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THE UNIVERSITY OF AUCKLAND

1979

THE ECOLOGY OF TWO NEW ZEALAND
OPISTHOBRANCH MOLLUSCS

RICHARD CARDEW WILLAN

A thesis submitted for
the degree of Doctor of
Philosophy in Zoology,
University of Auckland.
ABSTRACT

An intertidal population of the anaspidean *Aplysia dactylomela* Rang was followed for three consecutive years at the Leigh Marine Reserve, North Auckland, New Zealand. Field assessments were made of recruitment, growth (by recapture of tagged individuals), density, crawling rate, gonad index and mortality. These data allowed monthly estimates of the entire population within the entire study area (2.76 ha) to be made. Complementary laboratory studies investigated acceptable foods and an energy budget including data on energy of the food, growth rates, egestion, respiration and assimilation efficiency were also obtained in the laboratory. In conjunction with these studies, field work on the algal food of *A. dactylomela* (species of *Laurencia*) elucidated the entities present, their separate yearly changes in biomass and the causes. From this information, data on food requirements for *A. dactylomela* (species of *Laurencia*) elucidated the entities present, their separate yearly changes in biomass and the causes. From this information, data on food requirements for *A. dactylomela* were contrasted with standing crop estimates for *Laurencia* spp. in the same units to permit consideration of the theoretical grazing effects of *A. dactylomela*. Several lines of evidence show this environment to be suboptimal for *A. dactylomela*. Storms account for the greatest mortality, but some losses are due to predation by the asteroid *Cocinasterias calmaria* (Gray). Few individuals reach reproductive maturity and the population is not self-recruiting.

An intertidal population of a second opisthobranch, the Cephalaspidean *Haminoea zelandiae* (Gray in Dieffenbach) was followed for three consecutive years at Motukaraka Island, Hauraki Gulf, New Zealand. Field determinations of growth, annual abundance and reproductive cycles were made. The cryptogamic flora at Motukaraka Island has been characterised and annual patterns of cover and distribution presented for five major seasonal components. The relationship between *Haminoea zelandiae* and these algae is considered.

Additional studies on two less-common anaspideans were carried out. Field data on breeding, growth and density are given for *Aplysia parvula* Mörch which exists in separate, spatially-isolated intertidal and subtidal populations at Goat Island Bay. For these two populations differences exist in diet, colouration, size distribution, growth and survivorship. The intertidal habitat is marginal whereas the subtidal is close to being optimal. *Bursatella leachii* Blainville shows variable annual recruitment to the cyanophyte *Lyngbya majuscula* intertidally at Motukaraka Island. Growth rates have been determined for field and laboratory populations. In the field a deliberate offshore migration takes place whilst *L. majuscula* is still abundant. Speculations on the possibilities and causes for migrations amongst opisthobranchs are discussed.

A taxonomic revision of the New Zealand Anaspidea follows as an appendix. There are eight sea hares authentically recorded for New Zealand: *Aplysia* (Pruvotaplysia) *parvula* Mörch 1863; *A. (Varria) dactylomela* Rang 1828; *A. (V.) keraudreni* Rang 1828; *A. (V.) extraordinaria* (Allan 1932); *A. (Aplysia) juliana* (Quoy & Gaimard 1832); *Bursatella leachii* Blainville 1817; *Stylochaelis longicnuda* (Quoy & Gaimard 1825); *Dolabrifera dolabrifera* (Cuvier 1817). For each species a complete synonymy is given as well as full description, locality records and discussion.
ACKNOWLEDGMENTS

A great many people have assisted with this thesis. Owing to the diverse nature of their specialist aid I acknowledge them separately in the methods chapter and introductions to the relevant sections of the work. I wish to single out five people for very special thanks, without their help this thesis would not have been possible or produced: my supervisor, Dr M.C. Miller for encouragement, assistance, literature and specimens; Dr W.J. Ballantine for use of facilities at the University of Auckland's Marine Research Laboratory at Leigh; my mother, Mrs J.D. Willan for assistance in the field given so unstintingly; Mr G.W. Batt for his thorough preparation of photographs; Mrs Batt for typing the manuscript so thoroughly. Dr M.F. Barker very kindly read through the final manuscript. This research was supported by a New Zealand University Grants Committee Postgraduate Scholarship (1975-1977).
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*Aplysia dactylomela* Rang. Length 120 mm.

Specimen photographed in situ, Echinoderm Reef, Goat Island Bay, Leigh.

CHAPTER I
INTRODUCTION

Herbivorous tectibranchs have a tremendous capacity for feeding, food conversion, growth and reproduction. However, despite their important roles in shallow-water marine communities very little detailed or quantitative information is available on these attributes. The commonness of certain species in northern New Zealand has enabled me to investigate the second and third of the four attributes listed.

As a group, the molluscan subclass Opisthobranchia includes some of the most suitable organisms for study that exist anywhere amongst the Invertebrata. Their attributes are as follows: generally large in size and easy to locate; certain species are common enough to permit observations on large numbers and to allow removal of some animals without affecting the whole population; at times they reach high densities corresponding to what might be called "population explosions"; many live for only a single year and therefore exhibit annual cycles of density and reproductive state; remarkably close associations exist between some species (particularly Sacoglossa and Nudibranchia) and their food organisms that verge on ectoparasitism; their bodies are large and soft, many have prominent accessible nervous systems and display simple behaviour sequences so that sophisticated physiological studies can be undertaken.

According to these attributes, one could expect a study on a group of opisthobranchs, particularly on members of one of the herbivorous orders, to be relatively easy. But this is far from the case and research on them is beset with difficulties. If it were not for my interest in the group and experience with them beforehand it would have been impossible to undertake any problems of an ecological nature with opisthobranchs.

The difficulties of opisthobranch study stem from their opportunistic life cycles and frequently cryptic behaviour. It is unusual to come across an
adequately sized population for quantitative analysis. Population densities are liable to vary enormously throughout the seasons. The taxonomy of many species is in chaos. A planktonic phase is usually present in the life cycle. These difficulties arising from the field occurrence of opisthobranchs mean that rigorous sampling procedures are exceedingly difficult to maintain. It is often impossible to obtain samples of sufficient size that would satisfy the requirements of many statistical analyses.

However, from experience I chose two species that are common in northern New Zealand, and I studied them at selected localities where the populations were large enough for detailed and repeated observations to be made. The species were the sea hare *Aplysia dactylomela* Rang, 1828 (Frontispiece) and the White Bubble Shell *Haminoea zelandiae* (Gray in Dieffenbach, 1843) (Fig. 3.3). Data on two other opisthobranchs that were also encountered reasonably frequently are included - these secondary species being *Aplysia parvula* Mörch, 1863 and *Bursatella leachii* Blainville, 1817.

I studied the annual cycles of the major species for three consecutive years. Data were collected on changes in density (both in time and space), feeding, growth, competition and predation (only for *Aplysia dactylomela* in the latter three instances).

I attempted to go deeper into the relationships between these herbivores and their food. This is because the species under investigation here have considerable effects, seasonally, on the associations in which they occur. This is principally because their densities and ingestion rates mean they are potentially capable of altering the algal composition of their environment. *Haminoea zelandiae* browses on filamentous Cyanophyta, Chlorophyta and Phaeophyta. *Aplysia* species feed on larger Chlorophyta and Rhodophyta, and *Bursatella leachii* feeds on filamentous Cyanophyta and Chlorophyta.

The objectives of this thesis have been to determine the natural annual cycles displayed by populations of both of these herbivorous opisthobranchs and their food algae, in terms of changes in density and distribution both
through the year and from year to year. I have examined what effects the populations of herbivores have on their algal food resources, and if there is any degree of dependence so as to suggest incipient accommodation by the grazers to supplies of food. Thirdly I considered the effects that the edible algae have on their dependent opisthobranchs, and I attempted to detect any relationship that might suggest these algae could have produced growth strategies to mitigate grazing by opisthobranch predators.

This study has therefore considered the ecology of both marine animals and plants and investigated their interactions and the degree of dependence of each component upon the others. These investigations have been quantified for the *Aplysia dactylomela/Laurencia* sp. relationship, and the parameters of the energy budget have been determined for this herbivore.

From the outset, it was apparent that the taxonomy of the New Zealand species of sea hares (Order Anaspidea) was in great confusion, so a considerable portion of my time, and space in this thesis, has been devoted to a systematic revision of the Anaspidea (here presented as an appendix). The higher classification of *Haminoea zelandiae* has also been rectified.

There are few detailed ecological studies for herbivorous opisthobranchs that have been conducted over a reasonable length of time. Miller (1960) followed *Aplysia punctata* Cuvier for 19 months. Papers by Carefoot (1967a; 1967b; 1967c; 1970) describe the growth and nutrition of *Aplysia punctata* Cuvier, *A. juliana* (Quoy & Gaimard) and *A. dactylomela* Rang. Usuki (1970) studied the life cycles of seven Japanese species of Anaspidea. Growth of one of these species, *A. kurodai* (Baba), was investigated in greater detail by Nishiwaki et al. (1975). Of all these papers, only two by Carefoot (1967b; 1967c) really consider the herbivore and algae together. All the studies assumed algal food sources to be available continuously and to be of a consistent nutritional standard.

The Anaspidea have had hundreds of papers devoted to them. Many are essentially taxonomic but provide brief ecological information of the anecdotal
type (e.g. Allan, 1932b; Kay, 1964; Beeman, 1968; Bebbington, 1972; 1974; 1975; 1977; Neck, 1976; Strength & Blankenship, 1977). The greatest importance of the Anaspidea (particularly the species of Aplysia) in recent years has been for neurophysiological research, and these investigations have generated a plethora of papers (e.g. Arch, 1976; Kupfermann, 1965; 1968; 1974; Jacklet, 1972; Lickey et al., 1976; Strumwasser, 1967; 1971; 1973; Strumwasser et al., 1965). There are excellent reviews by Willows (1973) and Kandel (1976).

Knowledge of breeding biology, larval life and artificial rearing techniques has advanced very rapidly (Bridges, 1974; 1975; Krigstein, 1977; Krigstein et al., 1974; Lederhendler, 1977a; Smith & Carefoot, 1967; Strumwasser et al., 1976; Switzer-Dunlap & Hadfield, 1977); it has been most stimulating to read of progress in this field during the course of my thesis. Research on anatomy and function of the Anaspidean reproductive system is proceeding (Beeman, 1970; Brandriff & Beeman, 1973; Lederhendler & Tobach, 1977; Thomas, 1975; Thompson & Bebbington, 1969). There are several works on nutritional physiology (Chapman & Fox, 1969; Frings & Frings, 1965; Watson, 1973; Winkler et al., 1962; Winkler, 1969). And finally a great many good papers consider various aspects of behaviour amongst the Anaspidea (Hamilton & Ambrose, 1975; Lederhendler, 1975; 1977b; Lederhendler et al., 1978; Lowe, 1976; Martin, 1966; Tobach, 1978; Tobach et al., 1965; Van Weel, 1957; Winkler, 1959; Winkler & Tilton, 1962).

Each of the major fields has now become so specialised that any of them could suitably provide enough research material for a Ph.D. topic in itself.

Probably because of the nature of dietary differences, there is an imbalance in treatment between the herbivorous and carnivorous opisthobranch species. Many ecological surveys have been generalised and deal with a large number of species, each in little detail (Garstang, 1889; Swennen, 1961; Miller, 1961; Thompson, 1964; Schmeckel, 1968; Bertsch et al., 1972; Clark, 1975). Recently more detailed studies on a single carnivorous species have been undertaken and these are listed in Table 1.1. These works consider feeding behaviour, food preferences, food availability and food partitioning. Very full reviews have been prepared by Harris (1973) and Ottaway (1977a).
Table 1.1. Summary of detailed ecological investigations on carnivorous opisthobranchs and their prey species.

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<td>Retusa chrysoma Burn in Burn &amp; Bell</td>
<td>Foraminifera, Mollusca</td>
<td>Burn &amp; Bell, 1974</td>
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<td></td>
<td>Retusa pelyx Burn</td>
<td>Foraminifera</td>
<td>Burn, 1974</td>
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<td>NOTASPIDEA</td>
<td>Pleurobranchus membranaceus (Montagu)</td>
<td>Chordata, Protochordata</td>
<td>Thompson &amp; Slinn, 1959</td>
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<td>Coelenterata</td>
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<td>Crustacea</td>
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<td>NUDIBRANCHIA (sensu Minichev, 1970)</td>
<td>Aeolidia papillosa (Linnaeus)</td>
<td>Coelenterata</td>
<td>Stehouwer, 1952; Braams &amp; Geelan, 195</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>Edmunds et al., 1974; Edmunds et al., 1976.</td>
</tr>
<tr>
<td></td>
<td>Phestilla melanobranchia Bergh</td>
<td>Coelenterata</td>
<td>Harris, 1968; 1971; 1975</td>
</tr>
<tr>
<td></td>
<td>Phestilla sibogae Bergh</td>
<td>Coelenterata</td>
<td>Harris, 1973; 1975</td>
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<tr>
<td></td>
<td>Precuthona peachi (Alder &amp; Hancock)</td>
<td>Coelenterata</td>
<td>Christensen, 1977</td>
</tr>
<tr>
<td></td>
<td>Cuthona nana (Alder &amp; Hancock)</td>
<td>Coelenterata</td>
<td>Harris et al., 1975</td>
</tr>
<tr>
<td></td>
<td>Coryphella stimpsoni (Verrill)</td>
<td>Coelenterata</td>
<td>Morch, 1971</td>
</tr>
<tr>
<td></td>
<td>Lomanotus stauberi Clark &amp; Goetzfried</td>
<td>Coelenterata</td>
<td>Clark &amp; Goetzfried, 1976</td>
</tr>
<tr>
<td></td>
<td>Melibe leonina (Gould)</td>
<td>Crustacea</td>
<td>Ajeska &amp; Nybakken, 1976</td>
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</table>
CHAPTER 2
STUDY AREAS

Two localities were chosen for this study, both on the North East coast of the North Island of New Zealand. Observations on Aplysia dactylomela and A. parvula were made at Goat Island Bay, Leigh and those on Haminoea zelandiae and Bursatella leachii at Motukaraka Island, off Beachlands Beach.

2.1

Goat Island Bay, Leigh (36° 16'S; 174° 48'E) is 90 km north of Auckland, and is the site of the Marine Research Station of the University of Auckland. It is situated immediately outside the boundaries of the Hauraki Gulf and dominated by Goat Island which is 500 m² in area and 77 m from the mainland at its nearest point. The waters around Goat Island and to Cape Rodney to the South East and Okakari Point to the North West constitute New Zealand's first Marine Reserve which was established in November 1975. A review of knowledge and bibliography for the Marine Reserve has recently been published (Gordon & Ballantine, 1976), and a survey of the reserve initiated in 1976 is still in progress (Ayling, in prep.).

Goat Island itself is open to the South Pacific Ocean for an arc from the Northland Coast at Whangarei Heads through 90° to Little Barrier and Great Barrier Islands apart from small intervening groups of islands (Hen and Chicken Is, Moho Hinau Is) which do little to break the fetch of Pacific seas. Goat Island Bay lies to the South West of the Island and is therefore afforded some protection from North Easterly storms which tend to be the most severe of all. Within Goat Island Bay is a large intertidal reef platform, some 2.76 ha. in area and extending approx. 102 m seawards where widest. It is nicknamed "Echinoderm Reef" because echinoderms are abundant. This reef is probably the best-studied intertidal rocky area in New Zealand. Its physical characteristics and dominant biota have been described by Morton & Chapman (1968), Morton & Miller (1968) and Walsby (1977).
Echinoderm Reef slopes gently seawards. It is composed of alternating unfossiliferous felspathic sandstones, ripple-marked mudstones and carbonaceous shales, containing interbedded Mahurangi grits and basal conglomerates (Hopgood, 1961). These sediments accumulated in Upper Oligocene to Lower Miocene time (Ballance, 1974).

2.2

Motukaraka Island (36° 53'S; 174° 59'E) is known locally as "Flat Island". It is 5.7 ha in area, it lies 0.58 km off Beachlands, being 19.2 km from Auckland. The island is joined to the mainland by extensive shallow sand flats which become exposed for approximately one third of each 12 hr tidal cycle and allow foot access to the Island. Motukaraka Island is virtually surrounded by land with an inner string of the islands of the Auckland Harbour forming an arc approx. 8 km to sea (Rangitoto Id, Motutapu Id, Motuihe Id, Rakino Id, Waiheke Id, Ponui Id) and beyond that Coromandel Peninsula and Great Barrier Island which form an almost continuous outer barrier to the Hauraki Gulf.

Motukaraka Id is fringed almost continuously by a low-tidal reef platform cut in sandstones of the Waitemata Group. This reef is particularly large on the North Eastern side of the Island, extending to a maximum of 155 m seawards.

2.3 Physical Characteristics.

2.3.1 Water Temperature.

The oceanic waters of northern New Zealand are warm temperate in character. Sea surface temperature in the Hauraki Gulf is known to reach a summer maximum of 22.0°C (Paul, 1968) and a winter minimum of 13.0°C (Paul, 1968; Taylor, 1973). Dellow (1955) included a climate section in her large work on marine algal ecology of the Hauraki Gulf, this paper presenting the first records of sea temperatures, salinity, pH and oxygen concentration for waters in the Hauraki Gulf. Following Dellow's account
of monthly average sea surface temperatures (1935-1931) made by coastal vessels and her summary of air and sea temperatures for one location at Clifton Beach, north of Narrow Neck (1949-1950), Slinn (1968) gave monthly means for temperature, salinity, oxygen and nutrients from the Waitemata Harbour (made during 1963) taken from fixed stations within the Harbour.

Since 1967 the Leigh Laboratory has been taking daily readings of sea surface temperature to monitor changes in coastal climate. Monthly averages for the 11 years to December 1977 are shown in Table 2.1. The maximum monthly average during that time was 22.9°C while the minimum was 13.3°C. The average annual range was 7.1°C, whereas the range for each month was 2.1 - 3.6°C for the summer months and 1.4 - 2.2°C for the winter months. Dellow (1955) showed sea temperatures lag about one month behind air temperatures.

To complement the above data for ambient sea temperature conditions at Leigh, the water temperature of two of the study pools on Echinoderm Reef (near inner and outer extremes of the reef platform) were recorded at each visit and these are presented in Appendix III.1. These recordings emphasize the considerable significance in the intertidal region of the more extreme heating and cooling of exposed rock and shallow pools subject to strong illumination.

Water temperatures for fixed locations inside the Waitemata Harbour itself tend to be slightly cooler in winter, and warmer in spring and summer than those of the outer Hauraki Gulf because of the shallowness of the Harbour (Slinn, 1968). Slinn gives a maximum of about 21.8°C and a minimum of about 11.9°C. Recordings of seawater temperature in study areas were made on each visit to Motukaraka Island and are given in Appendix III.2. One point of note concerning temperature is that air temperatures for the 1975 Auckland summer were the coldest recorded since 1948 (N.Z. Meteorological Service).
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<td>1976</td>
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<td>17.4</td>
<td>17.1</td>
<td>17.0</td>
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<td>16.4</td>
<td>16.1</td>
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<td>1977</td>
<td>17.5</td>
<td>17.1</td>
<td>16.7</td>
<td>16.3</td>
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<td>15.4</td>
<td>15.0</td>
<td>14.7</td>
<td>14.2</td>
<td>14.2</td>
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<td>16.0</td>
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<td>1979</td>
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<td>16.2</td>
<td>16.0</td>
<td>15.7</td>
<td>15.4</td>
<td>15.1</td>
<td>14.8</td>
<td>14.5</td>
<td>14.1</td>
<td>14.0</td>
<td>13.9</td>
<td>13.5</td>
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<tr>
<td>1980</td>
<td>16.1</td>
<td>15.7</td>
<td>15.5</td>
<td>15.3</td>
<td>15.1</td>
<td>14.8</td>
<td>14.6</td>
<td>14.4</td>
<td>14.1</td>
<td>14.0</td>
<td>13.9</td>
<td>13.5</td>
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<tr>
<td>1981</td>
<td>15.6</td>
<td>15.3</td>
<td>15.1</td>
<td>14.9</td>
<td>14.7</td>
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<td>13.8</td>
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<td>13.2</td>
<td>12.9</td>
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<td>12.8</td>
<td>12.6</td>
<td>12.4</td>
<td>12.3</td>
<td>12.2</td>
<td>11.9</td>
</tr>
</tbody>
</table>

Table 2.1: Sea-surface temperature—monthly averages for the Great Island Region.
2.3.2 Sediment deposition.

The second physical parameter which was measured at each of the two study sites was sediment load, since this was considered to be of importance not only as an indicator of wave strength and water movement at each locality but also because the data could be used to compare each locality directly, provided both sites have the same horizontal topography and Corallina officinalis grows there. And this information could be used to predict events at other sites which lie in between or outside those of the two study sites examined in detail in this thesis.

At each locality ten $0.1 \text{ m}^2$ areas, five each made randomly on the inner and outer areas of the reef platform, were sampled. All sediment and algae were collected in a labelled plastic bag. Before collection, the area was photographed to obtain the percent cover of Corallina officinalis (an alga of the order Cryptonemiales with a low, tight growth habit) which acts as an excellent trap for sediments. At both localities counts were made of numbers and species of grazing molluscs in each area.

For the sediment analyses, determinations of total weight and total organic content were made, proportions of coarse sand, medium sand, fine sand and very fine sand were recorded, and calcium carbonate composition was determined.

Results for the sediment analyses themselves are given in Appendices IV.1 (Leigh) and IV.2 (Motukarakaka Island), and a summary of data for pooled means and standard errors is presented here in Table 2.2. Simply to facilitate construction of the above two appendices I have given data for the numbers and species of grazing molluscs in each of the areas in an appendix on its own (Appendix IV.3).
Table 2.2. Summary of comparative values for means and standard errors of sediment loads. Derived from each of ten 0.1 m^2 quadrats made on Echinoderm Reef Flat, Leigh and Motukaraka Island, Hauraki Gulf.

<table>
<thead>
<tr>
<th></th>
<th>Leigh</th>
<th></th>
<th>Motukaraka Id</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>S.E.</td>
<td>Mean</td>
<td>S.E.</td>
</tr>
<tr>
<td>Total weight of sediment (gm)</td>
<td>123.18</td>
<td>19.87</td>
<td>669.23</td>
<td>78.63</td>
</tr>
<tr>
<td>Total weight of organic material (gm)</td>
<td>67.57</td>
<td>11.96</td>
<td>113.89</td>
<td>10.78</td>
</tr>
<tr>
<td>% coarse sand (0.5 mm sieve)</td>
<td>10.60</td>
<td>1.52</td>
<td>6.17</td>
<td>1.56</td>
</tr>
<tr>
<td>% medium sand (0.25 mm sieve)</td>
<td>29.94</td>
<td>3.62</td>
<td>10.93</td>
<td>1.12</td>
</tr>
<tr>
<td>% fine sand (0.12 mm sieve)</td>
<td>31.14</td>
<td>4.09</td>
<td>38.69</td>
<td>1.31</td>
</tr>
<tr>
<td>% very fine sand (0.064 mm sieve)</td>
<td>18.27</td>
<td>8.09</td>
<td>33.92</td>
<td>0.73</td>
</tr>
<tr>
<td>% of mud</td>
<td>6.89</td>
<td>1.88</td>
<td>10.22</td>
<td>0.9</td>
</tr>
<tr>
<td>% of CaCO₃ in sieved sample</td>
<td>42.95</td>
<td>2.0</td>
<td>12.79</td>
<td>1.37</td>
</tr>
</tbody>
</table>
Figure 2.1.

Map of the Hauraki Gulf showing location of both the study sites with (inset) map of New Zealand.
Figure 2.2.
Survey map of Goat Island Bay, Leigh, showing location of study sites. Map courtesy of A.M. Ayling, from unpublished Marine Reserve Survey.

Points A, B, W and X indicate the position of the four intertidal study pools on Echinoderm Reef. Point C indicates the position of the subtidal study area North East of Knot Rock.

Insert shows the extent of Echinoderm Reef as exposed on a 0.1 m spring tide. Photograph taken from just below Marine Laboratory looking to the west. R.C. Willan, 16 November 1977.

Subtidal Survey Map - Scale 1 : 2000

KEY

**BOUNDARIES**

- Base of cliff
- Low tide line
- Outer sand/rock border
- Habitat demarcations
- Topographic features
- Depth contours (metres)
- Top of cliff

**TERRESTRIAL**

- Pohutukawa
- Macrocarpa erecta
- Pine
- *Pinus radiata*
- Cabbage tree
- *Koelmia australis*
- Flax
- *Phormium tenax*
- Fence line

**OTHER FEATURES**

- Permanent anchor/survey buoy

**MARINE HABITATS**

- Rock Flats, 1-12m. Flat or undulating, *Evechinus* abundant, *Ecklonia* sparse or absent.
- Sediment Covered Rock Flats, 3-15m. Flat, few *Evechinus*, *Ecklonia* sparse or absent, some sponges in deeper water.
- *Ecklonia* Forest, 5-15m. Dense *Ecklonia* cover on flat or undulating rock, *Evechinus* absent.
- Sponge Garden, 16-20m. Sediment covered rock flats, urchins and finger sponges abundant, *Evechinus* & *Ecklonia* sparse.
- Shallow Broken Rock, 1-16m. Large boulders and crevices, dense mixed brown algae on peaks, moderate *Evechinus*.
- Deep Reefs, 15-20m. Moderately broken, few *Evechinus* & *Ecklonia*, sponges, ascidians and brachiopods abundant.
- Cobble, Drifts of small boulders and sand.
- Sand and Gravel.
Figure 2.3.

Panoramic view of low tidal reef platform, as exposed on a 0.4 m spring tide, on the northern side of Motukaraka Island, Auckland, showing location of study pools B and C. Lower diagram names the inner islands of the Auckland Harbour. Photographs taken from cliff top, Motukaraka Island.

R.C. Willan, 8 January 1978.
CHAPTER 3

STUDY ANIMALS

3.1 Introduction.

This study has concentrated principally on the ecology of two species of opisthobranch mollusc - Aplysia (Varria) dactylomela Rang, 1828 and Haminoea zelandiae (Gray in Dieffenbach, 1843). Besides these two, two others have been sufficiently abundant at times, in the study areas to examine their ecology and thus make a comparison with the former two. These latter species are Aplysia (Pruvotaplysia) parvula Mörch, 1863 and Bursatella leachii Blainville, 1817. Initially, studies were going to be on the former two species only, but B. leachii fortuitously turned up in large numbers at Motukaraka Id during the H. zelandiae surveys and A. parvula was subsequently found subtidally at Goat Island Bay in sufficiently high densities to undertake some population studies on it. I have included a brief note on the life cycle of Melanochlamyx cylindrica Cheeseman, 1881.

Haminoea zelandiae and Melanochlamyx cylindrica are in the order Cephalaspidea (= Bullomorpha), this group being characterized by: the presence of a spiral shell that is more or less developed and external or internal, the head flattened dorsally into a head shield which is separated laterally from the foot by a groove in which is situated Hancock's organ. The anus and the genital pore opening towards the floor of the mantle cavity, the female genital orifice being in front of these apertures and on the right side, a retractile penis (not in the Acteonidae where it is permanently everted) in front of the female orifice, the vas deferens being either an open canal or a subepidermal tube, jaws are weak or absent (Thiele, 1931; Hyman, 1967; Odhner in Franc, 1968). It is probable that the order is polyphyletic (Rudman, 1970; 1971a; 1971b).
The two Aplysia species and Bursatella leachii are in the order Anaspidea (= Aplysiacea or Aplysiomorpha) which is almost certainly a natural and compact assemblage (Thompson, 1976). All are typified by the lack of a cephalic shield, the presence of parapodia enclosing a distinct pallial cavity in which is a conspicuous plicate gill, and by having a much reduced shell that is usually covered by the mantle, or lacking one altogether, a digestive system adapted for a herbivorous diet, and a hermaphrodite reproductive system, some of the species swimming with varying degrees of ability (Thiele, 1931; Hyman, 1967; Beeman, 1968; Thompson, 1976).

The Anaspidea are divided into two subgroups: Longicommissurata with very long pleurovisceral connectives and the Brevicommissurata with greatly reduced pleurovisceral connectives (Marcus, 1972). The genera Aplysia Linnaeus 1767, Dolabella Lamarck, 1801 and Syphonota A. Adams, 1854 form the first group whilst Bursatella Blainville, 1817, Stylocheilus Gould, 1851, Notarchus Cuvier, 1817, Phyllaplysia P. Fischer, 1872, Petalifera Gray, 1847 and Dolabrifera Gray, 1847 constitute the second group.

As is the case with most of the groups of New Zealand opisthobranchs, the Anaspidea received meagre treatment by early workers and have generally been neglected in favour of their shelled prosobranch and pulmonate kin. As no regional systematic studies have been presented for the order in this country, classification of the Anaspidea remains uncertain despite an abundance of published literature overseas. On the other hand, names have been proposed for five taxa, apparently unique to New Zealand (Aplysia brunnea Hutton 1875, Aplysia venosa Hutton 1875, Aplysia tryonii Meinertzhagen 1880, Aplysia hamiltoni Kirk 1881, Aclesia glauca Cheeseman 1878) and the status of these species needs to be evaluated with respect to overseas taxa.
For these reasons a complete taxonomic review of the order Anaspidea in New Zealand has been undertaken as part of this thesis and is presented in Appendix I. This systematic section is based on field collections made by the author supplemented by examination of as much comparative material residing in collections as possible. I am very grateful to the following people who have assisted me with this work: Mr W.O. Cernohorsky, Auckland Institute and Museum; Dr M.C. Miller, Zoology Department, University of Auckland; Drs R.K. Dell and F.M. Climo, National Museum, Wellington; Professor R.L.C. Pilgrim, Zoology Department, University of Canterbury, Christchurch; Mr G. Tunnicliff, Canterbury Museum, Christchurch; Drs J.B. Jillett and C.R. Boyden, Portobello Marine Laboratory, Otago; Dr W.F. Ponder, The Australian Museum, Sydney.

3.2 APLYSIA (VARRIA) DACTYLOMELA RANG, 1828. Frontispiece; Figs. 3.1A,B; 4.1a; 9.4F,G.
In her revision of the World species of Aplysia, Eales (1960) was the first to record the presence of this distinctive sea hare from New Zealand. Morton & Miller (1968) also recognized the species and gave a brief description and a coloured drawing of a living specimen. Morton & Chapman (1968) noted that A. dactylomela could be found in pools on the lower eulittoral terrace in Goat Island Bay. Miller & Batt (1973) recorded that "the red seaweeds Corallina officinalis and Laurencia are the favourite food of Aplysia dactylomela". The species has been admitted to the latest checklist of New Zealand's mollusca (Powell, 1976) on the basis of Morton & Miller's record. Gordon & Ballantine (1976: 112) recorded its presence in the Cape Rodney to Okakari Point Marine Reserve, the Aplysiidae in this work being listed under the vernacular name of "sea horses" because of an unfortunate printer's error.

Aplysia dactylomela has received more attention than any other Aplysia species because of its large size, wide distribution and striking appearance (Eales, 1960). It has also come into the hands of taxonomists
many times and Eales lists 21 synonyms. Engel (1921) was first to draw up a synonymy and showed the species to be circum-tropical in distribution. Eales (1960) records it from Bermuda, Florida, Mexico, the West Indies, Panama, Brazil, the Canaries, the Cape Verde Islands, Ghana, the Red Sea, Ceylon and India, Mauritius, South Africa, China, Japan, the East Indies, the Philippines, Samoa, Tonga, the Gilbert Islands, Australia and New Zealand. It has been recorded subsequently from South Texas (Neck, 1976; Strength & Blankenship, 1977), Bimini, Bahamas (Carefoot, 1970; Lederhendler et al., 1975), Puerto Rico (Lederhendler, 1977a; 1977b), Barbados (Marcus & Hughes, 1974), Brazil (Marcus, 1972), tropical West Africa (Marcus & Marcus, 1966), Ghana (Edmunds, 1977), Kenya (Bebbington, 1974), Gulf of Kutch (Narayanan, 1969), China (Guang-Yu & Si, 1965), Japan (Usuki, 1970), Queensland (Burn, 1966; Kenny, 1970), Micronesia (Marcus, 1975), and Hawaii (Kay, 1964).

In New Zealand *A. dactylomela* occurs on the East Coast of the North Island and so far is only known from Northland; it has not been recorded for the West Coast. This distribution is shown by numerous other gastropods (Powell, 1961) and is typical of warm temperate species (Dell, 1962). The pattern is related to the warm East Australian current flowing down the North East coast of the North Island running out to sea again at East Cape (Brodie, 1960; Powell, 1961; Knox, 1963). Willan (1976) listed 43 species of molluscs showing similar trans-Tasman affinities. A full list of New Zealand localities from which *A. dactylomela* has been authentically reported is included in Appendix I.

The species is essentially intertidal in New Zealand and its distribution just extending subtidally to approx. 8m; its bathymetric range apparently being correlated with that of its favoured algal food. Individuals occasionally stray into deeper water, one being recorded in 17m off Goat Island (P.J. Doherty, pers. comm., 1975). Kay (1964) noted a juvenile specimen that had been dredged from 183m in Hawaii. In New Zealand it is usual for *A. dactylomela* to reach a maximum size of 30cm and this
corresponds with a weight of 450gm, but exceptionally New Zealand specimens reach 45cm and attain a weight of 1.4Kg.

In recent years *Aplysia dactylomela* has been eclipsed as an aplysiid subject for ecological and physiological research by *A. californica* Cooper. Nevertheless, *A. dactylomela* continues to be intensively studied, Lederhendler et al. (1975) having reported on preliminary investigations of distribution, changes in locomotion and interspecific behaviour in the field at Bimini, Bahamas. Lederhendler (1977a) examined reproductive and intraspecific behaviour in the laboratory and parts of this study have subsequently been published (Lederhendler, 1977b; Lederhendler & Tobach, 1977). Tobach (1978) has provided field notes on pairing behaviour. Switzer-Dunlap & Hadfield (1977) have successfully cultured *A. dactylomela* through to metamorphosis.

3.3 APLYSIA (PRUVOTAPLYSIA) PAVULA MORCH, 1863. Figs. 3.2A,B; 9.1d; 9.4D,E.

This species, small when adult, has an enormous global distribution, ranging from approx. 40 N. to 40 S. latitude in all tropical and temperate seas (Eales, 1960; Barash & Danin, 1971; Marcus, 1972). Eales has compiled a very extensive list of authentic localities within these latitudinal limits; however it can also occur considerably beyond these latitudes. Bebbington & Brown (1975) have recorded it from British shores (50 10'N.), and in New Zealand it is found throughout the country as far south as Otago Peninsula (46 S.). Burn (1966a)records it from Tasmania. Another recent locality record is that of Lance (1971) for the Gulf of California.

Records subsequent to those of Eales are from Queensland, N.S.W., Victoria, Tasmania and South Australia (Burn, 1966a; 1966b; 1969), Hawaii (Kay, 1964), Brazil (Marcus, 1972), Japan (Usuki, 1970), Madagascar and West Mexico (Marcus & Marcus, 1970), Israel and Mediterranean Sea (Barash & Danin, 1971; Bebbington, 1972; 1975). Eales (1970) suggested that *A. parvula*
had recently entered the Mediterranean Sea via the Suez Canal; hence its spread into the Central and western Mediterranean (Bebbington, 1972). However, because of the possibility of earlier misidentifications Bebbington (1975) now doubts that it is possible to postulate the date of entry.

_Aplysia parvula_ is distinct from all but one of the other species in the genus, not only because of its small adult size, but also due to it exhibiting a number of characters (relatively small parapodia, anterior position of visceral mass, nidamental gland arrangement, large shell, conspicuous mantle foramen) interpreted as being primitive (Pruvot-Fol, 1956). It shares these characters with the European _A. punctata_ Cuvier. These characteristics are considered sufficient to place them in a separate subgenus _Pruvotaplysia_ (Engel, 1936).

_Aplysia parvula_ as such was first recorded from New Zealand by Eales (1960), but under the name of its synonym _Aplysia tyronii_ Meinertzhtag, it had been known from this country since 1880 (Meinertzthag, 1880; Suter, 1913; Appendix I). _Aplysia parvula_ appears in the New Zealand literature in works by Morton & Miller (1968), Morton & Chapman (1968), Gordon & Ballantine (1976), Powell (1976).

Eales (1960) states that _A. parvula_ rarely reaches more than 60mm in length, but the largest New Zealand specimens are double this figure (120mm; 41gm) although these are considered exceptional. In this country the species is common intertidally and subtidally.

3.4 **BURSATELLA LEACHII BLAINVILLE, 1817** Figs. 9.2a; 9.3.

The "Woolly Sea Hare" was first recorded from New Zealand under the name of _Aclesia glauca_ Cheeseman 1878, being described as a new species (the type locality was given as Auckland Harbour). The description was accompanied by a meticulously hand-drawn illustration. Subsequent overseas reviewers of _Bursatella_ Blainville have been more reactionary in their treatment of this genus than for _Aplysia_; so, although Eales & Engel (1935)
went a considerable way towards a taxonomic understanding of *Bursatella leachii*, they chose to recognize six geographical subspecies to which Bebbington (1969) added a seventh. Most of these subspecies have never been rigidly defined and are separated by the most subjective of characters, e.g. "*B. leachii africana* is very woolly in appearance" (Eales & Engel, 1935). When one examines the allometric changes that occur in body structure and pigmentation within a single population, it appears that these characters upon which subspecific distinctions have been based are more likely due to intra-specific variation. It follows, therefore, that this division of *Bursatella leachii* into subspecies is unnecessary and if continued would retard understanding of the species as a whole. All of the available evidence suggests that world-wide populations of *Bursatella leachii* have as much genetic contact as do those of other anaspideans of a very wide geographic distribution (e.g. *Aplysia dactylomela*, *A. parvula*, *A. juliana*, *Stylocheilus longicauda*). True subspecies have yet to be identified.

Bearing in mind this broader definition of *B. leachii*, its distribution is almost circumtropical; it appears to be absent from the Eastern Pacific (Kay, 1964; Marcus, 1965). Recent records of *B. leachii* are from Florida (Lowe & Turner, 1976), South Texas (Strength & Blankenship, 1977), Jamaica (Davis, 1967), Colombia (Bandel, 1976; Marcus, 1976), Mediterranean Sea (Barash & Danin, 1971; Bebbington, 1972), Kenya (Bebbington, 1974), Ghana (Bebbington, 1969; Edmunds, 1977). In New Zealand, *B. leachii* has the same geographic range as *Aplysia dactylomela*.

*Bursatella leachii* most resembles *Stylocheilus longicauda* (Quoy & Gaimard) amongst the other members of the order Anaspidea, and assemblages of these two species are occasionally encountered. *B. leachii* has an exceptionally wide range of diet and is strongly euryhaline. These two attributes permit it to tolerate conditions of lessoned salinity not exploited by other generalist molluscan herbivores and so it is regularly found in harbours, estuaries and brackish lagoons. Its occurrence in such situations is more
predictable than on cleaner, more open coasts. In New Zealand the maximum size is approx. 12cm and this corresponds with a wet weight of roughly 100gm. Depth range is intertidal and shallow subtidal to approx. 12m.

More than any other anaspidean, Bursatella leachii exhibits a high degree of social interaction; there are reported instances of mass migrations (Lowe & Turner, 1976) and dense spawning aggregations (Marcus, 1972) in this species. Descriptions of the spawn and hatching have been given for B. leachii in Jamaica (Davis, 1967) and Colombia (Bandel, 1976).

3.5 HAMINOEA ZELANDIAE (GRAY IN DIEFFENBACH, 1843) Fig. 3.3.

Members of the herbivorous opisthobranch genus Haminoea are found throughout temperate and tropical regions of the world. The genus is characterized by the thin bubble-shaped shell which is partially enclosed by lateral extensions of the foot, the wide radula of hook-shaped teeth, and the large gizzard containing three-sided chitinous plates (Rudman, 1971c). Approximately 70 species have been included in Haminoea sensu lato (Rudman, 1971c).

Unlike the three members of the Anaspidea examined in this thesis, the cephalaspidean Haminoea zelandiae is endemic to New Zealand. The vernacular name of "White Bubble Shell" is frequently applied to this species most appropriately to its fragile, ovoid shell. Haminoea zelandiae is found only in the intertidal zone. It is a very common and characteristic inhabitant of mud- and Zostera flats of protected harbours and estuaries (Morton & Miller, 1968; Miller & Batt, 1973), its plough-like form enabling it to glide over soft sediments or burrow shallowly just beneath the surface. It can also be found living on hard substrates amongst Corallina officinalis turf. Haminoea zelandiae is found throughout the North Island of New Zealand with its southern limit coinciding approximately with Cook Strait, and touching the very northern tip of the South Island since it is also present in Pelorous Sound (Suter, 1913) and Golden Bay, Nelson (Elliott, 1967; Bergquist et al., 197
When extended and crawling actively, *Haminoea zelandiae* can reach 45mm in length, and this corresponds roughly with a weight of 3.7gm. Maximum dimensions of shells examined personally are 24 x 19mm.

