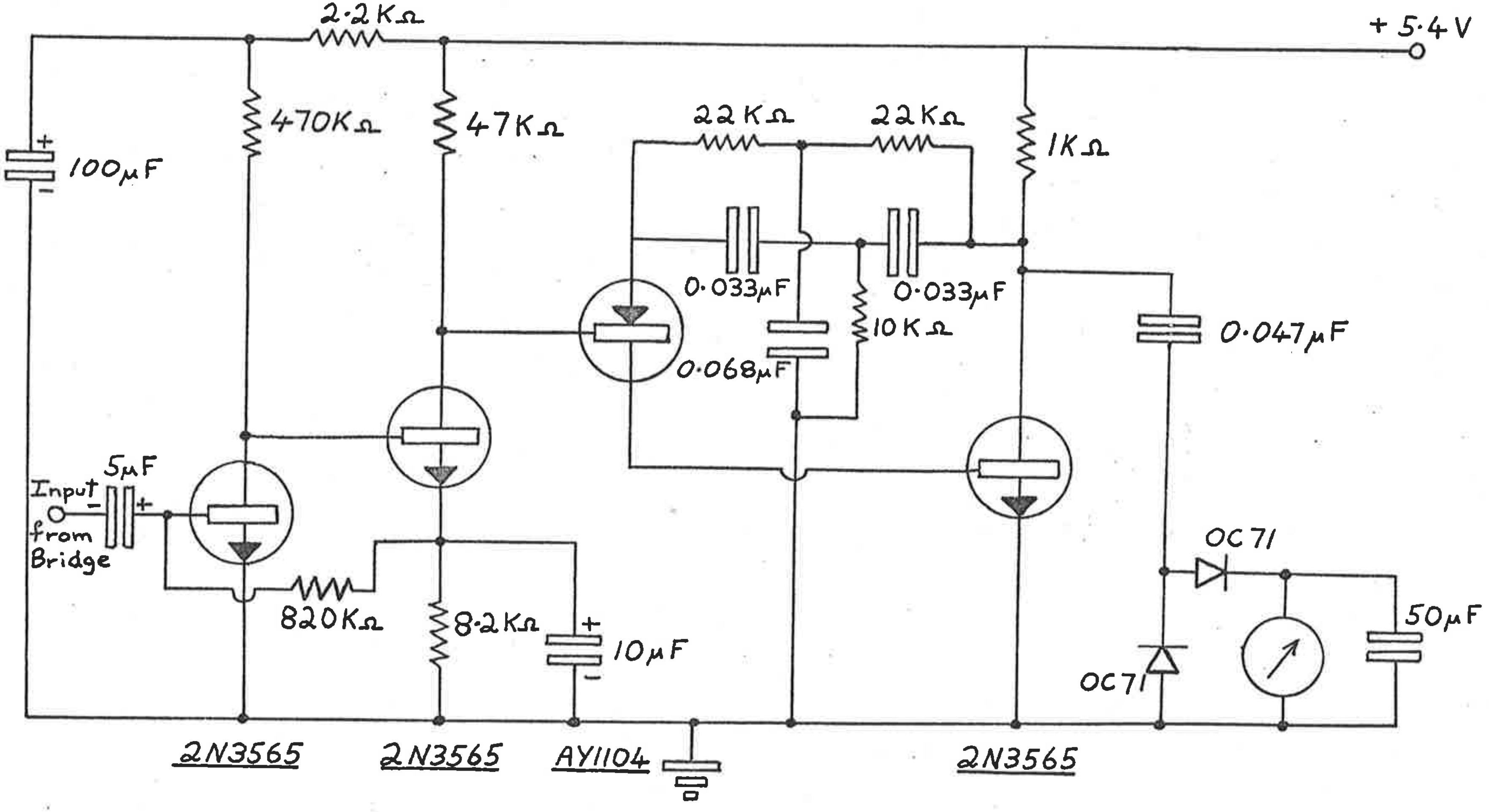
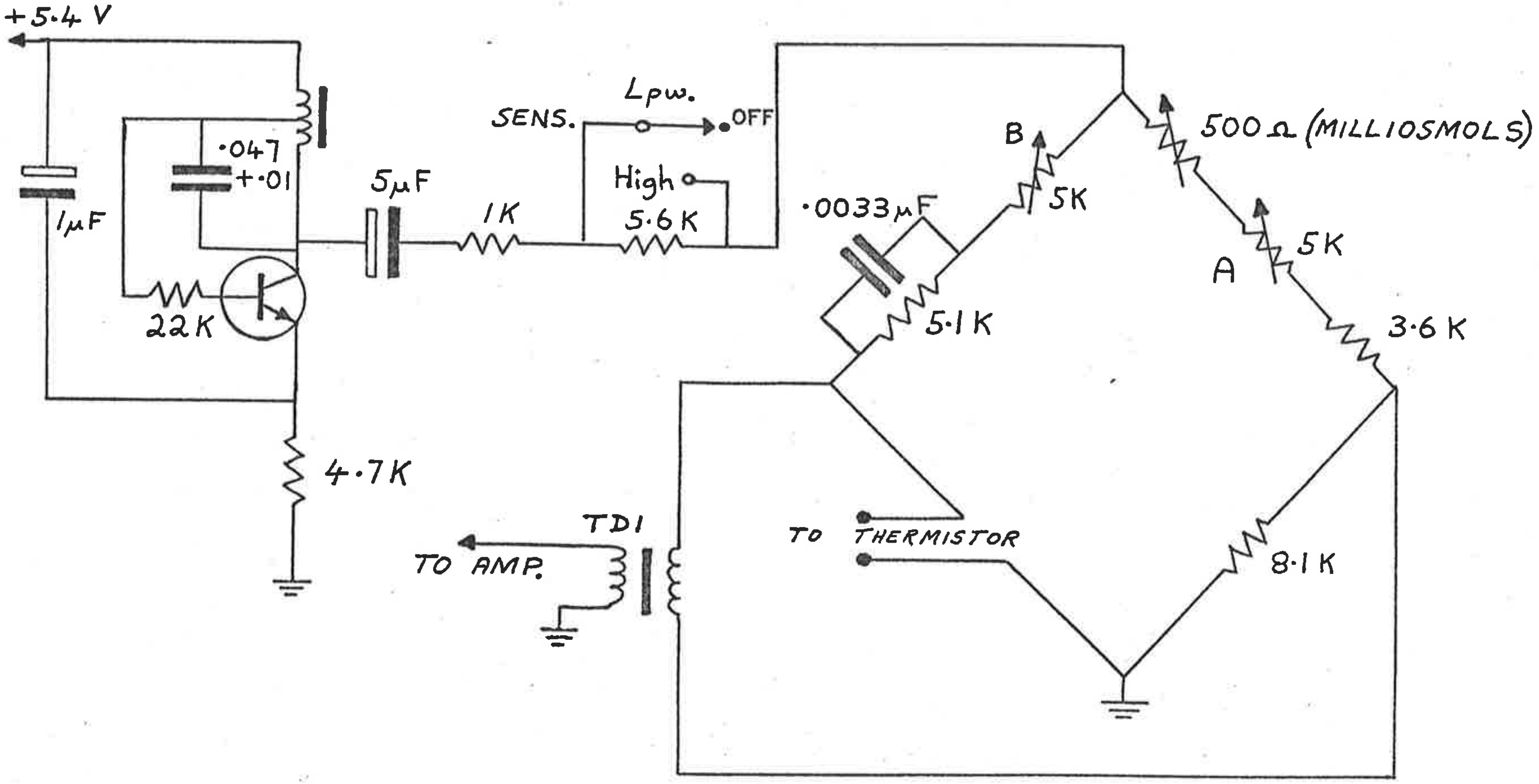

2·2KΩ
+5·4V
470KΩ
47KΩ
22KΩ
22KΩ
1KΩ
100μF
0·033μF
0·033μF
10KΩ
0·047μF
0·068μF
5μF
Input from Bridge
OC71
OC71
820KΩ
8·2KΩ
10μF
50μF
2N3565
2N3565
AY1104
2N3565

Figure 34

B. Circuit of Osmometer (Bridge).



+5·4 V
1µF
·047
+·01
22K
4·7K
5µF
1K
SENS.
Lpw.
OFF
High
5·6K
·0033µF
5·1K
B
5K
500Ω (MILLIOSMOLS)
A
5K
3·6K
TO THERMISTOR
8·1K
TD1
TO AMP.

hereafter referred to as the "osmometer".

Solutions of sodium chloride of known milliosmols per kg concentration were made up using quantities shown in Table 32, the figures being obtained from the "Fiske Osmometer Manual" 1962. The sodium chloride was analytical grade and the required accuracy was obtained by weighing it on a "Mettler" balance which read to 0.0001 gm and by mixing the solutions in volumetric flasks at 17°C.

The operational technique was as follows: 0.2 ml of fluid (standard solution, sea-water, or limpet blood) were placed in a small glass vial which was fitted over the end of the thermistor and taped in position. Thermistors used were STC F 23. In cooling, the procedure was carefully standardized to give repeatable results. Super-cooling was the major likelihood of error. To combat this, the sample was first frozen and then thawed until only a small crystal remained. The vial was then immediately placed into a salt-ice mixture which remained at -10°C to -12°C. The sample fluid in the vial immediately froze. After freezing, the sample was held in the air above the mixture, during which time the temperature of the sample reached a constant plateau. The reading was taken approximately one minute after the sample was frozen.

The calibration controls of the osmometer were set using the 100 and 500 milliosmols per kg water standard solutions;

Table 32. Relationship of standard solutions to freezing point.

Standard (milliosmols/Kg H_2O)	Sodium Chloride (grams/Kilogram Water)	Freezing Point (degrees C)
100*	3.089	-0.186
300	9.457	-0.558
400	12.70	-0.744
500*	15.93	-0.930
750	24.10	-1.395
1000*	32.23	-1.86
1200	38.76	-2.23
1400	45.22	-2.60
1600	51.62	-2.98
1800	58.01	-3.35
2000*	64.37	-3.72
2500	79.97	-4.65
3000*	95.40	-5.58

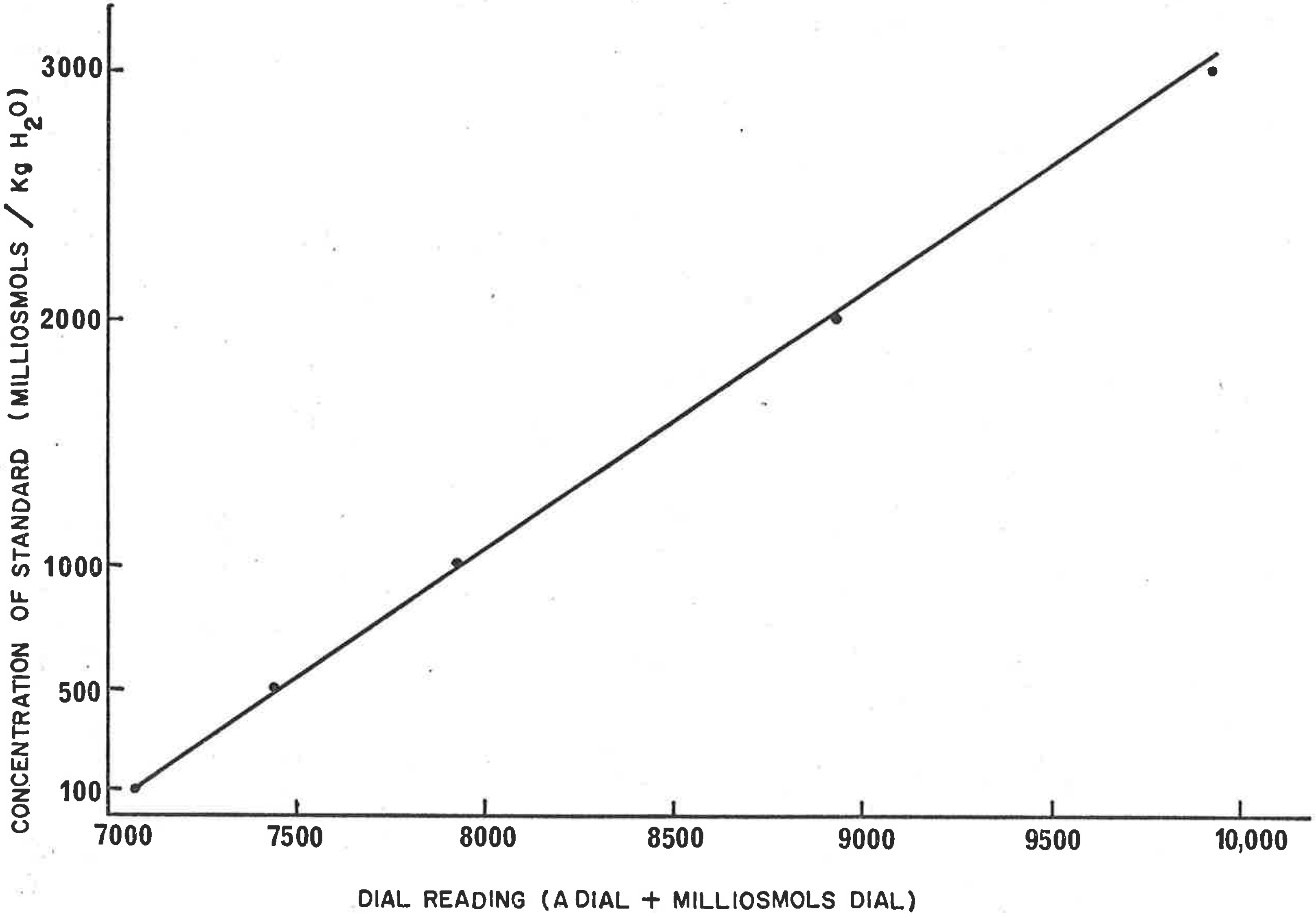
* Solutions used in calibrating instrument.

the procedure is outlined in section VI (Calibration) of the "Fiske Osmometer Manual" 1962. Once the dial calibration was completed the osmometer readings were checked against five of the standard solutions (see Table 32). The linearity so obtained (Figure 35) indicated the reliability of the technique and the accuracy of measurement.

Water of four concentrations was prepared, two above the concentration of sea-water and two below. The concentration was raised by evaporating over a flame and recooling; lowering of the concentration was effected by the addition of distilled water.

Specimens of Patinigera macquariensis (30 to 35 mm in length) were collected from the eulittoral zone and placed in holding tanks containing aerated sea-water, at a temperature of 5.0°C to 7.0°C. They were carefully checked, damaged or weakened specimens being discarded. After four hours, blood samples of 0.2 ml were extracted by a hypodermic syringe from the hearts of four limpets. The measurement of the blood concentration of these extractions was taken as the normal concentration. Twelve limpets were placed into each of four tanks containing the four experimental sea-water concentrations, at a temperature of 5.0°C to 7.0°C. At time intervals of 9, 24, and 48 hours, blood samples of 0.2 ml were extracted from the hearts of four limpets from each of the four sea-water concentrations. For any blood extraction,

Figure 35. Calibration of Osmometer.


CONCENTRATION OF STANDARD (MILLIOSMOLS / Kg H_2O)
3000
2000
1000
500
100
7000
7500
8000
8500
9000
9500
10,000
DIAL READING (A DIAL + MILLIOSMOLS DIAL)

a limpet was used only once and was then discarded.

Blood samples were also taken from limpets in the field. Results are discussed in section IV 2. (b) dealing with desiccation. The field investigation of blood concentration was to estimate the amount of water lost under natural conditions.

(ii) Results and discussion

Studies on other marine molluscs have shown that their blood is isosmotic with sea-water. Robertson (1964) listed data from the studies of other workers who made freezing point measurements on molluscs representing seven orders. In his own studies, Robertson recorded osmotic equilibrium in members of five additional orders (Robertson 1949, 1953).

Further studies have shown that, when subjected to abnormal salinities, marine molluscs usually acted as osmotic conformers (their body fluid concentration changed in conjunction with the change in concentration of the external medium); a few had limited osmotic regulation. (Osmotic regulation may be defined as the maintenance of the total particle concentration of body fluids at levels different from those of the external medium (Robertson 1964).) These other studies have also examined volume regulation, particularly in low salinities; the volume increase in some molluscs was shown to be reduced by the loss of salts, there being a subsequent decrease in weight on return to normal salinity.

Dakin and Edmonds (1931) showed that *Onchidium*, a marine pulmonate, swelled in dilute sea-water and regained its original weight after return to normal sea-water, demonstrating that little salt was lost.

For the opisthobranch, *Aplysia*, Bethe (1930) showed that, in dilute sea-water, there was an initial increase in weight followed by a decrease sometimes to below the weight the animal originally had in normal sea-water. Chloride analyses of the blood and the external medium showed that, after the initial osmotic uptake of water by the animal, salts began to be lost to the dilute medium. However, the final drop in weight was probably due to muscular contractions causing expulsions of water as shown in *Onchidium* by Dakin and Edmonds (1931) and not solely due to an outward transfer of salt with an accompanying osmotic loss of water as proposed by Bethe. Van Weel (1957) also suggested that since the eventual weights of some animals in dilute sea-water were less than the original weights, active water removal occurred in Bethe's experiments. Van Weel, in his own experiments on blood salinity measurements, showed that *Aplysia* could osmoregulate weakly in 95% sea-water.

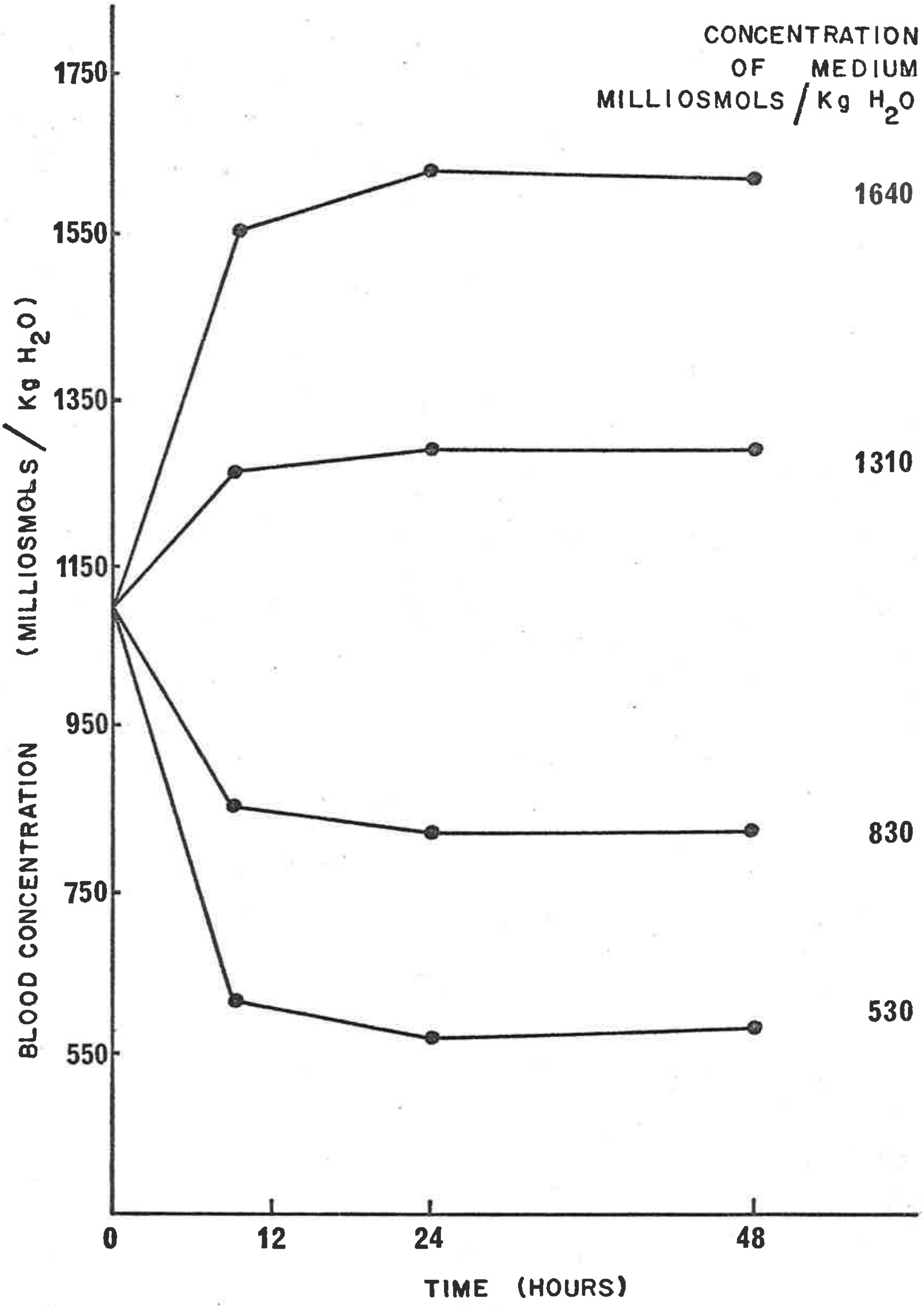
Bethe (1934) reported that the nudibranch, *Doris*, swelled rapidly in dilute sea-water and that there was essentially no volume regulation. However, Van Weel (1957) criticized the conclusions of Bethe and viewed the failure of some animals to reach osmotic equilibrium in 75% sea-water, as measured by blood chloride concentration, to mean that the blood remained hypertonic and thus the animals showed some regulation.