The external morphology, mantle cavity, reproductive and nervous systems of *Haminoea zelandiae* have been described by Rudman (1971c) and contrasted with that of other temperate and tropical representatives of the same genus. Rudman (1971b) has also detailed the structure and functioning of the alimentary canal in *H. zelandiae*, and reported it to be a vegetarian that ingests green algae and diatomaceous films. According to Rudman, *H. zelandiae* is unable to control its feeding responses, and when a plentiful supply of *Enteromorpha* sp. is provided the animal eats it all. The result of this rapid feeding is to have *Enteromorpha* entering the mouth and uniform lengths of undigested weed leaving the anus, bound as green faecal pellets. On the basis of the herbivorous habit and the structure of the reproductive system, Rudman (1971c) suggested that the group to which *Haminoea* belongs, Haminoeidae, shows a closer relationship to the Anaspidea than to many of the other forms at present classified within the order Cephalaspidea.
Figure 3.1.

Aplysia dactylomela Rang.

A - Specimen in detached posture.

B - Specimen in resting position.

Both specimens from Echinoderm Reef, Goat Island Bay, Leigh.

Figure 3.2.

*Aplysia parvula* Mörch.

**A** - Specimen of intertidal brown colour form.

Length = 60 mm. From "Echinoderm Reef", Goat Island Bay, Leigh.


**B** - Specimen of subtidal red colour form on alga *Plocamium costatum* J. Agardh. Length = 60 mm. From 12 m, 200 m N.W. of "Knot Rock", western end of Goat Island Bay, Leigh.

Photo: R.C. Willan, 6 July 1977.
Figure 3.3.

_Haminoea zelandiae_ (Gray in Dieffenbach).

Specimen from Motukaraka Island, Tamaki Strait, Auckland.

Photo: R.C. Willan, 18 November 1976.
CHAPTER 4
METHODS

4.1 Sampling Techniques.

4.1.1 Study Sites at Study Locations.

Surveys at Goat Island were done monthly, and at Motukaraka Island approximately twice on each month. On each visit observations were made at fixed sites on each shore. These sites were initially chosen as naturally occurring tide pools; four at each locality, the pools chosen are representative of the pools that exist on the platform at each tidal level.

This study pool approach was satisfactory at Leigh, but at Motukaraka Island where Haminoea zelandiae densities were higher and individuals smaller it was necessary to spend a longer search time so it became necessary to subsample the study pools using a 1 m² frame of tubular plastic which was placed randomly. Each 1 m² area took 15-20 min. to search thoroughly. A 0.1 m² iron frame was also used at Motukaraka Island, being placed randomly inside each study pool to gauge densities on a smaller scale and examine intraspecific variability in the chosen pools.

Goat Island Bay.

The location of the four study pools on Echinoderm Reef is shown in Fig. 2.2. Pool A is 5.2 m from the base of the beach on the eastern end of the Reef, it is 4.4 m² in area and consists of three triangular pools strung together. The chain is approx. at 45° to the beach, and the area just over 1 m wide at maximum. Its floor slopes evenly to the South to a maximum depth of 8 cm, and overall it is quite shallow with an average depth of 3.5 cm. The floor has a dense permanent cover of the alga Corallina officinalis but this may be obscured by seasonal bursts of growth of other ephemeral algal species (Enteromorpha sp., Laurencia spp.). Pool A is formed by every low tide, and at springs this pool is isolated from the sea for approx. 2.5 hr.
Pool A was monitored from May 1975 to November 1977. As the tide is ebbing there is a continuous flow of sea water from the gravel of the beach through the channel formed by pool A, and ultimately out to sea. Pool B is much larger, being 268 m$^2$ in area and situated at the north eastern extremity of Echinoderm Reef, it was monitored from August 1975 to November 1977. A raised rock finger projects into the pool from the South East; on the North Eastern side there is an extensive basin. Also, there is a series of steps on the South Western edge and several deeply gouged V-shaped wedges on the Western and South Western sides. A maximum depth of 50 cm is attained near the centre of the pool.

Pool B is isolated from the sea by tides of $\leq 0.2$ m, and so, because of its large area and relatively short time out of contact with the sea, its temperature changes little. Even at the lowest of spring tides, waves regularly break into pool B. Shallower areas bear a permanent turf of Corallina officinalis which supports seasonal outbursts of ephemeral algae such as Colpomenia sinuosa, Liagora harveyana, Glossophora kunthii, Lyngbya lutea, Laurencia distichophylla, Champa novaezelandiae and Gigartina macrocarpa. The deeper parts of the pool are dominated by patches of larger fucacean algae (Carpophyllum plumosum, C. mashalocarpum, Sargassum spinuligerum, Cystophora torulosa), and the occasional plant of the laminarian Ecklonia radiata.

Pools W and X lie on the inner part of the reef platform towards the western extremity of Echinoderm Reef, and are 33.9 m$^2$ and 5.7 m$^2$ in area respectively. They are ecological duplicates of pool A. Both were monitored from April to November 1977. Pool X is nearly circular with a maximum diameter of 7.1 m. An undercut rock wall bounds the pool in a straight line along the eastern side, and at this side the maximum depth of 22.5 cm is reached. At its closest point, pool X is 7.3 m from the base of the beach. Pool W is 1.7 m seawards of pool X, being basically V-shaped with its apex to the west and greatest depth of 14 cm is reached here as well. Both pools
are formed by every low tide, at springs they are isolated for approx. 2 hr.

The subtidal study site for *Aplysia parvula* in Goat Island Bay was located some 300 m offshore in 8-12 m of water. Personal observation, and the amount of silt on the bottom here indicate that this location is protected to some extent by Goat Island from rough northerly and easterly gales, and lies sufficiently far from the western end of Goat Island Bay to be beyond the reach of swells passing through the Goat Island channel. The area has an almost continuous canopy of *Ecklonia radiata* kelp at an average height of 1.5 m occasionally interrupted by solitary plants, or small patches, of *Carpophyllum maschalocarpum* or *Sargassum sinclairii*. This area supports a rich bottom flora and fauna. Dominant macroalgal species in the understorey are *Plocamium costatum*, *Pterocladia lucida*, *P. pinnata*, *Melanthalia abscessa*, *Corallina* spp., *Delisea compressa*, *Rhodymenia linearis* (all *Rhodophyceae*) and *Caulerpa sedioides f. novaezelandiae* (Chlorophyceae) and *Carpomitra* sp., *Zonaria angustata* (Phaeophyceae). Sponges figure prominently in this association, the dominant species being *Polymastia granulosa*, *P. fusca*, *Callyspongia ramosa*, *Raspailia* spp., *Ancorina alata*, *Biemma* sp. and *Aplysilla rosea*. The area is correspondingly rich in molluscs, echinoids, ascidians and crustaceans, but as observed by Ayling (1968), there is a marked paucity of encrusting forms beneath this kelp canopy. Inshore, in 4.5 to 9 m, the kelp canopy is broken and gives way to a *Corallina officinalis* turf/*Lithothamnion* sp. crust in which full establishment of a kelp canopy is inhibited by the grazing of the urchin *Evechinus chloroticus* (Dromgoole, 1964; Don, 1975). Offshore, in 14 to 16.5 m, the rocky areas are sparser and kelp passes into a sponge-dominated region intermixed with sand patches.
Motukaraka Island.

The location of the Motukaraka Island study sites is shown in Fig.2.3. Pool A is on the eastern tip of the Island, 16.5 m from the cliff edge, it is 8.4 m² in area. There is no beach zone between the reef platform and cliffs. The pool has a layer of sand over its floor, the greatest depth being 5.5 cm, and there is an area of *Corallina officinalis* stubble at the eastern extremity. Pool A is formed by every low tide, being isolated from the sea for approx. 2.5 hr.

Area A/B is on the northern side of the island, and at low spring tides, consists of a series of very shallow pools high on the reef platform at a distance of only 3 m from the cliffs. The greatest depth is 6 cm. The floor of this area is mostly bare sandstone with little silt or sand covering, however, there are patches of *Corallina officinalis* stubble which occasionally support growths of filamentous species of Chlorophyceae and Phaeophyceae. This area was monitored from July 1976 to February 1978 using a linear series of 41 m² quadrats extending seawards from 3 m to 6 m. At springs, pool A/B is isolated for approx. 3 hr.

Pool B is situated at 62 m across the reef platform, it is 14.82 m² in area and roughly rectangular in shape, the greatest depth being 13 cm. The pool has an extensive carpet of *Corallina officinalis* which is obscured seasonally by growths of *Lyngbya majuscula* and *Rhizoclonium* spp., especially in the shallows. Pool B is isolated for approx. 2 hr at springs.

Pool C is 105 m from the island (and is thus 58 m back from the edge of the reef platform), its area is 9.2 m², and it is part of a larger pool of standing water. The greatest depth is 10 cm. Here again the predominant alga is *Corallina officinalis*, although considerable amounts of *Lyngbya majuscula* and chlorophycean stubble cover the *Corallina* at times.

The first three sites are accessible at every low tide, but tides lower than 0.7 m are required for surveys of pool C. Observations were not possible at tides of ≥ 0.7 m in pool C because the pool is covered with 4 - 6 cm of
water through which it is not possible to locate Haminoea zelandiae properly. In fact, C is only formed at tides of \( \geq 0.4 \) m in magnitude. Pools A–C were monitored from March 1975 to February 1978.

### 4.1.2 Aplysia dactyomela sampling.

Each pool at Echinoderm Reef was searched thoroughly on each monthly visit. Visual searching was found to be adequate, with juvenile specimens down to 5-8 mm being detectable. All specimens collected were put into a separate bucket labelled according to their respective pool, and when the day's survey was finished were taken to the Marine Laboratory where they were measured and weighed. The specimens were then maintained in 18 perspex aquaria fitted with gauze covers and through which there was a continuous flow of fresh seawater from the laboratory's seawater system. The specimens were returned to their respective pools at low tide on the following day.

To supplement the data on A. dactyomela collected from the study pools, additional surveys were made on each visit along the inshore and offshore parts of the reef platform (zones of pools A, W, X and pool B respectively). Specimens of Aplysia parvula located either in the study pools or in these additional surveys were collected as well.

At the subtidal situation off "Knot Rock", one survey consisted of a series of SCUBA dives done radially outwards from a permanent marker buoy located at the study site (PB. 4). A series (12-15) of 1 m\(^2\) transects, using a 1 m\(^2\) fixed metal frame, was run through areas of maximum Plocamium costatum density and all the Aplysia parvula present in these areas were located by eye or touch. Specimens were either brought back to the laboratory for measurement and weighing or measured underwater and replaced immediately.

### 4.1.3 Haminoea zelandiae sampling.

All four study sites were surveyed where possible on each visit, in addition a deep V-shaped gulley, which completely intersected the reef platform, was surveyed for presence of opisthobranchs amongst drift algal
debris that tended to accumulate there, and a pool at the extreme outer edge of the reef flat was surveyed for opisthobranchs (Haminoea zelandiae, Bursatella leachii, Melanochlamys cylindrica) and algae. Visual inspection was employed on all surveys and specimens resting or crawling over the sediment surface were counted and collected for measurement, juveniles down to 2 mm in length were able to be detected by this method. Careful disturbance of the sediment by hand and paint brushes was also employed. Occasionally a sieve with a mesh size of 1 mm was used to search for buried juveniles. However, because collecting Corallina officinalis and incorporated sediment destroyed the habitat this sampling technique was used in pools adjacent to the study pools but never directly in the pools themselves.

When located, densities per pool or per m$^2$ were counted, then the Haminoea zelandiae were washed carefully to free them from slime and adhering mud and placed in a jam jar. Following the survey of each site the Haminoea were measured in situ and returned immediately. On the occasions when densities were higher than 50 m$^2$, only the first 40-50 specimens collected were measured.

4.1.4 Algal Sampling.

On each visit to study areas, the presence and density of algae were recorded, particularly of those species serving as prime foods for the study animals - three Laurencia spp. intertidally at Goat Island Bay and Plocamium costatum subtidally, Lyngbya majuscula and several filamentous species of Chlorophyceae and Phaeophyceae at Motukaraka Island.

At Goat Island Bay two areas of 0.5 m$^2$ each in pool A were photographed monthly from November 1975 to November 1977 to follow the changes in gross algal cover. A further seven areas of 0.1 m$^2$ (two in pool A itself and the remaining five on the inner area of the reef platform) were photographed monthly from November 1976 to November 1977 to record changes in density of species of Laurencia. In addition the lengths of the ten longest axes of Laurencia spp. in each 0.1 m$^2$ area were measured to add a height dimension to the values of percent cover. A transparent plastic ruler was used for
these measurements. Adjacent to pool B, a different quantitative method was used to ascertain seasonal algal cycles. Five random 0.1 m² quadrats were taken from August 1976 to November 1977 to record presence and measure percent cover for each species of alga present in the quadrat. Another method using a 1 m² rigid aluminium quadrat divided into 5 cm squares with a nylon grid so that there were 100 points of intersection, was used to obtain an estimate of percent cover for the Laurencia spp. on the inner and outer parts of the reef platform from September to November 1977.

This same point survey method was used to obtain a quantitative measure of Plocamium costatum cover subtidally in Goat Island Bay. A line transect of ten consecutive 1 m² quadrats was made both under the kelp canopy and in an area where the canopy was not continuous to measure simultaneously Plocamium costatum cover and Aplysia parvula density.

At Motukaraka Island one area of 0.5 m² in pool C was photographed monthly from October 1975 to February 1978 to establish gross algal changes occurring at this study site. This technique alone was found unsatisfactory because the small size and filamentous nature of many of the species of Chlorophyceae and Phaeophyceae in this area did not permit recognition of specific entities from a colour transparency. So from July 1976 to February 1978 once each month, a qualitative collection of algae from each study area was made and returned to the laboratory to determine the presence of species by microscopic analysis.

All photographs were taken using a Pentax SP 1000 camera with standard 55 mm lens. Colour films employed were Agfa CT-18 (50 ASA) and Kodak Ektachrome-X (64 ASA).

Analysis of percent cover was made by projecting the colour transparencies onto a white screen, on top of which was laid a 40 cm square transparent acetate sheet on which 400 gridded points had been marked (gridded point method). As a check on the accuracy of this method, percent cover values for Laurencia species obtained in this way were compared with those obtained by a second and more laborious method, and in turn with actual field estimates. Table 4.1 presents
these comparative values. The second method involved projecting the slides onto 15 cm squared graph paper marked in mm giving a total of 22,500 mm squares. The outlines of each plant were then drawn on the graph paper and the area occupied by each plant calculated to give total percent cover (mm squared method).

Algal identifications were made by reference to Laing (1939), Chapman (1956), Lindaeur et al. (1961), Chapman (1969; 1970) and Chapman & Parkinson (1974). And in addition I wish to express thanks to the following people who assisted with identifications - Miss N.M. Adams (National Museum, Wellington), Professor V.J. Chapman and Dr K.A. Johnson (Botany Dept., University of Auckland), Dr F.J. Taylor (Marine Laboratory, Leigh) and Dr M.H. Hommersand (University of North Carolina).
Table 4.1. Comparative estimates of total cover by *Laurencia* spp. in areas of 0.1 m\(^2\) on Echinoderm Reef, Goat Island Bay. Table is based on observations and photographs made on 2 June 1977. Note that figures for arcsine transformations of cover estimates (mm squared method) are included, these figures give an idea of the relative magnitude of changes obtained when this transformation is employed.

<table>
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<th>Area No.</th>
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<th>% cover (gridded point method)</th>
<th>% cover (mm squared method)</th>
<th>% cover (following arcsine transformation)</th>
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<td>73.75</td>
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4.2 Measurement of Standard Length.

Because of opisthobranchs' capabilities for contraction and expansion, and the lack of external hard parts in several of the "nudibranchiate groups" (sensu Cuvier, 1830) the collection of measurement data on these molluscs for comparative purposes is beset with difficulties. Unless a standard system is adopted the results are liable to be erroneous.

Nevertheless length data are easily collected in the field and useful where very small opisthobranchs are being considered, and if it is recorded
systematically by the use of a standard technique it is of comparative value. All length measurements refer to the distance between the anterior margin of the head, excluding oral tentacles, and the posterior tip of the tail. These correspond to the standard lengths "Ac" (aeolids) and "A" (dorids) of Risso-Dominguez (1963) who attempted to systematize length measurements for opisthobranchs. Potts (1970) measured mantle length for the dorids in his study. Miller (1962) measured "A" using a pair of dividers with very fine points, but in my experience when used against an opisthobranch there is often a localized contraction.

The field technique used in this study to obtain "Ac" values for the opisthobranchs is apparently novel. As Nishiwaki et al. (1975) recognize, the measurements must be made on the fully extended body in seawater. After collection, specimens were washed briefly to remove adhering mucus and sediment, they were then placed on slates of PVC - 2 mm thick which had their surfaces slightly roughened to allow them to be written on in pencil underwater. The slate was immersed horizontally in the water. When the opisthobranch was fully extended and crawling in a straight line on the slate a short pencil stroke was dashed in the path of the oncoming animal 1-2 cm ahead of it. When the slug reached this line a second mark was made at the point that the tip of the tail reached at that instant. The slate was then brought to the laboratory, dried and the distance between the two lines measured with a perspex ruler. Usually three measurements of length for each animal were made and the average recorded.

Repeatability of measurements using this technique was found to be good. Table 4.2 gives values to the nearest 1 mm for ten measurements made on each of seven specimens of Aplysia dactylomela and ten Haminoea zelandiae. To further reduce errors, measurement data were grouped into size-classes for length-frequency analyses. Size-classes of 5 mm increments being employed for the two Aplysia species and Bursatella leachii, and a size-class interval of 2.5 mm being used for Haminoea zelandiae. The most consistent results using this method
were obtained for *Haminoea zelandiae* and *Aplysia dactylomela* and results were less consistent for *Aplysia parvula* and *Bursatella leachii*, both for repeated measurements of the same specimens and comparative measurements made on different specimens.

*Aplysia dactylomela* can readily be encouraged to crawl in the laboratory, when detached from a substrate the body elongates and the foot expands presenting a large convex foot sole, the head and tail are extended so as to present a maximum surface area (Fig. 3.1A). Upon contact of any part of the foot sole with a solid substrate there is immediate adhesion of that area and gradually the whole foot. *Aplysia parvula* has a long "prehensile" tail which remains fixed to a substrate even when there is no contact of the anterior two thirds. When detached, *A. parvula* contracts the foot margins together and the whole body is humped up in a fully contracted posture. As long as there is any piece of substrate (e.g. algal fragments or sand grains) adhering to the tail, *A. parvula* will not extend fully and commence crawling even though it may be resting on a solid substrate. If there are no pieces of substrate adhering to the tail, the anterior foot margin extends and attachment is achieved by a backwards-directed wave until the entire foot is attached. Neither *A. parvula* nor *A. dactylomela* display "leech-like locomotory patterns" (Kupfermann, 1965; Bebbington & Hughes, 1973).

Small *Bursatella leachii* have a long narrow tail as a posterior extension to the foot, extending some 4-8 mm from the back of the visceral hump (Fig. 9.3) and this tail can be variously extended or retracted when the animal is actively crawling. Large-sized *B. leachii* appear to lack this posterior filamentous extension. The state of this extension has considerable bearing on the length measurement of this species.
Table 4.2. Evaluation of standard measurement technique for ten repeated measurements of the same animal.

Aplysia dactylomela:

<table>
<thead>
<tr>
<th>Specimen No.</th>
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<th>$\bar{x}$ length (mm)</th>
<th>S.D.</th>
<th>S.E.</th>
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</thead>
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<td>3</td>
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<td>67.1</td>
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<td>94.1</td>
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<td>1.3</td>
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<tr>
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<td>66</td>
<td>67.6</td>
<td>3.86</td>
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<tr>
<td>7</td>
<td>89</td>
<td>90.1</td>
<td>4.35</td>
<td>1.38</td>
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</table>

Haminoea zelandiae:

<table>
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<tr>
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<th>$\bar{x}$ length (mm)</th>
<th>S.D.</th>
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</thead>
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<tr>
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<td>0.3162</td>
<td>0.1</td>
</tr>
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<td>0.3162</td>
<td>0.1</td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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</tr>
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<td>19</td>
<td>19.2</td>
<td>0.4216</td>
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</table>
4.3 Establishment of weight.

Measurements of weight for opisthobranchs have greater reliability than those for length. Most of the previous workers who have considered opisthobranchs in an ecological context have employed a parameter of weight for their determinations - Carefoot (1967a; 1967b), Smith & Carefoot (1967), Carefoot (1970), Nishiwaki et al., (1975) all for Aplysia species; and as well Paine (1965) for Aglaja inermis, Potts (1970) for Onchidoris fusca; Carefoot (1967a) for Archidoris pseudoargus and Dendronotus fondosus.

For this study wet weight measurements of living animals were made employing a damp wet weight technique. Superficial water was gently blotted off the body with an absorbent cloth, not a tissue since Aplysia dactylomela and A. parvula adhere the soles of their feet onto the tissue and make separation difficult. Care was taken to remove any water remaining in the parapodial cavity of Aplysia species. For specimens up to 300 gm (wet weight) an Ohaus Dial-0-Gram balance was used; a spring balance or Avery pan balance was used to weight Aplysia dactylomela in excess of this weight. This technique caused no apparent irritation to the specimens for the three anaspidean species seldom "inked" when being weighed. Some Aplysia spp. will discharge a deep purple secretion when disturbed mechanically or chemically (Tobach et al., 1965).

Only one weight measurement was taken instead of an average of several. This is because in a series of trials where the same specimen was weighed repeatedly, fifteen time at ten minute intervals, over three successive days, it was found that weights decreased with successive weighings. Table 4.3 shows this effect, all three Aplysia dactylomela were first weighed within 2 hr. of collection. The reason for this continual weight loss may be that the technique of blotting the specimens prior to weighing removes not only superficial water but also a surface layer of mucus, and energy is expended in replacing this mucous coat. Continual replenishment of this mucus, costing considerable energy, results in a detectable weight loss.
Table 4.3. *Alyxia dactyliomela*: weight loss (gm.) through 15 successive weighings on three consecutive days.

<table>
<thead>
<tr>
<th>Weighing No.</th>
<th>Specimen 1</th>
<th>Specimen 2</th>
<th>Specimen 3</th>
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<tr>
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<td>61.18</td>
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</tr>
<tr>
<td>15</td>
<td>37.30</td>
<td>59.70</td>
<td>244.53</td>
</tr>
</tbody>
</table>

| 3/6/76       |            |            |            |
| 16           | 33.16      | 61.61      | 253.52     |
| 17           | 33.10      | 61.49      | 253.74     |
| 18           | 33.03      | 61.04      | 253.92     |
| 19           | 33.00      | 60.83      | 253.04     |
| 20           | 32.90      | 60.43      | 253.24     |
| 21           | 32.83      | 59.94      | 253.05     |
| 22           | 32.60      | 59.55      | 253.05     |
| 23           | 32.52      | 59.16      | 253.06     |
| 24           | 31.82      | 56.38      | 253.31     |
| 25           | 31.55      | 56.16      | 253.69     |
| 26           | 31.47      | 55.90      | 253.24     |
| 27           | 31.52      | 55.73      | 253.06     |
| 28           | 31.31      | 55.52      | 253.20     |
| 29           | 31.14      | 55.20      | 253.85     |
| 30           | 31.11      | 54.67      | 253.20     |
| 31           | 28.31      | 51.42      | 232.19     |
| 32           | 28.19      | 51.09      | 231.43     |
| 33           | 28.05      | 51.06      | 230.94     |
| 34           | 27.96      | 50.97      | 230.80     |
| 35           | 27.84      | 50.99      | 230.78     |
| 36           | 27.82      | 50.86      | 230.60     |
| 37           | 27.84      | 50.67      | 230.81     |
| 38           | 27.82      | 50.48      | 230.38     |
| 39           | 27.78      | 50.17      | 230.42     |
| 40           | 27.67      | 49.92      | 230.16     |
| 41           | 27.58      | 49.67      | 230.24     |
| 42           | 27.55      | 49.68      | 229.90     |
| 43           | 27.41      | 49.20      | 230.14     |
| 44           | 27.34      | 49.14      | 230.19     |
| 45           | 27.10      | 48.68      | 229.99     |

Total Dry Weight: 2.205 5.163 23.213
Dry weights were obtained by heating samples to constant weight in a Qualtex/Contherm oven at 85°C and all material was cooled in a desiccator. Ash-free weights were determined by heating dried samples in a muffle furnace for 6-8 hr.

4.4 Tagging.

This technique was used only for *Aplysia dactylomela* to observe growth and survivorship in the field and laboratory. Four methods for tagging *Aplysia* spp. have been reported in the literature. Beeman (1968:92) attached vinyl tube, with information printed on it, to a parapodium. Nishiwaki et al. (1975) attached numbered pieces of "Dymo-tape" to the posterior end of the foot with enamel wire. Hamilton & Ambrose (1975) attached a small marker through the end of the foot to follow swimming individuals of *A. brasiliana*. Lederhendler et al. (1975) and Lederhendler (1977b) inserted a colour-coded stainless steel safety pin through the left parapodium. The tagging method used by these two latter researchers served for their short-term laboratory-based studies on behaviour but would have proven unsuitable for extended field observations.

A basic prerequisite of any tagging system is that it does not affect longevity or behaviour of the animals (Southward, 1966). In particular, a method most suitable for field studies of *Aplysia* should fulfil three criteria:

1. the tag should be approximately neutrally buoyant;
2. it should not inhibit growth; and
3. it should not restrict locomotion. For these requisites a new technique was employed.

The procedure used involved cutting small circular discs 5 mm in diameter from sheets of 1 mm thick PVC. Two holes were driven through the disc approximately 3 mm apart with a red hot needle to produce a button tag. Each tag was then individually marked by a self adhesive number (Brady "Bluestreak" tape B. 700) and the upper surface sprayed with clear varnish to give an additional seal over the number. Actual attachment of the tag was made by threading monofilament nylon (Korbond "Colorblend" thread) through the tag, using
a needle to pass the nylon through the body wall, returning the nylon out
again through a second hole and passing the free nylon end through the second
hole in the tag. The tag was then secured in place by tying two double half-
hitch knots in the two free ends of the nylon on top of the tag. Tags were
attached, at different times, to the right parapodium and to the tail of the
sea hares by this method. In some trials where parapodial tagging was being
undertaken, a second blank tag was attached to the inside of the parapodium
in the style of a Petersen fish tag (Petersen, 1896). Analyses of this tagging
method per se are given in the results section (Ch. 6.1.2) of this thesis.

4.5 Caging.

To follow the natural cycles of growth and regression in intertidal
Laurencia spp. on Echinoderm Reef at Goat Island Bay in the absence of
modifying effects of grazing by Aplysia spp., a series of protective cages was
constructed. The cages used were 10 cm square and 4 cm high, of 5 cm square
stainless steel mesh welded to a 15 mm stainless basal flange with four holes
for bolting at the corners. Cages were attached in the following manner.
First four holes were made in a square with sides of 10 cm, these holes being
excavated in the sandstone with a 'Terrier' FE4 self-drilling masonry anchor
to a depth of 12 mm. Whitworth stainless bolts (¾ x 1½ in.) were then inverted
in the holes and seated in place with waterproof epoxy cement (Expandite
"Expocrete" UA). After 24 hr the nuts on these bolts were tightened with a
crescent to hold the cages firmly in place.

This arrangement allowed the cage to be lifted each month to measure algal
growth and remove any tiny Aplysia that may have either crawled in, or
metamorphosed on the Laurencia within the cage. Each area was photographed
monthly and measurements of the lengths of the ten longest axes of the Laurencia
plants were made within the area enclosed by each cage and within a 10 x 10 cm
control area immediately adjacent to each cage. Fig A.1b shows one of these
cages in place. The locations of the cages and duration of time each was in
Arrow indicates start of photographic data collection at cage and control areas.

- Experiment terminated.
- Cage removed because of water damage.
- Cage lost.

Pool B - Cage 4
Middle of Reef Platform - Cage 3
Pool B
Pool A - Cage 2
Pool A - Cage 1

Table 4.4: Summary of location and duration of cageing experiments on rhinoderm beetles.
place are given in Table 4.4.

For the most part the cages withstood the forces of waves in the intertidal well but some human interference was observed with the two cages located in pool A.

4.6 Feeding Techniques.

4.6.1 Determination of Acceptable Foods and Preferences.

All laboratory studies directly involving feeding and growth were done at the Leigh Marine Laboratory where specimens were maintained individually in 18 l. perspex aquaria with a constant flow of fresh water supplied from the seawater system. Daily temperature recordings are made of the seawater in the tankroom and those for the times over which the following laboratory studies were made are tabulated in Appendix III.3.

Initially it was important to ascertain the limits of food acceptability for Aplysia spp. when presented with the range of algae available at Goat Island Bay. Specimens of both A. dactylomela and A. parvula were presented with a choice of nine different algae covering the major taxonomic categories of macrophytic intertidal seaweeds: Cyanophyta

- Lyngbya majuscula (Dillwyn) Harvey

Chlorophyta

- Ulva lactuca Linneaus
- Enteromorpha sp.

Phaeophyta

- Glossophora kunthi (C. Agardh) J. Agardh
- Noethia anomala Harvey

Rhodophyta

- Plocamium costatum J. Agardh
- Laurencia distichophylla J.Agardh/Laurencia sp. 1

The Ulva lactuca, Enteromorpha sp. and Noethia anomala were collected intertidally on "Pump Reef" immediately below the Laboratory; the Lyngbya majuscula came from Motukaraka Id; the Glossophora kunthi, Laurencia spp., Champia laingii and Herposiphonia sp. 1 came from Echinoderm Reef; the Plocamium costatum was collected subtidally from Goat Island Bay.
Twelve replicate trials were conducted with Aplysia dactyomela and ten with A. parvula, groups of 2 A. dactylomela (approx. 150 mm in length) and 6 A. parvula (approx. 50 mm in length) being used respectively in each trial. Each animal was used only once. All of the specimens of Aplysia were starved for two days before the experiment. Trials were run for three days. Prior to each trial approx. equal quantities of all algae were wet-weighed, and after the trials uneaten algal remains were removed and reweighed.

In addition, because seaweeds suffer small weight losses whenever they are kept in the laboratory (Carefoot 1967a; 1967b), pieces of each alga were maintained separately to ascertain a correction factor for the trials, each control being replicated four times. Control samples were dry-weighed so that wet-weights could be expressed as their dry-weight equivalents.

4.6.2 Measurements of Food Intake and Growth Rate.

Series 1 - Comparisons of Growth on Selected Algae.

These trails were run only with Aplysia dactylomela. Animals were maintained in the laboratory for a month on mono-specific diets of three algal species that had already proved to be acceptable foods. In addition, a control group was starved for the same time to obtain a figure for the weight loss due to starvation over a comparable period. Each trial had three replicates. Algae chosen were Laurencia spp., Enteromorpha sp., and Herposiphonia sp. 1. All twelve animals were tagged and weighed on 19 May 1976 and maintained separately until 19 June 1976. Every three days the specimens were reweighed, the aquaria cleaned, and fresh food supplied in excess.

Attempts were made to duplicate these trials in the field by releasing groups of animals in areas where each of these algae had high cover and were almost mono-specific in occurrence. Three animals were liberated on Enteromorpha sp. in a pool on "Waterfall Reef", and groups of ten animals were liberated in restricted areas containing each of Laurencia spp. and Herposiphonia sp. 1 on Echinoderm Reef Flat. Unfortunately recapture rates were too low to obtain meaningful results for these field trials.
Series 2 - Comparisons of Absorption and Utilization of Food Energy.

A group of ten *Aplysia dactylomela* was maintained, each in a separate aquarium in the laboratory from 8 May 1977 to 15 June 1977. All were given known amounts of *Laurencia* spp. (predominantly *Laurencia* sp. 1), so that total ingestion could be calculated, the faeces were collected to give total egestion and regular weighings were made to obtain comparable growth rates.

All ten specimens were starved for two days prior to the start of the experiment to allow their guts to clear. An excess of *Laurencia*, free of extraneous debris such as rissoid gastropods, erycinacean bivalves, crustaceans and sand was supplied fresh at each weighing. The damp wet weight of unconsumed *Laurencia* including the remnants was recorded for each *Aplysia* at this time. Faeces were collected and weighed every 2-3 days and for a three-day period after the end of the experiment by siphoning them onto a 3.5 cm disc of Whatman No. 1 filter paper in a 250 ml Millipore filter and filtering through a Buchner filter using a vacuum pump. Faeces were dried at 100°C for a minimum of 48 hr, cooled in a desiccator and reweighed on a Mettler H6T balance dig Cap. 160 gm. Finally all wet weight values for growth and for food consumption were converted to their dry weight equivalents by applying appropriate correction factors obtained by drying known amounts to constant weight at 80-110°C.

4.7 Additional Energetics Parameters.

4.7.1 Respiration.

Measurements of the respiration rate were obtained by use of two independent techniques - a classical Winkler Titration method, and a Beckman automatic oxygen analysis. I am grateful to Dr R.M. Wells and Mr J. Moorhouse for use of equipment in the Physiology Section of the Zoology Department and for assistance with construction of apparatus. Miss P. Wong kindly helped with collection of data.
Experimental investigations of respiration rates were done at Auckland University. Seawater that had been collected at Goat Island Bay, and therefore less likely to contain impurities than Auckland Harbour water, was filtered through a Millipore filter by using a 4.7 cm disc of Watson Glass Filter Paper - GF/A. Oxygen consumption was measured by an oxygen electrode attached to a Beckman 777 laboratory analyser. This apparatus provides a direct read-out of dissolved oxygen concentration and has a high degree of repeatability (Day, 1974). The sensor was calibrated to give a reading of 100% saturation in well-aerated fresh sea water and the readings made during the experiment indicated the percentage of the total oxygen consumed. An oxygen saturation value of 5.6 ml O_2 litre^{-1} was derived for full scale (i.e. 100%) on the analyses following the nomogram given by Green and Carritt (1967).

A total of 32 trials was made using seven animals with a range of weights from 1.74 gm to 67.03 gm. Experimental animals had been maintained in the laboratory on a diet of Enteromorpha sp., but were starved for one day prior to the experiments. Animals were acclimated at 17°C for 1 hr, then weighed and placed in sealed "Agee" jars containing approx. 960 ml of water that had been siphoned in to avoid agitation. Trials were run at 17±0.2°C for times between 120-169 min. A control jar accompanying each set measured bacterial respiration. At the end of the experiment the jar was opened and the water siphoned off to a sealed chamber containing the oxygen probe and a mechanical stirrer. Water flowed continuously through this chamber to a waste bucket. Before each reading the chamber was flooded with seawater incubated in the open at 17°C and the analyser recalibrated to 100%. Fig. 4.1e shows this apparatus in operation.

Values for energy in calories were converted to their SI unit equivalents - Joules, using the conversion factor

$$1 \text{ cal. (c)} = 4.1868 \text{ Joules (J)}.$$
4.7.2 Bomb Calorimetry.

Dried samples of *Aplysia dactylomela* body tissues, *Laurencia distichophylla*, *Laurencia* sp. 1, mixed *Laurencia* material, and faeces were combusted in a standard Parr 1108 oxygen bomb calorimeter of the isothermal jacket type, using the methods outlined in the Parr Instrument Company Technical Manual. Calorimetric determinations were made in the Chemistry Department, University of Auckland and I am extremely grateful to Mr T.A. Turney, Dr G.A. Bowmaker and Mr A. Hardcastle for permission to use these facilities in the Physical Chemistry Laboratory and for assistance with this work.

Using benzoic acid as a standard the energy equivalent of the calorimeter was calculated as 2486.88 cal. degree C⁻¹. Dry weights of 0.5-1 gm of material were used for each firing. Oxygen pressure inside the bomb was 30 atm. Bomb washings were titrated to neutrality against 0.0970 M NaOH. using methyl red as an indicator. Thermochemical corrections for heat of formation of nitric acid and heat of combustion of fuse wire (Parr 45C10 nickel-chromium fuse wire) were applied to calculate the gross heat of combustion (Hg) of each sample. To eliminate the influence of non-combustible components in each sample the values of Hg were converted to calories gm⁻¹ ash-free material (see Section 4.3).

4.8 Breeding Observations on Haminoea zelandiae.

Since the spawn of *Haminoea zelandiae* were observed on the shore at Motukaraka Island for a considerable length of time each year (13 March – 3 October 1975; 10 May – 18 November 1976; 19 April – 21 December 1977) it was desirable to follow a cohort of individual egg masses from initial laying to final disintegration to give information on developmental time, laying rate and behaviour of specimens, and finally rate of loss of egg masses before the full completion of development. These data gives the time spent by developing larvae inside egg masses before release into the water as mobile
veliger larvae. These also provide an estimate of larval life to add to the estimate of total length of life and provide data on mortality of the very early stages.

Two study areas were established close to pool B at Motukaraka Island (thus approx. at MTL). The first lay 1.3 m north of pool B. On 20 August 1977 a 1 m² quadrat was established. The area consists of a wide, shallow pool that receives drainage from the upper shore pools during tidal ebb, its floor is mainly of Corallina officinalis turf (55%) with areas of small loose sandstone chips. The 1 m² areas had 56 egg masses and 50 were marked individually with an orange "DYMO-tape" label with an embossed number, one end cut so as to point towards the egg mass it was marking (Fig.4.1c). The remaining six masses were removed so that there were exactly 50 masses being monitored from the start of observations. The labels were attached to 3/4" silicon/bronze flat head belt nails which were hammered into the sandstone. Where egg masses had been laid in clumps a sequentially-numbered "DYMO-tape" strip was attached beside the clump and a sketch was drawn to enable identification of each mass subsequently.

The second study area was 10.5 m N.E. of the first. This area drained completely at low water and the substrate is uniformly of Corallina officinalis turf with plants of the fucacean Hormosira banksii. Egg mass density was considerably lower (roughly half) in this area than in the standing pools where the first area was situated, therefore the second study site was made larger, consisting of two contiguous 1 m² quadrats. This area was established on 21 August 1977, initial densities of egg masses in the two 1 m² areas being 39 and 28. Seventeen masses were removed from the second quadrat to adjust the initial total number being monitored to 50. All were individually marked with yellow "DYMO-tape" labels.

Both sites were then observed daily for a total of 35 days (observations were impossible to make on only five days during this period). To monitor developmental changes an arbitrary scale was defined that enabled a rapid field measurement on development to be made. In addition to observing each of these
already-tagged masses, a search of the study site was made on each successive
subsequent visit for newly-laid masses that appeared in the two study areas.
When found each was tagged, a numbered green "DYMO-label" being used at both
sites to mark these eggs laid since the commencement of observations. By the
end of the study a total of 124 masses had been labelled.

4.9 Predation Experiments.

Limited experiments were conducted at the Leigh Marine Research
Laboratory in May 1976 to verify field observations that the asteroid
Coscinasterias calamaria (Gray) is a predator on Aplysia spp. These experiments
also gave some data on feeding and digestion rates for C. calamaria predation
on Aplysia spp. Four 6 l aquariums were established in the tank room, each was
aerated and had the water changed daily. One Coscinasterias calamaria was
placed in each with two A. parvula. All animals were weighed at the start of
observations, and one month later when the experiment was completed the
C. calamaria and remaining A. parvula were reweighed. During the experiments
the behaviour of all animals was observed four times each day and when a
C. calamaria was seen to be preying upon an A. parvula observations were made
at 3 hr intervals.

4.10 Crawling Rate Measurements.

A series of 20 determinations on the crawling rate of Aplysia dactylohomela
were conducted, all were made subtidally in 9 m of water near P.B.4 (western
end of Goat Island Bay) between 15 May and 14 June 1977. In the area chosen
the substrate consists of uniform, nearly horizontal rock flats with 90%
cover of Corallina officinalis turf, this being interspersed with patches
of Lithothamnion sp. Specimens used ranged in weight from 10 gm to 1410 gm.
A 'Seiko' diver's watch was used for time-keeping and distances were measured
using a 50 m "Eslon" fibreglass reinforced plastic tape held in a non-
corrosive plastic housing.
Each specimen was allowed to crawl for 10 min. to acclimate, after which time a small marker weight was placed immediately behind each animal indicating its starting position. Animals were allowed to crawl for 40-60 min. after which time their position was again marked and total distance travelled was measured.

4.11 Gonad Index.

Specimens of _A. dactylomela_ of a variety of sizes (and therefore reproductive states) were taken from May 1977 to May 1978 and used for construction of a gonad index. This index includes data on body weight, shell length, gonad condition and histological state. Since the index employs data on external characteristics it can therefore be used to assess the reproductive status of a population without having to sacrifice the individuals.

Each animal was measured (standard length to nearest 1 mm) and weighed (damp wet weight to nearest 0.01 gm). Animals were then placed in a 10% neutral formalin solution for 10 minutes to kill them. The mantle cavity of each was opened and the shell removed, measurements of maximum shell length and width (across the broadest area just below the anal sinus) were made. The visceral cavity was then opened and the ovotestis and gonoduct were dissected out. The relative state of maturity of the reproductive system was designated an arbitrary condition factor (from 1-4) based on degree of development of organs and colour. The digestive gland was also removed by anteriorly cutting the oesophagus behind the crop, and posteriorly cutting where the rectum leaves the digestive gland mass. The damp wet weight for all these dissected organs was then obtained. Ovotestes from representative specimens of three of the four categories of condition were immediately fixed in Bouins fluid. Subsequently they were embedded in Ester wax (Smith & Carefoot, 1967; Grange, 1974), cut at 8 µm and stained with Mallory and Heidenhein. This procedure allowed histological information to be incorporated into the gonad index.
Histological terminology for developmental processes in the acini of the ovotestis follows Thompson & Bebbington (1969).