Segal and Dehnel (1962) reported the lack of osmotic regulation in the blood of the acmaeid limpet, <u>Acmaea limatula</u>, when subjected to high and low salinities, the blood becoming isosmotic to the medium (range 150 to 25% sea-water) within twenty-four hours.

Todd (1962) demonstrated osmotic regulation in <u>Littorina littorea</u> at low salinities. This periwinkle was isosmotic in salinities of 17-36%o but in dilute sea-water (8.8%o), it maintained a mean blood freezing point depression of 1.06°C as against 0.48°C for the medium, after 3-7 days.

In the present study, there was little variation in the osmotic concentrations of the blood among the four specimens of <u>Patinigera macquariensis</u> sampled at any time in any of the sea-water concentrations. The blood of limpets kept in normal sea-water was isosmotic with sea-water, the osmotic concentrations of both limpet blood and sea-water being in the order of 1100 milliosmols per kg water. This value represented the normal osmotic concentration of the blood of limpets and designated the starting point of the graphs in Figure 36. These graphs showed the change in osmotic concentration of

Figure 36. Change in blood concentration of <u>Patinigera macquariensis</u> in four different concentrations of sea-water.


CONCENTRATION
OF MEDIUM
MILLIOSMOLS / Kg H_2O
1750
1550
1350
1150
950
750
550
BLOOD CONCENTRATION (MILLIOSMOLS / Kg H_2O)
1640
1310
830
530
0
12
24
48
TIME (HOURS)

the blood, with time, for limpets in the four experimental sea-water concentrations. Each point represents the mean value for four animals.

The graphs in Figure 36 showed that Patinigera macquariensis did not osmoregulate in abnormal salinities. The blood concentration was closely aligned to that of the external medium after twelve hours. The greatest concentration difference between the blood and external medium was at the lowest salinity (= 530 milliosmols) when the osmotic concentration of the limpet blood decreased to 570 milliosmols and this gradient of approximately 40 milliosmols between the blood and the external medium persisted. This could be interpreted as indicating a slight hyper-osmotic regulation at this low salinity but, as the advantage of maintaining such a gradient would appear to be of no value to the animal, no biological significance is attributed to this difference.

Mucus on the body of the limpets may act as a buffer to changing external conditions particularly with regard to desiccation. Any possible buffering action of the mucus during immersion was hardly effective as shown by the short time in which limpets equilibrated with external conditions.

(f) Reproduction

(i) Materials and methods

The examination of reproductive cycles for marine invertebrates has many methods of approach. Giese (1959a) reviewed those centering on the criteria of spawning, numbers of larvae, appearance of ripe gametes in the gonads, brooding of eggs, and relative size of gonads.

In extensive studies on *Patella vulgata*, Orton *et al*. (1956) drew a classification scheme for gonadial stages based on microscopical and cytological characteristics. The percentage of animals in each reproductive stage (resting, developing, spawning, completely discharged) plotted against time outlines the reproductive cycle.

The ratio of gonad size to body size has been used extensively and is applicable to animals where an immature or spent gonad is small and a ripe gonad, large. This ratio gives a "gonad index" and has been calculated in a number of ways. Lasker and Giese (1954), Farmanfarmaian *et al*. (1958), and Giese *et al*. (1959) have used the volume of the gonad divided by the wet weight of the animal multiplied by 100. Kowalski (1955) and Pearse and Giese (1966) took the weight of the gonad divided by the weight of the animal multiplied by 100. Moore (1934) used volume of the gonad divided by volume of the animal. For abalones, Boolootian *et al*. (1962) used the ratio of gonad area (at any given cross-section of the cone) to shell length, multiplied by 100. Plotting the gonad index against time gives a graphical representation of the average state of the reproductive population.

Observations of spawning in the field and the sampling for released larvae were not suitable for a study of the reproductive cycle of *Patinigera macquariensis* for both practical reasons and the object of the investigation, which was to record the overall growth of the gonads and maturation of the gametes. Spawning observations and the census of larvae would tend to reflect briefer periods of causal action. Gonad index, microscopical examination and slide smears of fresh gonad were used for investigating the reproductive cycle of *P. macquariensis*.

Specimens of *P. macquariensis* were gathered at monthly intervals from the eulittoral zone and from diving stations of 3 to 6 metres in depth by snorkeling and SCUBA diving. All sampling was done on the east coast. Large limpets of 35 mm in length and over were selected to ensure adulthood.

Each limpet was first flicked and blotted dry to remove excess water. Its body was removed from the shell over a previously weighed petri dish. Care was taken that no flesh remained attached to the shell. The mantle skirt was severed at its junction with the foot muscle and pulled forward. The posterior aorta was cut and the visceral hump and underlying gonad pulled out and forward, and the gonad carefully removed. Weights of whole body, shell, and gonad were taken.

There were no secondary sexual characters for *P. macquariensis*, although males at the peak of development often showed a pale, longitudinal streak down the centre of the foot (externally). This apparently was the result of pressure from the enlarged gonad. On examining gonads of limpets not in the resting stage, sexes were easily separated on the basis of colour. Testes were light yellow while ovaries were brownish orange. Spent gonads of both males and females in the resting stage had a similar yellow colour. Sexes could still be distinguished at this stage by microscopical examination as remnants of gametes, seminiferous tubules, and ovarian tissue could still be recognized.

The morphology of the shell varied considerably, particularly in shape. Limpets from the eulittoral had significantly higher shells than those from diving stations (see section V (h)). Shells often had encrustations of the calcareous tube worm, Spirorbis aggregatus, coralline algae, and/or various other algae. The gonad index was defined here as the weight of the gonad divided by the total wet weight of the soft parts multiplied by 100. Different numerical values in gonad indices for equivalent reproductive stages of the eulittoral and deeper limpets could be the result of different shell and body proportions. However, it was the actual reproductive state of each population that was sought here and this would be adequately shown by the gonad index definition employed. In addition, if the shell was included in the gonad index calculation, careful removal of all shell encrustations would have been necessary to avoid weight errors. Removal of coralline algae was particularly time consuming.

Some of the dissections were further analysed for lipid content (section V (g)). In all, gonad indices for ten males and ten females from each of the habitats were determined each month. Data for the deeper zone limpets were not obtained in May, July (1968) and March (1969).

Artificial fertilization studies were conducted on P. macquariensis. The sea-water used was filtered through a coarse filter paper to remove detritus and was kept at 7.0°C to 9.0°C. No food was added at any stage. The aim was not to record stages of development and metamorphosis but to establish whether fertilization can occur between limpet populations from different locations in which the limpets differed markedly in shell shape, see section V (h).

For female limpets, a ripe ovary was removed and then broken up in a petri dish containing filtered sea-water. This was then added to a litre of filtered sea-water and stirred for approximately 30 minutes. The eggs were than collected by filtering through 118 micron gauze and added to a large beaker containing 5 litres of filtered sea-water constantly stirred at a moderate speed.

For male limpets, the testis was removed and placed in a petri dish containing a small amount of filtered sea-water. An incision was made in the testis and a suspension was allowed to form for 15 minutes. Then, 10 drops of it were added to the eggs. Samples were removed at regular intervals and viewed under a microscope to check for fertilization and development.

(ii) Results and discussion

The gonad indices were grouped by sex for each month for both eulittoral and diving station samples. The data were processed by computer to give the mean and standard deviation for each group, variance ratio about the means for each male-female combination, and t-values comparing means of each male-female combination.

Table 33 lists the variance ratios and t-values with their resulting probabilities in testing differences between means. Figure 37 plots the mean gonad index of males and females from the two locations over 12 months. This gives an indication of general reproductive states, clearly showing a phase difference existing between the two populations. In each locality, males and females were harmonious for changes in reproductive condition. Males had larger gonads than females. This was tested for significance in the following way. Variance ratios (F-values) were first obtained by the formula, $F = \frac{s1^2}{s2^2}$ (Bailey 1959, p. 50). All resulting values were within the tabulated value obtained from the F Distribution Table giving 2.5% points working at 5% level of signifi-

Table 33. Statistical comparisons of gonad indices.

Month	F	t	P
Males vs. Females - Eulittoral (N = 10 males and 10 females for each month)			
Apr.	1.082	2.842	< 0.05
May	1.689	0.568	> 0.10
Jun.	2.144	3.430	< 0.05
Jul.	1.450	0.849	> 0.10
Aug.	1.993	4.868	< 0.05
Sep.	1.703	5.202	< 0.05
Oct.	1.307	4.758	< 0.05
Nov.	3.540	3.430	< 0.05
Dec.	1.756	5.114	< 0.05
Jan.	4.210	3.342	< 0.05
Feb.	1.576	4.734	< 0.05
Mar.	3.941	3.302	< 0.05
Males vs. Females - Diving Stations (N = 10 males and 10 females for each month)			
Apr.	1.718	3.121	< 0.05
May	-	-	-
Jun.	1.662	2.123	< 0.05
Jul.	-	-	-
Aug.	1.003	0.184	> 0.10
Sep.	1.018	0.115	> 0.10
Oct.	1.921	4.993	< 0.05
Nov.	1.888	3.650	< 0.05
Dec.	1.383	5.756	< 0.05
Jan.	3.527	2.087	0.10>P>0.05
Feb.	2.305	2.725	< 0.05
Mar.	-	-	-

Figure 37. Monthly mean gonad indices for *Patinigera macquariensis* (male and female) from the eulittoral zone and diving stations of 3 to 6 metres in depth.

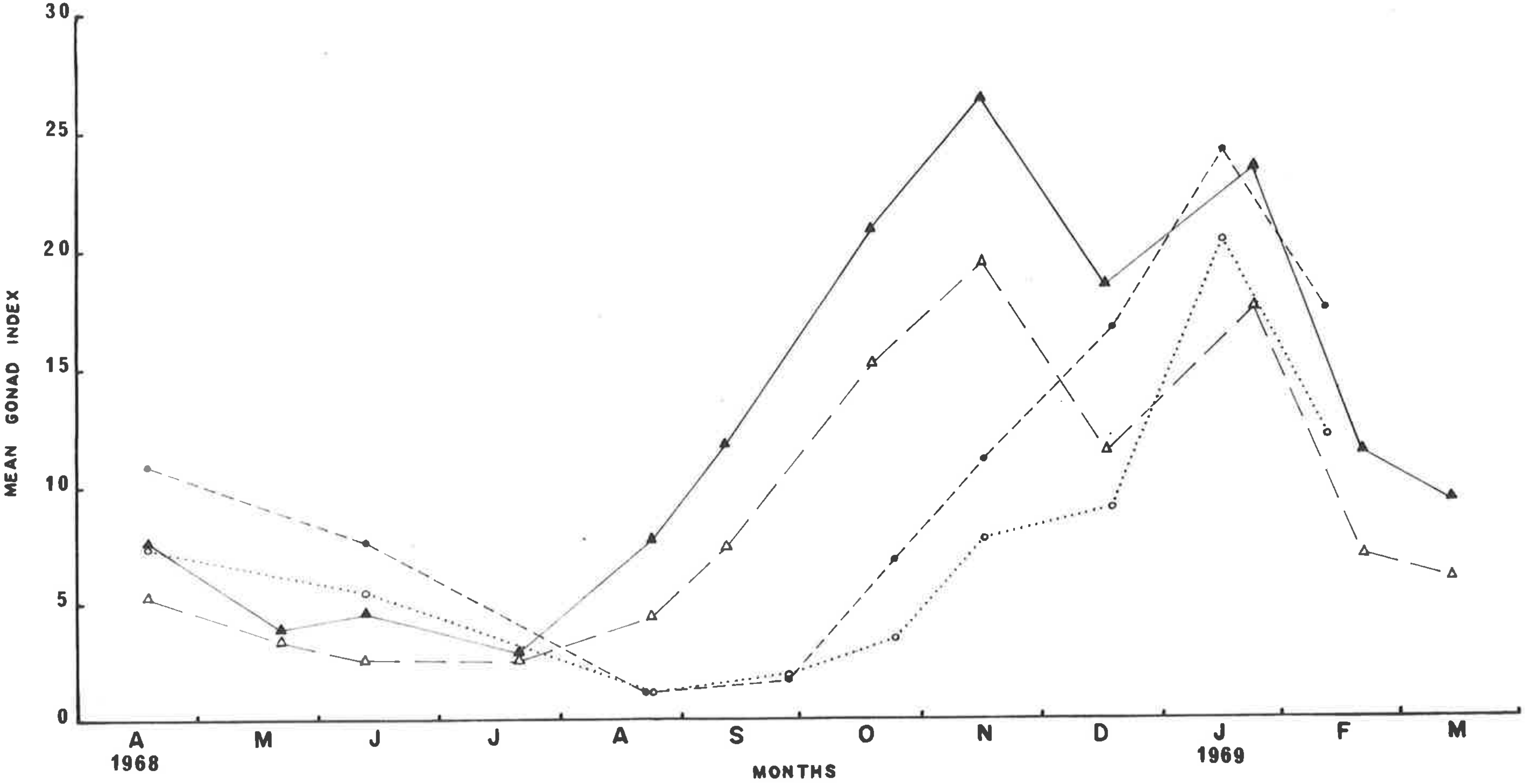
Key:

▲——▲ Males (eulittoral zone)

△— —△ Females (eulittoral zone)

●- - - -● Males (diving stations)

○·········○ Females (diving stations)


30
25
20
15
10
5
0
MEAN GONAD INDEX
A
1968
M
J
J
A
S
O
N
D
J
1969
F
M
MONTHS

cance in a two-tailed test (F Distribution Table from Snedecor 1956). Thus, the degree of homogeneity of variance for each male and female group was acceptable for applying a t-test on the means between males and females in each combination when a sample size of 20 was used (Bailey 1959, p. 50). Formula and distribution table for t were obtained from Bailey (1959). There were significant differences between male and female gonad sizes from both the locations except for May, July (eulittoral) and August, September (diving station). A marginal difference occurred in the January figures for the diving station sample.

The mean gonad index cycles (Figure 37) showed that, when active, male gonads were larger than female ones; as shown by the above tests, this difference is a significant one. The progressive stages in the reproductive cycles were evident in the shape of the graphs in Figure 37. Limpets in the eulittoral zone had a resting stage from May to July. Development of the gonads commenced in August, peak maturation being reached in November; the following sharp drop in gonad index indicated the first spawning. A second peak occurred in January, indicating that, during the spawning period limpets were still developing gametes, and in early January, the stimulus inducing limpets in the eulittoral zone to spawn abated and gonad size increased. Orton et al. (1956), in their histological studies, noted bursts of development alternating with spawning in Patella vulgata.

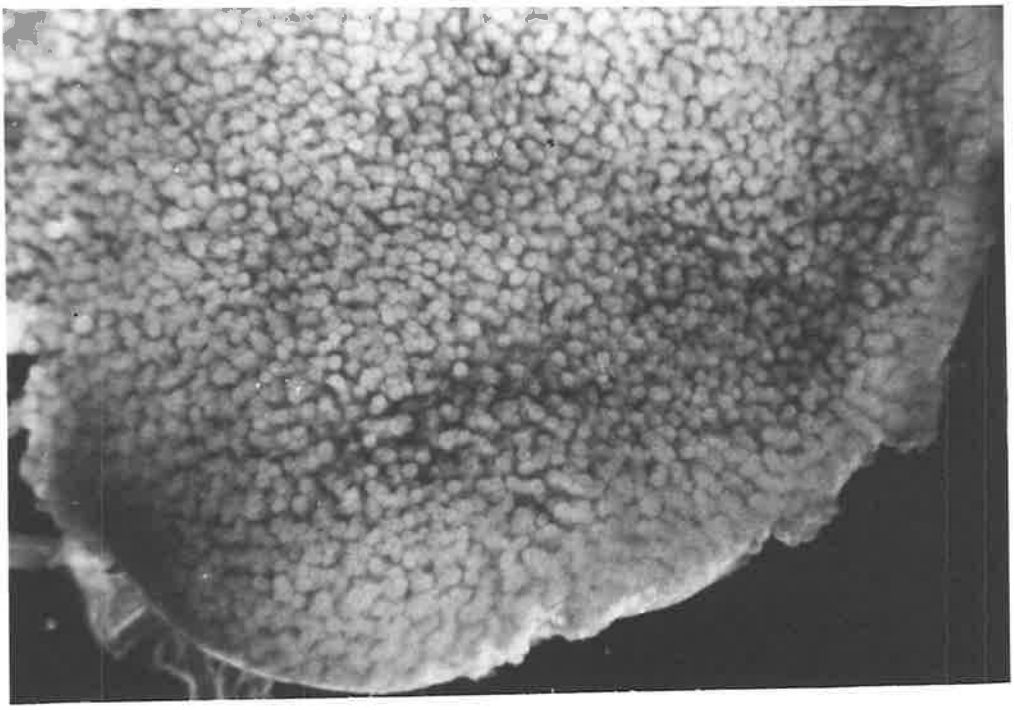
The decline of the curve after the January peak continued into March. The first part of the curve in the previous year indicated a decline until May i.e. five months after the first spawning. Limpets from diving stations had a resting stage from about July to September. Development of the gonads commenced in October and peak maturation was reached in January. A secondary development peak may well have occurred in March as the previous stages in the cycle corresponded to those prior to the secondary peak for the eulittoral limpets. The sharp drop after the January peak indicated the first spawning. In the first part of the curve, the decline continued through till June, again, five months after the first spawning.

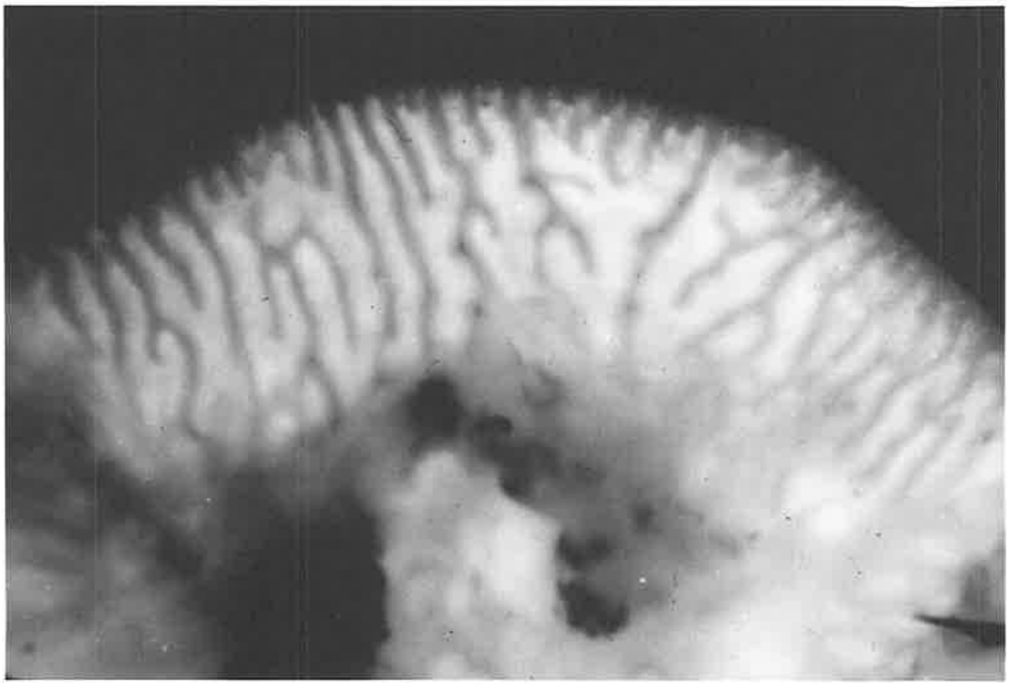
Information on the reproductive state of all limpets and the phase difference between populations from the two localities obtained from the mean gonad index cycles were supported by microscopical examinations of whole gonads and smears. Developing oocytes and spermatocytes were noted in the gonads of limpets from the eulittoral zone in August-September while, simultaneously, the gonads of limpets from the diving stations were in a spent and resting condition. The commencement of development in these was not observed until October. In October-November, the gonads of the eulittoral zone limpets were building up to their peak. In October, the eggs were individually visible to the naked eye but were not uniform in size and were still tightly packed and held by the germinal tissue. In November, the whole ovary was a mass of uniform eggs, each egg enclosed by a chorion; those on the surface were quite loose. Plate 24B shows the surface of a female gonad at this stage. In males, fully developed spermatozoa were present in October but there was still a high proportion of spermatids. In November, the testes were very soft and even a slight mishandling caused rupture and the release of a milky fluid with a high proportion of spermatozoa. Plate 24A shows a dorsal view of the male gonad at this stage with the seminiferous tubules very distinct. The corresponding stages for limpets from the diving stations were not observed until December-January. In December, eulittoral zone limpets had obviously spawned. Eggs on the surface of the ovary were extremely loose with noticeable gaps amongst them. Testes often had patches, darker in colour, and lacking in the "explosive tension" exerted by the milky fluid in other parts of the testis. January saw the second peak for the eulittoral zone limpets when gonads closely resembled those of November. A further sample between the December and January ones should have shown gonads with an increased amount of developing gametes. Developing gametes were present in November and January but formed a very small part of the gonadial tissue. The February sample

Plate 24.