4.12 Sediment Analyses.

Sediment analyses were kindly performed by Mr D. Pryor of the Department of Geology. Prior to processing, the bulk sample was split into two portions. For each, as much organic material (e.g. thalli of Corallina officinalis and other algae, annelids, amphipods etc.) as possible was removed to give a measure of the organic content of the sediment. The subsample then had all the mud removed, the mud and remaining subsample being dried separately. The subsample of sand was passed through a series of nested sieves and the proportions of coarse sand, medium sand, fine sand and very fine sand that were retained by the 0.5 mm, 0.25 mm, 0.12 mm and 0.064 mm sieves respectively was recorded. Addition of the separate weights for the sand series and mud of the subsample gave the weight of the sieved sample and this was added to the weight of the sand and mud of the remainder of the sample to give the total weight of the bulk sample. Analysis of the calcium carbonate composition was made by weight loss after adding a 12% hydrochloric acid solution to the sample after it was recombined following sieving.

During processing of the bulk sample a distinction was made between the 'resident' sediment fraction (including mineral components; non-living calcareous and siliceous invertebrate remains; calcareous algae and molluscs boring or nestling in the sediment, e.g. Lithophaga truncata, Diplodonta striatula, Notirus reflexus) and the 'transitory' fraction (including mobile grazing and carnivorous gastropods, isopods and amphipods). All members of the latter fraction were separated immediately and the only weights considered were those for the 'resident' fraction.
4.13 Data Analyses and Tests of Significance.

Because of the intrinsic variability of biological systems, large numbers of observations must be made on any phenomenon before one can confidently reach a decision as to its meaning, this is particularly so in any ecological context. Statistical procedures and computing techniques are useful tools to aid in the analysis of this data, they can act as a guide to interpretation of results.

The simplest piece of statistical information, and frequently the most useful, is the mean. The mean is the simple average of the observations in a group. Frequently I also quote deviation of points about the mean by use of a standard error term. The standard error is the standard deviation of the sampling distribution of a statistic from random samples of size $n$ (Remington & Schork, 1970). Occasionally 95% confidence intervals of the mean or the standard deviation are used instead of standard error, but it is clearly pointed out where these alternatives are used. Throughout this thesis I abbreviate standard error to S.E. and standard deviation to S.D., rather than referring to them as $\sigma$ or S respectively.

An arcsine transformation has been applied to values for percent cover of algae. This transformation, also known as the angular transformation, is appropriate for percentage and ratio data which is assumed to be binomially distributed. However, mean and variance ($S.D.^2$) are linked for such data and so have non-normality. An arcsine transformation makes these parameters independent. This transformation stretches out both tails of the distribution and compresses the middle thereby turning the transformed variable into a normally-distributed variable (Sokal & Rohlf, 1969). Arcsine transformations were applied uniformly to all data for cover values since the transformation only produces noticeable changes over the ranges of 0-30%, and below 70% to 100% (Snedecor & Cochran, 1968). Tables of arcsine transformations presented in Steel & Torrie (1960 : Table A.10) were followed consistently.
Throughout this thesis, whenever the term 'significant' is used, it denotes that the statement referred to has been verified by means of an accepted statistical test. As is standard practice, a significance level greater than 0.05 is not accepted, and in such cases a null hypothesis cannot be rejected.

The most simple test of significance used has been the t-test or student's t-test based on the t distribution of variables (Gosset, 1908).

More complex tests of significance that have been used are regression analyses and analysis of variance techniques. Regression analysis is a means of studying the variation of one quantity (the dependent variable) at selected levels of another quantity (independent variable) (Remington & Schork, 1970). More generally it is used to describe relationships between variables.

Analysis of variance (ANOVA) techniques have been employed as a second form of significance test. For ANOVA, one initially presents the null hypothesis that there is no difference in the means of the populations from which a series of separate samples have been drawn. ANOVA examines whether there is significantly more variation among the group means than within the groups (Remington & Schork, 1970). ANOVA tests were carried out using the 'Teddybear' programme developed by Wilson of Otago University, on Auckland University's B6700 computer and I am extremely grateful to Mr J. Paynter for his assistance and persistence in running the ANOVA programmes. Use of ANOVA techniques for analysis of time series is not strictly correct because one of the fundamental assumptions of ANOVA, that of independence, is violated by a time series (Ayling, 1976). Therefore a series of 'samples' of the same pool or caged area or study quadrat through time cannot be regarded as completely independent. This fault is acknowledged and results of ANOVA analyses treated with due caution.

Besides acknowledging the assistance of Mr Paynter with the analysis I wish to extend considerable thanks to Dr B.A. McArdle and Mr R.J. Fulton for assistance with the statistical and computing techniques.
Figure 4.1.

Apparatus and Techniques Employed.

a - *Aplysia dactylomela* tagged through parapodium (right) and tail (left);
b - Cage for exclusion of *Aplysia* species and other grazers from *Laurencia*
  species; c - Dymo-tape labels identifying separate egg masses of *Haminorea*
  zelandiae; d - *Coscinasterias calamaria* catching an *Aplysia dactylomela*;
e - Respirometer apparatus in operation; f - the aglajid *Melanochlamys*
  cylindrica and egg mass.
CHAPTER 5
ALGAL STUDIES

5.1 Introduction.

Besides monitoring the population cycles of herbivorous opisthobranch molluscs in this thesis, detailed observations have been made on the algae upon which their lives depend. This work has concentrated on the distribution and seasonal abundance of those algal species which serve as recruitment sites, as cover and as direct food sources for the animals under study.

In any marine habitat one must acknowledge the dual contributions of the seasonal and the perennial plants. Several schemes have been proposed to classify algae so as to reflect their seasonal growth patterns. Groupings have differed depending on the directions from which workers have approached their classifications but the categories of long-lived, large forms and delicate, ephemeral (seasonal) forms are always distinguished. Sears & Wilce (1975) based their groupings of benthic algae on thallus longevity, plant form during the adverse season and period in which each species population was present in the community. Their terminology is followed here because of its ecological basis, definitions of their four classes being:

1. Thalli persisting less than one year.
   a. Plants passing adverse season in a resting or juvenile stage or completely absent from the community for part of the year
      - Seasonal annuals
   b. Population present year-round as overlapping generations, formed from the immediate germination and subsequent maturation of reproductive cells
      - Aseasonal annuals

2. Thalli persisting for more than one year
   a. Most plants of the population passing adverse season in a reduced perennating form
      - Pseudoperennials
   b. Major portion of the thallus present year-round and persisting for more than one year
      - Perennials
In this study the definition of seasonal annuals is used in the widest sense - to cover both those species that disappear completely (the ephemeral component) and those that are present virtually throughout the year but have greatly reduced abundance during the adverse season (this component tends towards pseudoperennial character). These latter species behave ecologically like the ephemerals in their abundance cycles. All the component species are typified by a sudden seasonal upsurge in growth, a plateau of high density, then a regression phase and finally virtually complete disappearance for the remainder of the year. Throughout this section all these components are termed "seasonals".

At both Motukaraka Island and Leigh perennials were found to be of less direct importance to the opisthobranchs than the smaller seasonal species.

The seasonal algal species encountered, and of ecological significance, are introduced in the following sections. There are numerous species for Motukaraka Island but only the Laurencia species at Leigh. Distinctive characters at the microscopic level are given briefly, and criteria for identification and discrimination in the field are stressed. These sections will clarify the status of the seasonal species considered in this thesis, even if subsequent studies reveal the nomenclature used here to be incorrect. Briefer diagnoses are given for those species whose identifications are unambiguous (e.g., Lyngbya majuscula; Colpomenia sinuosa; Scytosiphon lomentarium).

In later sections, zones of dominance and growth patterns are described. All descriptions and measurements given refer specifically to, and are based upon, living plants from the Motukaraka Island or Echinoderm Reef populations; therefore these details are only likely to reflect the character of the Auckland and North Auckland populations at the most. Accordingly these details will differ in some respects from other published accounts whose descriptions have been prepared to encompass the variability of species throughout their entire geographical range. Determinations to the specific and varietal level have not been possible for some of the filamentous Rhodophyceae, not only because of uncertainty about the entities in New Zealand but also because sexual
stages were not encountered.

5.2 Characterization of the flora at Motukaraka Island.

The total number of algal species (belonging to all of Sears & Wilce's four categories) recorded at Motukaraka Island over the entire three years of this study is approximately forty-five. This total includes filamentous Cyanophyceae and colonial tube- of filament-forming Bacillariophyceae. The contribution by perennials to this total is low (approx. 17%) with Corallina officinalis and Hormosira banksii consistently contributing the greatest biomass. However, owing to the disproportionate contributions of certain seasonal species, total algal cover values were often high.

CLASS CYANOPHYCEAE, ORDER NOSTOCALES, FAMILY OSCILLATORIACEAE

Lyngbya majuscula (Dillwyn) Harvey.


Thallus filamentous (up to 13 cm long), dark green almost brownish. Trichomes unbranched with an overall diameter of 25-30 μm and sheath width of 5-12 μm (Motukaraka Island population), sheaths colourless. Apices rounded, not capitate. L. majuscula is determined in the field by its dull green colouration filamentous or floccular nature and felt-like feel. The species is cosmopolitan and apparently only intertidal.

CHLOROPHYCEAE, ULOTRICHALES, ULVACEAE


All plants of the Motukaraka Island population small, being consistently less than 2 cm in height. Other characteristics of this taxon are that the cells are not arranged linearly, the thallus is simple and is never branched nor does
it proliferate, colour grass-green, cell diameter (including membranes) is 30-40 \( \mu m \). The form is endemic to New Zealand.

**CHLOROPHYCEAE, SIPHONOCLADALES, CLADOPHORACEAE**

**Cladophora repens** (J. Agardh) Harvey f. *tenuis* Hamel.


Thallus erect, often amongst coarse sand and pebbles in conjunction with *Corallina officinalis*; growing to 3 cm in height. Axis slightly expanded at nodes. Branches alternate, but often opposite on main axis, branching more dense distally, upper branchlets erect, apices rounded and finger-like. Cells of main axis 600-800 \( \mu m \) long and 70-90 \( \mu m \) wide in the Motukaraka Id material. In the field, branching readily discernible, colour a characteristic vitreous that approaches dark green, the plant rigid and appearing glassy. The species and form are apparently worldwide in distribution.

**CHLOROPHYCEAE, SIPHONOCLADALES, CLADOPHORACEAE**

**Cladophora cf. laetivirens** (Dillwyn) Kützing.

1966, Gyr a, *Les Algues des Côtes françaises*: 119, fig. 20A.

Similar in many respect to *C. repens* f. *tenuis*: thallus erect; branching alternate or opposite; apices rounded, but maximum size smaller (2-2.5 cm) and the branches more slender. Dimensions: length of cells 450-600 \( \mu m \); width of axis 60-90 \( \mu m \) (Motukaraka Id material). In the field *Cladophora cf. laetivirens* can be distinguished from *C. repens* f. *tenuis* by its more numerous branches and consequently more matted texture, and by being yellow-green in colour rather than olive-green. Chapman (1956) introduced the varietal name 'regularis' based on a single drift plant from Nelson because the diameter of the filaments was constant from base to apex, however this is not the case with the population at Motukaraka Id which is held to be more akin to *C. laetivirens* s. str. which is world-wide in distribution.
CHLOROPHYCEAE, SIPHONOCALDALES, CLADOPHORACEAE

Cladophora crinalis Harvey.

Fig. 5.1b


Plant to 1.5 cm high. Branchlets fine, much divided, filaments lax but often held together by intertwining Rhizoclonium spp. Cells of main axis approx. 240 μm long by 50 μm wide (Motukara Id population). Colour pale green to grass-green. Branching irregular, mostly alternate, sometimes opposite, sometimes 3 or even 4 branchlets arise from one side of axis. In the field branching can just be detected, a clump of C. crinalis resembles a piece of loosely-coherent, hirsute sponge. Endemic to New Zealand.

CHLOROPHYCEAE, SIPHONOCALDALES, CLADOPHORACEAE

Rhizoclonium kernerii Stockman.

Fig. 5.1f


Thallus a mass of exceedingly fine filaments. Rhizoids and branches absent. Individual cells short and numerous, several hyaline pyrenoids in each cell. Dimensions of cells in Motukara Id specimens: length 25-40 μm; width 8-12 μm. In the field, single threads not discernible, the distinguishing characters for this species being its fineness and softness, colouration dull-green to whitish. It has a felt-like texture, often forming flocks up to 7 cm in diameter. The species is never filamentous in appearance. Its distribution is world-wide.

CHLOROPHYCEAE, SIPHONOCALDALES, CLADOPHORACEAE

Rhizoclonium hookeri Kützing.

Fig. 5.1e

1853. Kützing, Tab. Phyc. 3, tab. 67, fig. 2.

Thallus tubular, rigid, rhizoids absent. Cell dimensions: length 110-190 μm; width 40-50 μm (Motukara Id population). Chloroplasts numerous, spherical,
placed around periphery of all walls. Distinguishable in the field by size and pale green colour, texture thread-like and stringy resembling tangled fishing line. This species and *R. kernerii* often form mixed clumps, both being intertwined to form a fleecy layer. World-wide in distribution.

**CHLOROPHYCEAE, SIPHONOCLADALES, CLADOPHORACEAE**

*Chaetomorpha aerea* (Dillwyn) Kützing.


Filaments erect, rigid, almost cylindrical throughout. Maximum height of Motukaraka Id material 8.5 cm. Filament widths 200-280 μm. Cell lengths variable, some cells long (300-340 μm), others short (50-250 μm), both types occurring beside each other, intermediates readily found. Filaments shiny, colour bottle green, vitreous, cell walls thin and clear. Distinguished by its solitary character, erect filaments and large cells that are visible in the field. World-wide in distribution.

**PHAEOPHYCEAE, ECTOCARPALES, ECTOCARPACEAE**

*Ectocarpus granulosus* (J.E. Smith) C. Agardh. Fig. 5.2b


Filaments elongate, 80-100 mm in length, flexible, branching fairly regular, alternate or sympodial but never opposite. Colour pale straw-brown. Cells rather short with length varying between 150 μm and 320 μm and widths of 70-100 μm (Motukaraka Id population). Chloroplasts reticulate, entirely peripheral, regular in outline; conspicuous green pyrenoids easily visible. Plurilocular sporangia ovoid, 60-120 μm long and 30-70 μm wide. In the field *Ectocarpus granulosus* grows as long straw-coloured tufts, the filaments being much paler than those of *Bachelotia fulvescens*, and considerably more lax so they are easily displaced by water movement. World-wide in distribution.

Although thallus structure and cell dimensions of the Motukaraka Id
population correspond with those given by Lindaeur et al. (1961), I have not found any secondary branches that are arranged oppositely.

PHAEOPHYCEAE, ECTOCARPALES, ECTOCARPACEAE

Bachelotia fulvescens (Bornet) Hamel. Fig. 5.2a


1961. Lindaeur, Chapman & Aitken, Nova Hedwigia 3(2/3): 141, fig. 1B.

Filaments short, linear, 1.5-2 cm in height, branching sparse, apices rounded. Filament diameter 25-40 \( \mu \)m, cell length 40-90 \( \mu \)m (Motukaraka Id population). Sporangia intercalary. Chloroplasts distinctive, stellate, with cytoplasmic filaments radiating outwards to the cell's limits. In the field \( B. \) fulvescens is recognisable by its rather low, turf-forming character, filaments tending to be short and parallel, and quite high, chocolate brown colour and filaments not displaced by water agitation. World-wide in distribution.

PHAEOPHYCEAE, SPHACELARIALES, SPHACELARIACEAE

Sphacelaria limicola Lindaeur. Fig. 5.2e


Filaments erect, rigid, forming a tight spherical clump. Filaments 10-15 mm in length, apices rounded. Measurements of filaments: widths 30-45 \( \mu \)m; cell lengths 30-55 \( \mu \)m (Motukaraka Id population). Straw-coloured to chocolate-brown. In the field growing as an epiphyte (often on Corallina officinalis) or directly on the substrate, distinguishable by its short, close cropped texture like fur, its rigidity and chocolate-brown colouration. Endemic to New Zealand.
Colpomenia sinuosa (Roth) Derbes & Solier.

1806. Roth, Catalexta Botanica 3: 327, pl. 12, fig. 9.


Characterized by its more or less lobulate and thin thallus which can reach 6 cm in diameter (Motukaraka Island population). Tight and globular when young, lobed and convoluted when mature. Outer wall frequently ruptured in larger specimens. Colour light yellow to golden-brown.

Juvenile C. sinuosa resembling the basket-like dictyosiphonaceous Hydroclatrus clathatus (C. Agardh) Howe that has recently been recorded from northern New Zealand waters (Johnson & Dromgoole, 1977). However H. clathratus was not present at Motukaraka Island during the years of this study. Leathesia difformis (L.) Areschoug is another brown alga of similar growth form to C. sinuosa, but this latter chordariaceous has a fleshy-gelatinous thallus. C. sinuosa is cosmopolitan in distribution. It is found throughout New Zealand.

It occurs across a broad spectrum of exposure classes, being absent only from the most sheltered or open shores. Maximum densities are reached between ELWN level and 3 m, but the alga does grow to approx. 8 m subtidally although its occurrence is very patchy towards this lower level. C. sinuosa is a characteristic element of the flora of many shores throughout the winter because it undergoes seasonal "macroalgal blooms" (Walsby, 1977). The alga appears unselective as to substrate; although it occurs most frequently as an epiphyte on other algae, it can also grow on hard bare substrates.

Scytosiphon lomentaria (Lyngbye) J. Agardh.

1819. Lyngbye, Tentamen hydrophytologiae danicae: 74, pl. 18.


Characterized by its tubular, tapering thalli with regular constrictions.
Specimens from Motukaraka IId reaching 15 cm in length and 5 mm wide. Colouration olive-green or brownish. *S. lomentaria* is cosmopolitan in temperate and colder seas.

RHODOPHYCEAE, CERAMIACEAE, RHODOMELACEAE

**Polysiphonia sp.**

Fig. 5.2c, d

Thallus to 1.5 cm in height, pale brown in colour. Usually only four siphonous cells. Branching generally alternate or sometimes two or three branches arise from the same side of axis. Axis widens towards the base: width of axis near base 140-170 µm; width of axis of ultimate branch 70-80 µm. Length of individual cells increases similarly towards the base: length of cells near base 200-240 µm; width of cell of ultimate branch 100-150 µm.

RHODOPHYCEAE, CERAMIACEAE, CERAMIACEAE

**Laurencia sp. 3.**

Maximum height of branches 8 cm. Colour chocolate brown or deep reddish brown. Plant tall, open and flaccid. Bases and axes terete, approx. 1 mm diameter, main axis predominates throughout. Branching opposite (2-3 branches per node) or subalternate but never strictly alternate, branches rather long, and bearing short sub-branches (1-5 mm long), occasionally sub-branches bear tiny lateral shoots near tips. Branching occurs all down main axis, not being continued to apical third only.

This *Laurencia* is the only species of the genus at Motukara IId with terete axes and branches, therefore it cannot be confused with any other species. Distinguished by its brown colouration, laxness of branches and bushy appearance.

*Laurencia* sp.3 is very near *Laurencia* sp. 2 from Leigh in taxonomic status (see description later in this section) and is probably conspecific with it. However, I maintain them as distinct species because *Laurencia* sp. 2 grows much larger and its branching is coarser than for *Laurencia* sp. 3. Seasonal
cycles of the two species differ. Laurencia sp. 2 attains maximum cover in October and November at Leigh whereas Laurencia sp. 3 has greatest cover in July and August.

RHODOPHYCEAE, CERAMIALES, CERAMIACEAE

Ceramium sp.

Branching dichotomous. Apices bifurcated, invariably hooked towards each other with one side consistently larger. Pinkish in colour overall, nodes of corticating cells pinkish-red, internodal cells clear with weak, irregular surface striations. Measurement data for plants from the Motukaraka Island population are tabulated below and it is obvious that although length of internodal cells decreases upwards, axial diameters remain constant. In the field appearing as short pinkish-brown filaments that are rather lax in form, never being in tight clumps.

Table 5.1. Measurement data for Ceramium sp. from Motukaraka Island.

<table>
<thead>
<tr>
<th></th>
<th>Basal regions (µm)</th>
<th>Distal branches (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of internodal cells of axis</td>
<td>280 - 330</td>
<td>40 - 70</td>
</tr>
<tr>
<td>Diameter of axis (internodal regions)</td>
<td>50 - 65</td>
<td>40 - 60</td>
</tr>
<tr>
<td>Diameter of axis (nodes)</td>
<td>80 - 90</td>
<td>70 - 90</td>
</tr>
<tr>
<td>Diameter of corticating cells at nodes</td>
<td>60 - 110</td>
<td>60 - 70</td>
</tr>
</tbody>
</table>

BACILLARIOPHYCEAE, PENNALES

Grammatophora marina (Lyngbye) Kützing

Cells rectangular, symmetrical with four slightly wavy chloroplasts projecting towards the centre, appearing like two tuning-forks; remainder of cell hyaline, corners rounded. Approx. length 40 µm; width 10-15 µm. Most characteristic feature of G. marina is alignment of cells - forming chains end on, each cell nearly at right angles to those on either side but each displaced so as to leave a gap between the two adjacent cells. In the field appearing as a chocolate-brown fuzz up to 40 mm thick. Epiphytic on most other algal species studied.
Figure 5.1.
Photomicrographs of filamentous Cyanophyceae and Chlorophyceae from Motukaraka Island.

a - Lyngbya majuscula (Dillwyn) Harvey. x 125;
b - Cladophora crinalis Harvey. x 50;
c,d - Enteromorpha compressa (L.) f. australiensis (Chapman) Chapman. x 20;
e - Rhizoclonium hookeri Kützing. x 50. Note single filament of R. kernerii for comparison.
f - Rhizoclonium kernerii Stockman. x 50.
**Figure 5.2.**

Photomicrographs of filamentous Phaeophyceae and Rhodophyceae from Motukaraka Id (a – e) and Echinoderm Reef (f).

- a - *Bachelotia fulvescens* (Bornet) Hamel. x 50.
- b - *Ectocarpus granulosus* (J.E. Smith) C. Agardh. x 50.
- c - *Polysiphonia* sp. with sporangium. x 50.
- d - *Polysiphonia* sp. detail of axes. x 20.
- f - *Herposiphonia* sp. detail of apical region. x 200.
Besides those species defined above there is a number (c. 10) of bacillariophyceans that were not considered to be sufficiently numerous or ecologically important to warrant their counting or to establish their nomenclature. Six other algal species were encountered spasmodically and whilst none achieved importance, their presence at Motukaraka Is should be recorded:

**CYANOPHYCEAE, NOSTOCALES, OSCILLATORIACEAE**

- *Spirulina subtilissima* Kützing.

- *Lyngbya lutea* (J. Agardh) Gomont.

**CYANOPHYCEAE, NOSTOCALES, OSCILLATORIACEAE**

- *Lyngbya lutea* (J. Agardh) Gomont.

**CHLOROPHYCEAE, SIPHONALES, BRYOPSIDACEAE**

- *Bryopsis plumosa* (Hudson) J. Agardh.

**RHODOPHYCEAE, CERAMIACES, CERAMIACEAE**

- *Spyridia filamentosa* (Wulfen) Harvey.

**RHODOPHYCEAE, CERAMIACES, CERAMIACEAE**

- *Callithamnion sp.*

**RHODOPHYCEAE, PORPHYRIDIALES, BANGIACEAE**

- *Erythrotrichia carnea* J. Agardh.

#### 5.3 Seasonal Growth Patterns of Dominant Components of this Flora.

#### 5.3.1 *Lyngbya majuscula.*

For each of the three years of this study the filamentous cyanophyte *Lyngbya majuscula* always became abundant across the entire reef flat during the late summer and autumn months although it was entirely absent over winter and spring. This cyclic pattern is presented in Fig. 5.3.

Each year, at the height of summer, the first clumps of *Lyngbya majuscula* appeared as short dull green tufts in pools on the middle and outer parts of the reef platform. First plants of the 1976 summer were noted in both pools B and C on 31 January; the first for 1977 were noted in both pools B and C on 5 February; the first for 1978 were seen in pool B on 11 January.

Initially *L. majuscula* appear as discrete, lax, filamentous clumps with a density of approx. 1 m\(^{-2}\). An initial phase of very rapid growth occurs from March to May with maximum cover being reached by mid-May. Throughout May and early June a growth plateau is reached and this is typified by particularly high cover and merging of the filaments so that discrete clumps are no longer discernible. At this time the longest filaments can reach 110 mm. After June
a third phase is reached and there is a rapid decline through late June and early July so *L. majuscula* becomes absent by the middle of July.

The pattern of rapid growth, a short period of high cover and rapid decline, was exhibited each year with only minor differences in the dates of appearance and disappearance; the standard deviation for each year being in the order of two weeks. This pattern was exhibited most clearly in 1976. Total cover reached at the height of the plateau phase was less predictable. Maximum cover at each site is tabulated below (Table 5.2).

Table 5.2. Field estimates of maximum cover of *Lyngbya majuscula* at Motukaraka Island for 1975-1977.

<table>
<thead>
<tr>
<th></th>
<th>Pool B</th>
<th></th>
<th>Pool C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>% cover</td>
<td>Date</td>
<td>% cover</td>
</tr>
<tr>
<td>26 March 1975</td>
<td>70</td>
<td>14 May 1975</td>
<td>90</td>
</tr>
<tr>
<td>31 May 1976</td>
<td>60</td>
<td>31 May 1976</td>
<td>60</td>
</tr>
<tr>
<td>29 May 1977</td>
<td>60</td>
<td>19 April 1977</td>
<td>70</td>
</tr>
</tbody>
</table>

The estimate for pool C on 19 April 1977 was 60-70% *lyngbya* cover, but photographic analysis and transformation gave a cover value of 54-63%.

Therefore at times of peak abundance, actual cover of *L. majuscula* is between 60% and 70%, although the 1975 peak was considerably greater than this.

The phase of growth where a plateau is reached was expressed for a consistently longer time in pool C giving a broader overall curve and thus implying the first and third phases were faster for this alga on the outer areas of the reef platform.

Three of the curves in Fig. 5.3c show a sudden fall and sharp rise again after the plateau growth phase is reached (evident for both study pools in 1975 and pool C in 1977). This fall is directly attributable to the predation of *L. majuscula* by the anaspidean *Bursatella leachii*. As recorded in Ch. 6.3.5, *B. leachii* metamorphoses on *Lyngbya majuscula* at the time of peak abundance of the latter, then grows extremely rapidly utilising the alga
as a food source and densities of \textit{B. leachii} are so high that it soon affects the algal cover. The \textit{L. majuscula} is cropped to a short stubble 30-40 cm in height and discrete clumps become discernible. However, \textit{B. leachii} migrates offshore before the cover of \textit{L. majuscula} is entirely decimated and the alga regenerates. Out of the three occasions on which this phenomenon occurred, twice \textit{L. majuscula} did not reach the extent of its former abundance (in both pool B for 1975 and pool C for 1977 \textit{L. majuscula} regrew to only 70\% of its former cover value), and once subsequent regrowth of \textit{L. majuscula} enabled cover to exceed that value recorded prior to grazing (in pool C for 1975, \textit{L. majuscula} cover regrew to 24\% above that of its former value). This observation suggests that grazing could stimulate \textit{L. majuscula} growth, and that if grazing ceases early enough the eventual maximum cover is greater.

Enhanced algal growth, not by grazing per se, but by passage through the gut of the predator has been described by Porter (1976). No fall in cover was noted in pool B for 1977 despite the presence of \textit{Bursatella leachii}, this was because \textit{B. leachii} density was never found to exceed 2 m\textsuperscript{-2} (mean density = 0.5 m\textsuperscript{-2}, n=4), and this density was too low to effect a noticeable decrease in total \textit{L. majuscula} cover.

5.3.2 \textit{Colpomenia sinuosa}.

Seasonal distribution, density and growth in \textit{C. sinuosa} were followed on the shore at Motukaraka Island throughout 1976 and 1977. The first tiny "buttons" were noted early in May at ELWN level; initial densities were low (approx. 0.3 m\textsuperscript{-2}) and sizes small (max. diameter 15 mm). For the next two months vesicles appeared progressively across the shore (Fig. 5.4). Full abundance was achieved from August to December. At Motukaraka Island maximum \textit{Colpomenia} cover \textsuperscript{m\textsuperscript{2}} was never observed to exceed 30\%, except for some extremely localized patches (e.g. 65\% cover \textsuperscript{0.3 m\textsuperscript{2}} in pool B in November 1977).

Initially the \textit{C. sinuosa} "buttons" are small and discrete and they thus permit an accurate census of density to be made. However, as the vesicles
grow the lobes pucker and distort, adjacent plants abutting against each other so closely that individuals can no longer be discerned accurately. Consequently, cover values were obtained for *C. sinuosa* in preference to density measurements. One approximation relating densities of individuals and cover values is that for plants of approx. 10-20 mm diameter, a density of 60 plants \( \text{m}^{-2} \) is approximately equal to 10% cover. The maximum sizes attained by such vesicles originating from single plants differs across the shore; the plants in pool A never attained more than 24 mm in greatest diameter, whereas those at pool D (= ELWN level) often reached 55-60 mm in diameter. The appearance and regression phases of *C. sinuosa* distribution across the intertidal platform are not symmetrical; whilst the alga takes two months to spread across the shore in the inwards direction, its decline is more rapid occurring synchronously across the shore and lasting only one month. Patterns of distribution and abundance were similar in 1976 and 1977, however the time of peak abundance was attained later in 1977 (October - November) than in 1976 (September).

5.3.3 *Laurencia* species.

Two species of *Laurencia* occur sympatrically towards the outer part of the low tidal reef flat at Motukaraka Island. They were not distinguished specifically until July 1977 and so ecological observations prior to that time treat "*Laurencia* spp." as a composite category. Similarly, the species cannot be separated from photographs, so the cycle described below includes the two species as one.

The annual cycle of "*Laurencia* spp." was followed for two years from January 1976 to January 1978. "*Laurencia* spp." was virtually never present in any of the three inshore pools, only attaining significance towards the outer part of the platform. In pool C, the pattern was similar each year and consisted of an initial upsurge of growth from February to mid-May when maximum cover was approximately 20%. A rapid decline followed, so that by
June all plants had virtually disappeared. In 1976 cover remained low through winter and spring until the following year, however in 1977 there was a second burst of growth of lower total cover from August to September.

Subsequent to the discrimination of the two species, it was noted that *L. distichophylla* was present year-round in a narrow strip at the extreme outer edge of the reef platform. Here maximum cover (up to 50% occurred in August-October).

*Laurencia* sp. 3 appeared to grow preferentially in pools. In August 1977 51 m² quadrats were analysed for comparative densities of the two *Laurencia* species. *L. distichophylla* had mean numbers of 5.5 and 0.3 plants m⁻² in pools and on *Corallina* flats respectively, whereas *Laurencia* sp. 3 had means of 1.5 and 9.0 plants m⁻² respectively. Apparently the level in standing pools of water sets the height to which *Laurencia* sp. 3 can grow, plants in deeper pools being larger and more luxuriant. Perhaps exposure to air is deleterious to apices of this species?

During the times of rapid decrease in cover of *Laurencia* sp. 3, it was observed that the plants were dying from their bases and lateral branches of determinate growth were being lost. It is certain that this decline was not due to predation and appears to be a natural regression inherent to the species - that this sudden die-back is due to severe endoparasitic infection however, cannot be ruled out completely.

5.3.4 *Bachelotia fulvescens*.

This short tufting phaeophycean is present only on the inner third of the platform at Motukaraka Island and even there its density is skewed strongly shorewards. Observations on seasonal occurrence of *B. fulvescens* were made in January or February, simultaneously with the initial appearance of *Lyngbya majuscula*. Maximum cover (approx. 10%) was reached from May to July and this was maintained with only slight decreases for an extended period throughout the winter until September or October.
5.3.5 Green Algal Stubble Association.

The term "green algal stubble" is introduced to cover a group of filamentous algal species that occur together and display synchronous outbursts of growth. Thus the properties they possess as a group means they behave just as a single species - as *Lyngbya majuscula* or *Colpomenia sinuosa*, and so are given equal status as a dominant component of the Motukaraka Island seasonal flora despite being composite in structure. There are three dominant species - *Cladophora repens* f. *tenuis*, *Chaetomorpha aerea* and *Cladophora crinalis*, all belonging to one family (Cladophoraceae), so it is appropriate to set the group under a chlorophycean heading. These three have dominance of both numbers of species and cover. Subdominant species in the association are a further Cladophoracean, *Cladophora cf. laetivirens*, the single phaeophycean *Sphacelaria limicola* and three rhodophyceans - *Erythrotrichia carnea*, *Polysiphonia* sp. and *Ceramium* sp. All the species are filamentous and compact, and of the same turfing growth form as the surrounding *Corallina officinalis*. The second property, and one that is significant in field recognition, is that of the colouration of the dominants - bright grass green, contrasting markedly with the sombre dark green of *Lyngbya majuscula* and creamish-pink of *Corallina officinalis* together with which these green species are associated.

Despite the coherence of the group in terms of size, thallus structure, growth characteristics and times of abundance, the species involved do display some individual differences in distribution (Table 5.3). *Cladophora repens* f. *tenuis* occurs virtually only at the outer parts of the platform; although occasional specimens were picked up during algal collections further inshore its presence there is insignificant. *C. crinalis*, however, regularly occurs right across the platform though its cover is highest towards the outer areas. *Chaetomorpha aerea* and *Erythrotrichia carnea* occur across the entire width. The distribution of *Polysiphonia* sp. is uncertain.
Changes in abundance of this group were followed at Motukaraka Island throughout 1976 and 1977. The pattern was observed at pool C where it was representative of the outer part of the reef platform. Further inshore one encountered localized outbursts of other filamentous species (for example *Rhizoclonium kernerii*, *Scytosiphon lomentarium*, *Enteromorpha compressa f. australiensis* and the bacillariophycean *Navicula grevilleana*), but these patches were seldom extensive.

Green algal stubble first appears in May as *Lyngbya majuscula* regresses thereby exposing increasing amounts of underlying *Corallina officinalis* turf, bare patches of sandstone and depressions filled with intermixed silt, sand and shell material. Cover remains low (< 5%) for another month until *Lyngbya majuscula* vanishes completely. Growth of all species of green algal stubble is slow so that maximum cover (10-15%) is attained from August to mid-October. From late October onwards there is a decrease in cover, although no active regression (as noted for *Laurencia* sp. 3) was observed for any species of the green algal stubble association.

Unlike the ephemeral species, *Lyngbya majuscula* and *Colpomenia sinuosa*, components of green algal stubble are pseudoperennials in the terminology of Sears & Wilce(1975). At no time of the year is any species totally absent from the shore. Even at the height of the *Lyngbya majuscula* bloom, occasional dumps and filaments of these stubble-forming species can be found. But because of the reduced perennating form possessed by the species they are often inconspicuous, being overtopped by other annual or perennial species, or submerged under temporary silt accumulations during the adverse seasons. *Chaetomorpha aerea* appears to maintain highest cover for the greatest proportion of time.
Figure 5.3.

Lyngbya majuscula. Seasonal and horizontal changes in cover at Motukaraka Island.

A - Horizontal changes during 1977. "Distance" refers to distance across reef platform.

B - Seasonal abundance in 1977 at pool C (105 m), cover values were derived from photographic analysis.

C - Seasonal abundance cycles 1975-1977, at 62 m (upper) and 105 m (lower). Means and standard deviations plotted from field estimates of cover, arrows indicate times of first sightings of Bursatella leachi on the reef.

In A and B points plotted represent averages of monthly samples, in C data from all visits are included.
Figure 5.4.

*Colpomenia sinuosa.*

Schematic representation of annual distribution across an intertidal reef flat. Constructed from data collected at Motukaraka Island during 1976 and 1977. Letters A-D refer to sites of the four study pools.
5.4 Annual Patterns of these Dominant Algae.

5.4.1 Changes in Cover.

A shortcoming of many earlier cryptogamic surveys has been that the workers have failed to separate the perennial and annual components of the flora under study. They have largely ignored the important factor of seasonality with its resulting differences in species' composition at different times and, consequently, different patterns of biomass change. Previous algal studies in the Hauraki Gulf have concentrated on defining the levels at which species are encountered (Chapman, 1950; Dellow, 1950; 1955; Carnahan, 1952; Dromgoole, 1964) without considering the meaning of seasonal species as their distribution patterns change across the shore. Continuous monthly observations for several years particularly at Motukaraka Island have shown that this shore could not adequately be described or analysed in terms of one flora, but rather the algae form a suite of two or three seasonally replacing florae. Batham (1956) observed the sheltered shore at Portobello, Otago Harbour from mid-1952 to November 1955, she recorded brief seasonal outbursts of several algae.

In addition, even on this gently sloping reef, level is of great importance so that patterns of abundance, and sometimes distribution of dominant species even, are not uniform across the shore.

At Motukaraka Island five categories characterized by dominant seasonal algae are present at various times throughout the year. These categories are based on one or several species. The five dominant seasonal categories are:

1. *Lynghya majuscula*
2. *Colpomenia sinuosa*
3. Green algal stubble
4. *Bachelotia fulvescens*
5. *Laurencia* spp.
Each has a separate and predictable pattern of dominance and biomass change over the platform. Each equals or exceeds the *Corallina officinalis* turf in dominance for a time before regressing.

When the observations on annual cycles for the dominant seasonal categories are combined, an overall picture of seasonal algal patterns on difficult parts of the shore can be gained. This pattern will later be related to distribution and occurrence of the dependent herbivorous opisthobranch species.

5.4.2 A Graphic Model to Demonstrate Cycles of Dominant Seasonal Algae.

It is possible to depict changes in cover and biomass for the dominant algae in terms of a cyclic graphic model (Fig. 5.5). Here months and seasons are shown together with patterns of occurrences of algal categories. In the graphic summary the area of maximum width for each species corresponds with a period of maximum cover, narrower areas indicate decreases in cover. The full scale for each of the seasonal groups shown is as follows: *Lynghya majuscula* 65% cover; *Colpomenia sinuosa* 20% cover; green algal stubble 15% cover; *Bachelotia fulvescens* 10% cover. A vertical component (one that relates position on the platform to level on the shore) could be added to the model by having a series of concentric rings, each corresponding to a known study site or level, rather than the single sites as depicted here.

The *Laurencia* spp. are omitted from the model. This is because of the unpredictable seasonal growth burst and my failure to separate the two specific identities at Motukaraka Island until late in the study. This omission is unfortunate since the *Laurencia* spp. contributes significantly to the total algal biomass in pool C. However it is justifiable on two counts.

1. The model predicts only seasonality of occurrence, it does not predict density effects either of component species or total cover. Consequently removal of one species has no effect on the pattern, according to this model, of any other species.
Figure 5.5.

Graphic summary to demonstrate annual cycles amongst the dominant seasonal algal categories. A is for the inner reef flat (based on data from pool B), B is for the outer reef flat (based on data from pool C). Unshaded areas indicate the absence of cover by a dominant seasonal alga at that time.
2. *Laurencia* spp. are not used as a food by either of the opisthobranchs studied at Motukaraka Island.

Fig. 5.5

A

B

<table>
<thead>
<tr>
<th>Lyngbya majuscula</th>
<th>Bachelotia fulvescens</th>
<th>Colpomenia sinuosa</th>
<th>Green algal stubble</th>
</tr>
</thead>
</table>
With reference to the model it can be seen that at pool B, the first appearance of *Lyngbya* and *Bachelotia* is nearly identical, however *Bachelotia* outlasts the latter only to regress subsequently at the time *Colpomenia* is growing. Times of maximal growth for *Colpomenia* and green algal stubble overlap (August–October) through the season of minimum sea temperatures. *Colpomenia* and *Lyngbya* initially never occur together anywhere on the platform - in January if the first *Lyngbya* plants are early there will be a breif overlap phase of one or two weeks before the *Colpomenia* vesicles disintegrate completely. It appears that the conditions required for growth of these two species are precise opposites.

Carnahan (1952) suggested that the establishment of *C. sinuosa* in autumn may be due partially to the occurrence of the maximum periods of continuous submergence of the lower littoral areas. In Hawaii, Santelices (1977) found an irregular pattern of change throughout the year for *C. sinuosa*, biomass changes having no significant correlation with light intensity, temperature, water movement or salinity. Walsby (1977) noted how spring storms damaged *C. sinuosa* plants at Leigh, N.Z.