24A. Mature testis (dorsal side) of <u>Patinigera</u> <u>macquariensis</u>.

24B. Mature ovary (ventral side) of <u>Patinigera</u> <u>macquariensis</u>.





showed obvious spawning by both the eulittoral and diving station limpets. It was inferred from the early part of the mean gonad index curves that the time from peak development to the resting condition for each limpet population was 5 months. However, in female gonads of eulittoral limpets in April and of diving station limpets in May-June, the eggs regressed to a very irregular shape indicating degeneration and resorption. Thus in the final decline of the gonads, it would appear that gamete release was unlikely.

Out of a total of 504 limpets dissected, with a length of 35 mm or greater, 243 were females, 259 were males, and 2 were hermaphrodites. Thus, there was a 50:50 sex ratio at this age and beyond. The hermaphroditic limpets had distinct sections of both male and female gonadial tissue. Hermaphroditism has been studied in the genus _Patella_ (Dodd 1956), and it was found to be rare. A causal connection between sex change and hermaphroditism was rejected by Dodd as it was estimated that sex change occurs in 90% of individuals of _Patella vulgata_ and greater incidence of hermaphroditism would be expected if a causal connection existed. The above samples of _Patinigera macquariensis_ were restricted to a relatively large size-group, and sampling of smaller limpets would be needed to indicate whether hermaphroditism and/or sex changes occur.

The measurement of reproductive condition was possible for only 12 months but the end points of the cycle in Figure 37 indicated similar reproductive states at the same time in successive years. Studies of reproductive cycles of other marine invertebrates have shown that times for peak maturation, spawning, and resting stages can differ markedly in successive years, e.g. Farmanfarmaian *et al.* (1958), Giese (1959b). Orton *et al.* (1956) showed this to occur for the limpet *Patella vulgata*. It was also found that the time involved in maturation and spawning depended upon geographic locality. Ballantine (from Morton and Miller 1968, pp. 324-325) found that low tidal populations of *Patella vulgata* have earlier seasonal maturation of the gonads than high tidal populations. In contrast, Blackmore (1969a) found no difference in time of reaching peak maturation in *Patella vulgata* situated at different levels in the littoral zone.

Giese (1959a) reviewed the studies on causal mechanisms behind reproductive cycles of marine invertebrates. Most work centred around control by exogenous factors but Giese suggests that "the endogenous drive for a reproductive cycle appears to be plastic to the extent that the precise pattern it takes depends upon the external factors which entrain or time the endogenous events in such a way as to be effective for the survival of the species".

Temperature, light, salinity, pH, and food represent the external factors which have received the most investigation as control mechanisms on marine invertebrate reproductive cycles.

The phase difference in the reproductive cycles of Patinigera macquariensis from the two locations can be used to isolate possible mechanisms controlling the cycle. Correlations only are noted here.

The two cycles discounted any relation between onset of development and a primary causal stimulus acting on the species in the two habitats. For example, the diving station limpets were still subjected to good light penetration and photoperiodicity could not have acted as a single determining factor on the reproductive cycle pattern. Diving station limpets encountered very constant salinity and pH values. These factors were more variable for limpets in the eulittoral zone but the variation was small and sporadic and not likely to follow any seasonal trend under the influence of Macquarie Island's equable oceanic climate. The diet of limpets in the two habitats was essentially different. In the eulittoral zone, greenish algal film and diatoms were grazed while at a diving station, the staple diet was coralline algae. Whether these different diets had a causal effect on the reproductive cycles is unknown. However, it would be more likely for dietary differences to affect the duration of events in a cycle by influencing the build-up in reserves whereas the difference in these two cycles was in a phase offset of two months. The duration of the resting, developing, and declining periods was the same in each reproductive cycle. The eulittoral limpets had a secondary peak in their gonadial development but this may also have occurred in diving station limpets in March. [redacted] Spawning did occur in the eulittoral limpets over this period but the peak spawning for the diving station limpets occurred in February. There was little correlation between air temperature (see Figure 15, section III (c)) and the reproductive cycle of limpets in the eulittoral. The peak maturation of diving station limpets followed the high peak of sea temperature, yet there was no temperature rise to correspond with the onset of development. The increase in temperatures owing to radiation would affect limpets in the eulittoral zones and there was a sharp increase in average daily sunshine in August (see Figure 5, section II (b)), the 29th August having 7.6 hours of sunshine. Air and sea temperatures both rose unusually in August and this rise, coupled with the sharp increase in sunshine, may have caused the earlier start to the development of gonads in the eulittoral population. The heavy December spawning for eulittoral zone limpets occurred in a month that had a marked reduction in wave action on the east coast, from which all samples were taken, (see Figures 13 and 14, section III (c)). Correlations have been noted between the spawning of molluscs and sea conditions, both rough and calm (Giese 1959a). Calm seas on the shores of Macquarie would perhaps increase the possibility of the meeting of gametes and hence fertilization of eggs in the littoral zone.

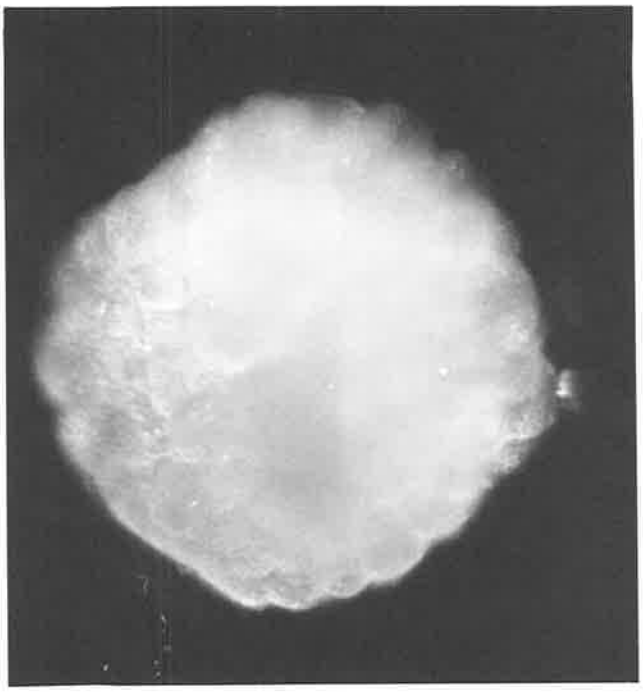
Artificial fertilization was invoked: (1) in December, between males and females from the eulittoral, (2) in January and February, between males and females from the eulittoral zone, the diving stations, and deep rock pools (both in each group and between groups). All fertilizations were carried to the trochophore stage. Plates 25A and 25B show cleavage and trochophore stages respectively. Gametes were taken from individuals by only slightly teasing ripe gonads (refer to Materials and methods). Thus, it was still possible for fertilizations to occur between the three populations examined.

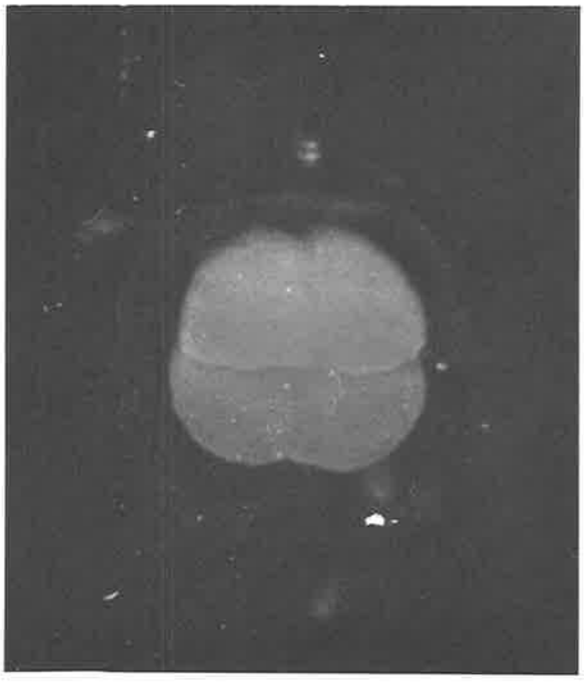
Such a phase difference, as shown in the reproductive cycles of limpets from two appreciably different habitats, i.e. eulittoral zone and from a depth of 3 to 6 metres, indicated the possible effects of environmental factors on speciation when one species is capable of colonizing a variety of habitats. Environmental factors in one habitat are likely to cause a population to be reproductively out of phase with a population in another location. If this is accentuated to

Plate 25.

25A. Development of *Patinigera macquariensis*: Second cleavage.

25B. Development of *Patinigera macquariensis*: Early trochophore.





the point where spawning does not overlap and such a situation is maintained, the reproductive isolation so incurred could well result in the eventual formation of two species.

The aim here was to record the type of reproduction and reproductive cycle of this sub-Antarctic limpet rather than determine underlying causes. Correlations were presented here for speculative discussion. Hitherto unknown information brought to light on the reproduction of _Patinigera macquariensis_ included: a 50:50 ratio of sexes in limpets of 35 mm length or greater; the rare occurrence of hermaphroditism in specimens of the above size; the release of gametes in late spring-summer; the duration of the developing, spawning, resorption, and resting stages in an annual reproductive cycle. Continuing data would show whether the stages in the reproductive cycle occur at the same time of the year in successive years. Further insight might then be gained into possible causal factors.

(g) Seasonal Variation in the Lipid Levels of Tissues

(i) Materials and methods

As two terms with very different meanings are used frequently in this section, it is important at the outset to define them. Lipid level refers to the percentage of lipid in a tissue per unit weight (in this study, per unit dry weight); lipid content refers to the total quantity of lipid in a body component.

Specimens of Patinigera macquariensis were dissected to obtain samples of gonad, digestive gland, and foot muscle for lipid determinations. Large limpets were selected to ensure adulthood as one of the aims was to investigate any relationships between the changes in lipid levels and the reproductive cycle.

The reproductive cycle was determined by measuring the gonad indices of limpets at monthly intervals (see section V (f)). Also, it was intended to compare the lipid content of both male and female gonads during the reproductive cycle. If the lipid level multiplied by the total weight of the gonad was used as a measure of gonadial lipid content, any size difference between males and females (not suggesting a sexual dimorphism by size but a difference occurring by sampling) would affect the values of lipid content of the gonads. As the gonad index gave the ratio of gonad size to body size, the lipid level of the gonad times the gonad index was used as a measure of lipid content in order to compensate for possible different body sizes between male and female samples. Collections of limpets for lipid analyses were made at the same time as the monthly collections of limpets for measurements of gonad index.

Digestive gland indices were not obtained. This gland was very soft and was wound around the intestine, making it difficult to measure the weight or volume of the gland accurately. A suitable section of digestive gland and small pieces from the middle of the foot muscle were removed for lipid determinations.

The limpets were taken from the eulittoral zone, transferred to holding tanks, and dissected within 24 hours. Collections were made at monthly intervals and always at low tide. Studies in section V (b) showed that the feeding activity of limpets in the eulittoral zone was regulated by conditions of submergence and emergence. This, in turn, would be related to tidal cycles except in the cases where the seas were unusually calm and the surge of waves did not reach limpets in the eulittoral zone. Thus, the limpets were at the same stage of their feeding cycle at each collection.

The tissue samples were weighed and then placed in a vacuum desiccator over concentrated sulphuric acid and dried for approximately 24 hours. The tissues were crushed in a small pestle and mortar, then enclosed in filter paper and transferred to the holding bucket of a micro-Soxhlet apparatus. Lipid was extracted by refluxing diethyl ether. The boiling vessel was placed in a water-bath which was kept at 55°C to 60°C. The temperature at the bucket where the sample was held was 34°C which was regarded here as the temperature of extraction. The tissue samples were about 100 mg when possible and 10 to 15 ml of diethyl ether were used for extracting from such a weight over a 2 hour period. (These quantities and the refluxing time were taken from the technique used by Greenfield _et_ _al_. (1958) in their investigation of lipids in echinoderms.) Weighings of tissue samples and lipid residues were made on a "Mettler" balance capable of reading to 0.0001 gm. At a particular setting of the laboratory room heater, the temperature varied from 18.2°C to 21.2°C and the relative humidity from 36% to 42% (from continuous recording instruments). The weighing of an empty collection vessel at various points in the above ranges showed no significant source of error, i.e. variation was ± 0.0001 gm.

Giese (1966a) noted the distinction between stored and structural lipids. Stored lipids (e.g. fats) accumulate in cells as free globules and serve as energy reserves. Structural lipids (e.g. sterols) are prominent in cell membranes and in membranes of the cell organelles. A Soxhlet extraction, using mild heat (34.6°C) with a non-polar solvent (ethyl ether) presumably liberates mainly stored or loosely held lipids. Increased temperature and polar solvents are supposedly needed for the removal of the bulk of structural lipids.

With the conditions of extraction used here (Soxhlet extraction at 34.0°C with diethyl ether), it was expected that mainly stored lipids were removed. Future reference to lipid levels obtained in this study should be viewed as those obtainable by the extraction method employed. As the same method was used in all cases, comparisons can be applied between any combination of results. Small traces of other organic compounds would have been removed but such contamination is negligible.

In the monthly lipid determinations, 3 males and 3 females were used. This sample size was not great. The main limiting factor was time, both in the preparation of the tissues and the extraction of lipid from them. Only one Soxhlet apparatus was available and laboratory deficiencies prevented the setting up of a bank of improvised units. To offset this small sample size, a quick measurement of gonad index was taken after weighing and only those with an average gonad index for that month were used for lipid determinations, a current record of mean gonad indices being compiled during the experimental period. As outlined in section V (f), gonad sizes were subjected to further statistical analysis on return to Australia and the mean values were valid indications of reproductive condition. Thus, lipid determinations were only undertaken on limpets in an average reproductive condition for the eulittoral population. At each month, gonads and digestive glands were processed, whereas lipid level of the foot muscle was determined at more widely spaced intervals.

Tissues in March 1969 were dissected and dried just before the relief ship departed. The samples were sealed in plastic tubes with a silica gel crystal and lipid was extracted at a later date. A control was obtained by sealing the left-over dried tissue from a previous extraction in the same way. Lipid extraction on this control did not differ significantly from the previously obtained percentage.

(ii) Results and discussion

The lipid levels in the body components of marine invertebrates have been noted to vary considerably. Giese (1966a) observed that marine invertebrates taken from the field are of "diverse genotypes and in various states of nutrition" and that these two factors will bring about variations in lipid levels of body components. (Nutritional state refers to the range encountered between animals that may have just eaten and animals that may have been starved for several days or weeks.) Giese also stated that it was not possible to conduct studies on marine invertebrates of inbred lines but suggested that animals in aquaria can be studied under more standard feeding conditions. However, in investigating cyclic variation in lipid levels, animals have to be taken from the field as life in aquaria would interfere with environmental variables of possible influence.

Nutritional state of animals in the field is likely to have greater influence on lipid levels in such animals as asteroids which feed irregularly in a predator-prey relationship. For example, some specimens of the starfish, *Pisaster ochraceus*, ate only a few mussels in an entire year even where food was fairly abundant (Feder 1956). However, nutritional state should be far less variable in grazing molluscs which feed with some degree of regularity as does *Patinigera macquariensis* (see section V (b)).

Giese (1966a) reviewed the work on lipids in marine invertebrates; in molluscs, there is considerable interspecific variation in lipid levels of particular tissues. The importance of lipid as a storage material apparently receives varying emphasis with different molluscs.

The increase in lipid level during the development of gonads has been followed in some chitons (Tucker and Giese 1962; Giese and Araki 1962) and in the limpet, *Patella vulgata* (Blackmore 1969b). More extensive work on cyclic biochemical changes (including lipid levels) has been done on echinoderms (see review by Giese 1966b).

Studies on the lipid levels of body components of the chiton *Katharina tunicata* have related these levels to nutritional state and reproductive condition (Lawrence *et al.* 1965; Giese and Araki 1962). Of particular interest is the relation to nutritional state as further deduction is made here on combining the results of the two studies. Lawrence *et al.* (1965) found an inverse relationship between the annual cycles of gonad index and digestive gland index in *Katharina tunicata*, and suggested that the reduction in size of the digestive gland could be due to nutritive demands of gonadial growth; also, variation in the size of the digestive gland could be influenced by a seasonal change in the amount of food ingested. Giese and Araki (1962) calculated the lipid level of gonads and digestive glands of *Katharina tunicata* for spent, ripe, starved, and freshly collected specimens. They found relatively little change in lipid levels of gonad and digestive gland before and after breeding, indicating that lipid was not transferred from digestive gland to gonad during reproductive development. Giese and Araki (1962) showed that both the size and the lipid level of the digestive gland decreased with starvation. Therefore, if a seasonal change in the amount of food eaten is postulated as causing a variation in the size of the digestive gland, then the lipid level of the digestive gland would be high when it was large and low when it was small. However, from the inverse relationship between digestive gland and gonad sizes (Lawrence *et al.* 1965), ripe and spent individuals have small and large digestive glands respectively; yet, as previously mentioned, Giese and Araki (1962) showed that the lipid level of the digestive glands of ripe and spent individuals was relatively constant. Thus, it appears that variation in the size of the digestive gland was not merely due to a seasonal change of food ingested.

Figures 38 and 39 show monthly lipid levels for gonad, digestive gland, and foot muscle of male and female *Patinigera macquariensis*, each point representing the mean value for three specimens. The graphs of gonad indices for males and females (from section V (f)) are added to the figures for quick reference to corresponding reproductive condition.

The analyses indicate that lipid is a prominent component in the gonad and the digestive gland. In the female gonads, lipid levels averaged from 8.6% to 25.6% of the dry weight while, in the male gonads, the variation was between 6.7% to 14.2%. In the digestive gland, the range was from 7.2% to 19.2% of the dry weight in females, and 5.8% to 18.3% in males. In foot muscle the lipid level was very low, the range of averages being from 2.6% to 4.8%, with no difference apparent between the sexes.

The lipid analyses were undertaken to gain information on the importance of lipid as storage material in tissues and whether or not variations in lipid levels were related to reproductive activity.

Giese (1966a) raised the question "when is a cell considered to store lipid?" Because the muscle cells of crabs appeared to accumulate no visible lipid inside or between them; he considered the lipid level of such cells to be indi-

Figure 38. Average monthly lipid level of gonad, digestive gland, and foot muscle of male *P. macquariensis*. The reproductive cycle (monthly gonad index) is included.

Key: ●- - - - -● Digestive gland.

■———■ Gonad.

▲ Foot muscle.

X—·—·—X Reproductive cycle.