In Hawaii, Santelices (1977) found *Lyngbya majuscula* to have a negative correlation with water movement and positive correlation with light intensity. These observations hold good for New Zealand populations and explain its occurrence in the sheltered waters of the Waitemata Harbour where it occurs only in the intertidal zone. Interestingly Santelices placed the rhodophycean *Spyridia filamentosa* in the same category of seasonality, and indeed, at Motukaraka Island *S. filamentosa* clumps were present with *L. majuscula* in 1975 and 1976 but none was present in 1977.
| A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z |
| A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z |
| A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z |
| A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z |
| A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z |
| A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z |

Table 5.3: Presence/absence records for age at Menorca balea. Data for your study area included, records both from field observations
and microscopic inspection. Examination, percentage included (based on monthly collection made from July 1976 to February 1977).
5.5 Characterization of the Flora on Echinoderm Reef Flat.

Algal diversity is higher at Goat Island than within the Waitemata Harbour, this is probably because the waters of the Hauraki Gulf are cleaner, or the situation is more exposed, or both. A preliminary list of algae (only Cyanophyceae, Chlorophyceae, Phaeophyceae, Rhodophyceae) collected from Goat Island, Leigh Harbour, Matheson Bay and Little Barrier Island by V.J. Chapman (unpubl. 1974) includes 145 species. I have prepared a personal list of 70 species (to November 1976) from the Leigh Marine Reserve alone. In comparison to Motukaraka Island, the one very conspicuous difference is cover of the fucacean Hormosira banksii - at Goat Island Bay cover is much less because of exposure.

Large phaeophytes dominate the flora on Echinoderm Reef, with the presence of both perennial and annual species. Amongst the perennials are Ecklonia radiata, Carpophyllum spp., Xiphophora chondrophylla, Cystophora retroflexa. Seasonal species attaining a significant height or diameter are Sargassum sinclairii, Glossophora kunthii and Colpomenia sinuosa. Several species of Rhodophyceae are seasonal dominants e.g. Asparagopsis armata, Hymenena variolosum, Herposiphonia spp. (2), Champia spp. (2), Laurencia spp. (3), Liagora harveyana and Gigartina macrocarpa. Bursts of members of both these orders occur towards the outer parts of the reef platform whereas Enteromorpha sp. (Chlorophyceae) are very common seasonally along the inner zones of Echinoderm Reef. For these annual species there is a distinct seasonal progression in dominance: a spring flora (September to October) of Asparagopsis armata, Splachnidium rugosum, Cladostephus verticillatus, Glossophora kunthii, Colpomenia sinuosa, Laurencia distichophylla, Laurencia sp. 2; an early summer flora (November to January) of Enteromorpha sp., Liagara harveyana; Gigartina macrocarpa and a mid to late summer flora (February - May) of Laurencia sp. 1 and Lyngbya lutea. Maximum algal diversity occurs at ELWS level (pers. obs., 1975). There is a general lack of fine filamentous ephemeral algae as already described for Motukaraka Island.
Subtidally off Echinoderm Reef the flora is reduced in the number of species, and those that are present tend to exist in layers: an upper canopy formed by *Ecklonia radiata* alone or in conjunction with *Sargassum sinclairii*; and an understorey of *Plocamium costatum*, *Pterocladia lucida*, *Pterocladia pinnata*, *Cladhymenia oblongifolia*.

Since *Aplysia* species are very selective as to the species of algae on which they settle and feed, I monitored only the annual cycles of the three species of *Laurencia* (Rhodophyceae: Ceramiales) on Echinoderm Reef. The algal flora of the Goat Island Bay region is well known, several prominent algologists having worked on the flora there (V.J. Chapman, F.I. Dromgoole, K.A. Johnson, R. Hall, D. Luxton, M. Begum, F.J. Taylor).

5.6 Introduction to Taxa of Laurencia Investigated.

*Laurencia* species are in the family Rhodomelaceae of the rhodophycean order Ceramiales; all members are cartilagenous. Characters defining the genus *Laurencia* Lamouroux, 1830 have been presented in works by Saito (1967) and Saito & Womersley (1974). The genus is worldwide with many species.

*Laurencia* species are common intertidally and often ecologically important (McKeon, 1966; Saito & Womersley, 1974). But despite their abundance, the species are very improperly known and regional taxonomic revisions have only appeared recently: Japan (Saito, 1964; 1965; 1967); Hawaii (Saito, 1969); Pacific North America (Saito, 1969); southern Australia (Saito & Womersley, 1974). However, no such revision has been attempted for the New Zealand forms, and because the concensus of published work is that *Laurencia* species mostly have small distributional ranges and tend to be confined geographically (e.g. 15 of the 16 species known from southern Australia are endemic to that continent; only approx. half the 20 species from Hawaii occur elsewhere in the Indo-Pacific area) then it can be predicted that many of the New Zealand taxa will be classed as endemic. Not only are the antheridial, cystocarpic and tetrasporic phases undescribed for New Zealand species but also it is not certain to which taxa
the available names should be applied (N.M. Adams, pers. comm. 1975; 1977).

This uncertainty of specific identification has caused the greatest problems with this project both at Leigh and at Motukaraka Island. Initially at Leigh it was thought that only two taxa were involved and sampling was undertaken according to this assumption, but subsequently it became clear that three species were in fact present. Two species exist at Motukaraka Island, one of these occurs at Leigh but it is not certain whether the other ("cylindrical") species is the same as either of the two similar species at Leigh.

Some Laurencia species show considerable intraspecific variation, for example the "filiformis complex" of Southern Australia. Here three forms of L. filiformis are recognized: forma filiformis based on the type which is generally a sheltered-water plant, epiphytic on seagrasses; forma heteroclada, based on L. heteroclada, a rough-water reef form; and a large, deeper-water form described as forma dendritica. These forms and their integrades appear to have a strong ecological, and to some degree, genetic, basis (Saito & Womersley, 1974).

Morphological descriptions of each of the four Laurencia species encountered during this study are provided in the following sections. Field characters and ecological information are included. It is felt that ecological data (on annual cycles and vertical distribution) should be used to supplement traditional morphological criteria to enable improved specific diagnoses to be made.

Only one species, Laurencia distichophylla J. Agardh, can be identified positively, the three remaining taxa have been designated numbers to standardize and simplify reference to them in the text that follows. As a further aid to subsequent taxonomic research in the genus voucher species have been deposited in the herbaria of the Leigh Marine Research Station, the Botany Dept, Auckland Institute and Museum, and the National Museum of New Zealand, Wellington.

Accession Nos: Laurencia spp. 1 - AK 150450; Laurencia spp. 2 - Ak 150451 and Ak 150452; Laurencia distichophylla - AK 150449.
5.6.1 Laurencia distichophylla J. Agardh, 1852. Figs. 5.6e,f.


There are two sections to Laurencia -

Section 1 Laurencia sensu stricto - thallus invariably radially branched, branches terete.

Section 2 Planae - thallus essentially branched in one plane, branches slightly or strongly compressed.

As its name implies, Laurencia distichophylla belongs to the section Planae, and is the only species of the four encountered to do so.

Description. Colour dull reddish-brown to pale pinkish-olive green. Maximum height of branches 5.5 cm. Bases of axes cylindrical, rhizoidal and epiphytic. Plants consisting of a clump of 3-12 branches. Main axes compressed, bearing closely-arranged alternate to subopposite distichous laterals, themselves with 1 or 2 further orders of branching at shorter intervals; ultimate branches terete to slightly compressed. Female plants bear cystocarps on lower laterals.

L. distichophylla extends to Pukerua Bay just north of Cook Strait (N.M. Adams, pers. comm. October 1975), and it is also known from Castle Point on the Wairarapa Coast. According to Saito & Womersley (1974) this species is the only Laurencia common to both New Zealand and Southern Australia.

It is probable that this species has been erroneously identified as L. botrychioides by New Zealand workers in the past, particularly in ecological investigations (Chapman, 1950; Dellow, 1950; 1955). Morton & Chapman (1968) leave no doubt as to this conclusion with their description of the species on the low-tidal platform at Goat Island Bay as having "flattened pinkish-brown axes and short bluntly divided branches."
Ecology. At Goat Island Bay, Leigh, *L. distichophylla* grows amongst turf of *Corallina officinalis* and on bare sandstone as well. This species extends subtidally whereas none of the other terete species do so. Low densities of *L. distichophylla* plants have been found amongst *Corallina* turf at 5-10 m below ELWS level at Goat Island Bay, Leigh Harbour and Matheson Bay. Immediately subtidally, off Echinoderm Reef, occasional plants have been observed as epiphytes of the fucacean *Carpophyllum plumosum*. Intertidally *L. distichophylla* occurs across the extent of Echinoderm Reef flat, however the microhabitats in which it occurs vary depending on its level on the shore. High on the platform (as in the vicinity of pool A), it is confined to pools, seepage flats and runnels; lower it grows on *Corallina* flats that become fully emersed at low tides.

This distribution appears to be caused through insolation effects, *L. distichophylla* is readily sunburnt as axes bleach white in 24 hr following a time of emergence and full sun. The dead axes are soon detached from the plant. Watts (1977) terms such partial loss of a plant "size-reduction mortality". This effect, whose prime cause is insolation, clearly serves to limit growth of *L. distichophylla* towards the upper parts of the reef platform where it is forced into habitats where shade or water submergence provide refuge.

Where *L. distichophylla* occurs subtidally, and in pools at ELWS level, plants have a pinkish-red colouration that is very different from the brown to olive-green tones of those occurring intertidally.

The main grazers of *L. distichophylla* appear to be *Aplysia* species and mesogastropods of the rissoacean family *Eatoniellidae* (*pers. obs.*).

Dellow (1950) noted that *L. distichophylla* (as *L. botrychioides*) occurred frequently in summer as part of the mid-tidal *Corallina-Hormosira* association. Dromgoole (1964) recorded *L. distichophylla* from Little Barrier Island, as abundant in the upper littoral fringe (ELWS to 3 m) and occasional in the lower midlittoral zone.
Growth and Annual Abundance Cycle.

*L. distichophylla* can be found as occasional small, isolated plants throughout the winter (June-August) and this species is virtually responsible, on its own, for the winter cover values of *Laurencia* recorded in my photographic analyses of total *Laurencia* cover. Despite its presence, cover is very low and growth probably negligible. *L. distichophylla* enters its growth phase in August and grows rapidly until October or November, the maximum cover values attained by this species during this time being approximately 20% (see Table 5.4 in which cover-values are given at three different sites for the time of maximum growth). Growth appears to halt over summer, and cover falls into a steady decline that leads to the winter minimum.

From monthly photographs of *Laurencia* observation areas it was possible to recognize individual plants and record their positions, and so I could follow increases in size of known plants to obtain their growth rates. Data for the growth of 33 separate plants was obtained for September to November 1977. Mean growth rate was 21.8 mm.month\(^{-1}\) (SE = 1.48, SD = 8.49). When increase in size for each plant was divided by the number of days between observations, a growth rate figure per day was obtained, this being 0.78mm.day\(^{-1}\) (SE = 0.053, SD = 0.304). Fig. 5.7 shows two series of slides taken on consecutive months showing growth of known *Laurencia distichophylla* plants.

The terete *Laurencia* species of section *Laurencia* sensu stricto present the greatest taxonomic difficulties. Apparently these "cylindrically-stemmed" species have been given various names in various herbaria and no one is sure what name should be applied (N.M. Adams, pers. comm., 1975; 1977).

5.6.2 *Laurencia* sp. 1.  Figs. 5.6a, b.

**Description.** Colour deep reddish-brown to greenish-brown. Maximum height of branches 3 cm. Plants erect, turfing. Bases cylindrical, rhizoidal and epiphytic on *Corallina officinalis*. Lower parts of axes nearly bare or with
sparse alternate laterals (0.5-1 mm in length); upper parts with laterals of greater length which are either simple or carry smaller branchlets. Branching much more dense than in Laurencia sp. 2. Apical cells tight without large gaps between the epidermal cells, trichocysts short (much shorter than in Laurencia sp. 2, secondary longitudinal pit present.

Where Laurencia sp. 1 is growing in pools (>25 mm in depth) it forms rather loose bushy clumps but is never consolidated into a mat. Where it is growing amongst Corallina officinalis out of water (e.g. the reef edge just off pool A) branching is more profuse and here Laurencia sp. 1 forms consolidated mats that attract sediment and so become even more compact, forming a thick, spongy turf. The turfing form appears more cartilagenous than the permanently immersed form.

Ecology. Laurencia sp. 1 is a conspicuous component of the reef platform flora during summer and autumn. It is the only species that is completely seasonal in character, being absent from June to November each year.

Most plants occur towards the inner part of the low-tidal platform at Goat Island (i.e. inner 30-50 m). Plants are present both in pools of standing water and on patches of Corallina officinalis turf that drain at low tides. Laurencia sp. 1 is an epiphyte on Corallina, no plants having been recorded on alternate hosts.

Aplysia dactylomela is the main grazer of Laurencia sp. 1, although A. juliana and A. parvula consume it as well. It appears to be unpalatable to Eatoniella species. An unidentified species of errant polychaete has been observed eating this Laurencia. This polychaete lives in sand amongst Corallina at the bases of Laurencia clumps, and it bites through axes close to their bases and pulls the branches down into its burrow.

Growth and Annual Abundance Cycle. Laurencia sp. 1 displays complementary seasonality to that already described for L. distichophylla. First appearance of Laurencia sp. 1 in November is due entirely to regrowth of basal portions that have overwintered amongst Corallina officinalis. Growth from sporeling
settlement is not apparent until February. Growth proceeds very rapidly, particularly in the warm shallow pools closest to the reef edge, so that by March or April maximum cover is of 80-100%. Much growth occurs by rhizoidal spreading and adjacent clumps merge to form extensive brown turf-like patches of this species alone. From June onwards a definite regression phase sets in, lateral branches fragment and fall away and the height of individual plants decreases, clumps becoming discrete. Soon the turf is at the same height as that of the Corallina officinalis that is supporting it, and eventually all the Laurencia sp. 1 apparently vanishes as tiny overwintering rhizoids are left amongst the bases of the Corallina officinalis plants.

5.6.3 Laurencia sp. 2. Fig. 5.6c, d.

Description. Colour deep chocolate-brown. Main branches several to many, up to 14.5 cm in height. Plants tall, open and flaccid. Bases and axes terete, approx. 1 mm diameter, barely tapering distally. Main axis predominates throughout. Branching irregularly alternate and radial. Lateral terete with stubby branchlets towards tips giving a dendroid appearance. Cells in vicinity of apical pits separated by larger intercellular spaces than in Laurencia sp. 1, and trichocysts much larger. Epidermal cells with secondary pit connections. This species keys closest to, and is most similar in morphological appearance, to Laurencia arbuscula Solander as interpreted by Saito & Womersley (1974) from Southern Australia.

Ecology. Owing to its large size and bushy appearance Laurencia sp. 2 is conspicuous on the shore. It occurs across the entire reef platform, but does not extend subtidally. Maximum densities from September to November occur in shallow pools and channels towards the inner areas (Table 5.4), and here it grows alongside Laurencia distichophylla. Other co-dominant algae at this time are the phaeophyceans Glossophora kunthi, Carpophyllum plumosum, Colpomenia sinuosa and Sargassum sinclairii. Inshore most plants grow amongst Corallina officinalis turf; but near the outer reaches plants are found growing directly
on the exposed sanstone, frequently in fissures.

Whilst both *A. dactylomela* and *A. parvula* have been observed feeding on *Laurencia* sp. 2, and the latter sea hare regularly lays its spawn masses on this alga, greatest grazing appears to be caused by minute rissoid gastropods of the genus *Etoniella*. Over December and January *Etoniella* species appear to congregate on *Laurencia* sp. 2 and reduce even the tallest plants to their base axes. It appears that those clumps of *Laurencia* sp. 2 that remain throughout the summer are existing in rough-water refuges where they are not exposed to grazing by *Etoniella* species.

**Growth and Annual Abundance Cycle.**

Minimum cover of *Laurencia* sp. 2 occurs from March until August; only occasional clumps are present and densities are as low as 1-2 plants.m\(^{-2}\), the longest axes being only 33 mm in length. The first new plants appear and start to grow gradually over July and August, and from September to November growth is rapid and plants are numerous. Cover of *Laurencia* sp. 2 alone can reach 20% in November. Therefore *Laurencia* sp.2 appears at a similar time to *L. distichophylla*, peak cover is reached slightly earlier, or at the same time, and regression in January and February is much more rapid than for *L. distichophylla*. Table 5.4 gives values for cover at three different sites on the reef platform, and comparable data for *L. distichophylla* is also presented. It can be seen that maximum cover values for *Laurencia* sp. 2 occur on the inner parts of the reef platform in submerged areas whereas maximum cover values recorded for *L. distichophylla* (in November) are on areas of emergent turf. For this latter species, cover is similar at these two levels on the shore.
<table>
<thead>
<tr>
<th>Month</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct. 1976</td>
<td>8 6.5 5.96 7.68 7.25 1.78</td>
<td>5 0.8 0.84 8.2 2.17</td>
<td>5 6.2 2.68 20.6 1.75</td>
</tr>
<tr>
<td>Nov. 1976</td>
<td>5 20.0 7.45 0.0</td>
<td>0</td>
<td>5 1.6 1.14 16.8 7.19</td>
</tr>
<tr>
<td>Sept. 1976</td>
<td>10 2.4 2.87 0.9 1.10</td>
<td></td>
<td>10 5.2 3.675 0.4 0.321</td>
</tr>
<tr>
<td></td>
<td>5 26.0 4.89 0.0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>SD</td>
<td>x</td>
</tr>
</tbody>
</table>

Regularly washed by seawater.

Site 3: Near ELMS Level, near outer edge of reef platform, Corallina officinalis turf areas in shallow pools and runnels.

Site 2: 5-10 m onto reef platform, Corallina officinalis turf areas elevated from areas of standing water.

Site 1: 5 m onto reef platform, Corallina officinalis turf areas elevated from areas of standing water.

**Mean values per m<sup>2</sup> at three different sites, derived from point quadrat data.**

**Table 5.4. Comparative cover values for T. distichophylla and Laurencia sp. 2, bothmoder reef flat, Leighton.**
Figure 5.6.
The three species of *Laurencia* found at Goat Island Bay, Leigh. Whole plants and detail of a single branch shown in each case.

a, b - *Laurencia* sp. 1.
c, d - *Laurencia* sp. 2.
e, f - *Laurencia distichophylla* J. Agardh.
5.7 Seasonal Growth Patterns of Laurencia spp.

5.7.1 Changes in Total Laurencia Cover.

On the inner part of the platform on "Echinoderm Reef", total cover of the three Laurencia species undergoes a yearly cycle of change. This pattern is described from monthly photographic analysis of seven sites (Fig. 5.8, Table 5.5) chosen so as to cover the spectrum of habitats occurring on the inner part of the reef flat: bare substrate versus Corallina turf substrate; pools versus dry flats; horizontal versus sloping surfaces. Total cover values are given because the species of Laurencia cannot be separated in photographs.

A plateau of high total Laurencia cover (40-50%) is attained throughout summer and autumn, but in late autumn there is a sudden decline to a winter low. Since three species are involved, this pattern of change for total Laurencia cover is a composite one, each species undergoing separate and pronounced oscillations in cover. As outlined previously, Laurencia distichophylla and Laurencia sp. 2 are annuals, Laurencia sp. 1 is effectively only seasonal in occurrence.

Table 5.5. Total Laurencia cover on Echinoderm Reef Flat. Transformed data for 7 0.1 m² areas from November 1976 to November 1977.

<table>
<thead>
<tr>
<th>Area</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>Mean</th>
<th>SE</th>
<th>SD</th>
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<td>-</td>
<td>-</td>
<td>45.09</td>
<td>1.97</td>
<td>3.94</td>
</tr>
<tr>
<td>Dec.</td>
<td>-</td>
<td>48.04</td>
<td>46.61</td>
<td>44.60</td>
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<td>-</td>
<td>-</td>
<td>46.42</td>
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</tr>
<tr>
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<td>39.82</td>
<td>42.13</td>
<td>25.33</td>
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<td>-</td>
<td>-</td>
<td>43.99</td>
<td>7.23</td>
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<tr>
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<td>37.76</td>
<td>43.17</td>
<td>38.23</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>2.50</td>
</tr>
<tr>
<td>March</td>
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<td>37.58</td>
<td>47.58</td>
<td>38.53</td>
<td>71.85</td>
<td>51.24</td>
<td>53.42</td>
<td>48.34</td>
<td>4.63</td>
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<td>54.03</td>
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<td>May</td>
<td>39.70</td>
<td>32.27</td>
<td>41.15</td>
<td>38.53</td>
<td>60.20</td>
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<td>64.01</td>
<td>47.68</td>
<td>4.77</td>
<td>12.62</td>
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<td>31.82</td>
<td>30.53</td>
<td>47.58</td>
<td>37.64</td>
<td>47.47</td>
<td>34.44</td>
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<td>10.38</td>
</tr>
<tr>
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<td>20.09</td>
<td>18.82</td>
<td>19.82</td>
<td>2.87</td>
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<td>19.82</td>
<td>15.06</td>
<td>2.00</td>
<td>7.94</td>
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<tr>
<td>Aug.</td>
<td>19.64</td>
<td>19.37</td>
<td>20.70</td>
<td>20.96</td>
<td>2.87</td>
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<td>13.56</td>
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<tr>
<td>Sept.</td>
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<td>35.67</td>
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<td>Nov.1977</td>
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<td>55.55</td>
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<td>33.85</td>
<td>37.53</td>
<td>7.43</td>
<td>19.67</td>
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</table>

When these data on relative seasonal abundances of the three Laurencia species are related back to those for total Laurencia cover (Fig. 5.8), it is seen that, in terms of biomass, Laurencia sp. 1 is the most important since it has nearly
total dominance on the shore from March to June; cover falls very rapidly through June and July. Total cover is lowest throughout July and August, but it gradually increases with the spring growth of \textit{L. distichophylla} and \textit{Laurencia} sp. 2, so that by November through January cover of these two species equals that formerly attained by the \textit{Laurencia species 1}. The drop in cover recorded for February is important, as this occurs during the lag phase when cover by the winter \textit{L. distichophylla} and \textit{Laurencia} sp. 2 is falling and that for \textit{Laurencia} sp. 1 is increasing. In some years this brief drop will be negligible, in others it will be accentuated.

5.7.2 Changes in Height.

Cover values for algae derived by photographic means are useful in following seasonal changes but their application in terms of availability of food to herbivores is limited. This is because a photographic representation is two-dimensional and assumes all the algae to exist as flattened, horizontally spreading or contracting sheets whereas algae are three-dimensional objects that grow upwards as well as outwards. Therefore cover values are most useful when supplemented with a measure of height or length of thallus so that values for biomass can be derived. Biomass data can then be utilized directly for studies on energetics and herbivore effects.

In the field, following photography of each of the seven study sites each monthly three additional sets of observations were made. A determination of which of the three \textit{Laurencia} entities was present and contributing to cover was made. A visual estimate of the proportion each contributed to total cover was made. Length of the ten longest pieces of thallus was recorded for each of the \textit{Laurencia} components. These data are summarized in Fig. 5.9 where average values for maximum height of each species together with 95% confidence levels are shown. There is an indication of an annual bimodality of heights in \textit{L. distichophylla}, the major peak in length is attained in spring (September to December), and a lesser one in Autumn (April to June). \textit{Laurencia} sp. 1 and
Laurencia sp. 2 display a unimodal pattern of length distribution throughout the year, with peaks in April and November respectively.

Since Laurencia sp. 1 and Laurencia sp. 2 were not present throughout the period followed, they could not be incorporated in an analysis of variance to test the significance of the changes. Similarly, *L. distichophylla* was absent from areas 4 to 7 for parts of the year so these data had to be excluded as well because the "Teddybear" Program (J.B. Wilson, 1976) employed cannot handle missing cells. However, a two-way ANOVA comparing heights and areas was performed on the monthly data for *Laurencia distichophylla* in areas 1-3 (Table 5.6). For these data, there was a significant change in height over the period under investigation, and the three areas were significantly different from each other thus validating their original choice. The interaction term was non-significant suggesting changes in height are correlated with some other factor (e.g. season) than sampling site. These results can be used to extrapolate for all three *Laurencia* species to show their thalli undergo significant changes in height as well as cover throughout the year.

Table 5.6. *Laurencia distichophylla*: Two-way ANOVA for comparisons of maximum length at three areas.

<table>
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<tr>
<th></th>
<th>DF</th>
<th>F</th>
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</tr>
</thead>
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<tr>
<td>T</td>
<td>10</td>
<td>65.5174</td>
<td>1.0 x 10^{-6}</td>
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<tr>
<td>S</td>
<td>2</td>
<td>3.4090</td>
<td>3.43 x 10^{-2}</td>
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<tr>
<td>Interaction</td>
<td>20</td>
<td>1.5349</td>
<td>6.84 x 10^{-2}</td>
</tr>
<tr>
<td>Error</td>
<td>297</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Where T equals monthly heights and S refers to the three sample areas.
5.7.3 Causes of Observed Yearly Cycles in Laurencia Cover.

When the fluctuations in total Laurencia cover on the reef platform of Echinoderm Reef, and the yearly abundance of Aplysia dactylomela are considered, one is led to ask if there is any causal relationship between the two. This consideration is particularly important with respect to the late autumn decline in total cover and winter low. In some years Laurencia was virtually absent over this time. Is this change in total Laurencia cover primarily caused by, or enhanced by grazing pressure from Aplysia dactylomela or does this Laurencia cycle reflect the actual pattern of growth?

During 1975, the first year for which records of total Laurencia cover were kept, all the Laurencia appeared to vanish over winter (from July until October). For this year too, Aplysia dactylomela densities were high, and it appeared that the decline in total cover (and especially for Laurencia sp. 1) was due to A. dactylomela grazing. This was especially so for Laurencia sp. 1, because most metamorphosis of A. dactylomela occurs on this species, and hence the alga suffers greatest grazing pressure from juveniles of A. dactylomela.

To examine quantitatively these grazing effects, Aplysia exclusion cages were established in different situations and on different levels on the shore (Fig. 4.1b). Close to each cage a control area of equivalent size was defined by four belts. The exclusion cages did not prevent settlement of A. dactylomela on the Laurencia beneath the cage, but because each caged area was inspected monthly any small A. dactylomela that had metamorphosed during the previous month could be detected and removed before they had the opportunity to have any significant grazing effects on the caged Laurencia. Juvenile specimens of other grazing gastropods (e.g. Turbo ammonius, Eatoniiella spp.) were free to move through the cage but larger specimens of grazing species were excluded.

Two cages were located in pool A, the first positioned over an area of Corallina officinalis turf. Cage 2 covered an area of C. officinalis turf that was permanently submerged beneath 5-6 cm of water at low tides. Both cages
were accessible at all low tides, *Laurencia* sp. 1 and *L. distichophylla* occurring at these sites. The third cage was positioned approximately half way across Echinoderm Reef Flat on a gentle slope. This site was accessible on tides lower than 0.6 m, only *L. distichophylla* occurring here. Cage 4 was positioned immediately beside pool B on a rock flat backed by a 20 cm high wall. This site was accessible on tides lower than 0.3 m, only *L. distichophylla* growing here. As explained in the Methods section, each treatment (i.e. caged and control areas) was photographed monthly and percent cover of all *Laurencia* species analysed by the point intersection technique.

Results for percent cover (following an arcsin transformation) for each of the areas are presented in Table 5.7. It will be noted that cover values derived from these data differ in some months when compared with those presented earlier for the seven *Laurencia* observation sites. There are two causes for these differences in cover. Firstly, the sizes of the areas monitored were different (*Laurencia* observation sites had areas of 0.25 m$^2$, i.e. 1056 cm$^2$; treatment sites had areas of 0.01 m$^2$, i.e. 100 cm$^2$). The increased resolution given by the smaller areas allowed recognition of *Laurencia* cover for one to two months after it could not be resolved in the observation areas. Secondly, the two sets of sites were in different situations on the shore, and it has already been shown that significant differences do exist in *Laurencia* cover at different sites even when sizes of areas considered are identical. Despite these differences there is a high correlation ($r = 0.91$) between the means for all *Laurencia* observation sites and treatment means for cages 1 and 2 over the period March to September 1977 when data from both methods were being gathered simultaneously.

To evaluate the effects of treatment (E), site (S) and time (T), a three-way analysis of variance was conducted on data for percent cover of *Laurencia* species that had been subject to an arcsin transformation. The analysis was performed under the null hypothesis that *Laurencia* cover is independent of the grazing effects of *Aplysia* species, i.e. that the annual cycles observed in cover
<table>
<thead>
<tr>
<th>Month</th>
<th>Treatment 1 Cage</th>
<th>Treatment 1 Control</th>
<th>Treatment 2 Cage</th>
<th>Treatment 2 Control</th>
<th>Treatment 3 Cage</th>
<th>Treatment 3 Control</th>
<th>Treatment 4 Cage</th>
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</tr>
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<td>13.56</td>
<td>17.76</td>
<td>16.74</td>
<td>0</td>
<td>23.19</td>
</tr>
</tbody>
</table>

0 = zero percent cover, i.e. all Laurencia spp. completely absent from study area.

- = data not able to be recorded.

Of Laurencia species are entirely due to endogenous factors for the species involved e.g. growth, reproduction. It was impossible to include all the cover data in this analysis. This was particularly so for treatments 3 and 4 where a total of 9 cells out of the 52 were missing (i.e. no data could be obtained because of weather, height of tide, inability to remove cage or unusable photographic transparencies). Similarly the data for treatments 1 and 2 each have a single missing cell (for January and February 1977 respectively) and therefore both these months had to be excluded from the analyses. Therefore the ANOVA was performed to compare the effects of two treatments, two sites and 13 time intervals (Table 5.8).
### Table 5.8.

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</tbody>
</table>

All three factors are significant. Thus there is a significant difference between each of the two sites, there is a highly significant change of cover through the 13 months sampled, and there is a significant difference between caged and control treatments. This latter difference is the most important one, here being interpreted as indicating that caging does have a significant effect in protecting the Laurencia beneath from grazing by Aplysia dactylophora. Therefore, the null hypothesis must be rejected.

This explanation of the significance of these differences is not the only one possible, others (such as shading, or exclusion of other herbivores or sand accumulation in caged treatments) could be responsible for the same effect. Indeed, some significant differences that were attributable to shading were noted in the treatments. For example, much less Enteromorpha sp. grew in the control sites than beneath the cages, and barely any Lyngbya lutea grew in the caged areas despite cover of up to 20% in the controls. In cages 3 and 4 (but not 1 and 2) there was considerable sand accumulation following periods of storms, the sand preventing regrowth or settlement of all algal species although Corallina officinalis appeared to be able to survive periods of submergence beneath sand.

When the interaction terms for the ANOVA are considered, it will be seen that the site/treatment analysis is non-significant, therefore it is probable
the same process responsible for change in *Laurencia* cover was occurring at both sites. However, the site/time and time/treatment analyses were significant and means have been graphed (Figs. 5.10, 5.11). Both graphs can be reduced to three phases: a decrease in cover from July to October 1976; an increase from November to April and May 1977; and a second phase of decreasing cover from June to September 1977. For the site/time interaction (Fig. 5.10) it is seen that site 1 (*Corallina officinalis* emergent at low water) has a higher cover of *Laurencia* overall, and this appears to be reached earlier. This is possibly due to the different growth form exhibited by *Laurencia* sp. 1 (see Ch. 5.6.2), the turfing form produced an emergent *Corallina officinalis* turf being denser than the pool form. The decline to low cover values over the autumn and winter months is similar at both sites. However, the increase at site 2 for September 1977 is anomalous - normally an increase in *Laurencia* cover (due to growth of *L. distichophylla*) is not noticeable until October to December. Perhaps this change is due to the effect of the small cage area?

For the time/treatment interaction (Fig. 5.11), the decline of total *Laurencia* cover in the first year in both caged and control sites was similar. I attribute differences in the increase of cover in the caged site to a shading effect on *L. distichophylla*. As has already been noted, *L. distichophylla* is sensitive to insolation and/or desiccation and generally only occurs inshore in pools and runnels where these sun-induced effects are lessened - perhaps the cage reduced the sun's effect sufficiently to enhance growth. However, differences in the subsequent decline phases cannot be due solely to shading because no such effect was apparent in 1976. Therefore, an alternative explanation for the more rapid decline in cover at the control site in 1977 must be sought, and again *Aplysia dactylomela* grazing can be invoked.

**Discussion.** It is apparent that total *Laurencia* cover naturally undergoes clearly defined annual cycles of increase and decrease. These cycles are related to the separate cycles of the three *Laurencia* species on the shore. Minimum cover is reached in mid-winter. However, there is virtually always some plants of one
Laurencia species at some region on the shore. Although the Aplysia exclusion experiments presented here are not sufficiently rigorous (because the analyses have been compromised through lack of replication because of missing cells in the data), they do suggest A. dactylorella grazing has a significant effect on total Laurencia cover - it enhances the autumn decline. In years when numbers of A. dactylorella are very high (e.g. 1975) the decline is accelerated and throughout the following winter there is virtually no Laurencia remaining. On the contrary, in other years when A. dactylorella numbers are lower the decline in cover will be natural and more gradual.

To improve discrimination between the effects of caging per se and grazing in the exclusion treatments larger cage sizes should have been employed and additional replicate treatments consisting of cage tops supported by an open frame should have been provided.

5.8 Summary.

1. The cyanophyte Lyngbya majuscula displays a pattern of rapid growth, followed by a brief plateau period of high cover and a rapid decline phase; cover at peak abundance being between 60 and 70%. Observations suggest grazing by Bursatella leachi may stimulate growth of L. majuscula.

2. Details of annual cycles of growth of the algae Colpomenia sinuosa, Laurencia spp. (composite) and Bachelotia fulvescens are given for the Motukaraka Id locality. Colpomenia sinuosa first appears at ELWN level in May, and greatest cover (30%) is reached from August to December and cover varies across the shore. Plants vanish during December and January. Two species of Laurencia (Laurencia distichophylla and Laurencia sp. 3) are present. In pool C, composite cover value appear to show one or two periods of maximum cover: one in May and a later one from August to September. Bachelotia fulvescens occurs only across the inner third of the intertidal platform, and maximum cover (10%) is reached from May to July.
3. The term "green algal stubble" is introduced to cover a group of filamentous algal species that occur together at Motukaraka Id and display synchronous outbursts of growth. Maximum cover (15%) is attained from August to mid-October.

4. At Motukaraka Id five categories of dominant seasonal algae are present in a cyclic fashion throughout the year and changes in cover and biomass are depicted in a model.

5. Three species of Laurencia are present on Echinoderm Reef, Leigh; morphological descriptions together with information on intertidal range, growth rate and grazers is given for each.

6. All three Laurencia species have endogenous cycles of abundance, these cycles differing seasonally for each species. Each contributes to a regular yearly pattern of change in Laurencia cover with highest values from March to May (40-50% cover) and a minimum in winter from July to September (10% cover or less).

7. From analysis of Aplysia exclusion caging experiments it is suggested Laurencia cover is altered by the grazing of A. dactylomela, although effects due to grazing and caging were not clearly separated.
Figure 5.7.

Change in cover of *Laurencia distichophylla* through four successive months on the inner part of the intertidal flat, Echinoderm Reef, Goat Island Bay. Right series = "L/o II/I"; left series = "L/o II/II".
Figure 5.8.

Figure 5.9.
Average values for maximum heights of the three Laurencia species. Means and confidence limits from field data. Echinoderm Reef, Leigh.

- Laurencia distichophylla
- Laurencia sp. 1
- Laurencia sp. 2
Figure 5.10.
Total *Laurencia* cover on Echinoderm Reef. Plot of ST means from ANOVA (Table 5.8). Comparison of sites.

Figure 5.11.
Total *Laurencia* cover on Echinoderm Reef. Plot of TE means from ANOVA (Table 5.8). Comparison of control and treatment areas.
CHAPTER 6
OPISTHOBRANCH POPULATION ECOLOGY

Introduction.

This chapter is on ecology, covering my observations on growth, density and reproduction for populations of opisthobranchs that were made directly in the field. This is the extent of my investigations on Haminoea zelandiae, Bursatella leachii and Aplysia parvula, but in Chapter 7 I present a detailed study of nutrition and food utilization for Aplysia dactylomela. All this latter work was laboratory-based and is more concerned with the individual's nutritional requirements and energy budget, but it does have implications for the populations of this sea hare and its algal food in the field. My reasons for looking in detail at A. dactylomela for this particular study were: that from the outset, it was known to be present annually on Echinoderm Reef in Goat Island Bay; numbers were assessed as being sufficiently high to allow both monthly samples and limited removal of specimens; specimens were known to reach a relatively large size so that a tagging programme could be undertaken; and, finally, comparative studies on population and individual parameters had been carried out overseas on differing species of Aplysia (Miller, 1960; Carefoot, 1967a-c; Usuki, 1970; Nishiwaki et al., 1975; Lederhendler & Tobach, 1975). As will be seen subsequently, a careful examination of the yearly changes occurring in the A. dactylomela population at Goat Island Bay showed several of these decisions to be incorrect.

Although the presentation and interpretation of the data on recruitment, growth and density for each species are the prime objects of this chapter, I have attempted also to elucidate the place of the species in the communities in which they occur (particularly the principal species Aplysia dactylomela and Haminoea zelandiae), using additional ecological information of mine. Examples of this ecological information are the sources of mortality in A. dactylomela, egg mass development rate in Haminoea zelandiae and migration in Bursatella leachii. My results are compared with those for other species of Aplysia.
Unlike other chapters, where a summary for the entire chapter is given at the end of that particular chapter, in Chapter 6 I have provided a separate summary for *Aplysia dactylomela*, *Harnonea zelandiae* and *Bursatella leachii* following the completion of the section on the ecology of that species.
6.1  **APLYSIA DACTYLOMELA RANG**

6.1.1  **Growth Parameters.**

a. **Length/Weight Relationship.**

Fig. 6.1 is a growth curve composed from standard length (to nearest mm) and damp wet weight (to nearest 0.1 gm) for 252 live *Aplysia dactylomela*. All of the animals were from the population of Goat Island Bay. When a logarithmic transformation is applied, there is a clear linear relationship between length and weight for this species. The regression equation is  
\[ W = 1.006 \times 10^{-4} L^{2.763} \]

where \( W \) = weight in gm and \( L \) = length in mm. The regression equation is highly significant (\( P < 0.001 \)).

b. **Wet Weight/Dry Weight Relationship.**

Table 6.1 summarizes data on the relationship between the damp wet weight of live specimens (to nearest 0.01 gm) and dry weight, including shell (to nearest 0.001 gm). Twenty individuals from the population of *A. dactylomela* at Goat Island Bay were measured. When the data are transformed, the resulting regression equation is  
\[ Y = 0.972X + 2.546 \]

which is significant (\( P < 0.001 \)). Dry weight has a mean value of 8.5%, \( SE = 0.4 \), when expressed as a percentage of the wet weight.

c. **Body Length/Shell Relationship.**

Although it is desirable to obtain a weight value as a relative statistic for live animals in the field (see Methods Chapter, Sections 4.2 and 4.3), the internal shell of *Aplysia* species is frequently all that is preserved of the whole animal, so I feel it is necessary to have some method of relating data on shell measurements back to those for animals. Shell length bears a close relationship to standard body length. In Fig. 6.2 I have plotted these data for 25 *A. dactylomela* and included a regression line for which the equation is  
\[ Y = 0.201X + 0.474 \]  \((r = 0.968)\). Shell length and width are linearly related.

A t-test, however, showed that the ratio of shell length to shell width has no significant relationship to standard body length \((r = -0.157, P > 0.256)\).
Table 6.1. Relationship between live damp weight and dry weight of A. dactylomela.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Wet Weight (gm)</th>
<th>Dry Weight (gm)</th>
<th>Dry Weight as % of Wet Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>44.01</td>
<td>5.862</td>
<td>13.32</td>
</tr>
<tr>
<td>2</td>
<td>1.13</td>
<td>0.082</td>
<td>7.26</td>
</tr>
<tr>
<td>3</td>
<td>4.07</td>
<td>0.309</td>
<td>7.59</td>
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<tr>
<td>4</td>
<td>81.32</td>
<td>6.367</td>
<td>7.83</td>
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<td>5</td>
<td>1.32</td>
<td>0.083</td>
<td>6.29</td>
</tr>
<tr>
<td>6</td>
<td>22.96</td>
<td>2.302</td>
<td>10.03</td>
</tr>
<tr>
<td>7</td>
<td>80.57</td>
<td>7.510</td>
<td>9.32</td>
</tr>
<tr>
<td>8</td>
<td>120.40</td>
<td>9.545</td>
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</tr>
<tr>
<td>9</td>
<td>9.71</td>
<td>1.059</td>
<td>10.91</td>
</tr>
<tr>
<td>10</td>
<td>42.98</td>
<td>4.190</td>
<td>9.75</td>
</tr>
<tr>
<td>11</td>
<td>380.2</td>
<td>41.080</td>
<td>10.80</td>
</tr>
<tr>
<td>12</td>
<td>43.60</td>
<td>2.775</td>
<td>6.36</td>
</tr>
<tr>
<td>13</td>
<td>7.38</td>
<td>0.459</td>
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<tr>
<td>14</td>
<td>62.61</td>
<td>4.867</td>
<td>7.77</td>
</tr>
<tr>
<td>15</td>
<td>6.91</td>
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<td>43.75</td>
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<td>38.48</td>
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<tr>
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<td>245.27</td>
<td>23.213</td>
<td>9.46</td>
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<tr>
<td>21</td>
<td>48.96</td>
<td>5.251</td>
<td>10.73</td>
</tr>
<tr>
<td>22</td>
<td>48.83</td>
<td>3.933</td>
<td>8.05</td>
</tr>
</tbody>
</table>

mean = 8.46  \quad SE = 0.40  \quad SD = 1.88
Figure 6.1.