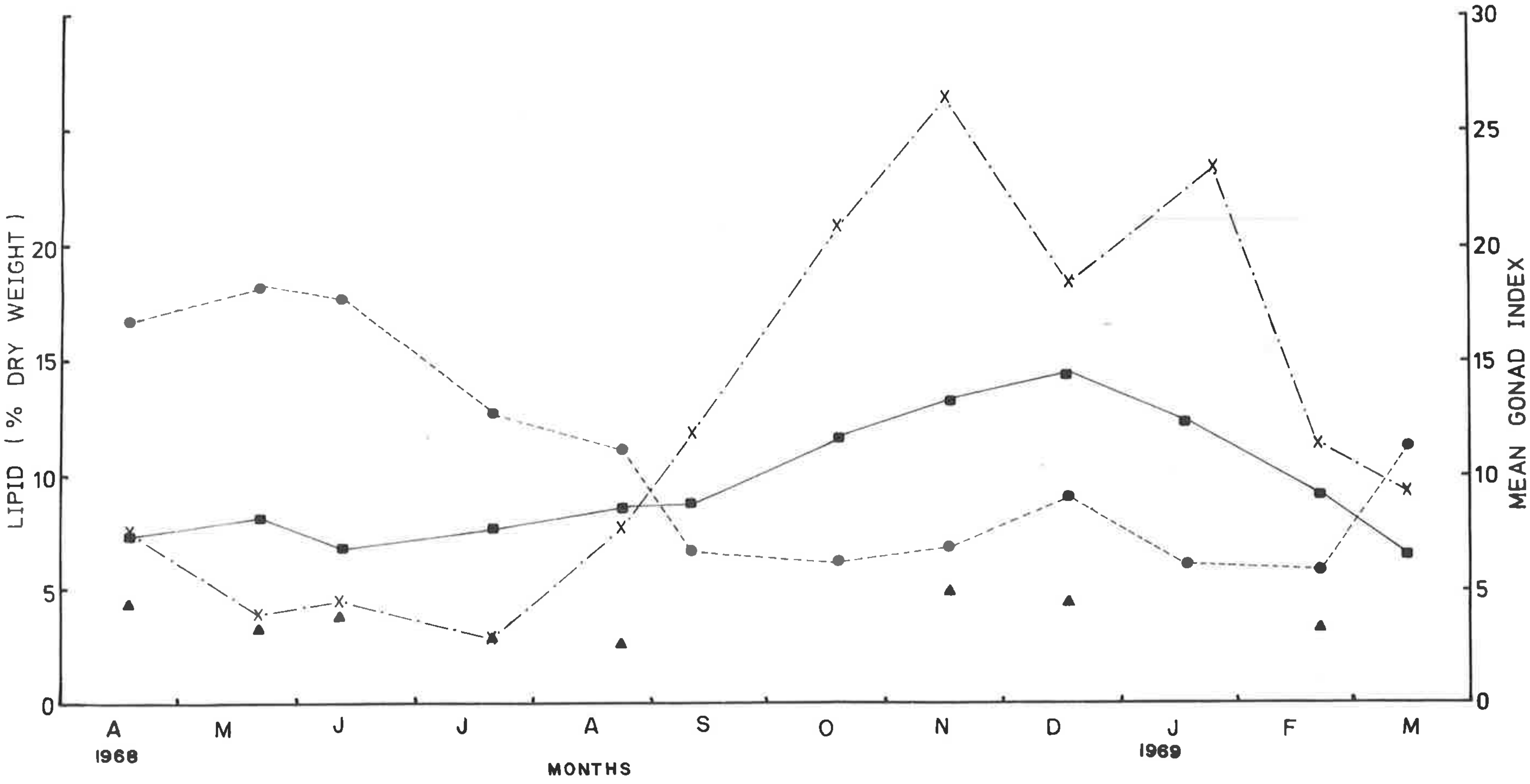
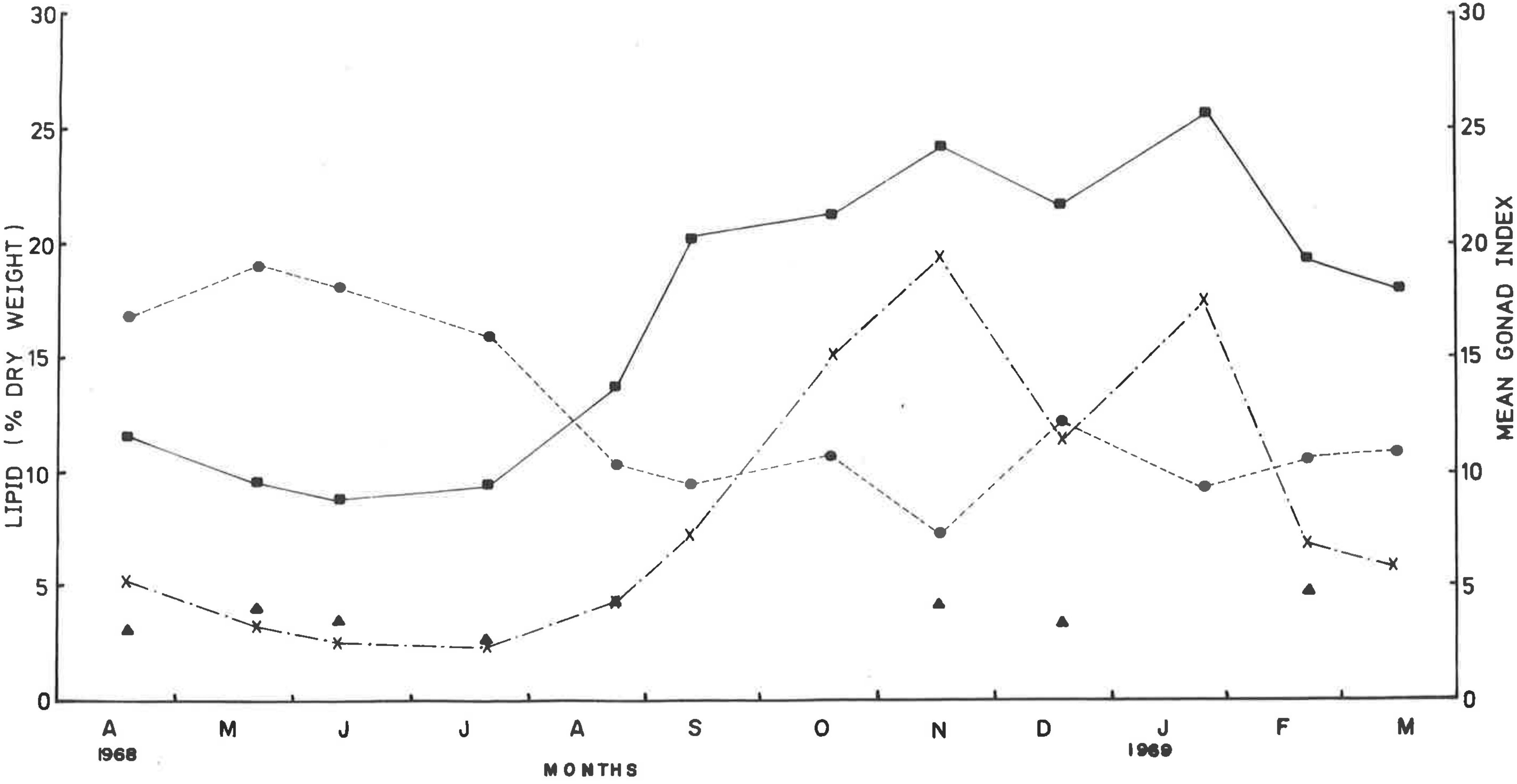

LIPID (% DRY WEIGHT)
0
5
10
15
20
MEAN GONAD INDEX
0
5
10
15
20
25
30
A
1968
M
J
J
A
S
O
N
D
J
1969
F
M
MONTHS

Figure 39. Average monthly lipid level of gonad, digestive gland, and foot muscle of female *P. macquariensis*. The reproductive cycle (monthly gonad index) is included.

Key:

●- - - - -●	Digestive gland.
■——■	Gonad.
▲	Foot muscle.
X—·—·—X	Reproductive cycle.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MEAN GONAD INDEX
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MONTHS

cative of the amount of structural lipid present in a cell. Crab muscle cells contained about 2.3% lipid per unit dry weight (Soxhlet extractable, using ethyl ether) to 5.2% (chloroform methanol - extractable). Lipid values above these amounts were therefore postulated as indicating stored lipids. Eggs of marine invertebrates are often found to accumulate stores of lipid to be used as nutritive reserves; values have ranged from 27% lipid per unit dry weight in the eggs of a sea urchin (Harvey 1956) to 14% lipid per unit dry weight in the eggs of a squid (Giese 1966b). Giese (1966a) suggested that lipids present in excess of that in crab muscle cells could be considered as reserve lipid while lipids in quantities equal to, or more than, those in marine eggs could be considered as large reserves. In the present study, the lipid level of the foot muscle was low and did not show any trend in variation. There was nothing to suggest that the foot muscle acted as a storage site for lipids. The gonad and digestive gland showed high lipid levels indicating an important role in the reserves of _Patinigera_ _macquariensis_.

It is appropriate here to comment on glycogen as a reserve material in marine molluscs. Some molluscs store large amounts of glycogen e.g. lamellibranchs and scaphopods (Masumoto _et_ _al_. 1934; Greenfield 1953; Srinivasan 1963; Giese 1966a) while others do not e.g. chitons and limpets (Barry and Munday 1959; Giese and Araki 1962; Blackmore

1969b). Giese (1966a) suggested that molluscs are probably of two kinds. Some have a prominent glycogen economy with a correspondingly lesser storage of lipid; others have a prominent lipid economy but store little glycogen. The studies by Barry and Munday (1959) and Blackmore (1969b) showed that *Patella vulgata* belonged to the second category. This suggested that the major food reserve in *Patinigera macquariensis* (also a patellid limpet) would be lipid. Although it would have been interesting to compare the seasonal levels of glycogen with the lipid levels in tissues of *Patinigera macquariensis*, the present study was confined to the expected major food reserve.

The variation in the lipid levels of both ovaries and testes showed a similar pattern to the variation in the gonad index of both females and males respectively. In ovaries, the highest lipid level occurred in the ripe condition. The lipid levels of the ovaries showed a variation in accordance with the resting, developing, and spawning stages of the ovary of the reproductive cycle (Figure 39); the lipid levels were low during the resting stage, increased during the developing stage, and fell during spawning. In the testes, the highest lipid levels again occurred in the ripe condition but the values were far below that of the females. Also, the pattern of variation in the lipid levels of testes did not show as close a similarity with the gonad index cycle as did the females. During gonadial development, the lipid levels of the testes only showed a small increase in comparison to the increase in the lipid levels of the ovaries (see Figure 38). These differences between female and male lipid levels of the gonads are understandable as more lipid would be required for storage in the eggs. In the December spawning, the lipid level of the testes actually rose. This could have been due to the male gonad storing lipids in greater quantity in tissue that was not shed at spawning (i.e. material other than spermatozoa), in contrast to the females where the greater quantity was stored in tissue to be shed (i.e. the eggs). If such were the case, a heavy spawning would increase the percentage of the extractable lipid in the male gonad. However, this view was not supported by the February percentage which decreased in line with spawning, although the February figure could have been indicative of a sharp decline in the lipid content of the germinal tissue of the testes.

Figures 38 and 39 showed that there was an inverse relationship between the lipid levels of the gonad and the lipid levels of the digestive gland of the female and, to a lesser extent, the male. Although investigation for direct evidence that lipid was transferred from the digestive gland to the gonad was outside the scope of this study, this inverse relationship suggested that the increase in lipid in the gonads during gonadial growth could occur, in part, at the expense of that stored in the digestive gland.

In investigating the lipid levels on a seasonal basis, it could be argued that any variation in the digestive gland is caused by a seasonal change in the amount of food ingested. Although no quantitative work was done on this topic, the gut of the limpets was seen to have food in it at all times of the cycle. However, it would be hard to reconcile the period of development and spawning (which in Patinigera macquariensis covers nine months) and the corresponding eight months of depressed digestive gland content, with a sustained period of decreased food intake.

The lipid levels of the digestive gland showed a similar pattern with time in both males and females. Although the lipid levels of the digestive gland in males were lower than those in females during the height of reproductive activity (September to February), the females showed a higher lipid level in the gonads during this period. This appears to be contrary to a hypothesis that lipid reserves of the digestive gland are utilized during gonadial growth. However, the mean gonad index of males was greater than that for females and thus, a comparison of lipid levels between them belied the total amount of lipid contained in the testes. From Table 34, in which the gonad index multiplied by lipid (percent dry weight) indicates the lipid content of gonads for both male and female, males still did not have as much lipid as females

Table 34. Gonad Index x Lipid Level of Gonad (% dry weight) for Limpets from the Eulittoral Zone

Month	Males	Females
April	55.5	61.2
May	31.3	33.5
June	30.5	21.6
July	22.0	23.9
August	64.6	37.0
September	102.5	147.2
October	243.0	323.1
November	351.7	471.6
December	245.7	247.5
January	217.3	447.7
February	102.2	129.8
March	58.5	107.2

during the height of reproductive activity. Materials from the digestive gland could still have been used in the manufacture of other substances for the testes, e.g. structural lipids, which as mentioned previously, were extracted at a low level here.

(h) Environment and Shell Height

(i) Materials and methods

Specimens of Patinigera macquariensis were taken from six habitats:

(1) exposed rock surfaces in the eulittoral zone on the west coast;

(2) exposed rock surfaces in the eulittoral zone on the east coast;

(3) sublittoral rock surfaces on the east coast;

(4) deep rock pools in the eulittoral zone on the east coast;

(5) high rock pools situated approximately 3.5 metres above the water-line on the east coast;

(6) diving station at a depth of 6 metres.

Plate 26A shows the sheltered aspect of a pool of habitat type 4, while Plate 26B shows heavy wave action on habitat type 2.

The shells of limpets preyed upon by Dominican gulls were also collected. These were divided into two categories: (1) shells from known Dominican feeding sites where the gulls

Plate 26.

26A. Deep rock pool (eulittoral zone) from which limpets were taken for shell height studies, (habitat 4).

26B. Exposed reef on the east coast under heavy wave action. Limpets were taken from this area for shell height studies, (habitat 2).

pecked out the flesh and left the shell behind and (2) shells from nest sites and roosting areas where the gulls regurgitated the remains, having swallowed the limpets whole.

Limpets in habitats 1 and 2 were exposed to a high degree of turbulence from breaking waves and were subjected to desiccation during emergence in sunny conditions. Limpets in habitat 3 were also exposed to a high degree of turbulence both from breaking waves and water flow; desiccation problems were minimal and would be encountered only in very extreme conditions. Habitats 4, 5, and 6 presented no desiccation problems for limpets. At a diving station situated at a depth of 6 metres, water currents were frequently strong. Habitat 4 was subjected to very little water movement from flow into the pools at high water. The pools of habitat 5 were replenished by splash during moderate to heavy seas; effect of turbulence was minimal.

Thus, the selection of these six habitats enabled the superimposing of sequences of gradations of desiccation and turbulence acting on limpets by studying the separate populations from each habitat. The effect of these gradations in environmental factors depended on the mobility of limpet populations. If limpets regularly moved from one habitat type to another, possible effects resulting from the particular environmental factors of any one habitat would be masked.

Studies on the activity and movement of populations were undertaken (sections V (b) and V (c)) and these showed that limpets tend to live in a fixed area. Movements over great distances by individual limpets were rare and, even when occurring, were usually within the same vertical zone and habitat. Limpets in rock pools in the eulittoral zone showed a very high constancy of location (see Table 30, section V (c)). Limpets in the sublittoral zone showed the greatest amount of movement. They were always in the same general area but individuals sometimes moved into the eulittoral zone above the *Durvillea* holdfast line.

No limpets from diving stations were marked but both the depth of collection and consistent heavy encrustation of coralline algae identified them and indicated their constancy of location. Encrustations of the tube-worm, *Spirorbis aggregatus*, were frequently but not always found on limpets in eulittoral rock pools.

When the existing limpet population of eulittoral and sublittoral rock surfaces was doubled by adding more limpets, the overcrowding resulted in the movement of original occupants over considerable distances, often into different habitats, see section V (c). Thus, by inducing movement between different habitats, periodic overcrowding could bring about increased variation in any phenotypic response to a factor peculiar to one habitat. Overcrowding also induced original occupants of eulittoral rock pools to migrate although mortality of those leaving was apparently high and, hence, the possibility of this resulting in a source of variation in limpet populations of other habitats was small.

A year's counting of limpets along set transects (see section V (d)) showed that there was no massive migration out of the eulittoral zone at any season. Slight differences in numbers indicated an increase in winter-spring and a decrease in summer-autumn in the eulittoral zone; this shift is discussed in section V (d). Possible reasons for this are recruitment and mortality and not migration of established adults.

Thus, the constancy of location exhibited by limpets was sufficient to validate sampling the populations from the selected habitats in order to gauge the effects on the limpets of the environmental factors characteristic of each habitat.

The variable character investigated here was shell height. As the range in length of specimens collected varied from 18 mm to 50 mm, possible differing proportions of age groups among the habitat samples had to be taken into account, i.e. those samples with a higher proportion of older shells would have a greater average height. The proportion of height to length was first considered as a measurement to compensate for differing proportions for age groups. A height index, equivalent to $\frac{\text{height}}{\text{length}} \times 100$ was used. Measurements were made with vernier calipers, accurate to 0.1 mm. Measurement of apex height was made with the jaws parallel to the breadth of the shell.

However, except for limpets from pool habitats, scrutiny of resulting measurements indicated a possible increase in height index with increase in length (i.e. age), the older the shell, the greater the height in relation to length. Scatter diagrams confirmed this and regression analysis of height index on length was applied to the measurements from all habitats and the two predation categories. The regression lines so formed would account for any growth pattern of increasing height proportion with age. Any environmental control on shell height could then be tested by looking for significant differences between the regression lines plotted for the limpets from habitat categories, these categories representing specific environmental characteristics.

(ii) Results and discussion

Table 35 gives the eight categories and the slopes of the regression lines of height indices against lengths. Tests were applied to determine possible significant differences between (1) each slope and a straight line and (2) two slopes in all paired combinations. Snedecor (1956, p. 125 and p. 136) gives the appropriate t-tests for each case. Results of these tests are included in Table 35.

Table 35. Regression analysis of shell heights of *Patinigera macquariensis* from eight categories (six habitats and two types of predation).

Sample category	N	Slope of regression line	*Results of significance tests: Each slope against a straight line	Slopes of all categories against each other						
1. Eulittoral West Coast	50	0.386	/	1vs2 x	1vs3 x	1vs4 /	1vs5 /	1vs6 /	1vs7 /	1vs8 /
2. Eulittoral East Coast	102	0.308	/		2vs3 +	2vs4 /	2vs5 /	2vs6 /	2vs7 /	2vs8 /
3. Sublittoral East Coast	41	0.481	/			3vs4 /	3vs5 /	3vs6 /	3vs7 /	3vs8 /
4. Deep Rock Pools Eulittoral East Coast	35	-0.072	x				4vs5 x	4vs6 +	4vs7 x	4vs8 /
5. High Rock Pools East Coast	23	-0.008	x					5vs6 /	5vs7 x	5vs8 /
6. Diving Station East Coast Depth of 6 m	134	0.174	/						6vs7 +	6vs8 /
7. Predation - Regurgitations	127	0.091	x							7vs8 /
8. Predation Pecked out	95	1.448	/							

*Significant difference (P < 5%) No significant difference (P > 5%)

When applied to testing slopes against each other:
/ = significant = both t values significant
x = not significant = both t values not significant
+ = applies only in testing slopes against each other when one t value significant, the other not.

In testing the slopes against each other, the difference between two slopes was divided by the Sb value for each slope thereby giving two t-values. Both t-values were considered in determining significance in order to allow for two slopes being tested against each other and not one slope against a whole number. For the combinations 2 v.3, 4 v. 6, and 6 v. 7, one t-value showed a significant difference at the 5% probability level, while the other t-value did not; significance here was regarded as marginal. In 2 v. 3 and 4 v. 6, large variance about the slopes of 3 and 4 (as shown by high Sb^2 values) reduced the second t-value in each case.

In all categories, the samples comprised post-juvenile specimens and therefore, regression lines only refer to shell growth in adults. The significant slopes and the significant differences between them suggested environmental control of shell form. The regression lines for samples from rock pools did not differ significantly from a straight line and the height index did not increase with length, i.e. age. The greatest increase (the largest slope) occurred in the sample from the sublittoral zone followed by, in descending order of magnitude: eulittoral zone (west coast), eulittoral zone (east coast), diving station. The slope for the diving station sample was significantly different from these other three. It was also significantly different from the high rock pools and marginally so from the deep rock pools in the eulittoral zone. Because desiccation had minimal influence on limpets from the sublittoral zone (largest slope) and none on those from both rock pools and the diving station (between which there was a significant difference), a greater shell height was not related to desiccation. However, it was correlated with an increase in water turbulence.

Few conclusions could be drawn from the predation samples. It was evident that different sized limpets were not treated the same by the Dominican gulls. Only small limpets were wholly swallowed and later regurgitated. Both small and large limpets were pecked out and the shells left behind. The slope of the regression line for the regurgitated limpets did not differ significantly from zero but the sample was restricted to a small size range which was probably not sufficient to indicate increasing height indices with age. The large slope for the pecked-out limpets showed that they definitely came from eulittoral or sublittoral areas.

Variation in shell heights of Patinigera macquariensis were noted by Dell (1964) when examining collections from Macquarie Island and he suggested that these differences might be ecologically controlled. Variation in shell heights of Patella vulgata have been noted by Russell (1907), Orton (1929, 1932), and Moore (1934b). It was found that the shells of adult limpets living on the upper shore were higher than those of individuals near the low water level or in rock pools. Orton (1932) correlated higher shell types with desiccation. He suggested that limpets inhabiting higher levels would hold their shells closer to the substrate to prevent drying out. The stronger grip pulls in the mantle which secretes new shell at its margin. Hence, a smaller peripheral increment of growth will be made and continued growth will consequently result in a steeper shell.

Correlation between shell heights of *Patinigera macquariensis* and water turbulence contrasted to Orton's suggestion that in *Patella vulgata*, wave action had negligible effect in the causation of shell shape although Orton recognized that wave action would also cause a limpet to adhere more firmly. This would have the same effect on shell growth as desiccation. The shell height of a limpet is probably the overall result of the degree to which it holds to the substrate. Orton's conclusions can only be interpreted as reflecting the greater importance of desiccation on *Patella vulgata*. It appears as though water turbulence is of greater importance in affecting the shell shape of *Patinigera macquariensis*.

VI. DISCUSSION: FACTORS LIMITING DISTRIBUTION

Macquarie Island experienced weather that, severe by temperate coastal standards, was quite equable. Such climatic conditions as 10°C with sunshine and -8.9°C with driving snow were extreme. A more stable environment could alter the importance of both physical and biotic factors likely to limit the distribution of species. For example, from studies of the benthic faunal zonation in the Antarctic, Dayton et al. (1969), found that, in proceeding from 0 to beyond 33 metres in depth, physical stability increased as did diversity and abundance of the fauna; biological interactions were more obvious. Dayton et al. suggested that, with a stable environment and a relatively homogeneous substrate, biological interactions would be most important in the evolution and maintenance of the benthic community. The physico-chemical environment of the littoral and sublittoral zones of Macquarie Island rocky shores was fairly stable, variability increasing toward the littoral fringe. This provided the opportunity to determine (i) how physical and biotic factors affected the distribution and abundance of animals and (ii) whether separate factors had the same effects as shown by studies in temperate regions where climatic conditions are more variable.