*Aplysia dactylomela.*

Length (standard crawling length) versus weight (wet weight) relationship (untransformed data) for the Echinoderm Reef population. Graph based on a total of 252 live specimens measured between April 1975 and November 1977. Curve fitted by least squares method.
Figure 6.2.

*Aplysia dactylomela.*

Relationship between length (standard crawling length) and shell length. Data derived from specimens from the Goat Island Bay population. Regression line fitted by least squares method.
$y = 0.20x + 0.474$
6.1.2 Analysis of Tagging Procedures.

As a byproduct of the nutrition and growth studies described in Chapter 7, records were kept of retention and loss of tags by animals which had been tagged either through their parapodium or tail. There was an indication that retention of a tag was longer when inserted through the tail. After 35 days, 6 of 12 parapodially-tagged sea hares had lost their tags and only 2 of 10 tail-tagged slugs had lost theirs.

However it is clear that tag loss does occur in Aplysia dactylomela regardless of where the tag is inserted and a hypothesis was formulated after observations, both on the tags themselves, and the appearance of the sea hares after they had lost their tags. All recovered tags still had the monofilament nylon attached to them and the knots were secure, so tag loss was not caused by the knots becoming undone. In all cases, when a tag was lost from the lower part of the parapodium an elongate hole was visible passing through at the site where the tag had been located, if the tag was lost from the upper area of a parapodium or the tail, a marked slit was present from the site of the tag out to the extremity of the organ. After 2-3 weeks these holes and splits would heal but always a conspicuous scar remained. It is postulated therefore, that tag loss in Aplysia dactylomela is a process where the tag is actively discharged from the site of attachment - presumably the tissue at the site of contact of the tag regresses to allow passage of the nylon. This method would serve whenever a piece of foreign or irritant matter became lodged in the body wall. Tag loss is not due to any mechanical removal by a piece of substrate since the tags were always placed flush with the body, and 2 out of 3 specimens that were starved in aquaria for a month in the absence of any substrate at all, had lost their tags after 3 weeks.

In a similar way, Nishiwaki et al. (1975) also experienced tag loss in Aplysia kurodai; the authors relocated approx. 8.5% of their tags in the field - all had been detached and yet were still as intact as before attachment.
The actual number of tags lost in my study would have been in excess of this figure. At Goat Island Bay in 1977, out of a total of 35 A. dactylomela tagged, 6 (16.7%) were recaptured with obvious tagging scars as evidence of tag discharge in the field but no lost tags were found. Greater tag loss, by any means, would be expected in the field because of the rougher topography which the sea hares encounter and greater water movement than that present in laboratory situations.

Active tag discharge is not peculiar to opisthobranchs only. Yamaguchi (1977) found the asteroid Linkia laevigata capable of ejecting monofilament nylon through the body wall within one month.

As noted in the introduction to the tagging methods section, it is a prerequisite of any tagging system that presence of the tag does not increase chances of mortality of the tagged individual. And it is in this respect that the disadvantages of use of tail-tagging procedures in Aplysia becomes obvious. Since all Aplysia species have an enlarged hind portion to the foot sole, and in some species this region is considerably expanded (e.g. in A. juliana where it is termed a "posterior sucker" (Eales, 1961; Marcus, 1972)), then any impediment to this region functioning properly must lessen overall adhesion and increase the chances of dislodgement by water movement. This undesirable side effect is clearly shown in the figure of a tagged A. kurodai provided in the paper by Nishiwaki et al. (1975:391). The whole posterior region of the foot is lifted off the ground and strongly contracted against the back of the visceral hump, the overall locomotion and ability for adhesion of this specimen would appear to be greatly impaired.

6.1.3 Analysis of Recruitment.

Recruits are here defined as those post-metamorphic individuals who are less than 3.5 gm in weight and/or less than 40 mm in length; all are at the stage I condition for the Gonad Index (Ch. 6.1.8). Individuals possessing these
characters are likely to be less than one month old, and so these figures represent specimens that have been recruited to the population since the last monthly census. This hypothesis assumes that the growth rate is constant and that individuals classified as recruits, according to the above classification, on one sample will have grown out of the recruit class by the subsequent visit. This assumption may not be valid because after the end of May as the water temperature is decreasing rapidly, the growth rate reduces (Fig. 6.8) and it is probable that some individuals may therefore have been classified as recruits on two successive samplings over these autumn and winter months.

Some of these data are plotted in Fig. 6.3 to show graphically the percentage of recruits in the total A. dactylomela population over the entire course of this study. From this illustration it can be deduced that recruitment in A. dactylomela is characterized by variations in intensity and tends to be sporadic in nature. First appearance on the shore of recruits occurs between January and March (at the height of summer) but recruitment may continue until July - i.e. recruits being found for over half of the year. Although the total number of recruits was higher in 1975 than 1977, the actual proportion of recruits in the whole population was higher in the latter year (reaching 86% in March 1977); 1976 was a low year both in terms of numbers of recruits and their proportion in the entire population (only reaching a maximum of 24% over February and March 1976).

6.1.4 Growth in the Field.

For Aplysia dactylomela at Goat Island Bay, Leigh monthly collections were made of as many specimens as possible for the construction of length-
frequency histograms. Echinoderm Reef was divided approximately into thirds — not simply arbitrarily, but because Laurencia sp. 1 was known to occur only on the inner third and it was suspected that changes in settlement, growth or density of Aplysia dactylomela could reflect this algal zoning pattern. Specimens were collected not only from pools A, W and X to establish these data for each month for the inner area of the reef platform, but also as many A. dactylomela as could be found along this inner zone between pool A at the eastern extremity, and pool X at the western limit, were collected. All specimens were returned to the laboratory for measurement and incorporation of these data into these overall growth data, all were maintained in the laboratory overnight and returned to the same area at low tide on the following day. Similarly data for the outer areas of the reef platform include specimens found not only in pool B but also in the zone in which pool B is situated along the outer margin of Echinoderm Reef. Figures 6.4 and 6.5 present the results graphically for the inner and outer parts of the reef platform respectively.

Results.

For the collections made on the inner areas, the three years show a distinct, repetitive pattern. High numbers of juveniles appear from January to March (i.e. mid-summer) and their growth is rapid. Small juveniles, presumably the result of recent settlement and metamorphosis, are present until July (1976) or September (1975, 1977). No specimens were found for several months over mid-winter or spring each year. The bulk of the population in the inner areas therefore consisted of
specimens below 150 gm in weight and were juveniles incapable of reproduction (Ch. 6.1.9). For the very few individuals heavier than this, the probability of them having been accidentally transported by storms to these inner parts of the reef platform cannot be ignored.

An annual pattern is much less clear for collections made on the outer areas. I have not included data for 1977 in the histogram because, apart from a single individual found in July (196 mm, 380.2 gm), no A. dactylomela were found in this zone throughout the entire course of the year's sampling. A yearly cycle is much less evident here and specimens were found (albeit in very low densities) continuously throughout the winter-spring months of 1976 when there was none on the inner reef areas. Secondly, for pool B, in general the size range of specimens was much greater than for the inner zone, in the outer zone only a few animals weighed less than 150 gm. This would indicate that the majority of specimens were at stage III or IV of the Gonad Index and therefore were probably capable of reproduction. Clearly there was in 1975, a much higher recruitment than in either of the two subsequent years and I have already considered the significance of this observation in the section on recruitment for this species.

Discussion.

Almost all the studies done previously on Aplysia species in the field have produced results indicative of extremely rapid growth, and high fecundity
and a life span of a single year (Miller, 1960; Carefoot, 1967c; Nishiwaki et al. 1975). Usuki (1970) suggested that generation time may be as short as six months so that there were two distinct spawning periods in a year.

It is axiomatic that such data refers to the situations where the species are thought to be living in ideal habitats. And as a corollary, with this knowledge, data on growth and fecundity can then be taken as an indication of the suitability of a local environment for a particular species of Aplysia.

These data show that the population of Aplysia dactylomela in terms of growth rate increments and size reached on the intertidal reef platform varies considerably in relation to what part of the reef is being considered. So does the state of sexual maturity - since the majority of the population occurs towards the inner part of the reef flat (Ch. 6.1.6) it is apparent that the bulk of the population never reaches reproductive maturity. Consequently, oviposition by A. dactylomela is a very rare event on Echinoderm Reef. The only copulation and spawning that may take place might occur at the extreme outer fringe of Echinoderm Reef or immediately subtidally.

The major recruitment occurs in early summer but small individuals (presumably newly-metamorphosed juveniles) are found until autumn. It would appear, therefore, that there is continual, sporadic settlement of young. These juveniles are produced by a population (or populations) of adults elsewhere. These adults probably breed throughout summer and early autumn, thus suggesting one reproductive season from approx. November to May each year. My data on recruitment do not suggest that two distinct spawning periods occur for Aplysia dactylomela.

I attribute the decline and loss of virtually the entire population on the inner areas throughout autumn and winter, primarily to storms with a small loss to predation. The factors contributing to mortality in A. dactylomela are considered separately in a later section (Ch. 6.1.10).
These results on growth in the field provide the first indication that Echinoderm Reef is a sub-optimum habitat for *A. dactylomela*. Further evidence presented in sections 6.1.5, 6.1.6 and 6.1.10 adds credence to this belief. I discuss the suggestion more fully in Ch. 6.1.10.

6.1.5 Field Growth Studies with Tagged Animals.

Determination of individual growth rates both in the field and laboratory is important if one wishes to consider population parameters such as longevity, fecundity and assimilation efficiency. Previous studies (Miller, 1960; Carefoot, 1967a; Nishiwaki et al., 1975) have found that samples taken at monthly time intervals were adequate to assess growth rates for the species of *Aplysia* each was studying. The impression gained from such surveys is of a rapidly growing species with a high growth rate and smooth growth curve (e.g. Krigstein et al., 1974). But do individual life histories sustain this impression? To look at growth patterns for known individuals a tag/recapture programme must be undertaken. Therefore, very early in my studies on *A. dactylomela* at Goat Island Bay I undertook an extensive tagging programme to obtain information on growth rates of individuals in the field.

In May 1975 I tagged 200 *A. dactylomela* and liberated them near pool B. None of these tagged animals was recaptured in June but I did find three specimens with tagging scars. In July I recaptured one (0.5% of the total tagged) animal that had been tagged in May, its tag was still intact but had small patches of pink *Lithothamnion* sp. growing on it. I tagged a further 75 individuals in July. In August six tagged *A. dactylomela* were recaptured (0.72%). From September onwards there were no further recoveries of tagged *A. dactylomela*. A plot of growth rate for all the 1975 recaptures is given in Fig. 6.6. Four of these specimens showed very little gain in weight over this period and three weighed less in August than they had done in July.

There are several reasons for the failure of the 1975 tagging programme. The causes can be attributed both to the tagging system itself (see Ch. 6.1.2),
and, as subsequently discovered, to environmental effects which for example
lead to an extremely high mortality of individuals.

Therefore, since a mass-tagging programme had proved impossible and was
time consuming besides, I chose to look in detail at the growth of a few
selected individuals. Sampling intervals were reduced to a week when, in 1977,
a second programme was undertaken and this allowed enhanced resolution of
overall changes in growth. In 1977, 35 *A. dactylomela* were tagged and liberated
within pools A, W and X.

The programme lasted for five weeks from 5 May to 16 June 1977. By
employing the shorter sampling interval, recapture rates were much higher, a
total of 19 animals (54.3% of the total tagged) being recaptured at least
once. In fact seven (20%) were recaptured once only, four (11.4%) were recaptured
twice, four (11.4%) were recaptured thrice, three (8.6%) were recaptured four
times and one (2.8%) was recaptured five times. Fig. 6.7 gives simple plots
of growth rates for the four animals recaptured four or five times. In Fig. 6.8
I have extracted values for growth rates for each of the five weekly intervals
based on recaptures for that week. It was necessary to adjust these values
to a standard seven-day time scale so that means could be comparable, even
though actual sampling time varied between five and twelve days as can be
seen from the graph. Although the plot shows variation (e.g. the sample taken
on 22 May) relatable to storms or temporary food shortages, the trend is
apparent. Growth rate was similar throughout May and early June, with a pooled
mean increase in weight of 3.71 gm.week$^{-1}$, SE = 1.02 (22 May rate excluded).
However growth rate dropped off after the middle of June and was actually
negative on the final sample of 16 June (-1.51 gm.week$^{-1}$, SE = 1.4).

These data describe changes in growth rate from May to June, when the
seawater temperature is falling (from Table 2.1 mean temperature decrease from
May to June is 1.8°C), supplies of *Laurencia* sp. 1 are dwindling and feeding is
not possible during autumnal storms which occur with increasing frequency.
Discussion.

The above are very probably some of the reasons why the growth rate in late autumn is less for field animals than for those maintained in the laboratory (Ch. 7.4.2). The only other field study on growth using a tagging technique is that by Nishiwaki et al. (1975) for the Japanese *Aplysia kurodai*. This work was successful in that out of 1,427 specimens tagged, 809 (57%) were recaptured with a frequency of one to four times. But the study was compromised because, instead of calculating growth rates derived from individuals, the authors obtained the average growth pattern by calculating the mean body weight at each time of tagging and/or recapture. I suggest the use of this method of analysis made all their tagging effort redundant - the authors have done no more than take regular samples of a section of their population (tagged individuals). In fact their results may be further biased because of probable tagging damage to their animals (Ch. 6.1.2) and because none of the smaller animals (below 10 gm) could be tagged, and hence sampled, by the methods described.

6.1.6 Annual Abundance Cycle.

As explained in Ch. 4 on sampling sites within study areas, population densities of *A. dactylomela* were monitored at study pools on the intertidal Echinoderm Reef flat in Goat Island Bay. Pools A and B were sampled once every month from June 1975 to November 1977 (29 months). Pools W and X were sampled every month from April 1977 to November 1977. As pools A, W and X were of a manageable size and *A. dactylomela* readily visible, actual density counts were possible for these pools. It is possible that because of the larger size of pool B, counts of *A. dactylomela* densities for that site may be slightly underestimated. But since densities here were generally extremely low, such underestimates are probably not significant.

Fig. 6.9 presents a summary of density data for *A. dactylomela* per m$^2$ for the four study pools. For each year the curves show a clear cycle of density
increase and decrease. The increase occurred throughout December to February, there may have been a couple of months in late summer when density stabilized at a high level, and then numbers dropped again equally rapidly through autumn and early winter. In 1976 no specimens were found in any of the study pools from August through the rest of the year, in fact no specimens were found at all on Echinoderm Reef over the long period from September 1976 until March 1977. However in 1975 and 1977, although the autumn/winter declines in densities were equally rapid the occasional specimen was found right through until October.

Considering the pools individually, it can be seen that the maximum density was nearly the same (2.3 to 2.7 specimens m\(^{-2}\)) for each of the three years of the study. The highest densities were recorded in March and April for the years 1976 and 1977, respectively. However, for pool B on the outer part of the reef platform it appeared that the maximum density was lower for each successive year. Densities were highest in July for 1976 and 1977 (it may also have occurred before monthly sampling began in 1975). For the 1977 data alone, it appeared that densities in pool X were similar to those for pool A, although peak density was displaced until May – June. Pool W appeared to have slightly lower densities than pools A or X.

It would appear that density is inversely related to pool size, highest densities are for pool A (with an area of 4.4 m\(^2\)) and pool X (5.7 m\(^2\)), slightly lower for pool W (33.9 m\(^2\)) and lowest for pool B (268 m\(^2\)).

Discussion.

Recruitment (in summer) and storms (in winter) are the two main reasons for the enormous yearly fluctuations in A. dactylomela densities on Echinoderm Reef in Goat Island Bay. Virtually all the increase in numbers from December to March is due to settlement of larvae out of the plankton, and in fact throughout the full year almost the entire population is of juveniles – i.e. reproductively immature animals (see Gonad Index, Ch. 6.1.9). The decline
throughout autumn and winter occurs largely as the result of storm-related mortality (Ch. 6.1.10). But it should be remembered that at this time too, sea temperatures are at their lowest (Ch. 2.3.1; Appendix III.1), growth has ceased (Ch. 6.1.4) and algal supplies are dwindling (Ch. 5.7). One could invoke an offshore migration to explain the sudden drop in numbers for the intertidal region, as with *Bursatella leachii* (Ch. 6.3.5). But following a series of snorkel dives done monthly from September 1976 to April 1977 at times of low water in the sublittoral fringe at to -3m in the immediate subtidal area off Echinoderm Reef to search for *Aplysia dactylomela*, none was found at all. So I reject this hypothesis. I only ever encountered a single *A. dactylomela* subtidally in Goat Island Bay and I know of only one other taken during the four years 1974 through 1977 (Ch. 3.1).

One possible reason for the significantly lower densities of *A. dactylomela* at pool B on the outer part of the reef platform concerns the presence of certain algae. At pool B only two *Laurencia* spp. occur, and only one (*Laurencia sp. 2*) is capable of inducing metamorphosis; whereas on the inner areas there are three *Laurencia* spp. altogether and two of these (*Laurencia sp. 1 and Laurencia sp. 2*) are capable of inducing metamorphosis. On the other hand, one could expect densities to be higher here, since the pools in this outer area are deeper and algal cover thicker (particularly for the perennial species) and one would expect storm-related mortality to be ameliorated.

Another interesting point to consider is the apparent decrease in *A. dactylomela* densities from 1975 to 1977 at pool B. The absolute number of *A. dactylomela* was never great. However, because the mean annual water temperatures fell by -2°C from 1975 to 1977 (Leigh Marine Laboratory, marine climate recordings), perhaps densities during these years were becoming less due to some effect of the lowered temperatures.
6.1.7 Estimate of Total A. dactylomela numbers on Echinoderm Reef.

Since the total area of Echinoderm Reef is known (2.76 ha.) and I have mean monthly values of *A. dactylomela* density for the study areas on both the inner and outer parts of the reef platform then it is a simple calculation to give a figure plus error term for the total *A. dactylomela* stock on the intertidal Echinoderm Reef flat. As density has been found to fluctuate so greatly, a series of monthly figures have been calculated rather than a single standing yearly mean. The only additional information required is the proportion of Echinoderm Reef which could be classed as "suitable", and therefore similar in nature to those of my study area. Therefore on 16 September 1977, a survey was carried out to determine the proportions, and hence (in combination with the total area of Echinoderm Reef), the total area of substrate that is suitable for *A. dactylomela*. Here "suitable" is defined by two criteria with respect to the life stages of *A. dactylomela*:

1. To be "suitable" an area must provide an environment adequate for settlement and metamorphosis of larval *A. dactylomela*.

2. The area must be able to sustain and promote growth of *A. dactylomela*.

Using these criteria I classified Echinoderm Reef into three categories of suitability. I acknowledge that this classification is not equal for newly metamorphosed larvae and larger post-metamorphic juveniles in that movement is ignored, and so the ability of larger individuals to deliberately select favourable sites is ignored. The classification is as follows:

1. **Suitable Areas** - Areas containing pools of standing water with a substrate of *Corallina officinalis* algae; pools or reef flat areas emerged at low tide but still moist - i.e. sites where most *Laurencia* spp. will grow. Either *Laurencia* sp. 1 or *Laurencia* sp. 2 must be present to induce settlement. Suitable areas were designated by the letter S.

2. **Marginal Areas** - Areas generally not in pools of standing water, such as those with a basal crust of *Lithothamnion* sp. (but not a *Corallina officinalis* turf) or boulder fields. These are areas of shelter and survival for *A. dactylomela* but they are not suitable for metamorphosis nor would they sustain prolonged growth.
These areas were designated by the letter M.

3. In hospitable Areas - Areas where no macroscopic algal growth is sustained (Corallina officinalis or Lithothamnion sp.), for example bare rock surfaces or rocks covered with sheets of barnacles. Such areas are suitable neither for metamorphosis nor growth and provide no shelter; in short A. dactylomela would not survive in such habitats should a uniform expanse be present. These areas were designated by the letter I.

A 0.2 m tide was chosen so that virtually the entire reef was exposed. A series of 20 linear transects was then run across Echinoderm Reef in a grid fashion, ten at right angles and ten parallel to the beach. For each transect the observer walked a distance of 9 m then classified the tenth metre into one of the three categories listed above. The longest transect was 280 m and 28 square metre determinations were made. Each quadrat was designated as S or M or I.

Out of a total of 368 lm² quadrats studied, 129 (c. 35%) were determined as being of suitable status, 114 (c. 31%) were marginal, and 125 (34%) were inhospitable. Therefore only approximately one third of Echinoderm Reef is designated suitable for settlement, metamorphosis and growth; one-third of the total area is available for shelter. A further third is inhospitable, no settlement could occur there and it is likely that if a crawling sea hare were stranded there by the ebbing tide, then death would result providing weather conditions (e.g. insolation, wind) were sufficiently unfavourable.

The actual estimates for total A. dactylomela density are given in Table 6.2. When data from the inner and outer areas are averaged, it will be seen that for approximately four months (March until June) total density was between 5,000 to 6,000 animals. These months correspond with a density plateau where losses were being balanced by recruitment, but on either side of these months one of these two processes was markedly dominant and numbers increased or decreased rapidly.

A fault in the density estimates is that they are derived from summation of three years' data, and because maximum densities did not correspond to the
exact month each year the overall effect has been to extend the period of
time for which the estimates hold beyond that time which they could be
expected to be obtained on any particular year. This is especially so for
the months of the increasing or declining population phases. Another
possible fault has been incorporated with use of the 1977 data, because in
this year there was considerable recruitment in pools W and X late in the
year (June to August). Such recruitment is thought to be exceptional as
it was not encountered on the inner part of the reef platform in 1975 or
1976. So the numbers for these months for my estimates are probably higher
than usual.

Table 6.2. *Aplysia dactylomela*: mean densities from inner and outer sections
of Echinoderm Reef based on monthly observations at study pools
from 1975 to 1977 and estimates of total population for each month.

<table>
<thead>
<tr>
<th>Month</th>
<th>Mean no. per m² ± SE</th>
<th>Outer Section</th>
<th>Pop. estimate for Echinoderm Reef ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>0.15 ± 0.076</td>
<td>0</td>
<td>580 ± 285</td>
</tr>
<tr>
<td>February</td>
<td>0.32 ± 0.21</td>
<td>0</td>
<td>1,205 ± 790</td>
</tr>
<tr>
<td>March</td>
<td>1.48 ± 1.25</td>
<td>0.011 ± 0.011</td>
<td>5,615 ± 4,750</td>
</tr>
<tr>
<td>April</td>
<td>1.48 ± 0.54</td>
<td>0.007 ± 0.007</td>
<td>5,600 ± 2,060</td>
</tr>
<tr>
<td>May</td>
<td>0.94 ± 0.48</td>
<td>0.011 ± 0.011</td>
<td>3,580 ± 1,680</td>
</tr>
<tr>
<td>June</td>
<td>1.58 ± 0.49</td>
<td>0.022 ± 0.022</td>
<td>6,035 ± 1,930</td>
</tr>
<tr>
<td>July</td>
<td>1.12 ± 0.56</td>
<td>0.005 ± 0.002</td>
<td>4,250 ± 2,118</td>
</tr>
<tr>
<td>August</td>
<td>0.58 ± 0.32</td>
<td>0.053 ± 0.053</td>
<td>2,358 ± 1,405</td>
</tr>
<tr>
<td>September</td>
<td>0.08 ± 0.05</td>
<td>0.002 ± 0.002</td>
<td>310 ± 195</td>
</tr>
<tr>
<td>October</td>
<td>0.006 ± 0.006</td>
<td>0.002 ± 0.002</td>
<td>30 ± 30</td>
</tr>
<tr>
<td>November</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>December</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
6.1.8 Crawling Rate.

The relationship between damp live weight and distance crawled (m.hr\(^{-1}\)) for 17 *A. dactylomela* is shown in Fig. 6.10. From these data it appears that crawling rate increases regularly with weight, and hence size, up to approx. 45 gm; beyond this value the rate declines. The fastest rate recorded was 5.05 m.hr\(^{-1}\), and this was for an animal weighing 44.31 gm. Overall mean crawling rate was 2.14 m.hr\(^{-1}\) (SE = 0.28, SD = 1.28). This rate corresponds with a mean size of 108.3 mm for all the animals tested.

It must be noted that some of the *Aplysia dactylomela* actually crawled further than the distances measured, but because I measured only the direct distance from start to finish it was assumed all had followed a straight path. This assumption was not correct in all cases because some crawled in a semicircular path and others changed direction suddenly. It is probable that large *A. dactylomela* can produce a crawling rate considerably faster than 2.14 m.hr\(^{-1}\) for short bursts.

Crawling speed in *A. dactylomela* is slow compared with that for the notaspidean *Pleurobranchaea maculata*, for which a rate of 32 m.hr\(^{-1}\) for a 52 mm long animal has been measured (Willan, 1975).

6.1.9 Gonad Index.

I have derived a gonad index for *Aplysia dactylomela* from specimens of the Goat Island Bay population. This index consists of a four-point scale and incorporates data on gonad condition (appearance of ovotestis, developmental stage of reproductive organs and colouration), histological state of ovotestis (level of oogenesis and spermatogenesis) and certain body measurements (live weight, shell length). Naturally changes in all of these characters occur slowly and gradually as *A. dactylomela* grows, and these take place at different rates. Nevertheless it is possible to divide all the developmental processes into stages and characterize each stage. The gonad index is as follows:
STAGE I. Ovotestis and gonoduct barely discernible, simply a white streak on the mesentery of the visceral mass. The ovotestis occupies a mean of 2.95% by weight of the damp wet weight of the digestive gland (SE = 0.8, SD = 2.47). Wet weight for live animals lies within the range 0-80 gm. Shell length is less than 28 mm.

STAGE II. A small orange ovotestis is present as a discrete entity at the surface and partially enclosed by the digestive gland. The hermaphrodite duct is present as a thin and almost straight tube. The nidamental glands appear as a single, undifferentiated, pale green sac off the hermaphrodite duct. The ovotestis occupies a mean weight of 6.11% (SE = 0.77, SD = 2.90) of the damp net weight of the digestive gland. Oocytes are less than 10 μm in diameter, yolk granules are present within the oocytes as pale spherules and they have a reticulate appearance, germinal vesicles are recognizable in only a few oocytes, each oocyte being surrounded by several nurse cells. Spermatids are already tailed, most are embedded in nurse cells but some may be present in the small collecting tubules leading to the hermaphrodite duct. Wet weight values lie within the range 80-150 gm. Shell lengths lie within the range 28-33 mm.

STAGE III. The ovotestis is considerably enlarged, it is golden-orange or brown in colour and still partially enclosed by the digestive gland. The hermaphrodite duct is well-formed and sinuous but not dilated. All components of the nidamental glands are now differentiated, being deep lime-green in colour. Oocytes are 20-90 μm in diameter, each has a conspicuous germinal vesicle and numerous distinct, full yolk granules, the oocytes being no longer surrounded by nurse cells. Autosperm are present in collecting tubules. Wet weight values for animals belonging to stages III and IV merge, and extend from 120 gm upwards, similarly shell lengths range upwards from 33 mm.
STAGE IV. This is the histologically and physiologically mature state - i.e. individuals are capable of reproduction. The ovotestis is in its terminal state and is no longer interlobed with the digestive gland; it is bright golden-orange with green areas. The hermaphrodite duct is sinuous and dilated. The nidamental glands are fully expanded and differentially pigmented - the albumen gland lime green, the membrane gland light pink and the mucous gland orange to brick red in colour. The receptaculum seminis is swollen and contains allosperm. A large proportion of the acini of the ovotestis contain empty follicles. The oocytes contain conspicuous hyaline germinal vesicles, and are alike those of stage III. Autosperm is almost absent from acini of the ovotestis, most of it being present in collecting tubules.

By stages III and IV the ovotestis occupies a mean weight of up to 12.19% (SE = 0.15, SD = 0.21) and above, of the damp wet weight of the digestive gland.

In Fig. 6.11 I have shown how gonad condition is related to standard length and wet weight of A. dactylomela. Here gonad condition is based only on state of the ovotestis and gonoduct as observed from dissections. Stages I and II appear to be distinct, there is some overlap between stages II and III, and stages III and IV cannot be distinguished externally by weight or length of the live animal.

Discussion on Gonad Index.

It is very probable that morphological changes chosen to construct the gonad index are reflections of synchronously occurring physiological ones - most particularly in reproductive behaviour. Newby (1972) maintained that copulation in A. dactylomela was never observed in animals less than 40 gm body weight. Frazier et al. (1976) noted a change in the bag cells with growth, this being the name for a group of neurohormonal-secretory cells located in the abdominal ganglion. These cells participate in the control of oviposition (Arch, 1976) and increase in number and secretory ability as the animals grow. It may be that reproductive behaviour develops some time after metamorphosis
(Lederhendler, 1977b); certainly there are significant changes in conspecific activity (e.g. contacts, copulation) as size increases (Lederhendler, 1977a; 1977b). Mazzarelli (1893) and Beeman (1970) have visualized the ontogeny of the female anaspidean gland mass but neither has speculated at what stage it develops.

Since apparently mature sperm were observed in the collecting tubules within the ovotestis of specimens in Gonad Stage II, and for which oogenesis was at a very early stage, it is possible A. dactyromela is partially protandrous. This suggestion would agree well with Lederhendler's (1977b) observation that animals that were most likely to initiate contact took on the role of sperm donors at copulation.

The reproductive system is developing at stages I and II. This system is the last to develop as other aspects of adult life (e.g. fully integrated adult feeding behaviour) develop much earlier (Krigstein et al., 1975; Switzer-Dunlap & Hadfield, 1977). The size range of animals belonging to stages III and IV overlap. At stage III all components of the reproductive system are differentiated but not as "mature" as in animals belonging to stage IV. Specimens in stage III can be termed "pre-copulatory adults". The change from stage III to stage IV could be either behaviourally initiated and related to seasonality e.g. temperature changes (Miller, 1960; Carefoot, 1967c; Smith & Carefoot, 1967; Strumwasser et al., 1969; Usuki, 1970; Nishiwaki et al., 1975) or physiologically based (Lederhendler, 1977a; 1977b). Naturally these two causes could act together. Lederhendler (1977b) suggested that a certain amount of contact may be necessary before juveniles could copulate; and as an extension to this suggestion, that egg laying need not follow the first instances of copulation. Copulation might induce a series of morphological and physiological changes that are necessary for egg laying at a later stage of development.
6.1.10 Sources of Mortality.

The mortality of the veliger larvae of *A. dactylomela* in the plankton must be extraordinarily high. All *Aplysia* species produce vast numbers of eggs. Beeman (1965) estimated a single adult *A. californica* could produce over three-quarters of a million eggs in one season. Switzer-Dunlap & Hadfield (1977) give a figure of 1,030,000 eggs per average egg mass in *A. dactylomela*. Veligers of *A. dactylomela* take 8-9 days to hatch and spend a minimum of 30 days in the plankton (Switzer-Dunlap & Hadfield, 1977). Only a minute fraction of these survive beyond metamorphosis and for those that do metamorphose successfully the chances of growing to reproductive maturity are slim. For the Echinoderm Reef population I have attempted to partition post-metamorphic and pre-reproductive mortality into its components. Two sources of mortality have been observed — storms and starfish predation.

Mortality due to Storms.

Owing to its relatively open nature, Echinoderm Reef suffers considerably from storm damage. Many *A. dactylomela* are removed by wave scour during storms and killed. So severe are the storms over winter that no *A. dactylomela* were able to be collected at all during some of my sampling visits, the population existing on the reef at these times must have been exceedingly low.

Following a storm from the North-West on 22 May 1975 many *A. dactylomela* were washed from the intertidal platform. Dozens were cast up amongst decaying algae. A check of one 25 m² area on 25 May near the stream at the eastern end of the Main Beach revealed 139 *Aplysia dactylomela*. Of this total 100 (72%) were still alive but would soon have succumbed to desiccation, fresh water or scavengers. I took a sample of 84 to the laboratory and found them to have the following characteristics:

mean length = 45.36 mm, SE = 1.85, SD = 16.74;

mean weight = 9.61 gm, SE = 1.18, SD = 10.75.
When these measurements are compared with the average for that month (mean weight = 30.31 gm; SE = 7.25; SD = 72.5) there was a significant difference at the .01 level between the storm-cast and shore populations (t = 2.818). This suggests that storms have different effects throughout the population and that the chances of mortality for smaller individuals through storms is greater than for larger ones. Perhaps this is related to stronger clamping action or improvement of dislodgement behaviour with increasing size?

As mentioned previously (Ch. 3.1), when _A. dactylomela_ is removed from a solid substrate it erects the parapodia to present greater resistance to the water and stretches or arches the foot maximally so that any region, upon encountering a solid object, is able to adhere rapidly.

During observations made in stormy conditions, _A. dactylomela_ were seen to seek refuges where wave force and sand scour are lessened. The sea hares retreat beneath stones and into cracks and recesses. At times animals have been noted not to leave such sanctuaries for three successive days. During these times they may become completely covered by sand. At low tide, animals may crawl from their hiding places or simply extend the head and neck to feed. The number of such retreats, particularly for larger animals, may limit the population on Echinoderm Reef.

Not only are storms responsible for massive mortality of _A. dactylomela_, some sublethal effects were observed that can be attributed directly to storms. Following winter storms in 1977 an _A. dactylomela_ was found with its oral tentacles and rhinophores worn down to their stumps. I believe injury had been caused by the abrasive action of storm-suspended sand. Since _Aplysia_ species have very sensitive chemo-receptors in the oral tentacles and rhinophores (Jahan-Parwar, 1975) then an injury of this kind must greatly impair their ability to find food.
Predation on Aplysia dactylomela.

Generally species of Anaspidea appear remarkably free from predators, particularly when the animals are healthy (Eales, 1921; Carefoot, 1967c; personal observations). In Australia, N. Coleman has observed the large volute *Melo miltonis* eating *Aplysia* sp. and *Dolabella* sp. at Coral Bay, south of Exmouth Gulf (pers. comm., 1976). Apparently the only report of predation in the literature is by Winkler & Tilton (1962) who found small *Aplysia californica* that had been eaten by the actinian *Anthopleura xanthogrammica*. However, when in the laboratory, live *A. californica* were fed to the anemones, the workers found that although the anemone would ingest the *Aplysia*, in all cases (except for a weak animal), the sea hares were subsequently able to escape. Winkler & Tilton (1962) also noted scavenging *Pachygrapsus* sp. crabs feeding on the bodies of dead sea hares.

I can confirm that whelks and crabs devour moribund Anaspidea in New Zealand, e.g. *Cominella glandiformis* and *Helice crassa* were observed scavenging the carcases of *Bursatella leachii* at Motukaraka Island on 6 July 1975. A partially ingested *B. leachii* was also recovered from a large individual of *Actinia olivacea* (a sea anemone) on the same date. I have observed a group of six asteroids (*Patiriella regularis*) feeding on a detached *Aplysia dactylomela* egg mass under a stone (9 June 1976).

6.1.10 (a) Field Observations on Predation of Aplysia dactylomela.

I can report here another predator of healthy *Aplysia* species in New Zealand - the asteroid *Coscinasterias calamaria* (Gray). At pool B (Echinoderm Reef) on 11 July 1975 I found two separate starfish each devouring an *A. dactylomela*. For one of these *Coscinasterias/Aplysia* pairs, the starfish had a maximum diameter of 147 mm and its sea hare prey had a length of 51 mm. Another starfish was observed in the process of capturing an *A. dactylomela* at "Knot Rock" on 7 June 1977. Fig. 4.1d is a photograph of *C. calamaria* capturing an *A. dactylomela*. 
This feeding behaviour of *C. calamaria* was tested in the field. A sea hare was placed in the path of an actively-crawling starfish, as the first outstretched tube feet on the leading arm of the starfish encountered the sea hare, the starfish increased its crawling rate. The leading arm was passed forwards over the head of the sea hare and the two arms on either side wrapped around the sides of its body. At this stage the slug produced an escape response by increasing its crawling speed and releasing amounts of purple "ink", but this had no apparent effect on the starfish.

The size relationships of the predator and prey appear more important than "inking" by the sea hare. Small *Aplysia* (less than half the diameter of the starfish) seldom escape, larger sea hares have increasing chances of escape. Starfish attempt to capture sea hares several times their size but the sea hares escape by crawling away rapidly. Edwards (1974) also recognized the existence of an upper critical prey size beyond which the possibility of capture is small.

It is not surprising that *Coscinasterias calamaria* predates sea hares. This carnivorous starfish is renowned for its catholic diet. It has been observed feeding on each diverse prey as the echinoid *Evechinus chloroticus* (Don, 1975), the bivalve *Atrina pectinata zelandica* (Barker, pers. comm., 1978), the large free-lying brachiopod *Neothyris lenticularis* (pers. obs., Stewart Island, Feb. 1977) and egg capsules of *Cominella* spp. (Larcombe, 1971).

6.1.10 (b) Predation Experiments with *C. calamaria* in the Laboratory.

To determine capture frequency and prey holding times for *Coscinasterias calamaria*, a trial was performed at the Marine Laboratory in 1976. Each of four aquaria (6 l in capacity) contained a single *C. calamaria* previously starved for three days) which was provided with two healthy *Aplysia parvula* for food. Data for sizes of prey and predators at the start of observations (15 May 1976) are given in Table 6.3. The trial ran for 32 days, fresh *A. parvula* being added as others were eaten.
Table 6.3. Coscinasterias calamaria predation on Aplysia parvula. Data for prey and predators at start of experiment (15 May 1976).

<table>
<thead>
<tr>
<th></th>
<th>Tank 1</th>
<th></th>
<th>Tank 2</th>
<th></th>
<th>Tank 3</th>
<th></th>
<th>Tank 4</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>length (mm)</td>
<td>weight (gm)</td>
<td>length (mm)</td>
<td>weight (gm)</td>
<td>length (mm)</td>
<td>weight (gm)</td>
<td>length (mm)</td>
<td>weight (gm)</td>
</tr>
<tr>
<td>Starfish</td>
<td>73</td>
<td>11.43</td>
<td>82</td>
<td>9.18</td>
<td>104</td>
<td>8.45</td>
<td>136</td>
<td>36.15</td>
</tr>
<tr>
<td>Aplysia parvula 1</td>
<td>50</td>
<td>3.42</td>
<td>56</td>
<td>5.25</td>
<td>61</td>
<td>4.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aplysia parvula 2</td>
<td>56</td>
<td>4.33</td>
<td>45</td>
<td>2.55</td>
<td>35</td>
<td>1.35</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Coscinasterias calamaria* length measured as maximum diameter between the two longest arms.

*Aplysia parvula* length is standard extended crawling length.

Table 6.4. Results for Coscinasterias calamaria predation on Aplysia parvula. Data for completion of 32 day trial.

<table>
<thead>
<tr>
<th></th>
<th>No. Aplysia eaten per day</th>
<th>Handling rate $\pm$ SD (hrs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tank 1</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Tank 2</td>
<td>0.031</td>
<td>23.5</td>
</tr>
<tr>
<td>Tank 3</td>
<td>0.062</td>
<td>21</td>
</tr>
<tr>
<td>Tank 4</td>
<td>0.062</td>
<td>19.25 $\pm$ 14.5</td>
</tr>
</tbody>
</table>

Results are given in Table 6.4. Digestion of *Aplysia parvula* was observed to be external. The shell and part of the digestive gland remained after feeding, these remnants amounted for a mean weight of 14.2% of the original *A. parvula*. It appeared that the "ink" of *A. parvula* produced a greater effect in deferring *C. calamaria* predation than had been noted in the field for *A. dactylomela*. On several occasions a starfish was observed to
grasp a sea hare, but expulsion of the purple dye appeared to retard
crawling by the starfish and the sea hare made a rapid escape.

6.1.10 (c) Defensive Responses of Anaspidea against Predators.

It is known that species of Anaspidea (and Aplysia spp. in particular)
possess both chemical and mechanical mechanisms to deter predators
(Eales, 1921).

A. Chemical Methods.

1. "Ink" Discharge - Anaspidea belonging to the genera Aplysia (Pruvotaplysia),
   Aplysia (Varria), Bursatella and Stylocheilus all possess the ability to
   produce a thick cloud of rich, deep purple fluid which is discharged into
   the water through the exhalent respiratory aperture. This "ink", which
   has been called aplysioviolin (Chapman & Fox, 1969) is produced in the
   purple gland situated on the underside of the free edge of the mantle.
   Its release is accompanied by much mucus. Particularly rough handling
   will stimulate inking. Tobach, Gould & Ziegler (1965) found for solitary
   animals, increased stimulation had little effect but paired animals or
   those in larger groups responded to a more intense form of stimulation.

2. Opaline Gland Discharge - Frequently a milky-white, acrid-smelling fluid
   accompanies the "ink". This secretion is from the opaline gland (or gland
   of Bohadsch) which is situated in the floor of the pallial cavity and
   discharges into it by numerous apertures.