Much attention has been directed to the causal relations of abundance and distribution of littoral molluscs in other climatic regions (particularly cool temperate). Fretter and Graham (1962, p. 477) concluded that "the evolution of the ability to endure variations in temperature, light, humidity, and salinity allowed the prosobranchs to escape from the sub-littoral areas and colonize the beach". They further suggested that their distribution is governed by the extent to which their emancipation has proceeded, while certain pre-adaptions, anatomical and behavioural, must have speeded this evolution. Their summary considered only physical factors. Chemical and biotic factors such as pH, food, predation etc. were neglected, though these may also affect distribution.

Studies on distributional limits and abundance of molluscs can be broadly grouped into two categories:
(1) those dealing with the effects of only one (rarely more) environmental factor on a range of species e.g. (a) physico-chemical factors (Broekhuysen 1940; Evans 1948; Southward 1958; Meyer and O'Gower 1963; O'Gower and Meyer 1965, 1971; Micallef 1966) and (b) biotic factors (Burrows and Lodge 1949; Southward 1956; Lodge 1958; O'Gower and Meyer 1965).
(2) those dealing with the effects of several factors on one species e.g. (a) environmental factors (Lewis 1954; Newell 1958a, 1958b; Evans 1961, 1965; Davies 1967a, 1967b) and (b) environmental factors together with physiology and/or life history, often as part of a population dynamics study

(Frank 1965; Phillips 1969; Sutherland 1970).

Studies from category (1) mainly investigated a factor affecting all species to different degrees, the sequence of which was compared with the limits of distribution; the strength of any resulting correlation indicated the importance of the factor in limiting distribution. Physical factors were often assessed by comparing physiological tolerances with environmental conditions. However, each physiological aspect was individually related to the environment and not in combination with others.

Although studies in category (2) provided more scope for assessing the importance of combinations of the effects of possible limiting factors, such factors were still largely considered separately. In contrast, Sandison (1967) studied (a) respiratory responses of littoral gastropods in conjunction with temperature tolerances, and (b) the increased effects of desiccation on the animals at temperatures inducing coma. Other studies seek explanations of distributional limits in terms of lethal points for each separate factor under study. The combination of sub-lethal effects of more than one factor have rarely been taken into account. Previous studies of population ecology have covered many aspects (behaviour, physiology, life history, and associations with environmental conditions) but these mainly deal with events within the population structure and rarely deal with limits of distribution. If it is assumed that there is a constant population pressure leading to exploration and marginal expansion (i.e. over-reproducing to effect spatial population increase), the factors limiting this expansion need further investigation.

Determination of limiting factors for littoral invertebrates is complex. Attempts at explanations have been summarized by Barnes (1969). The selection of one factor for study as a simplified basis of investigation tends to be biased and of limited value. To attempt an assessment of all factors is impracticable but *a priori* probables can be selected for a study of their individual effects and of the interplay of combined effects. In the present study, such a method was used and applied to six species of grazing molluscs.

Laboratory experiments were used to test studies made in the field. Too often, experiments on physiology are conducted in the laboratory and the results secondarily related to known or measured environmental factors. Such an approach can overlook the effects of separate factors acting together in the field to limit distribution. Prior detailed observations would give insight into the existence of such combinations.

The distributions of the molluscs have been plotted in relation to the universal zonation scheme of Lewis (1964) which has been adapted for the Macquarie shore (section III (b)). The zones in such a scheme are representative of ecologically distinct areas; thus, distribution was set to an ecological pattern. The six sub-zones on Macquarie shores, i.e. Lichen, Porphyra, Bare, Upper Red, Kelp, Lower Red, were also used in plotting the distributions of molluscs as these sub-zones were placed within the universal zonation scheme by determining which boundaries were common to both schemes.

The limits of distribution for different species were shown to vary. Of particular interest here, was the difference found in the upper limits recorded in the littoral and sublittoral zones. Abundances of each species within its distribution varied. This was associated with habitat differences. For example, numbers of P. macquariensis decreased with heavy Durvillea cover while numbers of H. setulosum increased; the numbers of K. lateralis increased in areas of creviced, rocky substrate apparently because of the availability of crevices as retreats during dry weather.

The investigations were conducted on adult molluscs as it was not intended to compile the effects of environmental factors on the different stages of development in the life cycle of each species but to ascertain the factors determining the extent of invasion of adult molluscs into the littoral zone. The degree of tolerance of marine invertebrates to physico-chemical factors may change during ontogeny. In terms of tolerances to abnormal salinity and temperature, it is often smaller in gametes and developmental stages than in the adult (Kinne 1964, 1970). Studies in resistance to desiccation have also shown a similar difference in tolerance between juveniles and adults (Newell 1970). Because of the lower resistances of juveniles to adverse environmental factors, their limits of distribution would be narrower.

However, even if recruitment zones were restricted to areas where conditions were less rigorous, the adult molluscs studied here could invade other areas. After such movement, the adults could still contribute reproductively to the population (e.g. spawning during high tides or during heavy wave action). If the molluscs laid eggs or brooded young and if the young were less resistant to environmental hazards, the adults would have to return to recruitment areas to either lay egg cases or release juveniles from a brood. Such behaviour would allow the adults to make more use of the habitat rather than be restricted in distribution to an area of recruitment. In other studies, littorinids especially have shown movement to particular areas for reproductive purposes. Living normally in the littoral fringe, some littorinids exhibit a seasonal migration downshore for the breeding season (Lebour 1945; Kojima 1958; Fretter and Graham 1962, p. 387).

The studies on the reproduction of the molluscs (sections

IV 1. (e) and V (f) showed that K. lateralis laid egg cases; H. setulosum brooded young; and P. macquariensis, P. aurata, and C. (P.) coruscans released gametes into the sea. Indirect evidence suggested that L. caliginosa laid egg cases.

The egg cases of K. lateralis were laid mainly in crevices. On hatching, the juveniles would be subject to less rigorous environmental conditions in such areas. Although adult siphonarids were found in crevices during dry weather conditions, during the more frequent conditions of wet weather and/or wave splash they were to be found in other open areas. It appeared that the mobility of the adults allowed them to graze a wide area and to return to crevices for protection against adverse environmental conditions and for egg-laying. Collections of H. setulosum did not show any bias to a particular area for brooding females, indicating that there was no restricted recruitment zone. The range of H. setulosum was not large, being mainly confined to the Kelp Zone. Although other factors (e.g. desiccation, salinity, food preference - see later in this discussion) contributed to the setting of the upper limit of distribution of H. setulosum, the brooding habit and lesser mobility of the chitons could have also resulted in their closer restriction to areas where juveniles can be successfully released.

Table 36 summarizes results from previous sections. Anatomical limitations alone precluded C. (P.) coruscans from

Table 36. Summary of factors of possible significance in limiting distribution.

Species	Body form suitable for emergence	Type of algae eaten	Predators	Effect of *Durvillea* removal on density	Tolerance to:			
					High Temp.	Low Temp.	Low Salinity	Desiccation
K. lateralis	Yes	Encrusting			High	High	High	High
L. caliginosa	No	Encrusting Frond- (minimal)	Birds Starfish- (minimal)		Medium	High	High	Low
P. macquariensis	Yes	Encrusting	Birds Starfish	Density increases	Low	High	High	High
P. aurata	Yes	Encrusting	Birds		High	Medium	Medium	Low
H. setulosum	Yes	Encrusting		Density decreases	Medium	Medium	Low	Low
C. P. coruscans	No	Frond	Birds Starfish		Low	Low	Low	Low

emerged rock surfaces where the trochids had difficulty both in attaching properly and in moving freely. Also, at such times, they were subjected to predation by birds. Their low tolerance to desiccation was not suitable for living in emerged areas. In addition, the trochids did not completely close their opercula in any situation and always endeavoured to attach to the substrate. Such behaviour would increase water loss from the body surface. The trochids fed on frond algae rarely found in high pools. Their temperature and salinity tolerances also showed that they were physiologically unsuitable for living in such pools. They had a low tolerance to prolonged exposure to high (yet sub-lethal) water temperatures, as could be found in high pools. Low salinity and/or high temperature weakened them and caused loss of adherence within a short space of time, thus rendering them liable to predation by birds or isopods. C. (P.) coruscans were unsuited for successful invasion of the littoral zone.

The littorinids (L. caliginosa) were characteristically found in rock pools and under stones in the eulittoral zone. This habitat reflected the physiological tolerances of the littorinids. They had adequate tolerances to high and low temperatures and low salinity but had a low tolerance to desiccation. Thus, although L. caliginosa had a high zonal level, the dangers of desiccation were reduced by the moist habitats. The food preference (encrusting film of algae and diatoms) of the littorinids was suitable for their living in such habitats as green algal film and diatoms formed the main cover of rocky surfaces. L. caliginosa had a shell with a high-spired whorl. Although the importance of this factor was not assessed, it may have been disadvantageous to free movement in emerged situations during periods of wave action.

The other molluscs (K. lateralis, P. macquariensis, P. aurata and H. setulosum) were anatomically suited to living in emerged conditions. The adhesive power of the limpet and the two chitons was strong, particularly the former. The attachment of specimens of K. lateralis was weaker when tested by dislodging with the hand. The siphonarids were shown to favour crevices or fragmented rock surfaces. They packed tightly into crevices when emerged during sunny weather (see Plate 4B, section I (c)). Movement away from these crevices on to smooth rock surfaces was made during moist conditions but, during periods of extreme wave action they kept to the fragmented and creviced surfaces. The behavioural adaptation to use crevices in the eulittoral zone probably compensated for the lesser degree of grip of K. lateralis and reduced the detrimental effects of temperature and desiccation whilst emerged. As previously mentioned, K. lateralis laid egg cases predominantly in crevices. However, because the mobile adults could move into other areas, this restricted recruitment zone was not limiting on the distribution of adult *K. lateralis*. The siphonarids were physiologically suitable for distribution high in the littoral zone. Deaths in the field occurred apparently from the combined effects of high temperature and desiccation when they were situated on fragmented rock surfaces in the *Porphyra* Zone during extreme conditions of sunny weather in summer. *K. lateralis* were found in high pools. However, they were absent in pools (or sections of pools) situated in the upper eulittoral and the littoral fringe where high alkalinity ($pH = 10$) was often recorded. Typically these pools contained only *Enteromorpha* sp. (alga), amphipods, and *Tigriopus angulatus* (copepod). Although the absence of *K. lateralis* could be correlated with high alkalinity, no causal relationship was tested experimentally. Though readily available, *K. lateralis* were not taken by avian predators. Dominican gulls were not observed feeding on them nor did remains and regurgitations at roosting areas and nest sites include their shells. This was confirmed by data recorded by Merilees (pers. comm.).

The chitons (*P. aurata*, *H. setulosum*) showed tolerances to increased temperatures comparable with those shown by *K. lateralis* and *L. caliginosa* which had a higher upper limit of distribution. However, their tolerances to low salinity and especially to desiccation were poor; these tolerances may have contributed to their exclusion from pools and rock surfaces respectively, high in the eulittoral.

The lack of *Durvillea* cover was limiting to *H. setulosum*. Their small size, close apposition to the substrate, and food preference (coralline algae) made more favourable the area of *Durvillea* holdfasts. *H. setulosum* often occupied an indentation in the coralline algae, though conclusive evidence of homing was not obtained. As previously mentioned, the brooding habit together with (a) no apparent migration by adults to release young and (b) the lesser mobility of the chitons, would restrict the distribution of *H. setulosum* more closely to areas suitable for juvenile recruitment, which were likely to be narrower than areas suitable for adults. The combination of a food preference for coralline algae, lack of *Durvillea* cover causing a marked decrease in abundance, reproductive habit, and mobility made up a strong set of biotic factors limiting the upper distribution of *H. setulosum* to the Kelp Zone. Predation by birds or starfish was not evident.

The density of *P. aurata* per square metre was not great at or above the *Durvillea* holdfast line, though they were more abundant in deeper water (section IV 1. (a)). These large chitons showed a preference for coralline algae in the field but survived on algal film common to the eulittoral zone; so, with respect to food, they would appear to be capable of living in the eulittoral zone. Physiologically, the low salinity tolerance of *P. aurata* limited their occupation of rock pools high in the eulittoral. They were commonly found in large, deep rock pools in the lower eulittoral where physico-chemical conditions were stable. As mentioned previously, their low tolerance to desiccation appeared to limit their upper distribution on rock surfaces. In addition, it appeared that the lower density of *P. aurata* in the eulittoral compared to the lower sublittoral and diving stations resulted from heavy predation by birds. Although *P. macquariensis* outnumbered *P. aurata* by from six to nineteen times in the upper sublittoral and eulittoral zones (section IV 1. (a)), Dominican gulls took approximately equal numbers (Table 19, section IV 1. (d)). Both species seemed to be equally visible and it was unlikely that a taste preference was involved. The higher proportion of *P. aurata* in the Dominican diet may be due to the greater ease with which the gulls could remove the chitons. Lesser holding power of the foot and/or the comparative softness of the girdle could have facilitated their removal. Although no figures are available for predation by wekas, they were observed preying on both limpets and chitons. Table 37 summarizes the predation of *P. aurata* and *P. macquariensis* in different localities.

Patinigera macquariensis could feed on algae present in the eulittoral and sublittoral zones. The limpets had a high tolerance to water loss and there was a suggestion of a

Table 37. Field observations of predation on *P. aurata* and *P. macquariensis*.

Location	*P. aurata*		*P. macquariensis*	
	*Average Density	Predators	*Average Density	Predators
Rock pools:				
a. large, in higher eulittoral	None		7/sq.metre	Isopods Dominican gulls Wekas
b. small, in lower eulittoral	None		21/sq.metre	Isopods At pool periphery: Dominican gulls, Wekas
c. large and deep, in lower eulittoral	6/sq.metre	At pool periphery: Dominican gulls Wekas	37/sq.metre	At pool periphery: Dominican gulls, Wekas
Rock surfaces:				
a. lower eulittoral (Upper Red Zone)	1/sq.metre	Dominican gulls Wekas	19/sq.metre	Dominican gulls Wekas
b. sublittoral (Lower Red Zone) and at depths of 3 to 10 metres	4 to 5/ sq.metre	No known predator	38 to 41/ sq.metre	Starfish

* Average densities are taken from (i) the counts of molluscs in pools in section IV 1.(a), and (ii) the densities of molluscs along vertical transects (section IV 1.(a)).

phenotypic increase in this tolerance for those located at the upper margins of their distribution. In contrast, tolerance to high temperature was not greater for limpets in such areas. High temperature could be lethal at the upper range of their distribution both in sustained submerged conditions and in combination with desiccation. More important was the sub-lethal temperatures often reached in nature which could result in coma and subsequent predation, especially by the isopod, E. gigas. The tolerance to low salinity for P. macquariensis was high. Limpets could physically cope with the dilution stresses likely to be encountered in high rock pools, but their narrow temperature tolerance precluded them from pools supporting populations of K. lateralis and L. caliginosa, which had higher temperature tolerances. Healthy specimens of P. macquariensis were subjected to predation in the eulittoral and sublittoral by birds and in the sublittoral and below by starfish (see Table 37). Whether numbers lost to these two different types of predators were similar would be largely speculative here. The effects (both proximate and ultimate) of increased temperature through radiation were apparently the most important factors limiting the upper distribution of P. macquariensis.

Thus, in all the species of molluscs, no one factor was found to limit the upper distribution and different factors varied in their importance for each species. Particular combinations of factors, both physico-chemical and biotic, were found to be limiting though each factor (or its level of adversity) was not limiting in itself e.g. K. lateralis: high temperature + desiccation; P. macquariensis: high temperature + predation, high temperature + desiccation; H. setulosum: brooding reproductive habit + low mobility; C. (P.) coruscans: lack of holding power when emerged + predation, high temperature + predation. Such combinations emphasized the danger of attributing too much interpretation to results from a study of one particular factor in limiting the distribution of a littoral species. The tolerances of the study molluscs to physico-chemical factors had a similar pattern as those of molluscs in the littoral zones of other climatic regions i.e. a sequence in physiological resistance corresponded to a zonal sequence (or, in some cases, a habitat preference) with a wide safety margin from conditions that were immediately lethal. However, biotic interaction had increased emphasis in this study as shown by the predation on molluscs weakened by conditions far below immediate lethal points.

APPENDIX I

(i) Introduction

In proceeding from lower to higher latitudes, the reproductive habits of littoral marine invertebrates show a tendency towards a protective form with the loss of a free-swimming larval stage i.e. egg cases, brooding (Thorson 1950). Thorson has suggested advantages of such reproductive habits to marine invertebrates living in colder climates e.g. 1) no larval stage to be exposed to the harsher climate, 2) no dependence of larvae on the seasonal phytoplankton blooms. However, this phenomenon still requires further evaluation and empirical data are required.

At Macquarie Island, a number of invertebrates (mainly molluscs and echinoderms) were collected in order to describe their reproduction. The type of reproductive development (i.e. whether by external larvae, egg case, or brooding) was examined in each species. Besides the collection of empirical data on this topic, a further aim was to describe hitherto unknown reproductive cycles of some of the species. Animals which had been reported as brooding in previous collections from Macquarie Island were included in the study.

(ii) Materials and methods

The methods of preservation were essentially the same as those outlined in section IV 1. (e) on the reproduction of the study molluscs. Briefly, immediately after collection, all specimens were preserved in formaldehyde-based solutions for later examination. Before the animals were dissected, they were transferred to a glycerol-alcohol mixture. (The composition of these preservatives is outlined in section IV 1. (e).)

The collecting procedure differed from section IV 1. (e) in that not all the species listed in this appendix were investigated for reproductive cycles. In such cases, samples were not taken over a full year and only a small number of specimens were taken. For the determination of the reproductive cycle of a species, specimens were collected at monthly intervals over a period of one year. In these cases, the sites for each collection were kept within narrow limits and were positioned with reference to the local sub-zones. The range of distribution and habitat of each species were also noted and these, together with the area of collection, are described in the "Results and discussion".

The methods of describing reproduction were the same as that used in section IV 1 (e) i.e. (1) egg sizes; (2) the state of gonads and of broods; (3) observations of egg cases laid in the field; and (4) gametogenic activity (particularly spermatogenesis) determined by microscopical examination of smears of gonadial tissue.

The taxonomic authorities for the species studied here are given by Dell (1964) - molluscs; Clark (1962), Koehler (1920) - starfish; Pawson (1968) - holothuroids; Koehler (1926) - echinoid; and Carlgren and Stephenson (1929) - coelenterates.

(iii) Results and discussion

MOLLUSCA
Cl. Gastropoda
F. Littorinidae

Macquariella hamiltoni (Smith)

M. hamiltoni were abundant on the fronds of red algae in the lower eulittoral and the sublittoral zones. These littorinids were uncommon on bare rock surfaces or underneath stones in rock pools. Specimens were collected from algal fronds in the Upper Red Zone, i.e. in the lower eulittoral.

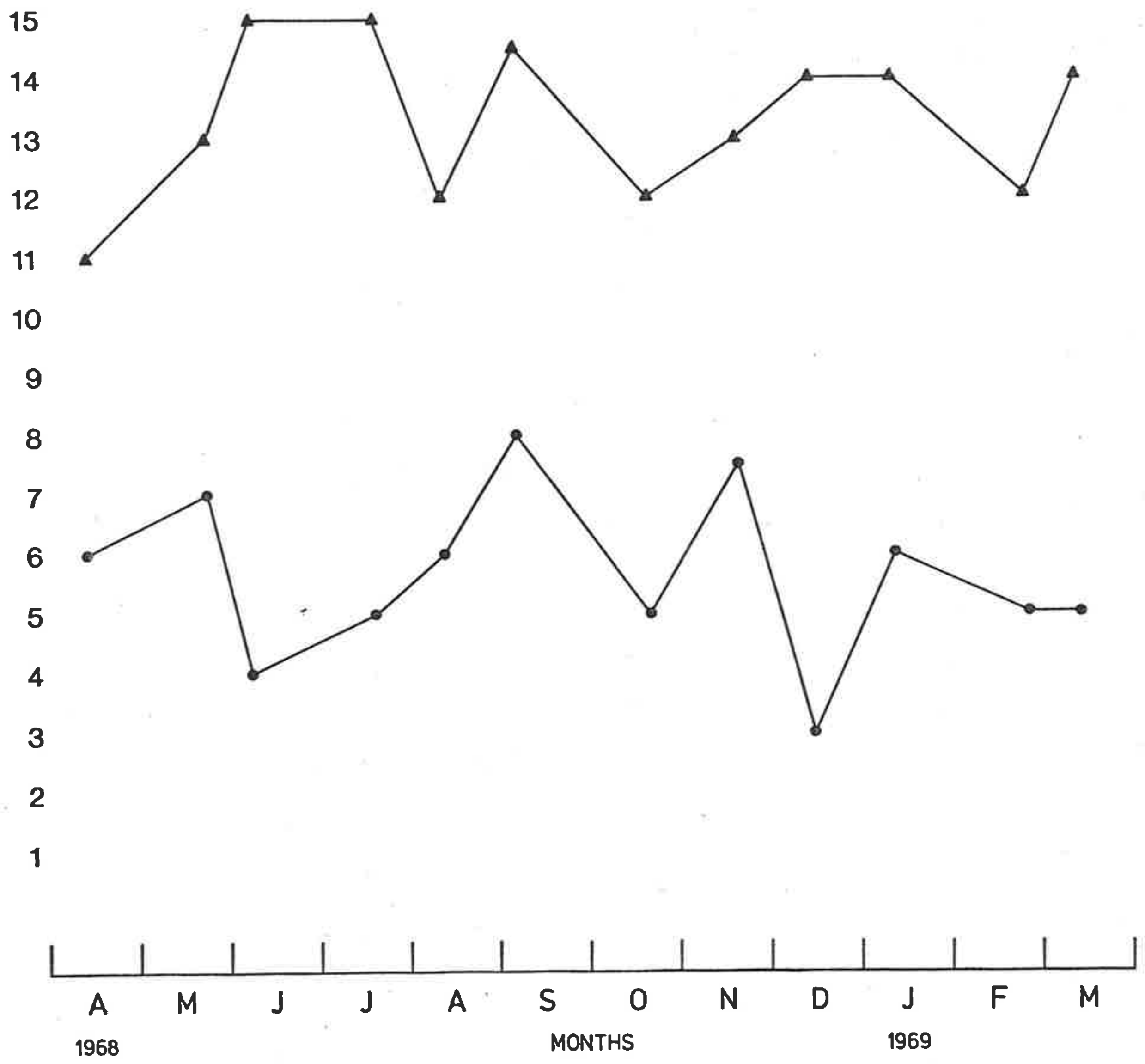
It is a small species; the length from the apex to the outer lip of the mouth of the shell of the largest adult was 4 mm. Their abundance enabled sufficient specimens measuring 3 to 4 mm in this dimension to be collected for reproductive studies.

In *M. hamiltoni* the sexes were separate, the male being easily distinguished by the relatively large penis behind the right tentacle. The gonad was alongside the digestive gland and occupied the apical section of the visceral mass.

Figure 40 shows the monthly reproductive condition of

Figure 40. Monthly reproductive condition of *Macquariella hamiltoni*.

Females: (N = 10, each month)	▲——▲	average number of mature eggs per individual.
Males: (N = 10, each month)	●——●	number with an abundance of mature spermatozoa in the testis.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M. hamiltoni over a period of one year as depicted by two features: (1) the average number of mature eggs in the ovaries per individual female and (2) the number of males with an abundance of mature spermatozoa in the testes.

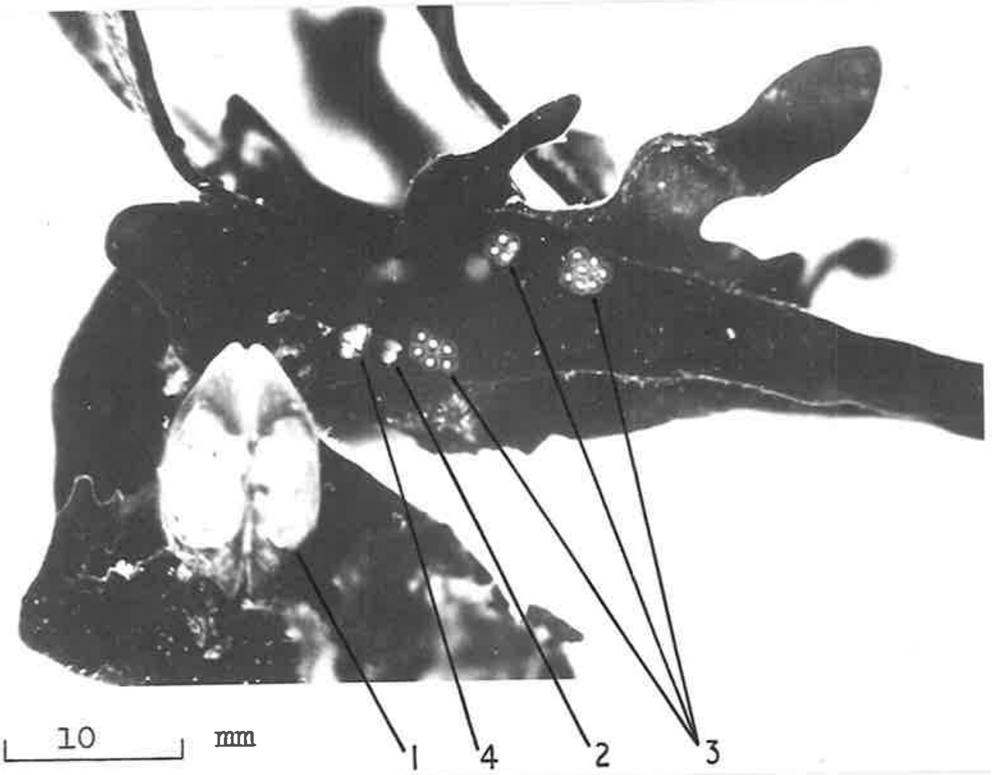
In females, a small number of mature eggs were present at each month. The number of eggs in any specimen varied from nine to eighteen, the size range being 100 µm to 200 µm. The dissections showed that embryos were not retained or brooded. The small number of eggs indicated that egg cases were laid and there was reasonable evidence to support this. Although M. hamiltoni were not observed laying eggs, red algae to which egg cases were attached were frequently collected and the only molluscs on the algae were adult specimens of M. hamiltoni. The most frequent deposition site for these egg cases was on the stipes of the alga near the holdfast. The narrowness and close proximity of the stipes suggested that the egg-layer was a small mollusc. Where developing embryos had proceeded to a juvenile stage, the shape and arrangement of the spire resembled that of M. hamiltoni. The eggs were laid in one-layered clusters of 4-10, usually 7 (see Plate 27).

In males, mature spermatozoa were common at any month and these were aggregated into clumps. No appreciable seasonal differences in either numbers of mature spermatozoa or spermatogenic activity could be detected.

Plate 27.

Frond of red alga from the sublittoral supporting:

1. adult *Gaimardia t. coccinea*.
2. released juvenile *Gaimardia t. coccinea*.
3. egg cases of *Macquariella hamiltoni* (early stage).
4. egg cases of *Macquariella hamiltoni* (late stage).


10 mm
1
4
2
3

From the dissections, it appeared as though the production of spermatozoa and eggs was constant throughout the year. However, egg cases appeared to be more common on red algal fronds in the spring and summer months, but this was only a subjective assessment as no quantitative survey was done on the algae and the fronds were under less scrutiny at the start of collections, i.e. in the autumn and winter months.

The reproduction of M. hamiltoni was similar to that for L. caliginosa (also F. Littorinidae, see section IV 1. (e)).

Cl. Lamellibranchia
F. Gaimardiidae

Gaimardia trapesina coccinea Hedley

G. t. coccinea were found attached by byssal threads to fronds of red algae in the lower eulittoral and the sublittoral zones. Their distribution was not uniform in these zones; they were also abundant in the Macrocystis algal beds about 250 metres offshore on the east coast (as shown by collections during ship to shore transit). Specimens for reproductive studies were collected from the top of the sublittoral zone. Only those with a minimum shell valve length of 1 cm were used in order to ensure that the animals were sexually mature.

In G. t. coccinea the sexes were separate. The gonad was situated lateral-dorsal to the foot, on both sides. Figure 41 shows monthly reproductive conditions in both males

Figure 41. [*]Monthly reproductive condition of *Gaimardia t. coccinea*.

A. Females:

(N = 5, each month)

X = very reduced brood, indicating release of juveniles
▲ = mainly red juveniles in brood
△ = mainly pale embryos in brood
○ = mainly eggs in brood
□ = no brood

B. Males:

(N = 5, each month)

X = spawning
● = ripe
○ = abundance of spermatids
■ = early spermatogenesis
□ = regressed
▲ = resorbing

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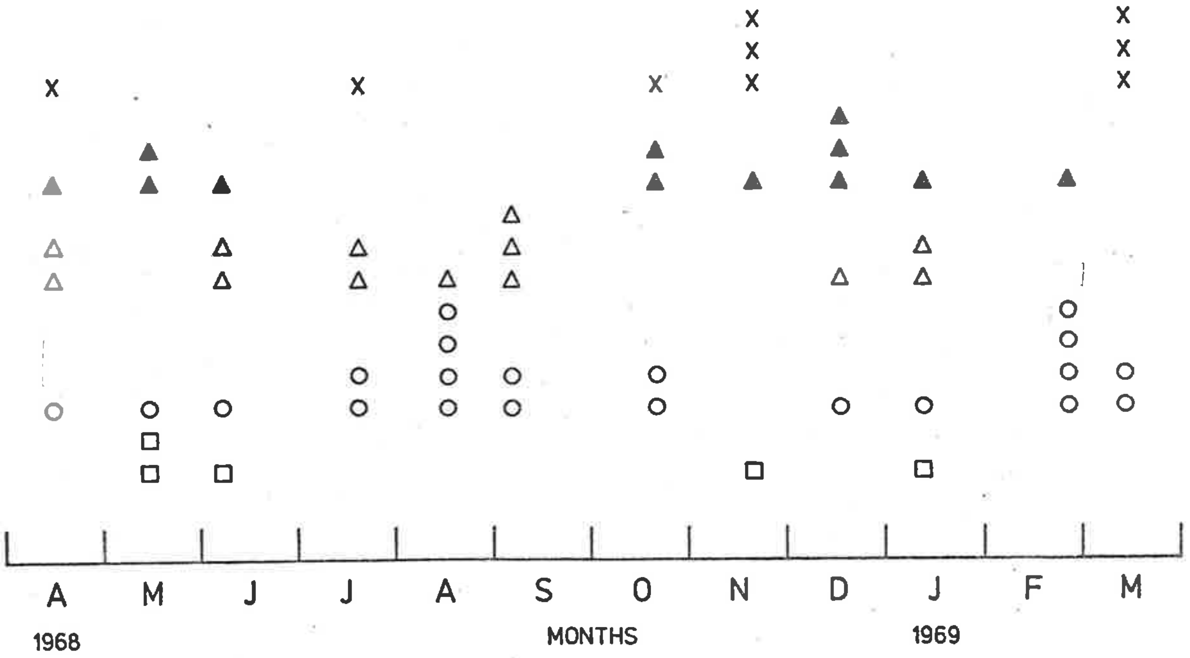
[*] A symbol is used to designate the predominant condition of the brood (females) or the testis (males) of each specimen. Sets of symbols are separated horizontally on the figure.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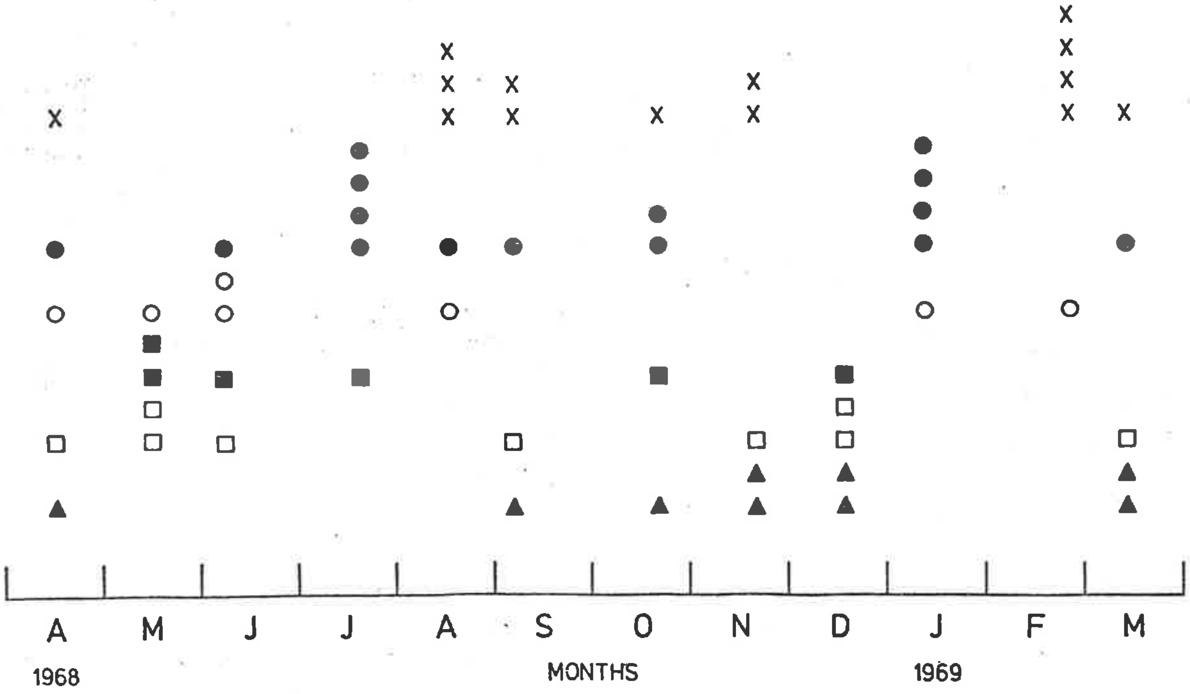
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and females. Symbols were used to designate particular states of the testes in the males and of the brood in the females. Sets of each symbol were separated horizontally on the figure. The monthly state of the testes (from microscopical examination of a smear of tissue, size, and turgidity) was used to determine the reproductive cycle of the species. Although the cycle was not well defined, there were two main breeding seasons - one in late winter, the other in late summer. In females, the monthly state of the brood was examined in order to determine any pattern in juvenile release.

In the males, the testes consisted of a branched network of tubules. When ripe, the testes were enlarged and extended over three-quarter the length and half the height of the animal on both sides; slide smears of these testes showed a predominance of mature spermatozoa. Spawning was indicated by a softer texture and a reduction in size of the tubules. The reduction of the tubules continued into a resting stage. A developing testis had enlarged tubules and slide smears showed a predominance of spermatogenic activity.

There were two peaks for ripe testes, in July and January, with spawning following each peak. The breeding season following July appeared to be more protracted than that following January. There was also a low level of breeding activity throughout the year as shown by the occurrence of males with ripe or spawning testes.

The female brooded its young to a well-developed juvenile stage in the interlamellar spaces of both the inner and outer demibranchs of the gills. Although not actually observed, it appeared as though the juveniles were released on to the algae in a clump of mucus, many such clumps being found. This would be more advantageous for settlement than being released to the open sea as Gaimardia attached by byssal threads to algal fronds subjected to almost constant wave action. Plate 27 shows two recently released juveniles, free of mucus, alongside an adult on a red algal frond.

Eggs were transferred to the gills where development proceeded through a pale, embryonic stage to a red, well-formed juvenile. (Adults were red.) The average sizes for these stages in the gills were: eggs - 0.4 mm, pale embryos - 0.6 mm, and red juveniles - 0.8 mm. The brood contained a large number of developing young; in broods from which juveniles had not recently been released, the number ranged from 430 to 500. The size of the brood was probably dependent on the size of the adult.

As the main spawning periods of the males (August and February) corresponded to an increase in the number of females with a predominance of eggs in the gills, it appeared as though fertilization occurred just after the eggs were transferred to the gills, i.e. females spawned into their gills for breeding.

A pattern to the progression of development in the gills and the release of juveniles was not well defined. There were two peak releases of juveniles in November and March, but these did not show a time sequence with the peak occurrences of eggs in the gills in August and February. The length of time for development from egg to red juvenile was obscure. Although one particular stage (egg, pale embryo, or red juvenile) was predominant, each brood almost always contained all three stages. This suggested that eggs were spawned into the gills of the one individual at all times of the year with an increase in this spawning at two half-yearly breeding seasons. This suggestion was further supported by the low level of breeding activity throughout the year as shown by the occurrence of females with a predominance of eggs in the gills. (The males also showed a low level of breeding activity throughout the year.)

Kidderia bicolor (Martens)

Specimens of *K. bicolor* were collected from crevices in the Bare and Upper Red Zones. This species was small; the average length of the shell of those examined was 4.5 mm.

The young developed to a well-formed juvenile stage in a brood in the interlamellar spaces of both the inner and outer demibranchs of the gills. Usually, a brood consisted of eggs, embryos and juveniles. The average length of a juvenile was 0.8 mm and the average number of all stages in a brood was 12, six on each side of the adult. The brood would have been restricted to such a number by size (cf. the brood of *Gaimardia t. coccinea*).

F. Erycinidae

Lasaea rossiana Finlay

Specimens of *L. rossiana* were collected from crevices in the Upper Red Zone. This species was small; the average length of the shell of those examined was 2.2 mm.

Again, there was direct development in a brood. The young were housed in the interlamellar spaces of the gills until reaching a well-formed juvenile stage. Juveniles averaged 0.4 mm in length and thus, the number of young in a brood was restricted by size; the average number was 10, five on each side of the adult (cf. the brood of *Gaimardia t. coccinea*).

ECHINODERMATA
Cl. Asteroidea
F. Asteriidae

Anasterias directa (Koehler)

The distribution of *Anasterias directa* extended from the top of the sublittoral to a depth of at least 10 metres, the lowermost depth not being determined. For reproductive studies, specimens were collected from channels, gutters, and pools at the top of the sublittoral zone. Only adults which were at least 19 mm across the central disc were used, in order to ensure sexual maturity.

The sexes were separate. A pair of gonads was situated in each of the five interbrachial regions. In the males, the testes had the appearance of a bunch of grapes while in the females, each ovary consisted of two compact round sacs. When ripe, the testes greatly enlarged and extended down into the arms. In the females, the sacs simply expanded to accommodate the enlarging eggs.

Figure 42 shows the annual reproductive cycle for A. directa. Symbols were used to designate particular reproductive conditions (at each month) of the gonads in both males and females and of the brood in females. Sets of each symbol were separated horizontally on the figure. Egg sizes indicated that the cycle was further advanced in 1969 than in 1968.

The female brooded the young from the egg to the juvenile stage, the brood forming a compact cluster overlying the oral region (see Plate 28A). Small eggs were present in the ovaries in April and May, the average diameter in April being 0.5 mm. The diameter of the eggs increased to 1.1 mm in early June and progressively increased until they were transferred to a brood at the oral region in July when the diameter of eggs ranged from 1.8 to 2.0 mm. Development of the embryos proceeded in the brood to a juvenile stage (October - November). The juveniles were released in the November - December

Figure 42. [*]Reproductive cycle of *Anasterias directa*.

A. Females:
(N = 5, each month)

X = release of juveniles
▲ = juveniles in brood
△ = embryos in brood
○ = eggs in brood
■ = eggs in ovary

B. Males:
(N = 5, each month)

X = spawning
● = ripe
○ = abundance of spermatids
■ = early spermatogenesis
□ = resting
▲ = resorbing

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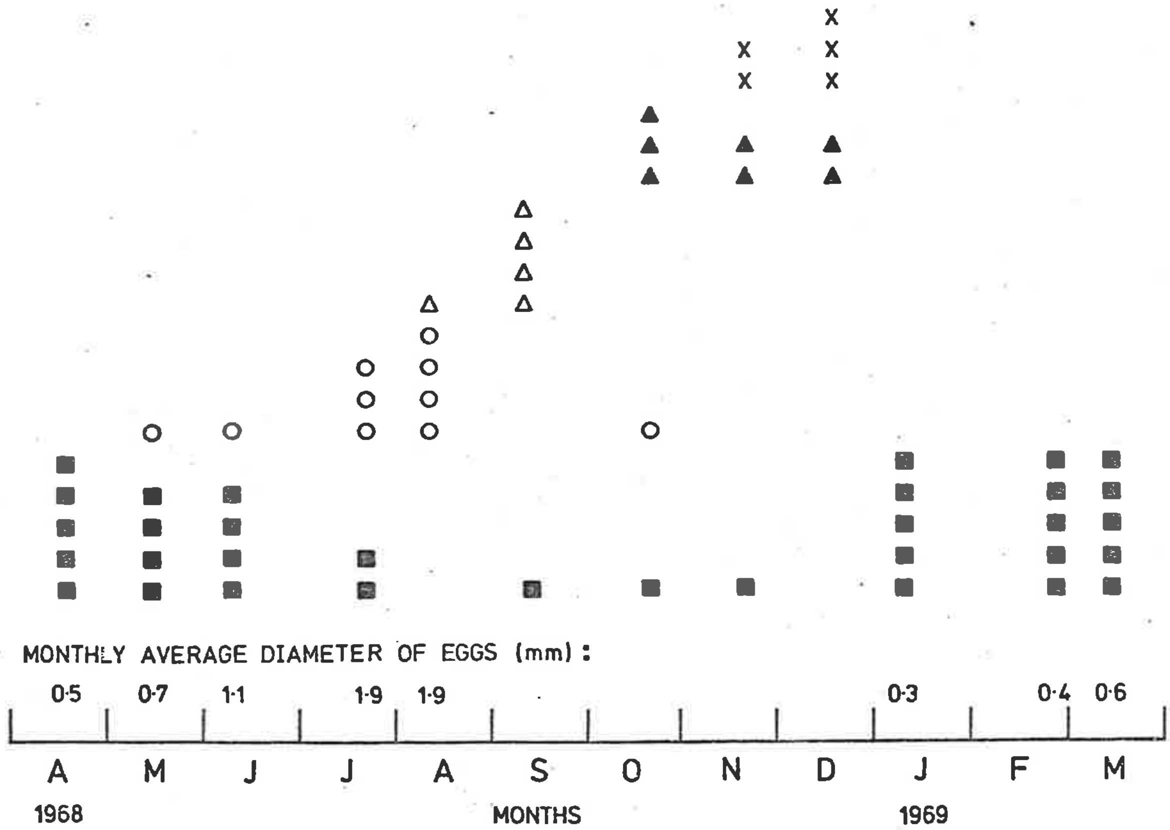
[*] A symbol is used to designate the predominant reproductive state of the gonad or the stage of the brood of each specimen. Sets of symbols are separated horizontally on the figure.