3. Toxicity of Secretions - In a preliminary trial on 5 June 1977 I put
   two Tripterygion varium, a blenny frequently found in the same habitats as
   Aplysia spp., in a 3 l. tank containing the total "ink" secretion from a
   single 130 mm (80.57 gm) Aplysia dactylostoma. After 10 min. it was evident
   that both were having respiratory difficulties because of the mucus fraction.
   Both fish were removed and the contents of the tank strained to leave only
   the water soluble fraction. At this stage one fish was placed in a second
   container of clean sea water, the other was returned to the inked solution.
After 90 min. the fish in the inked water had died, and did not recover upon being placed in fresh sea water. The control fish showed no ill effects. Therefore the "ink" produced by Aplysia dactylomela is not simply a harmless "smoke-screen" but does contain a toxic fraction that is water-soluble and poisonous to fishes.

Some studies have been undertaken to identify the chemical constituents of aplysioviolin and characterize the toxins. Chapman & Fox (1969) found aplysioviolin to be derived from the phycoerythrin pigment of red algae, so much so that Aplysia californica becomes "facultatively de-inked" on a diet of brown algae. These authors suggest aplysioviolin production is not a defense mechanism but probably a waste product.

4. Midgut Toxins. An acetone extract of Aplysia digestive glands, called aplysins (Winkler, 1961; Winkler et al. 1962) produces neuromuscular activity reminiscent of choline esters. Scheuer (1970) investigated the toxicity of aplysins further by considering symptoms and pharmacological responses. He found the extract from 2 species of Aplysia (A. dactylomela and A. juliana) showed no toxicity at all, toxicity of four others (Aplysia pulmonica, A. kurodai, Dolabella auricularia from Japan, D. scapula from Hawaii) was modest, that of three others severe (Dolabella auricularia from Hawaii, Dolabrifera dolabrifera, Stylocheilus longicauda). Watson (1970) isolated two separate lethal toxins (ether-soluble toxin and water-soluble toxin) from the digestive glands of sea hares.

Two naturally occurring bromine containing sesquiterpenes were isolated from Japanese Aplysia species by Yamamura & Hirta (1963) and named independently aplysins and aplysinol. Winkler (1961; 1969) has suggested these toxins are derived from the algae eaten by the Aplysia, and in support of this hypothesis is the isolation of several bromo-organics from Laurencia okamurae - amongst them aplysins, aplysinol and debromoaplysin. As discussed by Scheuer (1970) the structural similarities of various potential sesquiterpenes isolated from Laurencia with those sesquiterpenes of aplysids lends considerable weight to this hypothesis.
It would appear as though those species of Aplysia that feed on Laurencia species containing toxic compounds sequester some fractions for their own defense. This situation would then be analogous to the terrestrial case where certain caterpillars are able to sequester alkaloids from their plant foods, and these are used for their own defense (e.g. Ehrlich & Raven, 1965; Brower, 1968). Some ascoglossan opisthobranchs are known to sequester toxins from Caulerpa spp. (Doty & Aquilar-Santos, 1970). Since Aplysia species have very sensitive chemoreceptors located on the oral tentacles, and these are partially specific to food stimuli (Jahan-Parwar, 1975), then it is probable that these sea hares reach their preferred algae, such as Laurencia spp. by recognizing these bromo-containing compounds that are derived from them. In just the same manner a water-soluble material given off by Ulva spp. acts as a powerful attractant to Aplysia juliana (Frings & Frings, 1965).

B. Mechanical Methods - Swimming.

Several species of Aplysia, particularly members of the subgenus Varria, are able to swim (Strength & Blankenship, 1971; Bebbington & Hughes, 1973; Bebbington, 1974). Rather than swimming, species of Notarchus perform violent somersaulting behaviour (Allan, 1932b; Martin, 1966; Marcus, 1972). Since ejection of "ink" accompanies the first flapping strokes (personal observations on Aplysia extraordinaria) it would appear that the swimming escape and chemical defense responses are synchronized. Martin (1966) recognized the defensive significance of swimming as the escape from slower, non-swimming predators.

Discussion on Sources of Mortality.

To return to the question of partitioning sources of mortality in A. dactylomela. It appears that both storms and predators act more severely on the juveniles. Storm-related mortality is enhanced over winter when temperatures are lower and storms more frequent. Losses due to storms are so severe that in some years almost the entire population may be killed. On Echinoderm Reef it is likely that 90-95% of the post-metamorphic population will be killed by storms each year.
Overall mortality to predation is probably low. There are three reasons for this. Firstly, *A. dactylomela* outgrows the starfish predator. Secondly, *C. calamaria* has a catholic diet, and even when feeding solely on *Aplysia* species, its intake is low. Thirdly, toxins incorporated in the "ink" of *Aplysia dactylomela* have been shown to be lethal to potential predators (e.g. blennies) in limited areas such as rock pools. Toxins sometimes apparently deter starfish predators. Therefore over summer and autumn mortality due to predators would be less than 5%, and these losses probably drop even further in winter when most of the population has become too large for *Coscinasterias calamaria* predation.

6.1.11 Conclusion.

I have already intimated that Echinoderm Reef may present an unsuitable or marginal habitat for *A. dactylomela* and some grounds for this belief have already been presented. Here I will incorporate the evidence already presented along with some additional results that are anticipated (Ch. 7). Therefore these are some of the conclusions from chapters 5 to 7 on the behaviour of *A. dactylomela* populations on Echinoderm Reef and their relationships to algal cycles.

The first point to make is that the bulk of the population, whenever *A. dactylomela* is present on Echinoderm Reef, consists of juvenile animals that are at gonad stages I and II (sexually immature). Larger animals do occur on the outer parts of the Reef and it is only these specimens that could be reproductively mature and capable of reproduction. Subtidally there are virtually no *A. dactylomela* at any time of the year despite the presence of at least one species of alga (*Laurencia distichophylla*) upon which these sea hares could feed and grow. Therefore for the bulk of the Echinoderm Reef population, the chances of reaching maturity and producing eggs is very slight indeed.
It is unlikely that any of the newly-settled *A. dactylomela* on Echinoderm Reef are the progeny of the very few animals that may attain sexual maturity there. This is because the long-lived, obligatory planktonic larval stage would be expected to be far-removed by tides and currents from the adults that spawned them. Observed variations in numbers and settlement times are due to chance passage of masses of water containing larvae capable of settlement, over the reef. These waters would have most likely originated well outside the Marine Reserve boundaries. In the extreme it is possible that one year may pass in which there is no recruitment of *A. dactylomela* at all. A similar hypothesis will be presented for *Bursatella leachii* at Motukaraka Island (Ch. 6.3.5), and although this species was never observed on Echinoderm Reef in this three year study period, it has been noted there at times over the past twenty years (M.C. Miller; W. Tong; T.P. Warren, all pers. comm.).

When density data for *A. dactylomela* are related to values of total *Laurencia* cover for the same shore, it is seen that maximum numbers of *A. dactylomela* must occur throughout those months (March to June) when total *Laurencia* cover is highest and more precisely, exactly during those months that *Laurencia* sp. 1 has nearly complete dominance. The relationship between the presence of *Laurencia* sp. 1 and *A. dactylomela* must be considered more carefully. Each year it appears that settlement and metamorphosis of *A. dactylomela* occurs in mid-summer when cover by *Laurencia* sp. 1 is greatest. Grazing pressure by *A. dactylomela* on this algal species can accelerate the decline phase of the latter in autumn, but the decline is natural and not a direct result of predation. Since the highest densities of *A. dactylomela* are consistently found on inner areas of the reef platform and *Laurencia* sp. 1 only exists on the inner third, it is probable that *Laurencia* sp. 1 offers a stronger attraction to competent *A. dactylomela* veliger larvae than *Laurencia* sp. 2 or *Laurencia distichophylla*, and consequently relatively greater recruitment takes place on *Laurencia* sp. 1 than for either of the other species. All recruitment to *Laurencia* spp. occurs intertidally. Repeated monthly snorkel dives in the sublittoral fringe zone
immediately off Echinoderm Reef during the early part of 1977 revealed no juvenile *A. dactylomela* at all. Since it appears that the only subtidal alga that could serve *A. dactylomela* as a site for metamorphosis is *Laurencia distichophylla*, then the lack of recruitment suggests that this does not occur or is unsuccessful. Similarly in the intertidal, I never collected a tiny juvenile on *L. distichophylla* despite several thorough searches of discrete clumps. Perhaps there is no recruitment to *L. distichophylla* in the presence of *Laurencia* sp. 1?

The yearly pattern of density change illustrated for *A. dactylomela* shows none of the stability of that hypothesized for populations of *Haminoea zelandiae* at Motukaraka Island (Ch. 6.2.3). At Goat Island Bay, numbers of *A. dactylomela* initially show a rapid rise solely due to recruitment; then for approximately four months (March until June) density apparently remains constant but it is probable that during this time losses are being balanced by recruitment; following this there is a rapid decline so that virtually all of the animals are lost by the middle of winter. The very few *A. dactylomela* that persist towards the outer part of the platform, and perhaps immediately subtidally, appear to survive the winter and reach sexual maturity the following spring or summer.

I have already suggested that storms account for by far the greatest losses of *A. dactylomela* particularly in autumn and winter. But since storms can occur throughout the year, why should the effect be greater in these seasons? Firstly, seawater temperatures fall rapidly to a winter low and the growth of *A. dactylomela* virtually ceases; therefore the condition of the animals may be poor. Secondly, total *Laurencia* cover is decreasing rapidly, *Laurencia* sp. 1 disappears altogether and clumps of *Laurencia* sp. 2 and *Laurencia distichophylla* remain small and sparse. At this time it is probable that *A. dactylomela* widens its diet to include other algae normally passed over in favour of the three *Laurencia* species. For example, they accept another member of the Ceramiales, *Herposiphonia* sp. 1, at this time. However this alga only exists as a short,
delicate epiphyte on the *Corallina officinalis* turf. Other algae that may now be accepted as the result of this switch from a specific *Laurencia*-based diet to the more general algal-grazing one are *Ulva lactuca*, *Enteromorpha* sp., and drift *Plocamium costatum*. But during this time there is never a complete absence of *Laurencia* so that one could not conclude that either, the decline in total *Laurencia* cover could be related to winter mortality of *A. dactylomela* in a causative sense or that, total *Laurencia* cover exerts any specific density determining effects on the population of *A. dactylomela* on Echinoderm Reef.

### 6.1.12 Summary.

1. The regression equation relating weight to length \((W = 1.006 \times 10^{-4} L^{2.763})\) for *Aplysia dactylomela* is highly significant. Dry weight has a mean value of 8.5% of wet live weight. The regression equation relating shell length \((Y)\) to standard body length \((X)\) is \(Y = 0.201X + 0.474\).

2. First appearance of recruits on the shore occurs at the height of summer each year (January to March), but recruitment can continue until July. Since there is continual settlement of young throughout this period it is assumed that the adults breed continuously throughout summer and early autumn. Probably none of the recruits on Echinoderm Reef is the progeny of the few sexually mature adults there.

3. Different population structures occur on the inner and outer areas of Echinoderm Reef, differing in terms of recruitment, density and age structure. Reasons for these differences may be related to differing physical conditions or to different combinations of *Laurencia* species. In inner areas maximum density was nearly the same (2.3 to 2.7 specimens.m\(^{-2}\)) for each of the three years of the study. The estimated total stock of *A. dactylomela* on Echinoderm Reef from March until June is between 5000 to 6000 animals, but this drops to zero for November and December.

4. Gonad states I to III can be described on the basis of wet weight, developmental condition of the reproductive system and histological state. The difference between states III and IV could be behaviourally mediated or related to seasonality and/or temperature cycles. *A. dactylomela* appears to be partially
protrandrous.

5. It is suggested that the decline and loss of virtually the entire population on Echinoderm Reef each year is due primarily to storms (responsible for 90-95% mortality) and that predation by the starfish Corcinasterias calamaria may account for additional losses of juvenile A. dactylomela. Aplysia dactylomela outgrows predation by starfish.

6. It appears that Echinoderm Reef offers a sub-optimum habitat for A. dactylomela. Even in years when densities resulting from high settlement are greatest, there is not likely to be sufficient time for food shortage to exert a significant density-limiting effect in winter, this is because natural storm - and predator - induced mortality takes its toll before starvation could occur.
Figure 6.3.

_Aplysia dactylomela._

Percentage of new recruits in each monthly sample out of the entire population samples (given at top of figure) at Echinoderm Reef, 1975-1977.

Figure 6.4.

_Aplysia dactylomela._

Histograms of size distribution on the inner part of the reef flat (i.e. pools A, W, X) at Echinoderm Reef, 1975-1977. Numbers at top indicate number of individuals in each sample.
Figure 6.5.

*Aplysia dactylomela.*

Histograms of size distribution on the outer part of the reef flat (i.e. pool B) at Echinoderm Reef, 1975 and 1976. Numbers at top indicate number of individuals in each sample.
Figure 6.6.

Aplysia dactylomela.
Field growth rates for six tagged individuals at Echinoderm Reef, 1975.
Numbers in circles at end of lines indicate tag number of each individual.

Figure 6.7.

Aplysia dactylomela.
Field growth rates for four tagged individuals on Echinoderm Reef, 1977.
Figure shows only those individuals recaptured four or five times.
Numbers in circles at end of lines indicate tag number for each individual.

Figure 6.8.

Aplysia dactylomela.
Weekly field growth rate determinations from tagged animals for May and June 1977, mean and standard error plotted for each. Numbers in circles at top indicate the number of tagged individuals recaptured for each sample.
Figure 6.9.

Aplysia dactylomela.

Absolute density data plots for live animals per m² for four study pools at Echinoderm Reef, 1975-1977.

Note that Y-axis has a logarithmic scale.

- Pool A.
- Pool B.
- Pool W.
- Pool X.
Figure 6.10.

Aplysia dactylomela.

Graph of crawling rate for live individuals versus weight (wet weight) for 17 specimens with a weight range from 18.38 gm to 85.77 gm.

Figure 6.11.

Aplysia dactylomela.

Gonad index as related to standard length and weight (wet weight) for 26 specimens from the Echinoderm Reef population.

- Stage I.
- Stage II.
- Stage III.
† Transitional between one stage and a subsequent, later one.
6.2 APLYSIA PARVULA MORCH, 1863

This sea hare differs from Aplysia dactylomela in possessing separate intertidal and subtidal populations at Goat Island Bay. Both populations were studied, but in much less detail than for A. dactylomela.

6.2.1 Length-weight Relationship.

The relationship between standard length (to nearest mm) and damp wet weight (to nearest 0.1 gm) for 91 A. parvula from the intertidal and 92 from the subtidal populations respectively are linear when logarithmically transformed (Figs. 6.12, 6.13) both being highly significant (P < 0.001).

These regression relationships can be written in the forms:

Intertidal \[ W = 4.18 \times 10^{-4} L^{2.329} \]
Subtidal \[ W = 4.17 \times 10^{-4} L^{2.324} \]

where \( W \) = weight in grams and \( L \) = length in mm. The slopes of the regression equations for the two populations are not significantly different (\( P < 0.001 \), \( F = 68 \)) even though the subtidal animals grow larger.

6.2.2 Breeding and Growth.

Information on these properties for the intertidal and subtidal populations of A. parvula is summarised in Figs. 6.14 and 6.15 respectively. I have also incorporated the observations of copulation or presence of spawn made when the monthly sample was taken. Fig. 6.14 is based only on specimens found on the inner part of Echinoderm Reef (only across the first 20 m approximately), most especially in pools A, X and W. As a consequence I do not know whether the population structure alters across the reef platform as it does for A. dactylomela.

Although means and ranges for individuals measured over this period have not been plotted in a separate figure, the indications for weight distribution are clear from Figs. 6.14 and 6.15 alone. Subtidal individuals attain a much
greater weight, double that for the intertidal, and therefore they also have considerably greater overall size even though the period of growth for both populations in spring occurs over the same time (August to November).

At Leigh, *A. parvula* has a very long breeding season lasting virtually all the year. The data indicate spawning occurs subtidally from July to February. Records for the intertidal population are incomplete because of the small size of the population, but in 1975 and 1976 spawn was also observed intertidally from March to May, and in 1977 it was also noted in June. It is possible that spawning times of the intertidal and subtidal populations are not always in phase. In October 1977 no eggs were present on the shore whereas spawning was occurring subtidally.

In November 1977 I counted egg mass densities both intertidally and subtidally. Counts were made subtidally where *Plocamium costatum* densities were high in clearings where the *Ecklonia radiata* canopy was broken; measured densities were 1.5 masses.m\(^{-2}\), SE = 0.35, SD = 1.5 (n = 18), all masses had been laid on *Plocamium costatum*. Intertidally, counts were made near pools W and X where *Laurencia* sp. 2 was thickest, and all masses were laid on this alga. Here densities were 0.5 masses.m\(^{-2}\), SE = 0.40, SD = 1.27 (n = 10). Rarely individuals choose other algae upon which to oviposit, and I have found masses laid on *Hormosira banksii* intertidally and *Carpophyllum plumosum*, *Pterocladia lucida* and *Sporochnus* sp. subtidally. Whilst individuals never congregate to spawn en masse, it is not uncommon for one individual to oviposit ontop of an older, pre-existing mass. Where densities are high, it is usual to see groups of copulating *A. parvula* rather than pairs, and the numbers of individuals that are both copulating and ovipositing at the same time increases. I have seen a chain of seven copulating *A. parvula*.

Sexual maturity is attained by *A. parvula* whilst still comparatively small; animals of 0.49 gm have been observed to display copulatory behaviour, and copulation has been seen in animals of 1.5 gm. In the field, there is apparently no delay between the appearance of the first egg masses and settlement of larvae. Juveniles form a component of the population all the time.
6.2.3 Annual Abundance Cycles.

A. Intertidal Population.

Pool A was searched for *A. parvula* once each month from June 1975 to November 1977 (29 months). Pools W and X and the inner zone of Echinoderm Reef were searched from April to November 1977 (8 months).

Intertidally all individuals had chestnut brown ground colouration overlaid with white specks, all extremities being margined with black. *A. parvula* displayed a contagious distribution, always being encountered in association with species of *Laurencia*, mainly *Laurencia distichophylla* or *Laurencia* sp. 2, upon which it fed. In addition, this little sea hare was present most often where these species were growing in pools.

All the intertidal records are given in Table 6.5. Obviously *A. parvula* was uncommon on Echinoderm Reef and it is not possible to make quantitative analyses for the annual changes in density from such limited sample sizes. Low numbers of *A. parvula* were evidently present on Echinoderm Reef throughout the year but their abundance was very patchy. In spring *A. parvula* was most often found amongst the bushy clumps of *Laurencia* sp. 2.

In November 1977, ten quadrats were searched in the inshore zone where *Laurencia* sp. 2 was densest. Mean density for *A. parvula* was 3.74 animals.m⁻² (SE = 1.18, SD = 3.74); in these same areas numbers of egg masses were 0.5.m⁻² (SE = 0.4, SD = 1.27). Here mean cover of *Laurencia* sp. 2 was 8.7% and that for *Laurencia distichophylla* 10.8%.
Table 6.5. *Aplysia parvula*. Records of density in five areas on Echinoderm Reef, Goat Island Bay. Pools A, X and W refer to regular study pools (Ch. 4.1.1); Ch. is the channel 30 m north of pool A; In. is a series of pools in the inshore zone between pools A and W.

<table>
<thead>
<tr>
<th></th>
<th>Pool A</th>
<th>Ch.</th>
<th>Pool W</th>
<th>Pool X</th>
<th>In.</th>
</tr>
</thead>
<tbody>
<tr>
<td>August 1975</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>December</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>January 1976</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>1</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>1</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>April 1977</td>
<td>2</td>
<td>2</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td></td>
<td></td>
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<td>September</td>
<td>1</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>October</td>
<td>1</td>
<td></td>
<td></td>
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</tbody>
</table>

B. Subtidal Population.

Unfortunately this exceptional population of *A. parvula* was discovered too late during my field work at Leigh to be sampled over a significant period of time. The population was discovered in December 1976 by divers working on the Marine Survey mapping the submarine topography in the vicinity of P.B.4 (see Fig. 2.2).

Individuals of *A. parvula* here fed exclusively on the rhodophycean alga *Plocamium costatum* *J. Agardh*. All possessed a rich maroon-red background to the body colouration and frequently there was a bright cherry-red border to the parapodia. The density of *A. parvula* was found to be related to presence
of *P. costatum*. Where there was a canopy of the phaeophycean alga *Ecklonia radiata* and the bottom consequently shaded, cover of *P. costatum* was low, but where the *Ecklonia* canopy was interrupted by clearings, *Plocamium costatum* attained high cover itself as a virtually-continuous understorey plant. Table 6.6 gives comparative cover values for *P. costatum* beneath the *Ecklonia* canopy and in the clearings.

Initially I attempted to assess density by swimming along a fixed path underwater, starting from P.B.4 and working in a north-westerly direction. I usually spent 60-90 min. underwater. The results obtained using this method are given in Table 6.7. Carefoot (1967c) used a similar technique to follow the population density of *Aplysia punctata* subtidally in Trearddur Bay, Anglesea. However whilst still sampling, I felt my results were not adequately comparable because of the cryptic behaviour of *A. parvula* and the bias of the method towards larger individuals. So for the final two months of field work I chose a fixed site (of high *Plocamium costatum* cover) and searched every piece of *P. costatum* separately by eye and touch. Although the same site was not resampled exactly each month a similar location was always chosen. Every count was made in a clearing where the canopy of *Ecklonia radiata* was completely absent or there were up to three plants per square metre. Two quadrats searched beneath an *Ecklonia* canopy with 90-100% cover in November 1977 (with an understorey of a mean 30% *Plocamium costatum* cover) failed to produce any *A. parvula*. Results for these counts of density are given in Table 6.8.
Table 6.6. *Plocamium costatum.* Comparative values for cover (derived by point-intercept method) subtidally in Goat Island Bay for two months in 1977.

<table>
<thead>
<tr>
<th></th>
<th>% Cover</th>
<th>SE</th>
<th>SD</th>
<th>No. quadrats</th>
</tr>
</thead>
<tbody>
<tr>
<td>clearing</td>
<td>81.1</td>
<td>3.36</td>
<td>8.88</td>
<td>7</td>
</tr>
<tr>
<td>September canopy</td>
<td>47</td>
<td>3.48</td>
<td>1.78</td>
<td>5</td>
</tr>
<tr>
<td>clearing</td>
<td>79.72</td>
<td>1.75</td>
<td>7.41</td>
<td>18</td>
</tr>
<tr>
<td>November canopy</td>
<td>30</td>
<td>9</td>
<td>12.73</td>
<td>2</td>
</tr>
</tbody>
</table>

Table 6.7. *Aplysia parvula.* Densities by underwater survey method, January to November 1977.

<table>
<thead>
<tr>
<th>Month</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>56</td>
</tr>
<tr>
<td>February</td>
<td>19</td>
</tr>
<tr>
<td>March</td>
<td>3</td>
</tr>
<tr>
<td>April</td>
<td>0</td>
</tr>
<tr>
<td>May</td>
<td>0</td>
</tr>
<tr>
<td>June</td>
<td>1</td>
</tr>
<tr>
<td>July</td>
<td>6</td>
</tr>
<tr>
<td>August</td>
<td>1</td>
</tr>
<tr>
<td>September</td>
<td>16</td>
</tr>
<tr>
<td>October</td>
<td>50</td>
</tr>
<tr>
<td>November</td>
<td>40</td>
</tr>
</tbody>
</table>

Table 6.8. *Aplysia parvula.* Counts of density on *Plocamium costatum* in clearings subtidally in Goat Island Bay for two months in 1977.

<table>
<thead>
<tr>
<th>Month</th>
<th>Mean No. m$^{-2}$</th>
<th>SE</th>
<th>SD</th>
<th>No. quadrats</th>
</tr>
</thead>
<tbody>
<tr>
<td>October</td>
<td>3</td>
<td>0.79</td>
<td>2.49</td>
<td>10</td>
</tr>
<tr>
<td>November</td>
<td>4.94</td>
<td>1.19</td>
<td>5.07</td>
<td>18</td>
</tr>
</tbody>
</table>
6.2.4 Feeding Observations and Relationship to Algal Cycles.

In comparing the intertidal and subtidal populations of Aplysia parvula it can be seen that each population is distinct and exhibits different properties. As already noted, the intertidal animals eat Laurencia spp. predominantly (especially Laurencia distichophylla and Laurencia sp. 2, Laurencia sp. 1 being taken when present). Subtidally, the animals feed exclusively on Plocamium costatum. These different diets, even though both algae belong to the Rhodophyceae, produce a different background colouration-brown for the intertidal, red for the subtidal. Winkler (1959) demonstrated convincingly that diet and colouration are related in Aplysia californica.

The annual cycle of the subtidal population seems to be related to that of Plocamium costatum. Total cover of P. costatum was 70-80%, but this dropped to approximately 30% from May to July. These months were the same times that A. parvula density was lowest. However, because of the very high cover of P. costatum in spring and summer and the relatively low A. parvula density then, at no time did it appear as though P. costatum was actually a limiting factor to A. parvula density.

There was no evidence of the interchange of individuals between these populations: no directed migration or storm displacement was observed. But the different population size structures, densities and presumably abundance cycles of the two populations illustrate how this species is being controlled by its environment at different sites in Goat Island Bay.

In the intertidal loss of individuals attributable to storms is high. On the same shore small A. dactylomela are more likely to be lost by storms than larger ones (Ch. 6.1.10) and the small sized A. parvula must be vulnerable as well. In the intertidal A. parvula competes with Aplysia dactylomela, Eatoniiella spp. and polychaetes for its food algae (Ch. 5.6), and total cover of the Laurencia spp. is reduced considerably in winter. By contrast the subtidal
population would experience fewer losses in storms (no red subtidal individual was ever seen dead on Goat Island Beach after a storm), the food is less subject to an annual decrease in availability and there are fewer competitors (e.g. A. dactylomela and the Eatonella spp. are lacking). One must conclude that the subtidal environment is near optimum for A. parvula, but the intertidal is only marginal.
Figure 6.12.

*Aplysia parvula.*

Length (standard crawling length) versus weight (wet weight) relationship for the intertidal population at Goat Island Bay. Graph based on total of 91 specimens measured between September 1975 and November 1977. Double log plot. Regression line fitted by least squares method.

---

Figure 6.13.

*Aplysia parvula.*

Length (standard crawling length) versus weight (wet weight) relationship for the subtidal population at Goat Island Bay. Graph based on a total of 92 specimens measured between January and November 1977. Double log plot. Regression line fitted by least squares method.
6.12 Intertidal Population

\[ Y = 2.329X - 7.780 \]

6.13 Subtidal Population

\[ Y = 2.324X - 7.783 \]
Figure 6.14.

Aplysia parvula.

Changes in size throughout the year for the intertidal population on Echinoderm Reef, Goat Island Bay, January - November 1977. Numbers at top indicate sample size. Data on copulation and spawn included.

Figure 6.15.

Aplysia parvula.

Changes in size throughout the year for the subtidal population at Goat Island Bay, January - November 1977. Numbers at top indicate sample size. Data on copulation and spawn included.
6.3 HAMINOEA ZELANDIAE (GRAY IN DIEFFENBACH)

6.3.1 Introduction.

Haminoea zelandiae is undoubtedly the most abundant opisthobranch mollusc at Motukarakara Island, Waitemata Harbour, yet at certain times it is virtually impossible to find a single specimen. H. zelandiae can be found most easily in the middle of winter when breeding is at a peak. It inhabits a variety of shores: sandy-mud flats; Zostera flats; semi-exposed rocky shores (Rudman, 1971). At Motukarakara Island the majority of specimens occur across the intertidal reef that fringes the Island, here living amongst the low stubble of Corallina officinalis turf where sand, silt and comminuted shell fragments collect in local depressions on the sandstone basement. In addition, specimens can be found on the sand flats further off the Island, densities decreasing away from the Island.

When disturbed, a specimen of H. zelandiae, on a soft substrate will immediately burrow beneath the surface. Movement is by ciliary action. Rudman (1971) has shown the body to have a ciliated epidermis containing cells which produce a mucous tube in which the animal moves. The head shield lifts a thin layer of sand onto the mucus covering the dorsal region. Specimens come to rest completely buried in the mud, or embedded with just a trace of the shell uncovered. With its sandy-coloured, drab, mottled animal colouration (Fig. 3.3), H. zelandiae is thus extremely cryptic in such habitats. Its cryptic colouration and burying behaviour make it hard to detect by predators, and I have never seen living specimens being preyed upon at any time.

Haminoea zelandiae is a vegetarian, feeding on filamentous algae when on the surface. Feeding appears to be partially rhythmic.

Haminoea zelandiae lays its sausage-shaped jelly masses on solid objects such as rocks or Corallina officinalis turf. On mud, eggs are deposited on pebbles, empty bivalve shells or even waterlogged pieces of driftwood.

A graph illustrating the length to weight relationship of H. zelandiae is given in Fig. 6.16. These data were derived from animals sampled in May and June 1977. The regression equation relating length and weight is
\[ W = 2.43 \times 10^{-4} L^{2.564} \quad (n = 91, \, P=0.001) \]

where \( W \) = damp wet weight in gm, and \( L \) = extended crawling length of the live animal in mm.

For Haminoea zelandiae dry weight has a mean value of 15.5% damp wet weight \((n = 11, \, SE = 0.89, \, SD = 2.95)\), with shell weight included. The regression equation relating damp wet weight of live animals \((X)\) to dry weight \((Y)\) is \( Y = 0.1456x + 0.007 \).

6.3.2 Growth in the Field.

I have been able to maintain records of growth of field populations of Haminoea zelandiae, these records being the most complete for any of the species investigated by me. Growth of populations at three levels (pools A, B, C) on the intertidal reef platform off Motukaraka Island were maintained continuously for three years (March 1975 to February 1978); that of a fourth pool furthest inshore for eighteen months (September 1976 to February 1978). Results of these growth monitoring data are presented in Figs. 6.17 and 6.18. As mark/recapture techniques were not possible, growth rates could not be obtained for individual specimens.

Fig. 6.17 presents a series of monthly histograms of population growth in terms of size distributions at three of the four study pools. Where two or more samples were made in the same month I have included data for only that sample for which the largest number of measurements were made. These histograms show that in all study areas there was a clear pattern of size distribution within the population throughout each year. Considering pool B as an example. Over mid-summer (December to February) virtually all members of the population were juveniles (here "juvenile" was defined as non-reproductive individuals of less than 15 mm standard length); mean size steadily increased over the next three months, so that by May when the first eggs were laid there were virtually no juveniles; mean size continued to climb throughout June and July and egg production increased as well; by
August the first new juveniles were located and after that juveniles could be found continuously for the rest of the year. It would appear that for winter-settled juveniles, growth was retarded until spring or early summer, so that by then all juveniles (including those settling at that time) grew at the same rate. The presence of juveniles over this long time was related to the very extended breeding period. There is no evidence to suggest the first winter-settled juveniles grew very rapidly to participate in breeding for that winter (i.e. that they could have a faster growth rate than for summer-settled juveniles). The apparent downward shift in mean size each year following the mid-winter peak is related to numbers of specimens able to be collected in each sample and their combined contributions to the mean. Since the large individuals die after spawning their contribution to the larger size classes gradually diminished, and at the same time an increasing proportion of juveniles were settling and being detected. So the mean shifts downwards in favour of these juveniles until only they were present, at which stage it starts to ascend again.

Therefore the yearly cycle of growth for *Haminoea zelandiae* is interpreted as being an annual one, with a very extended period of overlap between generations because of the prolonged breeding season throughout autumn, winter and spring.

Several different observations have been made relating size distribution of populations to level on the shore. The first concerned sizes attained. When mean lengths were calculated for each of the pools for each sampling period (Fig. 6.18), it was seen that although the same general trends in annual increase and decrease in mean length were followed, mean size was seldom the same for all four pools. Generally at any one time, mean size in the outer pools (pools B and C) was greater than for the inner pools (pools A and A/B). Fig. 6.19 shows an example of this disparity in size for the pooled July 1977 sample, the histograms showing mean size between 22.5 and 25 mm for pool A/B, and mean size being two size classes larger at between 27.5 and 30 mm for pool B. To test the significance of differences between the four study pools and sample times, the data were subject to a two-way analysis of variance.
Table 6.9. **Haminoea zelandiae**: Two-way ANOVA comparing lengths between sites (S, =4) and Times (T, =47) at Motukaraka Island, Waitemata Harbour, 1975-1978.

Square root transformation applied.

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>386,761,009</td>
<td>3</td>
<td>129,587,202,86</td>
<td>333.1734</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>T</td>
<td>1367,637,650</td>
<td>46</td>
<td>29,731,692.4</td>
<td>76.4399</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>S x T</td>
<td>3744,296,314</td>
<td>135</td>
<td>27,132,596.48</td>
<td>69.7589</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>1046,440,174</td>
<td>274</td>
<td>27,422</td>
<td>0.38b946b76</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>5930,649,249</td>
<td>292</td>
<td>27,929</td>
<td>2.02480312</td>
<td></td>
</tr>
</tbody>
</table>

All results, including that for the interaction term, are highly significant. A Duncan's multiple range test on the raw data shows pools A and B have significantly greater combined means for length than for pools A/B or C at the P = 0.05 level. An objection to this analysis of changes in mean length by the ANOVA technique that could be raised concerns one of the fundamental assumptions of ANOVA, that of independence. This assumption is violated by a time sequence because of serial correlations, and because the samples cannot be regarded as completely independent. However I feel for these data on *Haminoea zelandiae* lengths serial correlations are not important because I did not sample exactly the same spot in each pool on each visit, and probably did not measure the same animal on each visit. A look at Fig. 6.17 shows the great fluctuations in numbers between consecutive visits to the same site.

Therefore, population structure in terms of sizes is different across the intertidal reef platform. To emphasize this difference in sizes I have presented histograms in Fig. 6.20 for two samples of *H. zelandiae* taken towards the outer part of the reef edge at Omana Beach (also in the Waitemata Harbour) only one day (10 Sept. 1976, Fig. 6.20 C, D) after a regular Motukaraka Island sampling visit (9 Sept. 1976, Fig. 6.20 A, B). These data show that size distribution at Omana Beach is more closely related to size
distribution at pool C at Motukaraka Island than the population at Pool C is related to pool B on the same Motukaraka Island reef. Therefore these data for growth and size distribution, and those I provide for densities in the subsequent section show that populations of the same species display very different properties at the same time at different levels on the same intertidal reef platform. I discuss the reasons for these different properties following the next section on abundance of live Haminoea zelandiae.

Two anatomical changes were noted for mature H. zelandiae. Shells of the oldest living specimens become rough and pitted on the dorsal surface in the area where the parapodia do not overlap, the periostracum being lost and a green algal film forming on the roughened shell surface. Secondly, mature animals often have crescentic areas missing from the posterior caudal lobe of the foot. These regions appear to be lost as the result of copulations but the method is not clear. On 3 May 1976, 2.3% of the H. zelandiae in pool A/B had parts of their caudal lobes damaged, whereas 30.9% of those in pool B displayed damage. Haminoea zelandiae will not voluntarily autotomize these caudal regions when irritated as do other opisthobranchs (Lewin, 1970). Should a worker want to assess the age and reproductive status of individuals in an unknown population of H. zelandiae that is being sampled once only, then observations on the ratios of both the above characters could be used, this method assumes that most of the individuals are in the reproductive phase.

6.3.3 Annual Abundance Cycle.

As explained in Chapter 4 on sampling sites within study areas, population densities of H. zelandiae were monitored at four study pools on the intertidal reef platform at Motukaraka Rd. A total of 28 samples was made during the period 22 September 1976 to 6 February 1978, therefore each site was sampled an average 1.5 times per month. In fact 1976 and 1978 samples were made once each month, those in 1977 being taken approximately twice each month.
Although records of *H. zelandiae* densities were kept continuously from 13 March 1975 for pools A, B and C I have excluded from analyses those for the first eighteen months because of sampling imperfections. However, the qualitative trends from those samples are included in my final considerations. The major cause for not using my early data is related to size of the sampling area.

There were four constraints on size of the area within each pool in which counts of abundance were to be made - area of pool, uniformity of substrate, time spent searching, position on the platform and hence the period available for searching as dictated by the tide. The eventual method chosen and the number of quadrats searched was therefore a compromise. For the first four months I attempted to search the entire pools for all live *Haminoea zelandiae*, but by June *H. zelandiae* were found in very great densities and searching time was insufficient to examine each pool thoroughly. Therefore a subsampling procedure was adopted; an iron frame giving a quadrat area of 0.1 m$^2$ was used to make random replicate counts of density. This system was employed until September 1976 by which time it was obvious a larger quadrat needed to be employed to overcome within-pool variability. Consequently a light tubular plastic frame giving a quadrat area of 1 m$^2$ was employed for the duration of the survey. The frame was assembled prior to sampling and several random quadrats (2-6) searched for live *Haminoea zelandiae*. A thorough search of a single 1 m$^2$ area took 15-20 min.

As a comparison of reliability, density figures measured by a close visual count (counts of numbers in a whole pool) and the second relative method (counts of numbers m$^{-2}$ for random quadrats) made on the same visit at the same pool were checked against each other. Both techniques were employed for samples made on 22/9/76, 10/10/76, 22/10/76 and 18/11/76. Results of density entries are tabulated below (Table 6.10).
Table 6.10. *Harnioea zelandiae*: Comparative data on population densities in two study pools at Motukaraka Id. Pool B has an area of 14.8 m$^2$, that of Pool C is 9.2 m$^2$.

<table>
<thead>
<tr>
<th>DATE</th>
<th>POOL B Density by direct counting</th>
<th>Density by relative estimate based on 1 m$^2$ subsamples</th>
<th>POOL C Density by direct counting</th>
<th>Density by relative estimate based on 1 m$^2$ subsamples</th>
</tr>
</thead>
<tbody>
<tr>
<td>22/9/76</td>
<td>61</td>
<td>138</td>
<td>22</td>
<td>43</td>
</tr>
<tr>
<td>10/10/76</td>
<td>158</td>
<td>215</td>
<td>65</td>
<td>92</td>
</tr>
<tr>
<td>22/10/76</td>
<td>22</td>
<td>44</td>
<td>32</td>
<td>46</td>
</tr>
<tr>
<td>18/11/76</td>
<td>43</td>
<td>133</td>
<td>35</td>
<td>55</td>
</tr>
</tbody>
</table>

From this table it can be seen that densities obtained by relative estimates are consistently higher than those derived from visual counts. It is probable that the relative counts more closely reflect the true densities because the whole pool could not be searched with anywhere near the thoroughness of a 1 m$^2$ quadrat. On the other hand, some estimates derived by the 1 m$^2$ sampling method may not reflect the true density because not all areas of the habitat were uniform and *Harnioea zelandiae* tended to be found more frequently in certain microhabitats rather than others (see later).

This element of microhabitat diversity combined with behavioural patterns are probably also the reasons for the diversity of counts made at the same time within a single pool, or for two closely consecutive visits to the same pool when densities could have been expected to have been similar. Example 1 in Table 6.11 is an extreme case of variation. However example 2 shows that estimates can be assessed as being fairly constant for a considerable length of time.
Table 6.11 Haminoea zelandiae: Counts of mean no. m$^{-2}$ on consecutive visits to demonstrate intraspecific variability within samples.

<table>
<thead>
<tr>
<th>Example 1 - Pool A/B</th>
<th>Example 2 - Pool B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>Mean no. m$^{-2}$</td>
</tr>
<tr>
<td>10/10/76</td>
<td>28.0</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>22/10/76</td>
<td>0</td>
</tr>
<tr>
<td>18/11/76</td>
<td>38.5</td>
</tr>
</tbody>
</table>

Means for relative densities (per m$^2$) for the four study pools have been plotted in Fig. 6.21. Considering these data, and that for 1975 and 1976, several points of interest emerge.

Firstly that H. zelandiae is present in all pools virtually throughout the year. A peak of abundance is reached in mid-winter (July-September) and there is a mid-summer paucity (January - March), but no clear annual cycle of presence and absence is detectable.

Secondly, Haminoea zelandiae density appears to be inversely related to position on the shore. The furthest inshore pool (A/B) exhibits overall highest densities with the pools successively further out across the reef flat exhibiting correspondingly low densities, so that on numerous occasions zero or very few H. zelandiae could be detected in pool C.

A two-way analysis of variance test was undertaken to test differences between sites and times under the null hypothesis that H. zelandiae densities did not change significantly in different areas at different times of the year. The ANOVA table is given below (Table 6.12).
Table 6.12 *Haminoea zelandiae*: Two-way ANOVA comparing site (4) and time (28) effects on density at Motukaraka Id. 1976-1978. Square root transformation applied.

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>T</td>
<td>250.02</td>
<td>27</td>
<td>9.259</td>
<td>10.551</td>
<td>0.000000</td>
</tr>
<tr>
<td>S</td>
<td>337.859</td>
<td>3</td>
<td>112.619</td>
<td>128.321</td>
<td>0.000000</td>
</tr>
<tr>
<td>B</td>
<td>282.785</td>
<td>81</td>
<td>3.491</td>
<td>3.9779</td>
<td>0.000000</td>
</tr>
<tr>
<td>Error</td>
<td>232.575</td>
<td>265</td>
<td>0.877</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1217.559</td>
<td>376</td>
<td>3.238</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Where T is time, S is site and B the interaction term.