MONTHLY AVERAGE DIAMETER OF EGGS (mm):
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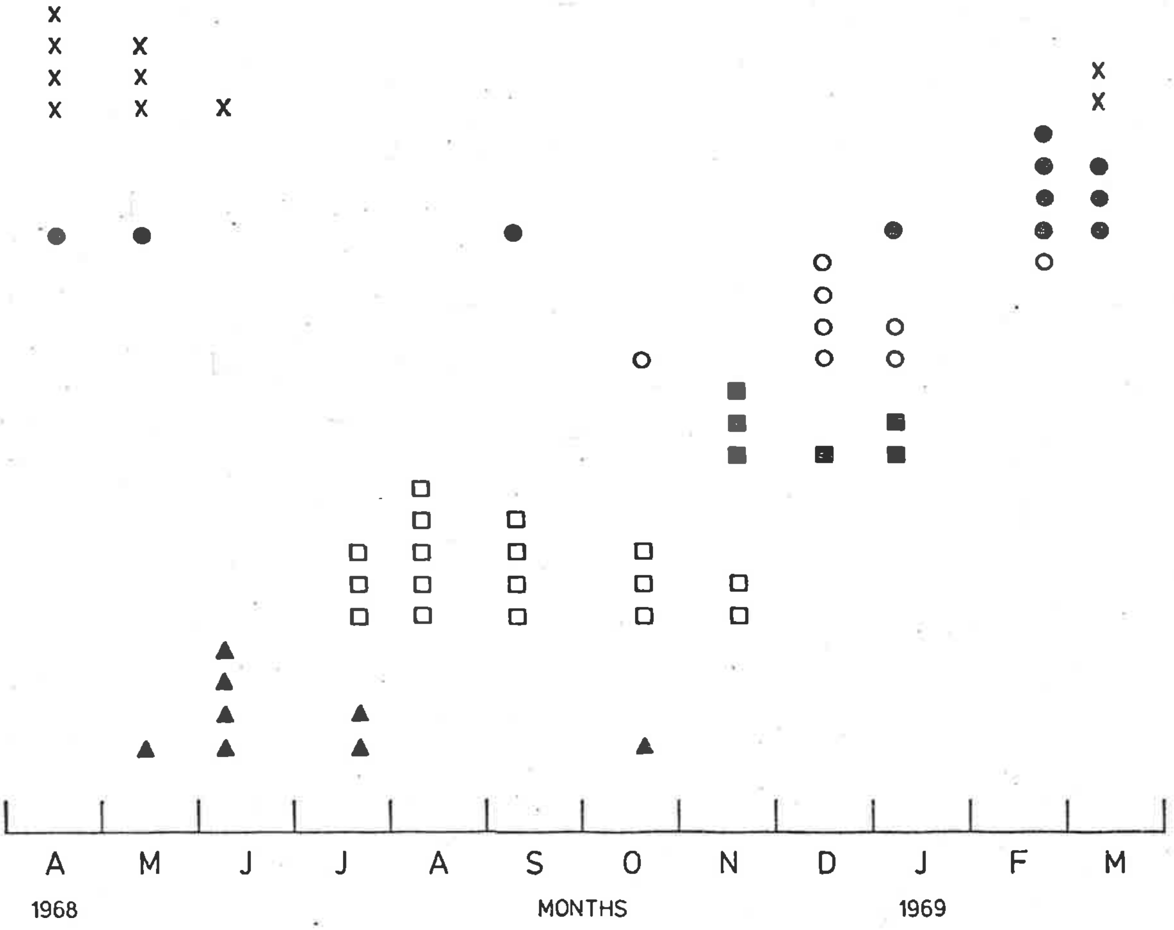
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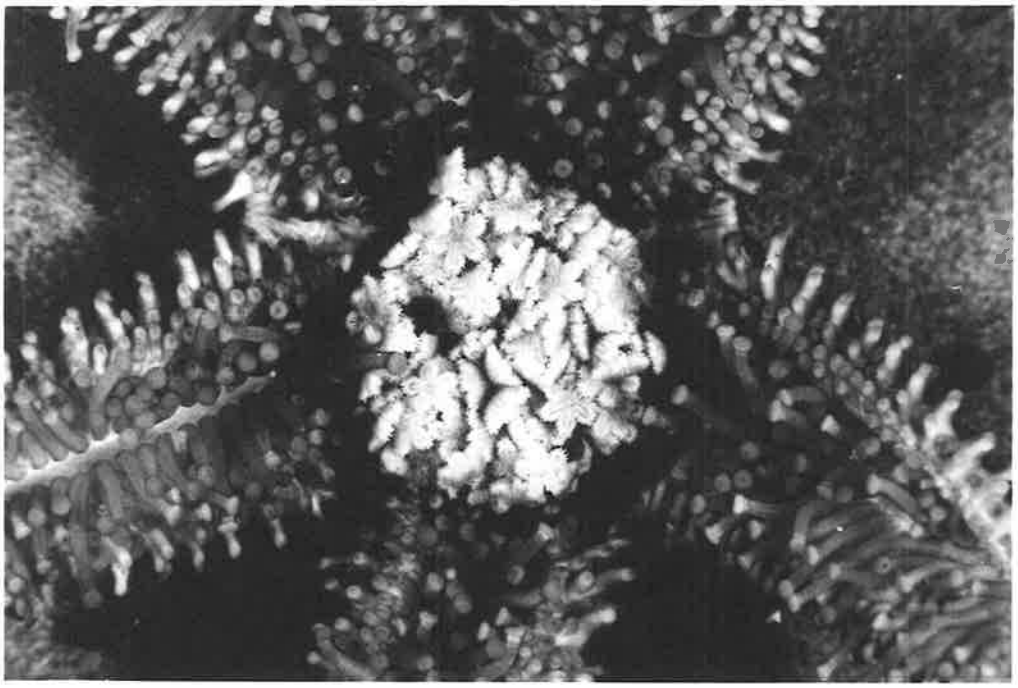
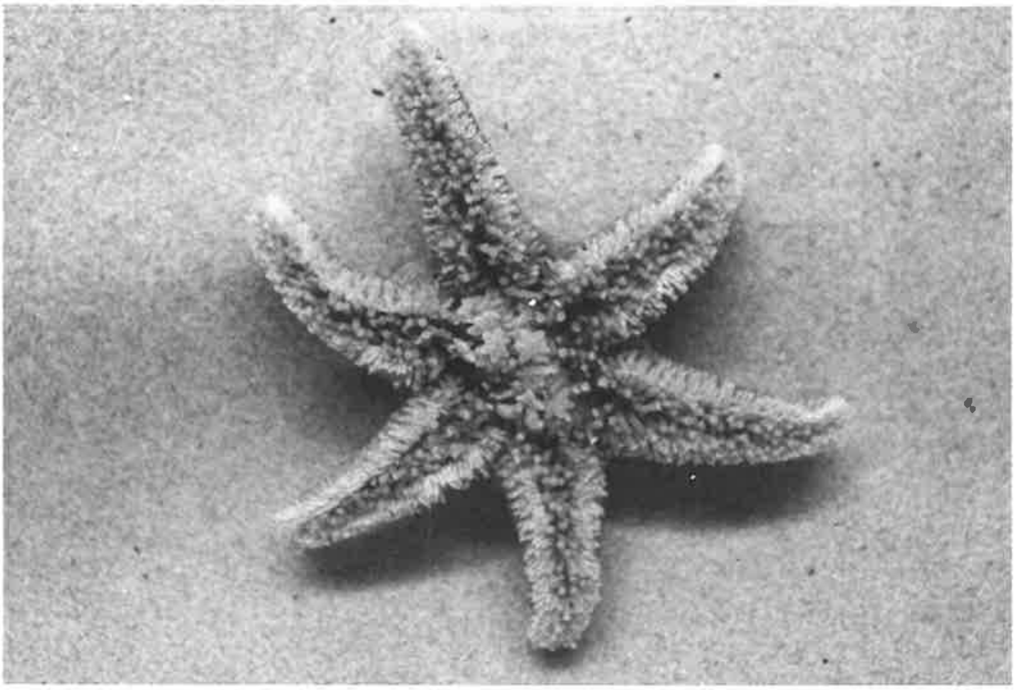
Plate 28.

28A. Brood of *Anasterias directa* (at juvenile stage just prior to release).

28B. Brood of *Anasterias mawsoni* (at juvenile stage just prior to release).



6 mm



20 mm

period. In January, the ovaries were small and the average egg size was 0.3 mm. The eggs progressively enlarged to an average diameter of 0.6 mm in mid-March. If the progression of the reproductive cycle continued at the same rate in 1969 as it did in 1968, juvenile release could be predicted as occurring one month earlier, i.e. in October - November, 1969.

In the specimens examined, the number of eggs in a brood varied from 174 to 220, depending on the size of the starfish. Females exhibited a distinctive arching posture when carrying a brood. The central disc was raised, the proximal parts of the arms being at a steep angle to the substrate and the distal parts horizontal and still attached to the substrate. This created a protected cavity over the oral region. The larger starfish were able to create a larger cavity and hence could accommodate a larger brood.

In males, during the corresponding period of brooding in the females, the testes were generally reduced in size and showed little signs of spermatogenic activity. Growth and spermatogenic activity were evident from November to February. Ripe testes were predominant in late February and March and they were present in April and May of the preceding year. In April and May, testes were mainly reduced and consisted of mature spermatozoa with little signs of spermatogenic activity, indicating that spawning had occurred. The monthly reproductive conditions of the testes showed that the breeding season occurred in the autumn months. During this period, the eggs were still mainly held in the ovaries.

Anasterias mawsoni (Koehler)

The distribution of A. mawsoni, like that of A. directa, extended from the top of the sublittoral to a depth of at least 10 metres. These two starfish occupied similar habitats, being found on coralline algae or other organisms encrusting solid rock substrate. For reproductive studies specimens of A. mawsoni were collected from channels, gutters and pools at the top of the sublittoral. Only animals with the diameter of the central disc at least 20 mm were, used, to ensure that they were sexually mature.

The sexes were separate. A pair of gonads was situated in each of the six interbrachial regions. In the males, the gonads had the appearance of a bunch of grapes while in the females each gonad consisted of two compact round sacs. When ripe, the male gonads greatly enlarged and extended down into the arms; in the females, the sacs simply expanded to accommodate the enlarging eggs. Thus, the shape, growth, and positioning of the gonads were similar in both Anasterias directa and Anasterias mawsoni.

Figure 43 shows the annual reproductive cycle for A. mawsoni. Symbols were used to designate particular reproductive states (at each month) of the gonads of both males

Figure 43. [*]Reproductive cycle of *Anasterias mawsoni*.

A. Females:

(N = 5, each month)

X = release of juveniles

▲ = juveniles in brood

△ = embryos in brood

○ = eggs in brood

▨ = eggs in ovary

B. Males:

(N = 5, each month)

X = spawning

● = ripe

○ = abundance of spermatids

▨ = early spermatogenesis

□ = resting

▲ = resorbing

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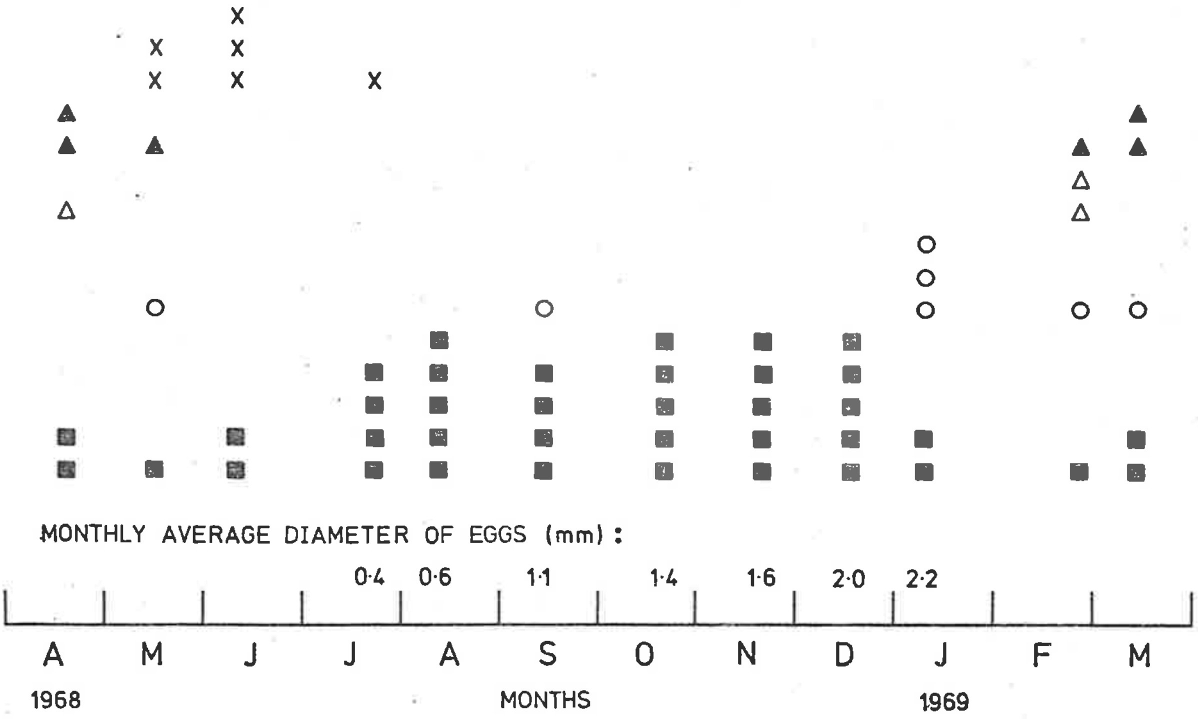
[*] A symbol is used to designate the predominant reproductive state of the gonad or the stage of the brood of each specimen. Sets of symbols are separated horizontally on the figure.


MONTHLY AVERAGE DIAMETER OF EGGS (mm):
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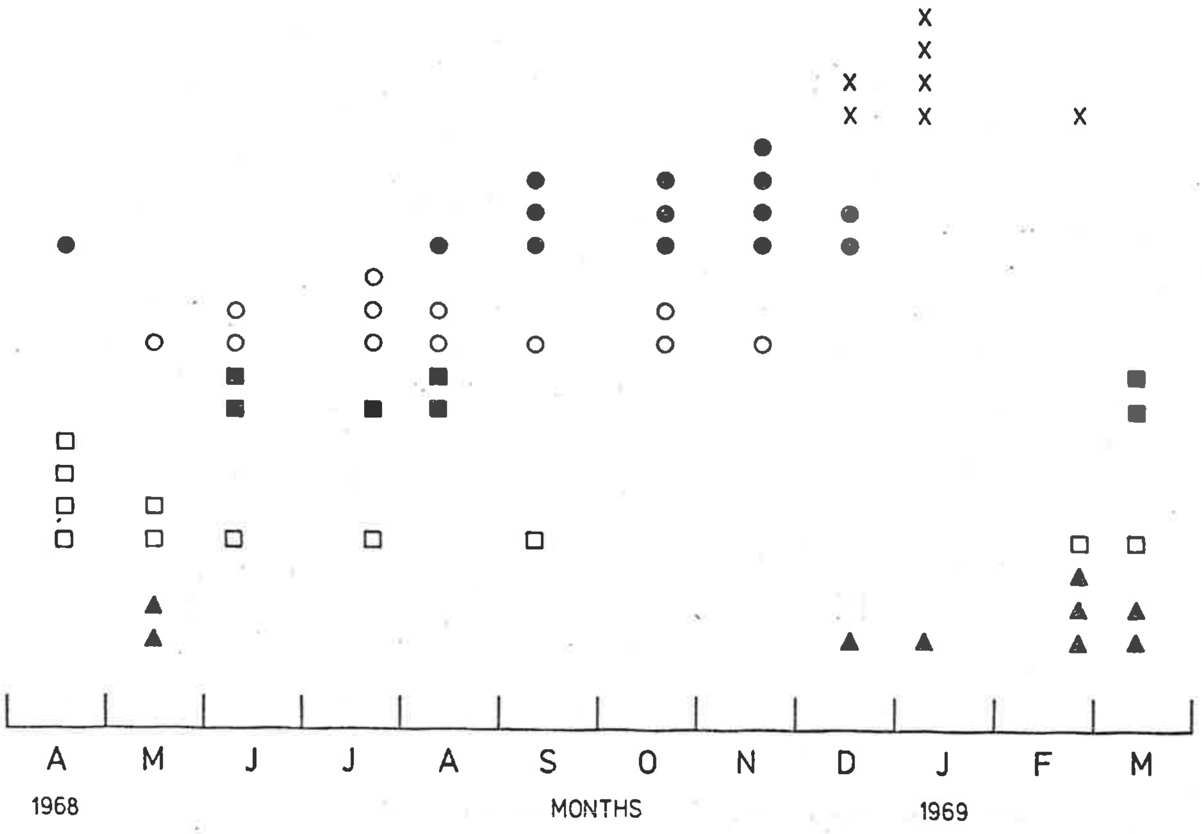
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and females and of the brood in females. The sets of each symbol were separated horizontally on the figure.

The female brooded the young from egg to juvenile stage, the brood forming a compact cluster overlying the oral region (see Plate 28B). Females assumed a distinctive arched posture (like that of A. directa) when carrying a brood. Larger specimens could form a more spacious, protected cavity over the oral region and hence could accommodate a larger brood. The number of eggs in a brood averaged 210 and the range was 168 to 296.

In July, the eggs in the ovaries averaged 0.4 mm in diameter. In the proceeding months, the eggs progressively increased in size until reaching a diameter of 2.0 mm in December. The eggs were transferred to the brood clusters in January - February. The diameter of eggs in a brood averaged 2.2 mm. Development proceeded in the brood to a juvenile stage in May and June when the juveniles were released.

In males, the testes were generally reduced from February to May. There was some spermatogenic activity during this period, but occurrences were few. The testes progressively increased in size and large, ripe ones were common from September to November. In December and January, they were reduced and mainly consisted of mature spermatozoa, indicating that spawning had taken place. The monthly reproductive conditions of the testes showed that the breeding season occurred in early summer. During this period, the eggs were being transferred to the brood clusters.

The reproduction of *Anasterias mawsoni* provides an interesting comparison with that of *Anasterias directa*. The arrangement and structure of the gonads were the same in both species. *A. mawsoni* had larger broods, suggesting that it could release more young per female. The most striking difference was the staggered reproductive cycles. The two species occupied similar habitats, had the same prey (see section IV 1. (d)), yet had markedly different breeding seasons. There was a time difference of four months between the peak release of young and hence recruitment of the two species.

F. Asterinidae

Asterina hamiltoni Koehler

This small starfish was commonly found in the sublittoral, attached to rock surfaces. Specimens were collected from pools and channels in the sublittoral for reproductive studies. To ensure sexual maturity only specimens measuring at least 22 mm in total body diameter were examined.

The sexes were separate. A pair of gonads was situated in each of the five interbrachial regions. The testes had the appearance of a bunch of grapes and when ripe, were large and extended into the arms. Each ovary consisted of a number of small sacs (typically seven) and each sac contained eggs of various sizes. The number of eggs per sac varied from 19 to 24, the average being 20. There were three distinct size categories in the diameters of the eggs: (a) less than 0.3 mm, (b) 0.3 to 0.5 mm, and (c) 0.5 to 0.8 mm. The smallest eggs were more plentiful than the largest. In grouping the figures from all specimens, the range of numbers in the three size categories was (a) 11 to 16 (Av. = 13), (b) 4 to 7 (Av. = 5), (c) 1 to 3 (Av. = 2).

The state of the ovaries did not vary from month to month. About 40% of the males had ripe testes at any one month. Thus *A. hamiltoni* appeared to have a constant production of spermatozoa and eggs throughout the year and no clearly defined reproductive cycle. This is unusual as starfish generally have a definite breeding season as part of an annual reproductive cycle (Boolootian 1966). In the list of breeding seasons of asteroids compiled by Boolootian, one of the two exceptions to this rule was also of the genus *Asterina* (*Asterina exigua*); this starfish appeared to breed continuously (Mortenson 1921). In *Asterina hamiltoni*, when considered as a population, the production of spermatozoa and eggs appeared to be constant. However, in the case of males, individuals did not breed continuously and spermatozoa could be released from only about 40% of the males at any one time.

It is not clear whether females released ova to the sea for external fertilization. In any average female, the number of eggs would be 20 x 7 x 10 = 1,400 (number of eggs per sac x number of sacs per gonad x number of gonads). However, from the size range of the eggs, it was apparent that only about 140 of these were mature ova. The release of even this number would hardly ensure successful fertilization if it were done externally in the open sea. A. hamiltoni may have had some particular reproductive behaviour to ensure successful fertilization but no extensive observations were carried out. No brood was found either enclosed in the body cavity or on the surface of the starfish.