Values for both times and sites are highly significant suggesting the four pools differ from each other in terms of *H. zelandiae* densities and that there is a significant change in density throughout the year. The interaction term is also highly significant. Both the parameters of site and time can be considered separately.

1. **Site.** Pool A/B is located at the extreme inner edge of the reef platform, very little silt accumulates on the floor of the very shallow pools, temperatures in the middle of summer can be exceedingly high (up to 30.9°C) because of the long period of isolation of this pool from the sea and its northerly aspect. Pools B and C are deeper, separated for less time from the sea and have a through-flow of water draining from the rest of the platform for a considerable time during each ebb tide. Neap tides do not uncover pool C at all.

2. **Time.** There is a significant difference in *Haminoea zelandiae* densities through time, this is probably related to size composition of *H. zelandiae*, and hence ability of the searcher to locate specimens. At the times densities are apparently lowest (in summer), there is the highest proportion of small juveniles since all sizes of *H. zelandiae* are secretive in nature, I suspect juveniles will be most difficult to find. Conversely, in mid-winter when densities are greatest, the average size is greatest, so is egg mass density (see later). Therefore one could expect to be able to locate the greatest numbers and
consequently expect greatest relative density figures.

I suspect that all four areas support a more or less constant population of *H. zelandiae* throughout the year, and apparent changes in density are the result of the inability of the searcher to locate all specimens. Very intensive searching over a quadrat area that had already been searched recorded one or two additional hidden *H. zelandiae*. Even though numbers may be relatively constant annually in any area, across the shore there appears to be a decline in density. Table 6.13 gives values for grand annual means at each pool derived for the 28 periods.

**Table 6.13. Haminoea zelandiae: Grand means for density (numbers.m⁻²) in four study pools across the low-tidal reef flat at Motukaraka Id.**

<table>
<thead>
<tr>
<th>Pool</th>
<th>Distance across reef (m)</th>
<th>Mean</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>A/B</td>
<td>3</td>
<td>14.482</td>
<td>1.913</td>
</tr>
<tr>
<td>A</td>
<td>16.5</td>
<td>2.987</td>
<td>0.459</td>
</tr>
<tr>
<td>B</td>
<td>62</td>
<td>9.004</td>
<td>1.955</td>
</tr>
<tr>
<td>C</td>
<td>105</td>
<td>1.469</td>
<td>0.461</td>
</tr>
</tbody>
</table>

Pool A is anomalous in that it could be expected to have a grand mean value between those of pools A/B and B, this being related to its position on the shore. But pool A has a large area of bare sandstone covered by an over-burden of sand and this situation appears inimical to *H. zelandiae*. Sieving the sand in such areas failed to record any hidden or buried *H. zelandiae*.

Therefore, it is hypothesized that *H. zelandiae* density is relatively constant throughout the year, and that maximum density occurs on the inner third of the intertidal reef platform. Maximum annual average densities here are approx. 14 animals.m⁻². The hypothesis assumes feeding and breeding aggregations do not occur, but there is some evidence to refute this assumption; the peak of *H. zelandiae* density at Pool B on 16 July 1977 (50.25 animals.m⁻²) is interpreted as a breeding-related phenomenon.
6.3.4 Reasons for Differences in Haminoea zelandiae Population Structure at Motukaraka Island.

As shown in the previous two sections, there are differences between growth rates and size distribution, and densities at different stations across the intertidal reef platform at Motukaraka Island and these differences are of a statistically significant magnitude. These data suggest that the populations are rather discrete in different areas of the reef. It is probable that migration laterally from inshore to offshore areas or vice versa would be very limited because of the animal's short-ranging burrowing/feeding activities.

These population differences could be mediated by the physical environment or by biological factors. In pool A/B which is farthest inshore physical fluctuations are extreme because of its shallowness and long time of separation by the tides, at the outer pools, oscillations of temperature and salinity would be damped. In this pool too, recorded densities of H. zelandiae were higher although lengths of individuals were smallest. Perhaps here, intraspecific competition for food could be invoked for the above differences. Initially algal cover would be low, or quality poor, because of the physical conditions prevailing in pools very high on the shore such as pool A/B; if Haminoea zelandiae densities were high there, then one would expect food resources to be limiting and so ultimate size distribution of the population would be depressed in the upper size classes. Since I have also shown algal types and abundance cycles to differ across the reef platform (see Ch. 5.4), diet could also be responsible for some of these differences. It is probable that both sets of factors are operating on Haminoea zelandiae causing the different population structures across the reef platform at Motukaraka Island.
6.3.5 Annual Breeding Cycle.

Egg masses were counted for each 1 m$^2$ quadrat in each of the four study pools from 22 September 1976 to 26 February 1978. Means for relative densities (per m$^2$) for the four study pools have been plotted in Fig. 6.22. They show a clear annual cycle with definite non-breeding and breeding phases. Egg laying occurs continuously over an extended period and reaches a clear peak in mid-winter (July and August). Throughout the year numbers of eggs were lowest in pool C, as were the animals (Fig. 6.18). Similarly for pool A, there was a correspondence between densities of live animals and egg numbers. The situations in pools A/B and B are reversed however. Egg mass numbers are consistently higher in pool B than in pool A/B where live Haminoea zelandiae numbers are significantly greater (Fig. 6.18). I suggest that the answer to this paradox lies in the nature of the environment and quality of food available. In pool A/B water temperatures oscillate greatly depending on the state of the tide and weather (Appendix III.2). The shallowness of the pool leads to a greatly varying salinity. Algal cover and composition are similar but not always the same (Table 5.3).

The data were subject to a two-way analysis of variance between both sites and times (Table 6.13). There are significant effects for both sites and times, and the interaction term is significant.

Table 6.13. Haminoea zelandiae: Two-way ANOVA comparing site (4) and time (28) effect on density of egg masses at Motukaraka Island, 1976-1978.

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>T</td>
<td>13995.397</td>
<td>27</td>
<td>518.348</td>
<td>16.993</td>
<td>0.000000</td>
</tr>
<tr>
<td>S</td>
<td>5994.5451</td>
<td>3</td>
<td>1998.181</td>
<td>65.508</td>
<td>0.000000</td>
</tr>
<tr>
<td>B</td>
<td>16756.571</td>
<td>81</td>
<td>206.871</td>
<td>6.782</td>
<td>0.000000</td>
</tr>
<tr>
<td>Error</td>
<td>8022.183</td>
<td>263</td>
<td>30.503</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>46973.386</td>
<td>374</td>
<td>125.597</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
To compare mean *H. zelandiae* egg mass densities over a larger area and contrast a different area to my study pools, I counted the total numbers of eggs per m$^2$ for a 10 m transect strip between pool A and pool A/B. This fixed transect was made on a gently sloping area of the reef platform, *Corallina officinalis* turf was uninterrupted by pools, dislodged rock slabs or clumps of *Hormosira banksii*. Data from July to December 1977 are given in Table 6.14. Figures on egg mass density would obviously have been higher had I chosen areas of pools or runnels to duplicate my study pools, unfortunately a single 10 m strip could not be run through any of these dissected areas.

**Table 6.14. Haminoea zelandiae: Counts of mean numbers of egg masses.m$^{-2}$ from a 10 m transect across a uniform, emerged area of *Corallina officinalis* turf between pools A/B and B at Motukaraka Island.**

<table>
<thead>
<tr>
<th>Date</th>
<th>Mean density (per m$^2$)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>30 July 1977</td>
<td>20.20</td>
<td>5.51</td>
</tr>
<tr>
<td>14 August 1977</td>
<td>29.36</td>
<td>2.63</td>
</tr>
<tr>
<td>31 August 1977</td>
<td>24.8</td>
<td>3.98</td>
</tr>
<tr>
<td>11 September 1977</td>
<td>28.4</td>
<td>4.56</td>
</tr>
<tr>
<td>26 September 1977</td>
<td>14.8</td>
<td>1.89</td>
</tr>
<tr>
<td>12 October 1977</td>
<td>0.40</td>
<td>0.22</td>
</tr>
<tr>
<td>27 October 1977</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td>6 November 1977</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>21 December 1977</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

6.3.6 *The Egg Mass and its Development.*

This section presents results of studies on the population at Motukaraka Island, Waitemata Harbour. Here individual egg masses were marked as they were laid and their development was followed through to hatching. These experiments were carried out in August and September 1977. Methods for recognizing individual egg masses are fully described in Ch. 4.8.
Egg Mass of Haminoea zelandiae.

The mass is semicircular, gelatinous, 25-35 mm in length. It is attached to substrate along ventral edge, oval in cross section, the base being slightly narrower than the top. Internally the irregularly-spaced strings of capsules are wound in spirals, each capsule containing a single larva. There is no hollow central position to the egg mass as in Haminoea elegans or H. antillarum (Bandel, 1976). For the Motukaraka Id population there are between 2,500 and 4,000 eggs per mass (mean = 3,597; SE = 1003; n = 4). In the masses examined none of the capsules had fine connections between them as in Haminoea virescens (Hurst, 1967) and neither were any capsules observed that contained two or more eggs as noted in H. virescens and H. antillarum (Bandel, 1976). In H. zelandiae all eggs hatch as free-swimming veliger larvae. However, Berrill (1931) claimed that for the European H. hydatis some larvae leave the egg masses as swimming veligers whilst others settle immediately to crawl for the rest of their existence.

Development Time for Egg Masses.

To monitor developmental changes of egg masses (from oviposition to hatching) an arbitrary scale of three stages was defined. This scale permitted a rapid field measurement to be made of the relative state of development of each egg mass. The scale is as follows:

Stage 1. Egg mass solid, sausage-shaped, clean or lightly covered with mud exteriorly, eggs golden in colour. This is the appearance of a newly-laid egg mass.

Stage 2. Mass flaccid, may be loosely attached, often ragged at the extremities. Outside encrusted with mud, larval colour and hence colour of whole egg mass, creamish-yellow.

Stage 3. Egg mass almost totally disintegrated, only small gelatinous fragments adhering to substrate, very ragged and loose. Pale creamish or uncoloured or so heavily coated with mud that colour is indiscernable.
Masses at each stage of development were brought back to the laboratory so that developmental processes could be examined.

When freshly laid, each mass has a clear, tough exterior layer; initially this is very adhesive and glues to anything it touches, subsequently although some adhesion is lost. Inside is a narrow zone of clear jelly and inside this again are chains of egg capsules in a gelatinous matrix. Larvae had not reached the trochophore condition by late stage 1 nor were they rotating inside their capsules.

Development proceeds rapidly between late stage 1 and stage 2. Early in stage 2, trochophores and veligers can be discerned and all larvae are rotating inside their capsules. When the mass is split open individual capsules cannot be shaken from the gelatinous matrix. Release of larvae, or swimming veligers, starts midway through stage 2.

Larval release peaks between stages 2 and 3. Veligers ready for release have transparent cap-shaped shells, an operculum and a small yellow larval kidney. Larvae are photopositive when liberated. Some development of veligers continues for those remaining inside the mass as it disintegrates. By stage 3 the mass is exceedingly flaccid and capsules and larvae can be shaken from the remnants of the egg mass.

Results.

Table 6.15. Haminoea zelandiae: Comparative data on development rate of egg masses at two different sites at Motukaraka Island.

<table>
<thead>
<tr>
<th></th>
<th>Site 1</th>
<th>Site 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial total egg masses tagged</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>No. of initials lost before development complete</td>
<td>10 (n=10)</td>
<td>27 (n=20)</td>
</tr>
<tr>
<td>Egg masses newly laid during observations</td>
<td>19</td>
<td>5</td>
</tr>
<tr>
<td>No. of newly laid masses lost before development complete</td>
<td>3 (n=15)</td>
<td>2 (n=10)</td>
</tr>
<tr>
<td>Time (days) spent in stage 1</td>
<td>23.5±7.71</td>
<td>-</td>
</tr>
<tr>
<td>Time (days) spent in stage 2</td>
<td>9.03±5.04</td>
<td>9.4±2.07</td>
</tr>
<tr>
<td>Time (days) spent in stage 3</td>
<td>7.5±4.07</td>
<td>8.0±4.66</td>
</tr>
</tbody>
</table>

(n = sample size)
The development time to commencement of hatching for *Haminoea zelandiae* is three weeks (plus or minus one week) which is remarkably long. Developmental times are shorter for other tropical species of *Haminoea*. Hatching occurs after two or three weeks in *Haminoea hydatis* (Berrill, 1931) and Bandel (1976) gives figures of four days development time for both *Haminoea elegans* and *H.* *antillarum* from Santa Marta, Colombia.

Conclusions.

The long developmental time plus the low oviposition rate in the second area (0.147 eggs laid per day) prevented the following of development of any single egg mass completely through all developmental stages to obtain an estimate of time taken at this site. However if it is assumed that each mass was tagged on the day it was laid, then a figure of 25.6, SD 4.08 days (n=24) is obtained for those masses which were observed to pass naturally into stage 2. This estimate is not significantly different (t = 0.777, \( P = 0.443 \)) from the mean for the first area. But since it is suspected that these masses had been laid prior to being tagged (probably approximately seven days earlier), then the developmental time is 32 days which is significantly longer (t = 3.258, \( P = 0.03 \)) than for eggs laid in pools. My results show that there are no significant differences in times taken for the hatching phase (stage 2) or final disintegration phases (stage 3) in either pools or emergent sites (t = 0.269, \( P = 0.68 \); t = 0.099, \( P = 0.922 \) respectively).

During the time of observations new egg masses were laid at a rate of 0.54 masses.day\(^{-1}\) at site 1 and 0.14 masses.day\(^{-1}\) at site 2. Assuming that no hatching or disintegration occurred and that no eggs were lost by any other means, it would take 104 days to reach a density of 56 masses.m\(^{-2}\) (starting density) at site 1 and 239 days to reach 33.5 masses.m\(^{-2}\) (mean starting density) at site 2. Since both these estimates are grossly high it suggests oviposition by *H. zelandiae* is not regular but occurs in bursts with all fertile members of the population at any one time laying their eggs synchronously. Perhaps oviposition is dictated by zeitgebers? Since egg
laying extends over six months it is probable that there are several of these bursts in any one oviposition season.

Finally, comment must be made on the losses of egg masses before all the larvae had been released or before the mass had disintegrated naturally. These losses summed to 18.8% at site 1 and 52.7% at site 2. The fate of lost egg masses was not followed and it is not known what proportion of larvae, if any, in such freely-drifting masses succeed in developing or hatching. Clearly there is a higher proportion lost in the emergent areas, and perhaps this explains the adult preference for oviposition in pools. The causes of such losses are probably physical. No organisms were ever observed eating *Haminoea zelandiae* egg masses although the carnivorous neogastropods *Lepsiella scobina*, *Hastrum haustorium* (Muricidae) and *Buccinulum vittatum*, *Cominella maculosa*, *Cominella virgata* (Buccinidae), the opisthobranch *Melanochlamys cylindrica* (Aglajidae), the crabs *Halicarcinus varius* (Hymenosomatidae), *Pilumnopeus serratifrons* (Xanthidae), *Notomithrax peroni* (Majidae) and the starfish *Coscinasterias calamaria* (Asteriidae) were all present and possibly could have been responsible for some egg losses. It is probable that most losses were the result of physical removal. During the period of observations there were two bouts of stormy weather (3, 4 September; 13, 14 September) and these storms created great losses. At site 2 for example, 17.2% of the total vanished during the first storm and 62% vanished during the second storm.

6.3.7 Feeding Observations and Relationship of *Haminoea zelandiae* to Algal Cycles.

Since *H. zelandiae* feeds only when emerged from the substrate, direct observations on food type and feeding behaviour can readily be made. *Haminoea zelandiae* is an extremely opportunistic feeder, eating filamentous algae belonging to the divisions Cyanophyceae, Chlorophyceae, Phaeophyceae and Rhodophyceae whenever available. Examination of faeces revealed recognizable remains of algae belonging to all four categories. Some undigested remnants of all
species are voided since, apparently trituration by the crop is incomplete, especially at times when food is abundant (Rudman, 1971). The only algae that appear not to be touched by H. zelandiae are filamentous colonial Bacillariophyceae. Naturally some benthic diatoms are ingested accidentally as epiphytes on other algal species, but I have never witnessed H. zelandiae grazing on filaments of chain-forming diatoms (e.g. Grammatophora marina) or colonial tube-dwelling forms (e.g. Navicula (Schizonema) grevilleana) that are seasonally dominant in certain areas at Motukaraka Island. Berrill (1931) noted Haminoea hydatis fed unselectively on small algae and encrusting diatoms.

Filamentous algae with diameters of 10-40 μm appear to be copepods with and ingested most easily, often several filaments being taken in at once. Algae containing cells of greater width (such as those of the Enteromorpha sp. described by Rudman (1971)) may not be disrupted by the gizzard as easily as filaments containing cells of lesser widths. It does appear, however, that in the field H. zelandiae prefers green algae (such as Enteromorpha compressa f. australiensis, Cladophora spp., Rhizoclonium spp.) to browns or reds or blue-greens. Haminoea zelandiae does not deliberately ingest macroscopic algae.

Since the algae eaten by H. zelandiae are microscopic, and almost always occur in mixed species associations with the thalli of one species intimately interwoven amongst those of several others, I did not attempt preference testing or growth rate determinations in the laboratory for H. zelandiae as I did with Aplysia dactylomela.

Now that the annual cycles for both Haminoea zelandiae and the dominant ephemeral algae have been described for Motukaraka Island, one can consider their inter-relationship. Maximum adult size for the bulk of the Haminoea zelandiae population is attained by June and July with a peak in August, and it would be during this phase that H. zelandiae grazing pressure could be expected to be having the greatest effects on their algal resources. Therefore, although I believe H. zelandiae has a relatively constant density for a
particular area and level, it is apparent that changes in grazing pressure will occur due to growth of the population. These changes are treated as a single factor in the following discussion and termed "grazing effect".

Greatest densities of _H. zelandiae_ occur on the inner third of the intertidal reef platform at Motukaraka Island. Grazing effect will then be building up at the very time _Lyngbya majuscula_ cover is decreasing and the two cycles could therefore be connected. However the zones of maximum abundances do not coincide, and by August when _Haminoea_ is exerting the greatest grazing effect, the _Lyngbya majuscula_ has virtually disappeared. Grazing by _Bursatella leachii_ does have a significant effect on _L. majuscula_ cover, but grazing by _H. zelandiae_ does not.

The annual cycle of _H. zelandiae_ appears related to that of the filamentous phaeophycean _Bachelotia fulvescens_ inshore, and to that of the "green algal stubble" association on the outer areas. If one considers the graphic summary for algal cycles at Motukaraka Island presented in Fig. 5.5, and one examines the inner and outer reef flat components separately, then these inter-relations are apparent. Inshore the grazing effect of _H. zelandiae_ forms a close match to that for _Bachelotia fulvescens_ cover - both cycles peak in July and August, and during this time faecal samples of _H. zelandiae_ often contain abundant _Bachelotia fulvescens_ filaments. Similarly, the spring decline in _B. fulvescens_ cover corresponds with the late reproductive phase of the _H. zelandiae_ cycle when many large adults are dying and the grazing effect is lessening. Whilst _B. fulvescens_ is absent on the shore from October to January, _H. zelandiae_ is exercising a minimal grazing effect, the juveniles present at this time having probably switched their diet to other filamentous species that are less abundant at these times.

_Bachelotia fulvescens_ does not occur towards the outer parts of the reef platform, its place being filled seasonally by green algal stubble association. It appears that green algal stubble fulfils the same role in the diet of _Haminoea zelandiae_ here as _Bachelotia fulvescens_ does on the inner parts of
the reef platform. Certainly *H. zelandiae* were frequently observed feeding
on plants belonging to the green algal stubble association. Perhaps the green
algal stubble sets a limit on the density of *H. zelandiae*? At pool C the low
average density for *H. zelandiae* (1.5 m⁻²) and the low tidal algal cover (10%)
derived from the green algal stubble appear to be correlated.

6.3.8 Summary.
1. A regression equation relating length and weight is provided for live
animals of this species. Dry weight has a mean value of 15.5% live weight.
2. *H. zelandiae* displays an annual cycle of growth, individuals living for
one year. In mid-summer all members of the population are juveniles (< 15 mm
standard length). Mean size increases until July or August when the first new
juveniles are located following settlement.
3. The breeding season is very long with extremes from March to December.
Peak breeding is in August (mid-winter) when densities of eggs can be in excess
of 50 m⁻². At this time *H. zelandiae* eggs have a long developmental time of
approx. three weeks. Higher numbers of eggs are laid in pools, and developmental
time here is shorter than for eggs laid on emergent areas of reef.
4. It is suggested that *H. zelandiae* density is more or less constant throughout
the year in any particular area, and fluctuations in relative density estimates
are due to inability to sample the smallest individuals successfully. Highest
densities occur on the inner third of the reef, annual average here being
approx. 14 *H. zelandiae* m⁻².
5. There are significant differences between growth rate, size distribution,
density and egg production at different sites across the intertidal reef platform.
The very limited migration capabilities of the species probably enhance such
differences at the population level.
6. The annual cycle of *Haminoea zelandiae* appears related to that of the brown
alga *Bachelotia fulvescens* on inner areas, and to that of the green algal stubble
association on outer areas of the intertidal reef platform.
Figure 6.16.

Haminoea zelandiae.

Length (standard crawling length) versus weight (wet weight) relationship (untransformed data) for the Motukaraka Island population. Graph based on a total of 51 live specimens measured between May and June 1977. Curve fitted by least squares method.
Figure 6.17.

_Haminoea zelandiae._

Monthly histograms of size (i.e. extended crawling length) distribution at three sites (pool A/B = upper figure; pool B = middle figure; pool C = lower figure) across the reef platform at Motukaraka Island, August 1975 – February 1978. Numbers at top of each figure indicate sample size.
Figure 6.18.
Haminoe zelandiae.
Graph of mean lengths for four study pools at Motukaraka Island, September 1975 - February 1978. Arrow indicates start of observations at pool A/B.

- Pool A.
- Pool A/B.
- Pool C.
- Pool D.

Figure 6.19.
Haminoe zelandiae.
Length (i.e. standard crawling length) frequency histograms for populations at two study pools (indicated on each figure) in the July 1977 sample. For pool A/B n = 137, for pool B n = 98.
Figure 6.20.

Haminoea zelandiae.

Comparison of length (i.e. standard crawling length) frequency histograms for separate populations from two adjacent localities (Motukaraka Island and Omana Beach) both in Tamaki Strait at the same time in July 1977. For each locality areas on the inner and outer parts of the reef platform were surveyed.
Figure 6.21.

_Haminoea zelandiae_.

Relative density data for live animals per m$^2$ for four study pools at Motukaraka Island, September 1976 - February 1978.

Figure 6.22.

_Haminoea zelandiae_.

Relative density data for egg masses per m$^2$ for four study pools at Motukaraka Island, September 1976 - February 1978.
6.4.1 Length-weight relationship.

To ascertain the relationship between standard length and damp live weight for *Bursatella leachii*, measurements of these parameters were made for individuals of the 1977 Motukaraka Island population. The resulting regression equation was \( W = 7.929 \times 10^{-6} \cdot L^{3.312} \) (\( n = 31, P < 0.001 \)), where \( W \) = weight in gm and \( L \) = length in mm.

6.4.2 Recruitment.

At Motukaraka Island I have found that larvae of *Bursatella leachii* settle from the plankton in autumn, and metamorphosis occurs on the filamentous cyanophyte *Lyngbya majuscula* which has reached peak abundance at this time. Greatest settlement occurs where *L. majuscula* cover is densest in shallow pools containing standing water at low tide towards the outer parts of the reef flat.

Yearly changes in absolute density of *B. leachii* at pools B and C are shown graphically in Fig. 6.23. However, because *B. leachii* displays aggregative behaviour from a very early age, recorded absolute densities vary greatly depending on where an aggregation happens to be present at the time of sampling. For example, on 19 April 1977, mean density for four quadrats in pool C was nine *B. leachii*.m\(^{-2}\); however densities recorded in two additional quadrats taken immediately adjacent were 4 and 63 *B. leachii*.m\(^{-2}\). The 1977 data for pool C is replotted in Fig. 6.24 which gives means and SD's for values obtained from 1 m\(^2\) quadrats. Aggregative behaviour is not the sole cause for the clumped distribution of *B. leachii*. When absolute totals for pools are compared with totals derived from estimates made by multiplying the mean densities derived derived from several 1 m\(^2\) subsamples by the total size of the pool (Table 6.16) it is seen that absolute numbers are less (58.5\%) than the predicted values. The greater discrepancies occur at the highest densities. These differences imply that *B. leachii* exhibits habitat selectivity in conjunction with its aggregative behaviour. In fact, *B. leachii* were almost
always found on *L. majuscula* in pools, virtually none was present where the 
alga was festooning emergent *Corallina officinalis* turf.

<table>
<thead>
<tr>
<th>Sampling Date</th>
<th>Absolute Total</th>
<th>Mean no. m$^{-2}$</th>
<th>Estimate of Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>19 April</td>
<td>46</td>
<td>9.0 (4)</td>
<td>82.8</td>
</tr>
<tr>
<td>3 May</td>
<td>32</td>
<td>6.25 (4)</td>
<td>57.5</td>
</tr>
<tr>
<td>17 May</td>
<td>7</td>
<td>1 (5)</td>
<td>9.2</td>
</tr>
<tr>
<td>29 May</td>
<td>1</td>
<td>0.2 (5)</td>
<td>1.84</td>
</tr>
<tr>
<td>10 June</td>
<td>1</td>
<td>0.2 (5)</td>
<td>1.84</td>
</tr>
<tr>
<td>21 June</td>
<td>1</td>
<td>0.2 (5)</td>
<td>1.84</td>
</tr>
</tbody>
</table>

Table 6.16. *Bursatella leachii*: Comparison of densities by direct measurement 
The number of quadrats searched is given in brackets following 
the figure for mean number.m$^{-2}$.

In contrasting the three years of observations on *B. leachii*, it is 
seen that maximum densities in pool C in 1975 and 1977 were nearly identical, 
but no stress can be placed on this observation because of the variations in 
density described above; it is thought that the closeness of these two counts 
is due to coincidence and fortuitous sampling. What is more significant is 
that there was no recruitment of *B. leachii* in 1976. The absence of the 1976 
population at Motukarak Island despite the presence of the species there in 
1975 implies that this population is not self-recruiting. Clark (1975) has 
suggested similarly that at Noank, Connecticut, populations of the nudibranchs 
Ancula gibbosa (Risso) and Onchidoris bilamellata (Muller) are not self-
sustaining.

In some years, therefore, there may be no animals present at any particular 
area even though settlement substrata and food may both be present. Such an 
observation supports a great deal of literature on variability of recruitment 
for organisms with planktonic larvae (e.g. Thorson, 1950; Coe, 1956; 
Loosanoff, 1964; Feder, 1970; Yamaguchi, 1973; Barker, 1977). Moreover,
the implications for annual species are more drastic than for longer-lived ones.

Following recruitment to intertidal *Lyngbya majuscula* at Motukarakar Island, *B. leachii* grow extremely rapidly and then migrates offshore. Each of these phases is considered separately in greater detail in subsequent sections of this work.

In 1975 several individuals of another anaspidean, *Stylocheilus longicauda* were present amongst the aggregations of *B. leachii* suggesting larvae of both species had drifted together to Motukarakar Island from a common place of origin. However no *S. longicauda* were observed in 1977.*

6.4.3 Growth in the Laboratory.

Three specimens of *Bursatella leachii* obtained as juveniles from the 1975 Motukarakar Island population were maintained in the laboratory at 20°C on a diet of pure *Lyngbya majuscula*. These individuals initially had standard lengths of 9, 15 and 23 mm. Fig. 6.25 is a graph of increase in standard length versus time for these three specimens. Mean growth rate for all three over this period was 9.66 mm.week⁻¹ (SE = 1.26). One individual actually doubled its length in one week growing from 15 mm to 33 mm.

Regression equations were calculated for each individual. The presence of serial correlation in the data makes any test or confidence limits on a line strictly speaking, invalid. However, notional 95% confidence limits are provided for the slopes as are correlation coefficients; both are simply aids to the interpretation of these data. These data are tabulated in Table 6.17.

*No settlement of *Bursatella leachii* occurred at Motukarakar Island in 1978.
Table 6.17. *Bursatella leachii*: Regression data and confidence limits of slopes for growth in the laboratory.

<table>
<thead>
<tr>
<th>Animal No.</th>
<th>r</th>
<th>m</th>
<th>b</th>
<th>Confidence limits</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.956</td>
<td>1.121</td>
<td>29.844</td>
<td>± 0.503</td>
</tr>
<tr>
<td>2</td>
<td>0.963</td>
<td>0.982</td>
<td>24.329</td>
<td>± 0.437</td>
</tr>
<tr>
<td>3</td>
<td>0.987</td>
<td>1.045</td>
<td>7.451</td>
<td>± 0.457</td>
</tr>
</tbody>
</table>

where \( r \) = correlation coefficient, \( m \) = slope (i.e. growth rate in mm.week\(^{-1}\)) and \( b \) = intercept of the regression equation (i.e. length at week 0).

It is essential to note that overall growth in *B. leachii* has a curvilinear pattern, but for the period under investigation it is assumed to be linear.

From the graph it is evident that *Bursatella leachii* has an enormously high intrinsic capacity for rapid growth in comparison with other molluscs and opisthobranchs (e.g: Laxton, 1968; Larcombe, 1971; Briggs, 1972; Hartley, 1978). When individuals are presented with a situation in which food is abundant and temperatures are high this ability is fully expressed.

6.4.4 Growth in the Field.

Data for size distributions of the 1975 and 1977 *B. leachii* populations are given in Table 6.18 & Figs. 6.27 and 6.28. Data for 1975 is plotted in Fig. 6.26. Since *B. leachii* numbers are densest towards the outer part of the reef flat only data for pool C are considered here.

The histograms of data collected at approximately fortnightly intervals (Figs. 6.27 and 6.28) show that in both years the *B. leachii* population was unimodal. This distribution suggests a single cohort of larvae settled en masse. The 1975 histograms initially (12 April and 20, 25 April) show a greater frequency of the smaller size classes (up to 50 mm) producing a skew to the left. However following the offshore migration of the larger individuals
this bias is removed and a more normal distribution attained (7 and 14 May). Accompanying the migration is a shift in mean size towards smaller size classes (Table 6.18 ) and approximately equal representation of all size classes. The 1977 data for B. leachii is even more compressed. Initial distribution of size classes (19 April and 3 May) appeared normal. This year class also exhibited a backshift of mean following migration (14 May).

To test the significance of the peak and backshift and compare size distribution between the two years a two-way ANOVA was undertaken (Table 6.19 ). The high variation of the data necessitated all length measurements for 1975 be pooled and 1977/into four time periods for each year. These time groupings were as follows:

- **Time 1** 1975: 12 April, 20 April, 25 April. 1977: 19 April
- **Time 2** 1975: 7 May. 1977: 3 May
- **Time 3** 1975: 14 May. 1977: 14 May
- **Time 4** 1975: 5 June, 12 June, 6 July. 1977: 29 May, 10 June, 21 June

Both logarithmic and square root transformations of the data were used but they did not remove correlation between the absolute values of the residuals and expected values. However, the derived significance levels were so high that this non-homogeneity of variance appears to have little effect on the results.


<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y</td>
<td>1</td>
<td>46.7683</td>
<td>1.0 x 10⁻⁶</td>
</tr>
<tr>
<td>T</td>
<td>3</td>
<td>35.6771</td>
<td>1.0 x 10⁻⁶</td>
</tr>
<tr>
<td>YT</td>
<td>3</td>
<td>5.7592</td>
<td>8.06 x 10⁻⁴</td>
</tr>
<tr>
<td>Error</td>
<td>242</td>
<td>249</td>
<td></td>
</tr>
</tbody>
</table>

Where Y = years, T refers to the four groupings of sampling times and YT is the interaction term.
This ANOVA shows there is a significant difference in the way size of the four classes changed over time for 1975 and 1977.

A Duncan's Multiple Range Test showed that the *B. leachii* measured within the second pooled group of sampling dates had significantly higher (\(p = 0.01\)) mean sizes than for those on any of the other three pooled sampling groups.

The regression equation for growth of the 1975 field population is \(Y = 1.477 \times X + 37.158\), where \(X\) is length in mm and \(Y\) is time in days, confidence limits for the slope of this line being \(\pm 2.53\).

The various ontogenetic changes that accompany growth of *B. leachii* are discussed separately in Appendix I.
Table 6.18. *Bursatella leachii*: Size distribution of individuals across the shore at Motukaraka Island in 1975 and 1977. No settlement occurred in 1976. In samples where the age classes are represented (as defined by body size and gonad state) on any one visit each is given on a separate line.

<table>
<thead>
<tr>
<th>Date</th>
<th>Pool B</th>
<th></th>
<th></th>
<th>Pool C</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sample Size</td>
<td>Mean</td>
<td>SE</td>
<td>SD</td>
<td>Sample Size</td>
<td>Mean</td>
</tr>
<tr>
<td>1975 DATA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13/3/75</td>
<td>1</td>
<td>81</td>
<td></td>
<td></td>
<td>1</td>
<td>79</td>
</tr>
<tr>
<td>6/4/75</td>
<td>3</td>
<td>14.87</td>
<td>2.99</td>
<td>5.95</td>
<td>1</td>
<td>91</td>
</tr>
<tr>
<td>12/4/75</td>
<td>3</td>
<td>25.2</td>
<td>5.1</td>
<td>11.4</td>
<td>47</td>
<td>30.4</td>
</tr>
<tr>
<td>20/4/75</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>112</td>
</tr>
<tr>
<td>25/4/75</td>
<td>3</td>
<td>51.66</td>
<td>14.4</td>
<td>25.03</td>
<td>12</td>
<td>49.58</td>
</tr>
<tr>
<td>7/5/75</td>
<td>5</td>
<td>42.4</td>
<td>10.5</td>
<td>23.46</td>
<td>28</td>
<td>71.36</td>
</tr>
<tr>
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<td>23</td>
<td>54.87</td>
<td>2.66</td>
<td>12.75</td>
<td>17</td>
<td>47.47</td>
</tr>
<tr>
<td>5/6/75</td>
<td>5</td>
<td>53.6</td>
<td>4.48</td>
<td>10.01</td>
<td>11</td>
<td>57.09</td>
</tr>
<tr>
<td>12/6/75</td>
<td>2</td>
<td>56.5</td>
<td>3.5</td>
<td>4.95</td>
<td>4</td>
<td>53.35</td>
</tr>
<tr>
<td>6/7/75</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>213</td>
</tr>
<tr>
<td>24/7/75</td>
<td>2</td>
<td>82.5</td>
<td>5.5</td>
<td>7.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1977 DATA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>92</td>
</tr>
<tr>
<td>19/4/77</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>31.73</td>
</tr>
<tr>
<td>3/5/77</td>
<td>2</td>
<td>33.5</td>
<td>6.5</td>
<td>9.19</td>
<td>32</td>
<td>45.25</td>
</tr>
<tr>
<td>17/5/77</td>
<td>2</td>
<td>69.5</td>
<td>1.5</td>
<td>2.12</td>
<td>7</td>
<td>28.9</td>
</tr>
<tr>
<td>29/5/77</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>25</td>
</tr>
<tr>
<td>10/6/77</td>
<td>1</td>
<td>43</td>
<td></td>
<td></td>
<td>1</td>
<td>30</td>
</tr>
<tr>
<td>21/6/77</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>32</td>
</tr>
</tbody>
</table>
6.4.5 Migration.

The subject of directed migration in post-metamorphic opisthobranchs has evoked considerable controversy in the past (Garstang, 1890). Eales (1921) and Yonge (1949) held that mature adults of the anaspidean Aplysia punctata underwent a definite onshore migration for spawning. However, Miller (1960) and Carefoot (1967c) described subtidal populations of A. parvula that did not reveal any shorewards migration. Miller (1962) subsequently concluded that migrations of nudibranchs for the purpose of spawning did not occur and Potts (1970) confirmed this in his detailed study on Onchidoris fusca.

When 'nudibranchs' is used in the strict sense (e.g. opisthobranchs belonging to the order Nudibranchia) the above assertion that migrations do not occur may well be true. However there is evidence that populations of certain of the larger Anaspidea may deliberately undergo directed migrations. The evidence for this statement is strongest for Bursatella leachii. This species exhibits considerable intra-specific social communication by performing such behaviours as trail following, queue formation and aggregation (Lowe & Turner, 1976). These authors were fortunate to witness queues of B. leachii coming from deeper water to aggregate in less than 1 m depth (density counted in one such aggregation was 6,600 animals m$^{-2}$). This was not an onshore spawning migration however, because few of the animals were sexually mature and most were juveniles, dry body weight for the majority being below 0.01 gm.

Similar but less spectacular cases of intraspecific social behaviour have been observed in B. leachii during the course of this study, and serve to substantiate the claim that this species undertakes deliberate migrations. The first two observations are casual, the third more lengthy.

1. At a depth of 8 m near High Island, Taurikura, Whangarei Heads on 21 June 1975, a group of four B. leachii were followed for 30 minutes. Judging from their sizes and plump appearance all were adults. When first encountered
they were crawling over the sand in single file with the tail of the one in front touching the oral tentacles of the one behind. When the leader encountered a clump of filamentous red alga (a species of *Polysiphonia* (Rhodophyceae)) the group would stop and all members would graze it. After eating, the group would move off as before. In this particular subtidal habitat algae of all types were sparse and not more abundant than one clump. $5 \text{ m}^{-2}$.

2. At 4–6 m on the southern side of North Cove, Kawau Island, Hauraki Gulf on 11 May 1977, high numbers of *B. leachii* were observed. All were juveniles (8–50 mm standard length) and many were aggregated or in large masses crawling in the same direction. Some were grazing on filamentous algae of the genera *Derbesia* (Chlorophyceae) and *Lyngbya* (Cyanophyceae) that were growing on the mud.

3. **Offshore Migrations at Motukaraka Island.** As recorded in the section on settlement and growth of *Bursatella leachii*, larvae metamorphose from the plankton on *Lyngbya majuscula* and grow very rapidly on this diet. The first juveniles were noted in mid-April of 1975 and 1977. Growth on the shore at Motukaraka Island continues until there is a mean wet weight of approx. 2.09 gm. At this stage a sudden decrease in numbers on the shore occurs and in the space of one or two weeks virtually the entire population migrates from the reef platform. Individuals involved in the migration frequently travel in long lines or groups and form dense aggregates at approx. ELWS level.

This migration is not due to direct food shortage because *Lyngbya majuscula* is still present on the reef platform, and undergoes considerable further growth when the grazing pressure exerted by *B. leachii* is reduced through migration. Nor is this emigration an artifact caused by the decimation of the population through storms, disease or predation. In both years the weather was quite settled over this period although sea water temperatures were dropping rapidly and none of the specimens observed was in an unhealthy state. The *B. leachii* that migrated were only 1–2 months old and examination
of their ovotestes and reproductive tracts showed them to be sexually immature.

Storms that blow up soon after B. leachii moves offshore wash many back onto the beaches. For example, following a storm in early June 1975 still-living B. leachii were cast up amongst drift algal debris at Motukaraka Island; within an area of 60 m² the density of stranded individuals was 2.1 m⁻². Although there was no predation by birds on the stranded individuals, it is unlikely that any survived.

In 1977 very high densities of newly-settled juveniles were first recorded on 19 April. Mean density in pool C at that time was 9 ± 3.36 m⁻² (n = 4). This estimate is likely to be a minimum because the great amounts of silt that had fallen out of suspension in the water onto the Lyngbya majuscula made detection of juvenile B. leachii a very difficult task. On 11 May 1977 great aggregations were observed in pools and gullies at ELWS level, this seaward movement being interpreted as a migration by these juvenile B. leachii.

A subsequent visit one week later on 17 May 1977 revealed a mean density for B. leachii of 1.0 ± 1.22 m⁻² (n = 5) in pool C, none of those remaining was clumped. Fortunately the tide was sufficiently low to make observations at ELWS and here there were high B. leachii densities (8-10 m⁻²) and most were aggregated. Later visits in May and June showed that these individuals moved out to sea. In both years none of these young individuals was ever observed copulating.

Although the vast majority of B. leachii present on the shore in both years were newly-metamorphosed individuals, a very low proportion of large animals were present as well. Dissection of these animals showed them to be sexually mature, and indeed in 1975, an egg mass was found on Lyngbya majuscula just outside pool C. Two interpretations of the presence of these sexually-mature individuals are, either they are adults from a previous year's spawning that migrated ashore to crop the extensive intertidal beds of Lyngbya majuscula.
or the products of a cohort that settled in extremely low densities very early in the year (in January or February) when the \textit{L. majuscula} was just becoming established, and the sea hares had grown to full size and attained sexual maturity in only two months. The first proposal is preferred, because the other would need an unrealistically high growth rate for \textit{B. leachii}.