Cl. Holothuroidea
F. Cucumariidae

Pseudopsolus macquariensis (Dendy)

Pseudopsolus macquariensis were common in pools and rock surfaces encrusted with coralline algae and in the Kelp and Lower Red Zones of the sublittoral. Snorkeling and SCUBA dives showed that extensive patches of rock surfaces were almost completely blanketed by a dense cover of these holothuroids. For reproductive studies specimens were collected from channels and gutters encrusted with coralline algae in the sublittoral zone.

Adult holothuroids were commonly 25 mm in length from the base of the tentacles to the anus. Such a length measurement was desirable for comparing animals as the extension of the tentacles varied considerably. For reproductive studies, specimens of at least 15 mm were used.

This species was hermaphroditic. The gonad consisted of a cluster of unbranched tubules uniting basally into one tuft. When a gonad was mature, the tubules were swollen with either spermatozoa or eggs, never both. There remained a number of small tubules which contained immature material opposite in sex to the mature products in the swollen tubules. Thus, it appeared that an individual alternated between a male and female role. Mortenson (1925) also showed that Pseudopsolus macquariensis produced eggs and spermatozoa alternately.

Young were brooded to a well developed juvenile stage in deep incubatory sacs. Juveniles were released through ventral pores, moving out from underneath the parent on to the surrounding rock surface (see Plate 29B).

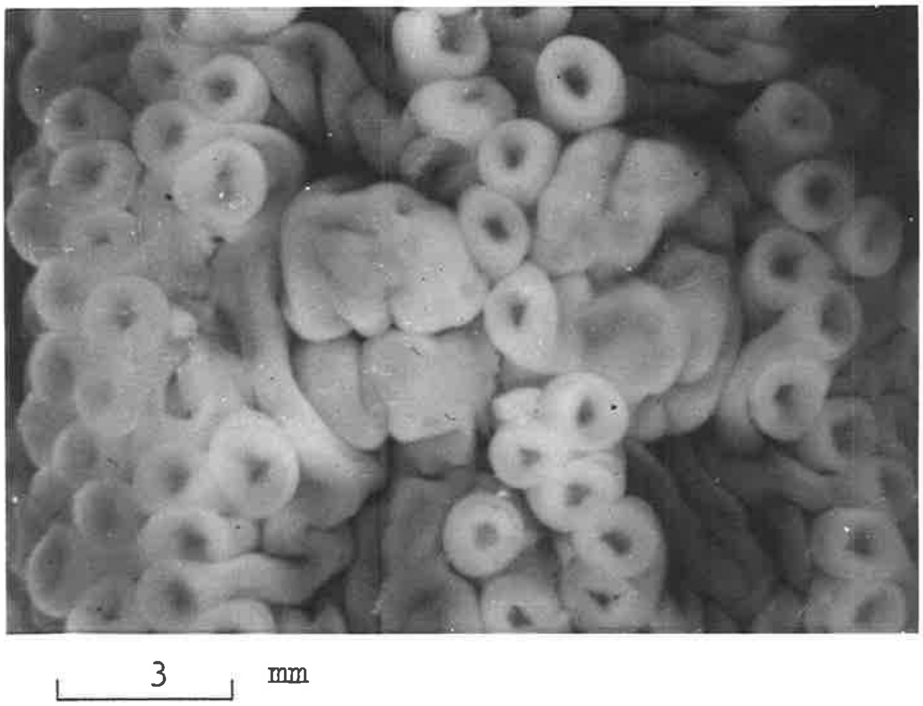
Figure 44 shows the annual reproductive cycle for Pseudopsolus macquariensis. Symbols were used to designate particular reproductive states (at each month) of both testes and ovaries and of the brood. Sets of each symbol were separated horizontally on the figure. The similarity of the reproductive states at the end points of the cycle indicated that a similar synchronization could be expected in 1969.

Eggs were developing in the ovaries from November to June. In December, the eggs were distinctly separate and were situated one after the other down the length of the tubules, resembling a string of beads. At this stage, the

Plate 29.

29A. "Protuberances" on ventral surface of the holothuroid, *Pseudopsolus macquariensis*.

29B. Released young (*Pseudopsolus macquariensis*) coming out from underneath parent on to rock surface.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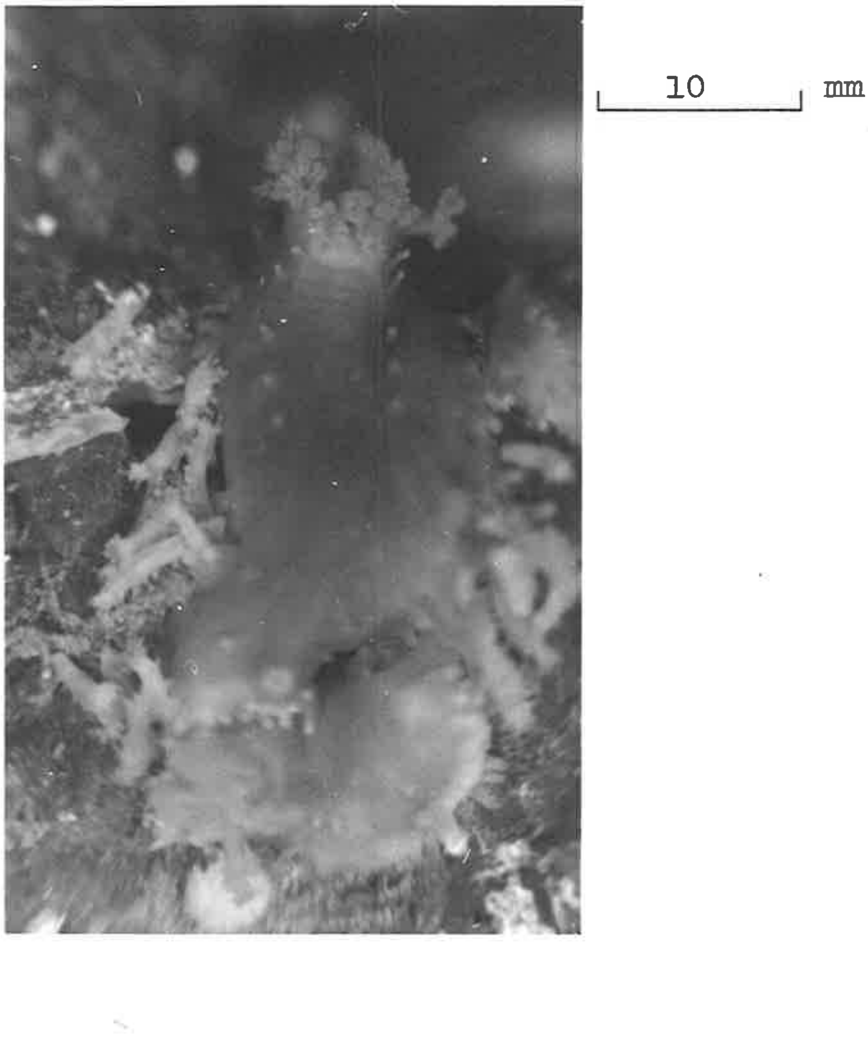
10 mm

Figure 44. *Reproductive cycle of *Pseudopsolus macquariensis*.

A. Females:

(N = 5, each month)

X = release of juveniles

▲ = juveniles in brood

△ = embryos in brood

○ = eggs in brood

▨ = eggs in ovary

B. Males:

(N = 5, each month)

X = spawned

● = ripe

○ = abundance of spermatids

▨ = early spermatogenesis

☐ = regressed

▲ = resorbing

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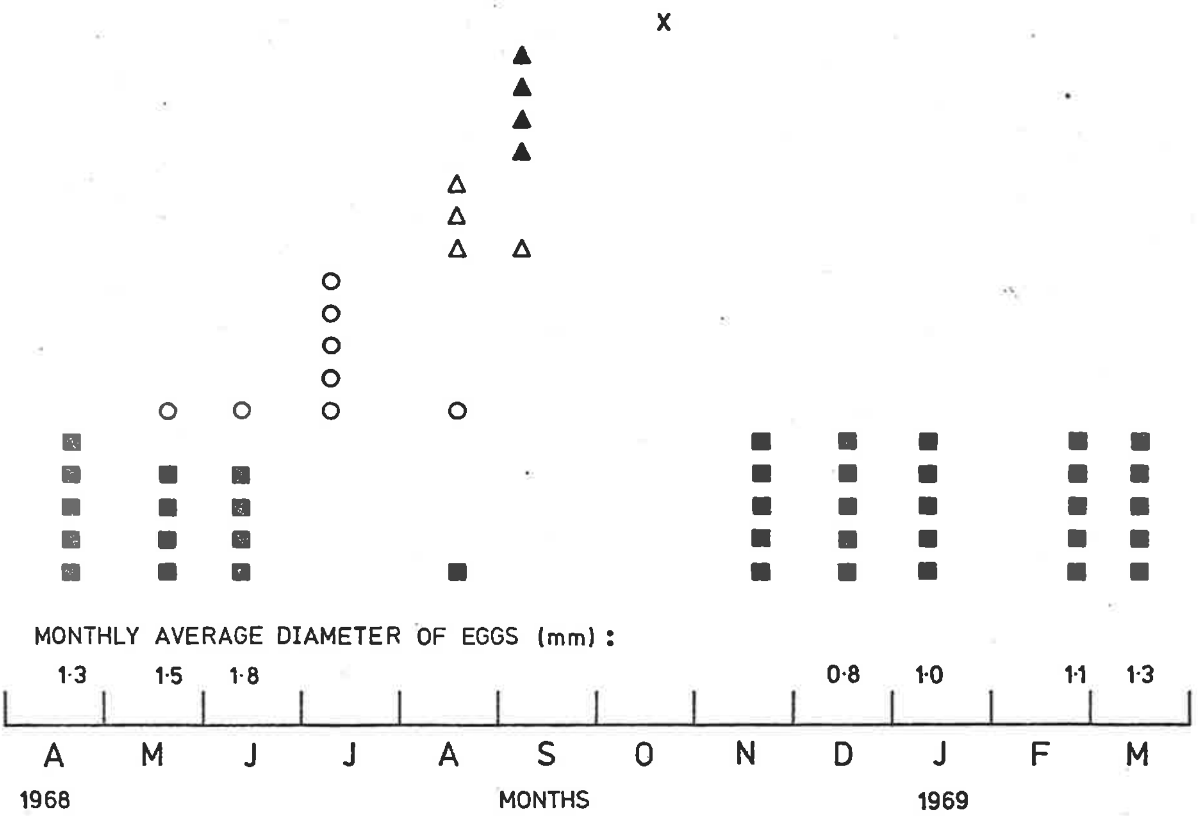
* A symbol is used to designate the predominant reproductive state of the gonad or the stage of the brood of each specimen. Sets of symbols are separated horizontally on the figure.


MONTHLY AVERAGE DIAMETER OF EGGS (mm) :
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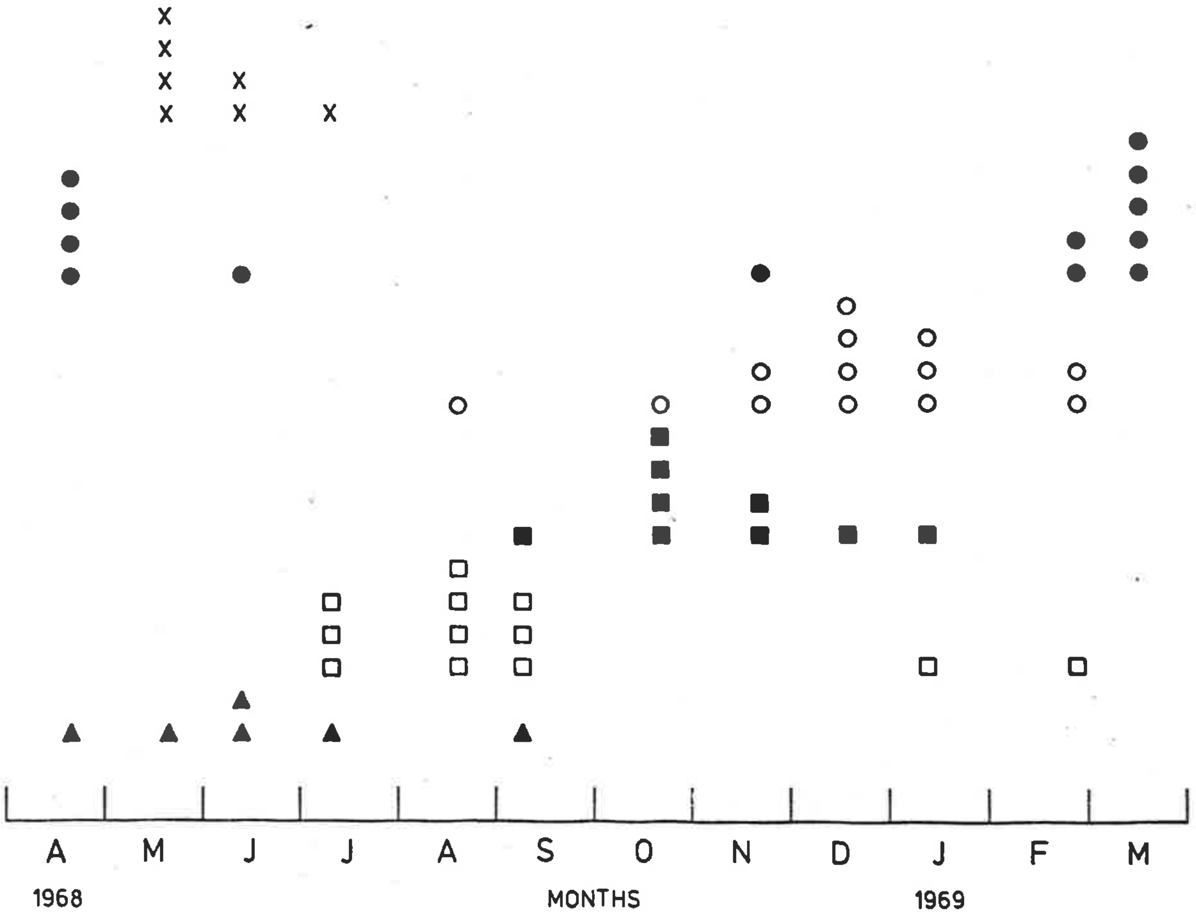
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eggs were small (diameter = 0.8 mm). The size of the eggs progressively increased in the following months and in May, their diameter was 1.5 mm. In May and June, eggs appeared in internal brood pouches and at this stage were 1.8 mm in diameter. There was negligible variation in the size of eggs in an individual at any particular phase of the cycle. In the first week of July, all specimens assuming the female role had their eggs housed in the internal brood sacs. External transference was not observed nor did any specimen collected show an intermediary phase of some eggs in tubules and some in incubatory sacs. Dissections did not show any evidence of internal connection to these sacs.

Further development proceeded in the brood sacs, the September samples showing advanced embryos. Release of juveniles occurred in late September - October. A high degree of synchronization appeared to be enforced during juvenile release. Juveniles were found underneath adults on 22nd October and large numbers of adults were collected. Forty specimens from this collection were dissected and not one contained any juveniles.

The resting period of the testes was from July to September. Activation of spermatogenesis was evident in October. Growth and spermatogenesis progressively continued, large, ripe testes being predominant in March - April. In May and June, testes were in an obvious post-spawning condition i.e. reduced, not firm, and full of mature spermatozoa with little spermatogenic activity.

The cycle in the testes indicated that the breeding season occurred in May - June during the transfer period of the eggs from tubules to incubatory sacs. Whether fertilization depends on this timing or whether the breeding season coincidentally falls at the same time are unknown.

Two large, often convoluted, protuberances appeared on the ventral surface of many individuals, about half-way down the body (see Plate 29A). In preliminary observations, it was thought that these were "brood pockets" from which the young were released as the bulges coincided with the openings to the incubatory sacs. However, the protuberances were present for specimens assuming both male and female roles just prior to or at the time of release of juveniles. The number of specimens with these growths increased during the juvenile - release phase of the cycle but with no bias to those acting as females. Histological sections showed that the extra growth in these areas was largely a result of increased connective tissue. The significance of these protuberances is unexplained.

Each brooding specimen had two incubatory sacs. They were deeply internal and were not surface pockets. Each sac exhibited compartments but there was only one duct and ventral opening for each. The opening was a simple hole, half-way down the ventral body wall, and coincided with the previously described protuberances (if they were present).

The walls of the sacs were transparent and of light texture and appeared to be similar to that described by Mortenson (1894) for *Cucumaria glaciatis*. He showed that such sacs consisted of thinned inturned body wall in which the connective tissue had undergone the greatest reduction. Internal incubatory sacs have been described in a number of species and these descriptions are summarized by Hyman (1955) and Boolootian (1966).

Pseudocnus laevigatus (Verrill)

Only four specimens were collected from rock pools in the lower eulittoral zone. The largest individual (35 mm in length, from the base of the tentacles to the anus) contained young in internal brood pouches. The brooding habit in this species has been previously described by Pawson (1968).

Trachythone macphersonae Pawson

Ten specimens of this species were collected from rock pools in the lower eulittoral zone. The sexes were separate and the females had a small number (110 to 130) of eggs in long, unbranched ovarian tubules; these eggs were large, diameters measuring from 0.2 to 0.8 mm. (The size of the egg would depend on the stage in the reproductive cycle.) Although none of the specimens were found with a brood, the small number and the size of the eggs suggested that this species had direct development with no planktonic larval stage (probably a brooding habit).

Cl. Echinoidea
F. Echinidae

Notechinus novae-zealandiae Mortenson

Four specimens of N. novae-zealandiae were examined. Two were from collections during the present study (one from the sublittoral, the other from a diving station of seven metres) and two were obtained from the National Museum of Victoria. Typical for regular echinoids, there were five gonads suspended by mesentery along the inner surface of the interambulacra. Three of the specimens were males, the other, female. In the female, the ovaries were large and projected well down ventrally, filling a large part of the available space. The ovaries were full of numerous eggs (diameter = 0.1 mm) and such a quantity of eggs indicated that this echinoid had a planktonic larval stage in its life history.

COELENTERATA
Cl. Anthozoa
Sea anemones

Halianthella kerguelensis (Stud.), Kwietniewski
Parantheopsis cruentata (Couth.) McMurr.

Both these sea anemones were collected from pools in the lower eulittoral and the upper sublittoral zones.

Specimens of both species were found with embryos in the coelenteric cavity. Such an occurrence was previously reported for *H. kerguelensis* by Carlgren and Stephenson (1929).

. . . .

Table 38 gives a summary of the type of reproductive development for each species. This table also includes the molluscs which were the subjects of the main studies. New descriptions of direct development have been made for (a) brooding: *Gaimardia t. coccinea*, *Kidderia bicolor*, *Lasaea rossiana*, *Anasterias directa*, *Anasterias mawsoni*, *Pseudopsolus macquariensis*, *Parantheopsis cruentata*; and (b) egg-cases: *Kerguelenella lateralis*, *Macquariella hamiltoni*. These descriptions of reproductive development substantiate or add to the data for marine invertebrates of higher latitudes. With the increase of records, possible reasons for the increase in direct development in colder climates can be further assessed. An important factor to arise from future accumulation of data will be whether animal groups with a phylogenetic affinity for a protective reproductive habit have spread to colder seas or whether this habit has developed in colder seas among widely represented groups.

Table 38. Summary of the reproduction of all Macquarie Island marine invertebrates examined in the present study.

Species	Type of reproductive development.				Breeding season (Period of fertilization of gametes.)			
	Brooding	Egg Cases	External larvae	Unknown	Summer (Dec.-Feb.)	Autumn (Mar.-May)	Winter (Jun.-Aug.)	Spring (Sep.-Nov.)
MOLLUSCA								
Cl. Amphineura								
Plaxiphora aurata			✓		▬	▬		
Hemiarthrum setulosum	✓				▬	▬		
Cl. Gastropoda								
Kerguelenella lateralis		✓			▬	▬	▬	▬
Laevilitorina caliginosa		✓*			▬	▬	▬	▬
Patinigera macquariensis			✓		▬			▬
Cantharidus (P.) coruscans			✓		▬	……	……	……
Macquariella hamiltoni		✓			▬	▬	▬	▬
Cl. Lamellibranchia								
Gaimardia t. coccinea	✓				▬	……	▬	……
Kidderia bicolor	✓							
Lasaea rossiana	✓							
ECHINODERMATA								
Cl. Asteroidea								
Anasterias directa	✓					▬	▬	
Anasterias mawsoni	✓				▬			
Asterina hamiltoni				1	▬	▬	▬	▬
Cl. Holothuroidea								
Pseudopsolus macquariensis	✓					▬	▬	
Pseudocnus laevigatus	✓							
Trachythone macphersonae				1				
Cl. Echinoidea								
Notechinus novae-zealandiae			✓					
COELENTERATA								
Cl. Anthozoa								
Halianthella kerguelensis	✓							
Parantheopsis cruentata	✓							

* Indirect evidence from number of eggs.

1 Size and number of eggs suggested direct development, probably by brooding.

▬ = breeding season

.... = period of low level breeding activity.

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