Careful observations of individuals and consideration of literature do not readily present answers for either the aggregation nor the active migration phases of \textit{B. leachii} behaviour. If food is limiting (Clark, 1975) or if individuals are uncommon (Miller, 1969) it is advantageous for members of the one species to aggregate prior to reproduction. But neither of these explanations hold for the population of \textit{B. leachii} observed at Motukaraka Island. Food in the form of \textit{L. majuscula}, was abundant on the shore during and after the offshore migration, and throughout the time \textit{B. leachii} was present growth rate for the cyanophyte was high and may have possibly been stimulated by grazing (Ch. 5.3.1). The majority of individuals were sexually immature and on no occasion was copulatory behaviour by individuals within aggregates ever witnessed. It is possible that an amount of social contact with conspecifics is required before copulation can occur, Lederhendler (1977a; 1977b; 1977c) having already suggested this for \textit{Aplysia dactylomela}. It does not seem possible to advance a hypothesis that unites all the observations on migratory behaviour of \textit{B. leachii}. Migrations appear directed but are sometimes onshore (Lowe & Turner, 1976) or sometimes offshore (Motukaraka Island 1975; 1977) and they do not appear to be correlated with food.
6.4.6 Summary.

1. Settlement and metamorphosis of *Bursatella leachii* are accomplished on the filamentous cyanophyte *Lyngbya majuscula* at Motukaraka Island.

2. *B. leachii* were only recruited to the population in 1975 and 1977, in both years maximum the absolute densities on the outer part of the reef platform being approximately equal. In both years only one major recruitment took place. Failure of the 1976 population suggests there is no self-recruitment.

3. Regression equations have been calculated to show length/weight relationships of *B. leachii*, similar equations being presented for growth data from laboratory-reared animals and the 1975 field population. *B. leachii* possess an extremely high intrinsic capacity for rapid growth.

4. *B. leachii* displays behavioural characteristics of habitat selectivity and clumping into aggregates.

5. In both years there was an almost synchronous offshore migration of the largest individuals despite the continued presence of *L. majuscula* on the shore.

6. It is not possible to give one hypothesis to unify observations on aggregation behaviour and directed migrations in *B. leachii*. It may be that a certain amount of social interaction between conspecifics is required before successful mating or oviposition can be accomplished.
6.5 A Note on the Life Cycle of *MELANOCLAMY M. CYLINDRICA CHEESEMAN* at Motukaraka Island.

The jet black aglajid (Fig. 4.1f) was encountered sufficiently abundantly during the course of *Haminoea zelandiae* sampling at Motukaraka Island during 1975 to warrant collection of records of numbers and standard lengths of all specimens encountered from then until February 1978, and as well to make notes on the presence of their characteristic white spawn masses (Fig. 4.1f).

These data are shown in Fig. 6.29. *Melanochlamyms cylindrica* turned out to be of very sporadic occurrence at Motukaraka Island, with no specimens being observed over the summer months of any year. This, combined with the cryptic burrowing behaviour of juveniles, means no satisfactory quantitative description of its annual cycle on this shore is possible. Large individuals were present in winter and spring of 1975 together with their spawn (maximum spawn numbers were noted on 15 October 1975 when six masses were observed in an area of one square metre). By contrast, in 1977 no individuals or spawn were observed at all over this time.

Few generalizations about the life cycle of *Melanochlamyms cylindrica* can be made. It is possible, however, that the species is an annual with mature individuals present in the population from August to November and that copulation and oviposition occur then in these winter and spring months. Therefore the annual cycle of *M. cylindrica* parallels that of *Haminoea zelandiae*. As with *Bursatella leachii*, it is apparent that the population of *M. cylindrica* at Motukaraka Island is not self-sustaining and numbers are very low in certain years, so that there is virtually no evidence of spawn being produced in those years.

*M. cylindrica* is a carnivorous opisthobranch that sucks up its prey using a buccal pump action, the prey consisting of polychaete and nemertine worms (Rudman, 1972). Another member of the same family *Aglaja* (*Navanax* *inermis* (Cooper) from Southern California to Mexico hunts other opisthobranch molluscs for its food (Paine, 1965), and it is quite possible therefore that *Melanochlamyms cylindrica* may prey on juvenile *Haminoea zelandiae* as well.
Figure 6.23.
Bursatella leachii.
Yearly changes in absolute density in pools B and C at Motukaraka Island, 1975-1978. Arrows indicate times of offshore migrations.

Figure 6.24.
Bursatella leachii.
Density changes for the population in pool C and adjacent areas at Motukaraka Island, 1977. Mean and range plotted. Number of 1 m² quadrats searched is given in circle at top of figure.

Figure 6.25.
Bursatella leachii.
Laboratory growth data for three individuals from the Motukaraka Island population. Regression lines (derived by least squares method) are included.

Figure 6.26.
Bursatella leachii.
Mean size of the population in pool C plotted against time at Motukaraka Island, 1975. Mean and 95% confidence levels plotted. Bar at top indicates time of main offshore migration.
Figure 6.27.

*Bursatella leachii.*

Monthly histograms of size (i.e. extended crawling length) distribution for the onshore population in pool C at Motukaraka Island, 1975. Samples are grouped in approximately fortnightly time intervals.
Figure 6.28.

*Bursatella leachii.*

Monthly histograms of size (i.e. standard crawling length) distribution for the onshore population in pool C at Motukaraka Island, 1977. Samples are grouped in approximately fortnightly time intervals.

Figure 6.29.

*Melanochlamys cylindrica.*

Monthly histograms of size (i.e. standard crawling length) distribution for the population on the outer parts of the reef platform at Motukaraka Island, May 1975 - November 1977. Data on copulation and spawn included.
6.28

19 April
n = 61

3 May
n = 44

14 May
n = 7

Size class (mm.)

6.29

■ = 1 individual
population
spawn

1975
1976
1977
CHAPTER 7

NUTRITION AND FOOD UTILIZATION

7.1 Introduction.

The experimental investigations outlined in this chapter were all conducted on *Aplysia dactylomela* at the Leigh Marine Research Laboratory. They examine the energy content and energy flow for the Goat Island Bay population of this sea hare. These results, expressed in terms of colorimetric measurements were obtained for individuals and then extrapolated to the population level.

The first sections of this chapter deal with quantitative studies on nutrition and growth, the latter sections deal with the components of the energy equation.

7.2 Acceptable Foods.

This investigation was carried out early on in my study. It tested the null hypothesis that *A. dactylomela* shows no selectivity in its feeding - i.e. this sea hare would ingest equal amounts of any algae present provided they were all equally available.

Results for six duplicate trials for each of ten different algal species are given in Table 7.1.

Table 7.1. Food selectivity in *Aplysia dactylomela*.

<table>
<thead>
<tr>
<th>Alga</th>
<th>Mean Percent Consumed in 3 days ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>CHLOROPHYTA:</td>
<td></td>
</tr>
<tr>
<td><em>Ulva lactuca</em></td>
<td>92.7 ± 2.58</td>
</tr>
<tr>
<td><em>Enteromorpha</em> sp.</td>
<td>96.4 ± 2.02</td>
</tr>
<tr>
<td>CYANOPHYTA:</td>
<td></td>
</tr>
<tr>
<td><em>Lyngebya majuscula</em></td>
<td>13.1 ± 4.44</td>
</tr>
<tr>
<td>PHAEOPHYTA:</td>
<td></td>
</tr>
<tr>
<td><em>Glossophora kunthii</em></td>
<td>7.4 ± 2.54</td>
</tr>
<tr>
<td><em>Noethia anomala</em></td>
<td>6.4 ± 2.68</td>
</tr>
<tr>
<td>RHODOPHYTA:</td>
<td></td>
</tr>
<tr>
<td><em>Plocanium costatum</em></td>
<td>73.6 ± 5.34</td>
</tr>
<tr>
<td><em>Laurencia</em> spp.</td>
<td>100</td>
</tr>
<tr>
<td><em>Herposiphonia</em> sp.</td>
<td>70.3 ± 10.74</td>
</tr>
<tr>
<td><em>Champia laingii</em></td>
<td>71.98 ± 6.94</td>
</tr>
<tr>
<td><em>Pterocladiad pinnata</em></td>
<td>9.2 ± 3.43</td>
</tr>
</tbody>
</table>
These results show that *A. dactylomela* is selective, with respect to algae, in its feeding, in fact extremely so. From this investigation the algae could be grouped easily into two categories - some were acceptable as food (*Ulva lactuca*, *Enteromorpha* sp., *Plocamium costatum*, *Laurencia* spp., *Herposiphonia* sp., *Champia laingii*), the others not. A one way ANOVA gave a highly significant result ($S = 78807.5$ with $F_{8,47} = 48.64$ and $P = 0.0$) enabling a clear rejection of the null hypothesis. The low values for consumption but high standard errors for data on the algae *Herposiphonia* sp. and *Champia laingii* can be explained partially by these algae dying rapidly when held in the laboratory - initially they are consumed by *A. dactylomela*, but when dead they are not touched.

Because samples of algae used for feeding experiments in the laboratory tend to lose weight (Carefoot, 1967a), a correction factor was determined for each of the species used in the above investigation, this factor being employed in each case. These are given in Table 7.2. It appears that *Herposiphonia* sp. and *Ulva lactuca* lost least weight and *Champia laingii* lost most. *Lyngbya majuscula* actually grew in the laboratory during the investigation.

Table 7.2. Weight changes for algal samples maintained in the laboratory.

<table>
<thead>
<tr>
<th>Algal species</th>
<th>Mean weight change $\text{day}^{-1}$ (gm damp wet weight)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ulva lactuca</em></td>
<td>-0.012</td>
</tr>
<tr>
<td><em>Enteromorpha</em> sp.</td>
<td>-0.018</td>
</tr>
<tr>
<td><em>Lyngbya majuscula</em></td>
<td>+0.06</td>
</tr>
<tr>
<td><em>Glossophora kunthii</em></td>
<td>-0.031</td>
</tr>
<tr>
<td><em>Noethia anomala</em></td>
<td>-0.020</td>
</tr>
<tr>
<td><em>Plocamium costatum</em></td>
<td>-0.045</td>
</tr>
<tr>
<td><em>Laurencia</em> spp.</td>
<td>-0.034</td>
</tr>
<tr>
<td><em>Herposiphonia</em> sp. 1</td>
<td>-0.011</td>
</tr>
<tr>
<td><em>Pterocladia pinnata</em></td>
<td>-0.026</td>
</tr>
<tr>
<td><em>Champia laingii</em></td>
<td>-0.064</td>
</tr>
</tbody>
</table>
7.3 Laboratory-based Growth Studies.

7.3.1 Growth on selected algae.

Having shown that *A. dactylomela* is selective in choosing its food, it is now necessary to examine the basis of this selectivity. Undoubtedly *A. dactylomela* would exhibit preferences in nature between those algae species tested in the last section, and very likely numerous others which were not available in adequate quantities for laboratory trials. Notwithstanding the practical problems with laboratory-based preference experiments for generalist marine herbivores (Vadas, 1968; Clark, 1975) and the uncertain extrapolation to the field situation (Ayling, 1978; Leighton, 1960), I have gone one step further to examine the effect on growth of different algae that are eaten in the field.

The methods used in setting up these experiments for growth on selected algae are described in the methods section (Ch. 4.6.2). The algae chosen, with mean wet weight at the start for each batch of *Aplysia* that were maintained on that diet in brackets are: *Enteromorpha* sp. (35.82 gm); *Herposiphonia* sp. (65.67 gm); *Laurencia* spp. - mostly *L. distichophylla* and *L.* sp. 2 (71.1 gm). All these seaweeds are known to be eaten by *A. dactylomela* in the field but the first two are very patchy in occurrence, both temporally and spatially, on Echinoderm Reef, and their short filamentous growth habit would preclude *A. dactylomela* from cropping them exclusively for long periods of time.

The results are presented in Fig. 7.1, each point representing the mean of three individuals. During the first 20 days of the trial a diet of *Laurencia* spp. produced good growth with a resulting gain in weight of approx. 40 gm during that time, *Herposiphonia* very little growth and *Enteromorpha* sp. moderate growth with a gain of approx. 15 gm. For the entire 31 days of this trial, sea hares maintained on *Laurencia* spp. increased their weight by 60%, those on *Enteromorpha* sp. increased by 48%, but those on *Herposiphonia* only 2%. For the final few days of this trial there was a drop in growth on all three diets and this was probably related to the time of year as identical growth halts were observed from mid- to late June in both the field (Ch. 6.1.5) and laboratory (Ch. 7.3.2) cases.
Growth rates were not calculated for these graphs because of the different starting weights. Smaller animals have higher growth rates but larger animals ingest a greater bulk of food. Nevertheless the extremes of growth produced by animals of approximately the same starting weights on diets of Laurencia spp. and Herposiphonia sp. are obvious.

7.3.2 Details of Growth on Laurencia spp.

Data presented here on growth of A. dactylomela are based on the observations on ten individuals: for each, separate recordings were made of growth, food intake (only Laurencia spp.) and defecation. These data are used here in conjunction with the results on the energy budget for these same individuals. Data were recorded for 40 days (i.e. from 7 May to 15 June 1977). Seawater temperatures during this time are given in Appendix III.3; these ranged from 9.8°C to 14.0°C.

Cumulative growth, food consumption and faecal production are shown in Fig. 7.2. No spawn was produced at any time during these studies. From the graph it is apparent that growth was more or less constant for the first 32 days (i.e. to 6 June), and following that time ceased so that little new flesh was added over the final eight days. On two of the later sampling times growth was actually negative. The reasons for this growth stoppage are considered in the discussion on growth (Ch. 7.5.2).

Food intake and faecal output were constant and relatively equal at approx. 0.3 gm dry weight.day⁻¹. Actually the mean quantity of food ingested was 0.353 gm dry weight.day⁻¹, SE = 0.02, SD = 0.067. Both lines show a peak after 26 days but this is caused by an unusually long sampling interval, the experimental animals being left for eight days instead of the customary three. However, in neither case did the rate of feeding or egestion alter during this time.

My only record for growth of a known individual in the laboratory for an extended period is for one A. dactylomela whose length and weight were monitored
weekly from 18 January to 14 June 1976. This specimen was maintained on a diet of *Laurencia* spp. During these five months, its length increasing from 33 mm to 165 mm and its wet weight from 1.24 gm to 112.27 gm (Fig. 7.3).

To examine how the growth rate is affected when food is unavailable three *A. dactylomela* (66.8 gm, 80.7 gm, 102.7 gm wet weight) were starved for 31 days (19 May – 19 June 1976), each in a separate aquarium. Each tank was scrubbed every 3 days and its water was changed to remove any accumulations of epiphytic algae or faeces that the sea hares could use as nutriment. No egg masses were laid during these starvation trials. At the end of the time, the mean loss of weight was a mere 3.2% of the original (mean loss = 0.086 gm wet weight day$^{-1}$, SE = 0.029, SD = 0.05). Clearly *A. dactylomela* is able to survive for very long periods without food, fasting producing little decrease in overall body weight. Apparently *Aplysia* species require only very small amounts of energy for body maintenance – i.e. the quantity of food required for normal metabolism without change in weight. Carefoot (1967b) estimated that the maintenance requirement of *A. punctata* was approx. 0.02 gm dry weight per individual over a 35-day period.

7.4 The Energy Budget.

In any living organism the components contributing to the functioning of that organism must be equal in input and output – the quantitative study of these components (ingestion, growth, reproduction, respiration, excretion) is termed energetics. Measurements of these components are relatively easy to obtain and can be used to describe the energy content of, or flow through, biological systems (Macfadyen, 1963). Results for an individual can easily be extrapolated to the population level. Different species populations can be directly compared using these common energetics units – formerly calories, now Joules. This technique can provide a useful approach in assessing the structure, productivity and functioning of communities.
The theoretical considerations of ecological energetics have been treated fully by Slobodkin (1962), Odum (1963), Paine (1965) and Phillipson (1966). Following I.B.P. terminology (Petrusewicz, 1967; Ricker, 1968) the energy budget of a population may be summarised by the equation:

\[ C = P + R + F + U \]

where \( P = Pr + Pg \)

and \( Pg = B + E \)

where the definition of each term is as follows:

- \( C \) = energy content of the food consumed by the population.
- \( P \) = total energy produced by the population as flesh or gametes.
- \( R \) = energy lost to the population due to metabolism (represented by respiration).
- \( F \) = energy leaving the population as faeces.
- \( U \) = energy lost vis mucus, excreted urine or other exudates.
- \( Pr \) = energy content of the gametes liberated during spawning.
- \( Pg \) = energy content of the tissue added to the population due to growth and recruitment.
- \( B \) = net increase in energy content of standing stock.
- \( E \) = energy content of the individuals lost to the population through mortality, also called elimination.

Also, following standard terminology:

- \( C - F \) = that part of the food that is absorbed into the body through the wall of the alimentary canal.
- \( C - F - U \) = the proportion of ingested energy which is assimilated (A) by the population and has been called energy flow (Smalley, 1960) or gross production (Engelmann, 1966).
- \( C - (F + R + U) = P \) which is total energy produced or production, it is also termed net production (Engelmann, 1966).
In many studies it has been impossible to estimate every component in
the energy equation for a single species population. This has deprived the
studies of internal checks, on their accuracy (Odum & Smalley, 1959; Smalley,
1960; Kuenzler, 1961; Teal, 1962; Golley & Gentry, 1964; Mann, 1965).

Energy loss via nitrogenous excretion and other exudates (U) has,
in many studies, been assumed to be negligible. However, mucus is known to
form a major part of the biological production in some species (Teal, 1957).
And with all opisthobranchs there is a considerable loss of energy through
mucus secretion (see Ch. 4.3), and in the Anaspidea by the production of
exudates by the purple and opaline glands - thus U cannot be ignored. However,
due to analytical difficulties U has not been determined here, and its value
must be estimated by difference in the energetic equation.

7.4.1 Energy of the Food (C).

Approximately one quarter of the Laurencia ingested by Aplysia dactylomela
is composed of inorganic material that cannot be assimilated. Laurencia
distichophylla has a mean ash value of 24.57%, SE = 1.59 (n=5), and Laurencia
sp. 2 has a slightly higher value of 27.04%, SE = 2.48 (n = 6).

A dry weight conversion factor of 12.55% was applied to mixed samples of
Laurencia spp., this is because dry weight was found to have a mean value of
12.55%, SE = 1.00 (n = 37) of damp wet weight.

Calorimetric determinations were made on "mixed" Laurencia samples - i.e.
mixtures of Laurencia distichophylla, Laurencia sp. 1 and Laurencia sp. 2 similar
to those used in the nutrition and food utilization trials of 1976 and 1977,
and also for pure samples of L. distichophylla and L. sp. 2. These results
are given in Table 7.3 below. A one-way ANOVA showed no significant difference
caloric values between the three sets of combustions, the analysis, giving an
F statistic of $F_{2,10} = 1.22$ with a probability of 0.336. These figures
fortunatley justify the use of samples containing mixed Laurencia spp. in the
feeding trials with A. dactylomela because the above figures show both Laurencia
distichophylla and Laurencia sp. 2 to have approximately the same food value. Accordingly, caloric content for Laurencia spp. used in the energy budget calculations has been derived from pooled values for all Laurencia combustions - i.e. mean calorific value for Laurencia spp. = 17,690.78 J.g\(^{-1}\), SE = 138.25 (n = 13). However acting against this standardizing element in my energy budget calculations is the report by Himmelman & Carefoot (1975) of significant seasonal changes in percent dry weight, percent ash content and calorific value in three North American Pacific coast seaweeds.

Table 7.3. Comparison of Combustion Values for Laurencia spp.

<table>
<thead>
<tr>
<th>Algal sample</th>
<th>Mean calorific value (J.g(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mixed Laurencia spp. (n = 5)</td>
<td>17,856.291</td>
</tr>
<tr>
<td>Laurencia distichophylla (n = 4)</td>
<td>17,416.2</td>
</tr>
<tr>
<td>Laurencia sp. 2 (n = 4)</td>
<td>17,799.878</td>
</tr>
</tbody>
</table>

7.4.2 Growth (P).

A dry weight conversion factor of 8.56% was used for tissues of Aplysia dactylomela, as dry weight was found to have a mean value of 8.56%, SE = 0.44 (n = 19) of damp wet weight.

For calorimetry, separate combustions were made on pieces of tissue from the parapodium, oral tentacles, head and buccal mass, and visceral mass. These tissues had a mean energy content of 21,260.11 J.g\(^{-1}\), SE = 553.49 (n = 12).

Since none of the A. dactylomela spawned during the growth and energetics studies a separate output component for reproduction cannot be assessed. Of course, energy required for development of the reproductive organs and maturation of gametes are incorporated with the growth component (P).
7.4.3 Egestion (E).

Separate combustions were made of faecal samples from the *Aplysia dactylomela* used for the energy budget investigations, these faeces being retained following dry weighing. Faeces were homogenized before calorific determinations, and they were found to have a calorific content of 11,422.64 kJ gm\(^{-1}\), \(SE = 204.53\) (\(n = 12\)).

The calorific value of whole *Laurencia* spp. tissue was 17.689 kJ gm\(^{-1}\), that of faecal material 11.417 kJ gm\(^{-1}\) or a reduction of 64%. This drop is indicative of considerable selection of energy-rich nutrient in the digestive process. The calorific content of faecal matter was, therefore, calculated as 36% of the summed dry weight defecated multiplied by the appropriate kJ gm\(^{-1}\) value.

7.4.4 Respiration (R).

The results are given in Fig. 7.4, the line of best fit being determined by least squares. The relationship between dry weight and oxygen consumption gives the regression equation:

\[
O_2 = 0.1488 W + 0.034
\]

where \(O_2\) = oxygen consumption and \(W\) = dry weight of *Aplysia dactylomela*.

To convert oxygen consumption to calories a value of 5.0 cal.ml \(O_2\)\(^{-1}\) was used (Paine, 1965). Therefore, for each individual the calories lost in respiration per day were calculated by multiplying the weight specific oxygen consumption per hour by 24 x 5.0.

The control containers that were incubated for the same times as experimental runs but without an *Aplysia* inside gave a mean respiration value of 0.140 ml \(O_2\) hr\(^{-1}\) (\(SE = 0.05\), \(SD = 0.186\), \(n = 14\)). To test the significance of the differences between the control and experimental respiration chambers, a standard t-test could not be employed because the variances differed so greatly. Therefore, an alternative test based on the work of Scott & Smith (1971) was used, this test producing a close approximation to a Z statistic.
The value of obtained was $Z = 4.2357$ which gives a probability less than 0.0000 and shows there is clearly a significant difference between the respiration of *Aplysia* and that attributable to bacteria alone.

My measurements produced a mean rate of $0.177 \text{ ml } O_2 \text{ gm}^{-1}\text{ hr}^{-1}$ (SE = 0.013, SD = 0.035, $n = 7$) which is well within the range of standard metabolism for molluscs given by Prosser (1973).

7.4.5 **Calculation of the Energy Budget for Individuals.**

Production of an energy budget is the culmination of much experimental work in the laboratory. For the energy budget of *Aplysia dactylomela* the value for respiration for each animal was based on its mean dry weight during the experiments. The separate energy budgets for the ten *A. dactylomela* are given in Table 7.3.

From this table it can be seen that during the 37 days of this trial mean dry weight showed a 54% increase. Mean values calculated for four of the components of the energy equation are: ingestion (C) = 249.3 kJ; ejection (P) = 52.7 kJ; respiration (R) = 103.4 kJ; growth (P) = 53.4 kJ. Therefore, the energy required for respiration is nearly double that combined as lost to egestion and used in growth.

Although the energy lost through the various forms of excretion (U) (i.e. mucus, urine, opaline and purple gland discharge) could not be determined independently, it can be calculated using the equation $C = P + R + F + U$, where P covers the energy requirements for both somatic and reproductive growth. Substituting known values into the equation gives us U = 39 kJ.

Since all the ten animals employed in these trials were juveniles, none produced spawn during the experimental period. Therefore, it is not known how much of the energy referred to the growth component is diverted to development of reproductive tissues.

With regard to the metabolic component (R), it is well known that the rate of oxygen consumption is influenced by activity, temperature, body size, stage
<table>
<thead>
<tr>
<th>Net Assorption</th>
<th>Cross Section (cm²)</th>
<th>Assorption Coefficient (g/cm²)</th>
<th>Infiltration Rate of Water (cm/hr)</th>
<th>Flow (cm³/hr)</th>
<th>Infiltration (cm)</th>
<th>Infiltration (cm/hr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.28</td>
<td>3.3</td>
<td>4.5</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
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<td>2.66</td>
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<td>4.4</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
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<td>2.94</td>
<td>3.1</td>
<td>4.3</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
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<td>3.22</td>
<td>3.0</td>
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<td>0.3</td>
<td>0.0</td>
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<td>3.49</td>
<td>2.9</td>
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<td>0.3</td>
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<td>0.0</td>
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<td>3.5</td>
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<td>0.0</td>
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<td>5.90</td>
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<td>2.8</td>
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</tr>
<tr>
<td>7.97</td>
<td>1.2</td>
<td>2.4</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
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<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
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<td>8.48</td>
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<tr>
<td>8.74</td>
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<td>2.1</td>
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<tr>
<td>8.99</td>
<td>0.8</td>
<td>2.0</td>
<td>0.3</td>
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<tr>
<td>9.25</td>
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<td>10.00</td>
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<td>0.3</td>
<td>0.0</td>
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</tr>
</tbody>
</table>

**Notes:**
- All data measured for 37 days. **X = X** (X).  
- Table 7.4. Adjusted to account for energy budgeted for forest product resources of Louisiana.  

*All values are in cm.*
in life cycle, season, time of day, as well as previous oxygen experience and genetic background (Prosser, 1973). Although no controls can be placed on heritable variables such as genetic background I attempted to ensure all the others were standardized and controlled adequately. Fortunately the animals themselves all acted in the same manner during the respiration experiments - after a short period of acclimation (approx. 10 min.) inside the sealed respiratory chambers, the animals remained quietly motionless for the rest of the time on the lids of the jars so that activity levels were constant (i.e. low) during all respiratory determinations.

The summations of all the energy budgets appear in the three columns to the far left under % efficiency. It is these terms that permit comparisons to be made between different species in different habitats and utilising different foods. Assimilation (A) is simply food ingested minus faeces i.e. \( A = C - F \), and so % assimilation efficiency is \( \frac{C - F}{C} \times 100 \). Calculation of gross and net efficiencies of growth (actually of formation of new protoplasm) follows Richman (1958), Paine (1965) and Carefoot (1967a). The efficiency of growth may be expressed in either of the following ways:

1. **GROSS EFFICIENCY** is the percentage of energy consumed that is converted into new protoplasm - i.e. \( \frac{P}{C} \times 100 \), where \( P \) is the sum of growth and reproduction. Gross efficiency is also called the energy coefficient of the first order (Ricker, 1946).

2. **NET EFFICIENCY** is the percentage of energy assimilated that is converted into new protoplasm - i.e. \( A \times 100 \), where \( P \) is the sum of growth and reproduction. Net efficiency is also called the energy coefficient of the second order (Ricker, 1946).

**A. dactylomela** has a very high value for assimilation of food (79%). However, mean gross and net efficiencies are low - 22% and 28% respectively. It is apparent that assimilation efficiency is related to weight with smaller **A. dactylomela** having a higher efficiency per gram weight than larger ones.
One would expect a priori that assimilation efficiency would be related to the type of food eaten, indeed Carefoot (1967a) suggested herbivores would have lower efficiencies because of the presence of more indigestible material in their diet. However this view does not appear to be correct (Table 7.5).

Table 7.5. Values for assimilation efficiency for molluscs from a variety of trophic levels.

<table>
<thead>
<tr>
<th>Species</th>
<th>Feeding strategy &amp; order</th>
<th>Mean assimilation efficiency (%)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nerita spp. (3)</td>
<td>herbivorous archaeogastropods</td>
<td>40</td>
<td>Hughes, 1972</td>
</tr>
<tr>
<td>Littorina irrorata</td>
<td>herbivorous mesogastropods</td>
<td>14</td>
<td>Odum &amp; Smalley, 1959</td>
</tr>
<tr>
<td>Cominella spp. (2)</td>
<td>carnivorous neo-gastropods</td>
<td>75</td>
<td>Larcombe, 1971</td>
</tr>
<tr>
<td>Amphibola crenata</td>
<td>detritus-ingesting basommatophoran</td>
<td>13</td>
<td>Briggs, 1972</td>
</tr>
<tr>
<td>Limax flavus</td>
<td>herbivorous stylommatophoran</td>
<td>77</td>
<td>Davidson, 1976</td>
</tr>
<tr>
<td>Arion hortensis</td>
<td>herbivorous stylommatophoran</td>
<td>89</td>
<td>Davidson, 1976</td>
</tr>
<tr>
<td>Aglaja inermis</td>
<td>carnivorous cephalaspidean</td>
<td>62</td>
<td>Paine, 1965</td>
</tr>
<tr>
<td>Aplysia punctata</td>
<td>herbivorous anaspidian</td>
<td>67</td>
<td>Carefoot, 1967a</td>
</tr>
<tr>
<td>Aplysia dactylo-mela</td>
<td>herbivorous anaspidian</td>
<td>79</td>
<td>Present study</td>
</tr>
<tr>
<td>Archidoris pseudo-argus</td>
<td>sponge-rasping dorid</td>
<td>52</td>
<td>Carefoot, 1967a</td>
</tr>
<tr>
<td>Dendronotus fondosus</td>
<td>hydroid-eating dendronotacean</td>
<td>86</td>
<td>Carefoot, 1967a</td>
</tr>
<tr>
<td>Mercenaria mercenaria</td>
<td>filter-feeding lamellibranch</td>
<td>29</td>
<td>Hibbert, 1977</td>
</tr>
<tr>
<td>Scobicularia plana</td>
<td>deposit-feeding lamellibranch</td>
<td>61</td>
<td>Hughes, 1970</td>
</tr>
</tbody>
</table>

Davidson (1976) concluded that food quality and age were the factors most strongly influencing assimilation efficiency in the land slugs he was studying. The view that food quality affects efficiency is very strongly supported by Carefoot's works on Aplysia species (1967b; 1970) in which he
showed that *A. punctata* had 73% efficiency on a diet of the alga *Delesseria sanguinea* but only 15% on *Cryptopleura ramosa*; also he found *A. dactylophora* to have 84% efficiency on *Cladophora* sp. but only 43% on *Galaxura oblongata*. Clark (1975) suggested gut modifications might relate to changes in assimilation efficiency.

It can be concluded that *A. dactylophora* achieves its rapid growth by its ability to absorb a great amount of the food it eats. Its ability to convert this food into tissues and hence grow larger is low. In other words it achieves its growth success in bulk absorption rather than skill in selective absorption.

7.5 **Discussion.**

7.5.1 **Discussion on Acceptable Foods.**

The diet of an organism in many cases is probably one of the most important limiting factors to any species' geographic range (Edmunds, 1977). It is not surprising to find that many of the most widely-distributed species within the order *Anaspidea* have a very wide range of diet. Species of *Aplysia* feed on members of the divisions Chlorophyta and Rhodophyta and are extremely wide-ranging in their choice of food within these categories. However, it has been demonstrated that these seaweeds differ in their growth-supporting value for *Aplysia* species (Carefoot, 1967b, 1970), even to the degree that when a choice is offered, *Aplysia* species eat preferentially those species most compatible with their capacity to utilize the contained nutrients.

All authors have reported *A. dactylophora* to accept several different algae. These sea hares can switch to other species of Rhodophyta or even Chlorophyta when the preferred species is unavailable. In the literature, the association between *Aplysia dactylophora* and various species of the rhodophycean family Rhodomelaceae appears over and over again, particularly for the genera *Laurencia* and *Acanthophora*. Carefoot found that on Barbados,
A. dactylomela grew most quickly on a diet of Enteromorpha sp., but this alga was scarce in the habitat. Growth and percentage absorption figures were high as well for A. dactylomela feeding on diets of Laurencia papillosa and Cladophora Lederhendler (1977a; 1977b). collected Aplysia dactylomela from the South West corner of Puerto Rico near La Parguera, and he suggested that Acanthophora spicifera was the main foodstuff, with supplements of Laurencia obtusa and L. papillosa when available. In Hawaii, Switzer-Dunlap & Hadfield (1977) maintained A. dactylomela on Ulva spp., Acanthophora spicifera, Laurencia sp. or Spyridia filamentosa. These workers found success of metamorphosis was highest on Laurencia sp. collected in the field. In New Zealand, A. dactylomela feeds predominantly on three species of Laurencia. One could generalise to say that although many species of algae are eaten by species of Anaspidea, those of the Rhodomelaceae seem to be selected preferentially, and this may be because they give the best growth.

Finally one should note that this catholicism of diet is not the sole strategy within the Anaspidea, and there are some species that show dietary specializations. Certain members appear to exhibit obligate relationships with specific plant species either for food or camouflage, for example Phyllaplysia tayloiri lives only on the phanerogam Zostera marina (McCauley, 1960; Beeman, 1968; 1970; Bridges, 1974; 1975), and Phyllaplysia smaragda is always closely associated with another spermatophyte - Syringodium filiforme (Clark, 1977).

7.5.2 Discussion on Growth.

Aplysia dactylomela grows continuously like all other anaspideans. By contrast, some mesogastropods of the family Cymatiidae alternate between feeding phases when saltatory growth occurs, and reproductive phases when no feeding or growth takes place (Laxton, 1968). Aplysia dactylomela is not obliged to feed every day however, and it can undergo prolonged periods of starvation - perhaps the latter happens during rough weather or whilst in search of food, with little loss of weight (Ch. 7.3.2).
Aplysia dactylomela has a high intrinsic rate of growth manifested by its large adult size and short life span of a single year, this growth pattern is seen in all other Aplysia species. Krigstein et al. (1974) have elegantly depicted the laboratory growth of A. californica and I have repeated part of their illustration (Fig. 7.3) to give an idea of the high rate of growth possible. Indeed, under such ideal conditions A. californica has a generation time as short as 19 weeks.

I have calculated the growth rate of A. dactylomela from known individuals independently three times during this study—once in the field and twice in the laboratory. All determinations were made during May and June when seawater temperatures were between 14-17°C (Table 2.1). In the field there was an increase in mean weight of 3.71 gm wet weight.week⁻¹,

SE = 1.02 (Ch. 6.1.5). If my results for laboratory growth are expressed on a comparable wet weight basis, then the ten A. dactylomela maintained on Laurencia spp. for the energetics studies (from 7 May - 15 June 1977) displayed an increase in mean weight of 5.14 gm wet weight.week⁻¹,

SE = 0.39. Similarly, the three A. dactylomela maintained on Laurencia spp. to study growth on that particular diet (19 May - 19 June 1976) showed an increase in mean weight of 12.7 gm wet weight.week⁻¹. The closeness of growth rate for all three trials, particularly for the field data and ten laboratory-fed individuals is most pleasing. It was to be expected that growth rates produced in laboratory trails would be higher than for the field. In the laboratory, animals were provided with a continuous and abundant food supply that was available and accessible (i.e. feeding was not curtailed because of low tides), and thus no time was lost to searching and unfavourable physical conditions (storms).
From the growth shown by the single individual in the laboratory (18 January - 14 June 1976) it is apparent that the growth rate can be much higher in summer when temperatures are greater. The other laboratory trials show growth drops to virtually nil over winter when temperatures reach their minimum. What is clear is that *A. dactylomela* displays a variable growth pattern during its short life. Initially all the assimilated energy is channeled into growth in size of the body but beyond a certain size (80-150 gm wet weight, see Gonad Index Ch. 6.1.9) a disproportionate amount of energy is diverted into growth for reproduction. Even though, the maximum growth rate is achieved in summer immediately after settlement, only a very few individuals reach the prerequisite size and attain sexual maturity before the falling temperature halts growth in mid-June. Not only is growth dependent on temperature, but it is also related to the species of food being eaten (Carefoot, 1967a; Ch. 7.3.1).

Growth is not determinate and once a portion of energy has been allocated for reproduction, excess energy derived from food is again used for somatic growth. Consequently, individuals that never find a mate reach enormous proportions. The only *A. dactylomela* ever seen subtidally at Knot Rock (15 May 1977) during the entire course of my studies there measured 450 mm and weighed 1410 gm when found! Such giants are exceptional.

Growth efficiency is the efficiency with which energy from assimilated food is turned into new protoplasm. It is calculated by dividing the total growth increment by the food consumed minus faeces and converting to a percentage. Carefoot (1967b) found growth efficiency declined markedly as animals grew larger. He also showed that growth efficiency was related to the species of alga being consumed, and that in general growth efficiencies decreased in accordance with the order of decreasing value of an alga for growth.

Because *Aplysia* species display flexible growth patterns according to the dictates of the local environment, comparisons of growth published overseas are of limited value. On the Island of Barbados in the Caribbean Sea, Carefoot
(1970) found *A. dactylomela* to add an increase in mean dry weight week\(^{-1}\) of 1.3 gm on a diet of *Cladophora* sp., 2.6 gm on *Enteromorpha* sp., 1.34 gm on *Ulva fasciata* and 1.34 gm on *Laurencia papillosa*. However, on the basis of mean percentage increase in dry weight from mean dry starting weight, *A. dactylomela* produced an increase of 100% over a 14-day period on a diet of *Enteromorpha* sp. This must be close to the maximum rate possible for *A. dactylomela*. During these trials seawater temperature varied between 27-28\(^\circ\)C.

7.6 *Energy Budget for the Population.*

Once the energy relations have been determined for a number of experimental animals it is usual to extrapolate these results to the whole population by calculating \( P_g \) (= energy added to the population due to growth and recruitment), \( \Delta B \) (= net increase in energy content of the standing stock) and \( E \) (= energy content of individuals lost from the population through mortality) (see Ch. 7.4). However, data on recruitment and mortality must be incorporated. Implicit in the reckoning is the assumption that \( \Delta B \) is almost zero and that the population of the species being examined is in a steady state (Slobodkin, 1962).

It is doubtful that the *A. dactylomela* population on Echinoderm Reef could ever be considered to be in a steady state. I have calculated figures for growth (Chs. 6.1.4, 7.3), for recruitment (Ch. 6.1.3) and mortality (Ch. 6.1.10), and all show extremely high variation from month to month. Changes in all of these processes occurs suddenly and have great magnitude (due to death in storms, or sudden high recruitment). Phillipson (1966) felt it was desirable to consider energy relations on a yearly basis for the compilation of a population energy budget (e.g. in terms of \( \text{kJ.ha}^{-1}.\text{year}^{-1} \)).

In his studies on the basommatophoran pulmonate *Amphibola crenata*, Briggs (1972) calculated \( \Delta B = -5.2 \text{kJ.m}^{-2}.\text{year}^{-1} \) between 1970 and 1971, thus showing the population in his study area to be essentially in a steady state condition.
Because of the dynamic structure of the *A. dactylomela* population throughout the year separate sub-budgets relating food and *A. dactylomela* density have been constructed (Ch. 8).

Here the energy budget for the population can be visualized in terms of a balance sheet. If the total energy ingested over a certain period is taken as 100% (i.e. C = 100) then the various outputs can be calculated as proportions and these are depicted in the following flow chart.

![Energy Budget Diagram](image)

The mean ingestion rate per month for an average-sized juvenile *A. dactylomela* (55 gm) on Echinoderm Reef is 11.34 gm *Laurencia* dry weight month$^{-1}$ (and this is equal to 200 hJ.month$^{-1}$). Therefore a population of 500 animals would possess the following energy flow for one month.

![Energy Flow Diagram](image)
In Chapter 8, actual values for population densities per month will be compared with the standing crop of Laurencia spp. for the same period, thus allowing the interactions between A. dactylomela density and Laurencia spp. cover to be considered together.

7.7 **Summary.**

1. Aplysia dactylomela discriminates amongst those algae upon which it feeds.

2. The association between A. dactylomela and various species of the family Rhodomelaceae (particularly the genera Laurencia and Acanthophora) occurs repeatedly in the literature. It is probable that all sea hares eat preferentially those algae most compatible with their capacities to utilise the contained nutrients.

3. A diet of pure Laurencia spp. produced a 60% increase in wet weight for specimens maintained in the laboratory for 40 days, Enteromorpha sp. gave 49% and Herposiphonia sp. gave 2%.

4. Growth rates are calculated on three independent occasions between 3 and 12 gm wet weight.week\(^{-1}\). There is close agreement between rates for field (3.71 gm. week\(^{-1}\)) and laboratory (5.14 gm.week\(^{-1}\)) animals.

5. A. dactylomela ingests a mean dry weight of 0.35 gm Laurencia.day\(^{-1}\) and defecation rate is similar. Starved specimens loose only 0.085 gm wet weight. day\(^{-1}\), so the maintenance energy requirement is exceedingly low.

6. Calorimetric determinations, on which the data for absorption and growth are based, yielded the following values for ash-free material: A. dactylomela body tissues 21.26 kJ; Laurencia spp. algal foods 17.69 kJ and faeces of A. dactylomela eating these foods 11.42 kJ. There is no significant difference in energy value between Laurencia distichophylla or either of the two terete species.

7. For an individual, if food intake (C) = 100%, then proportional energy losses are: egestion (F) 22.9%; respiration (R) 41.5%; growth (F) 21.4%; excretions (U) (calculated by substitution) 14.2%. 
Figure 7.1.

*Aplysia dactylomela.*

Laboratory growth on three selected algal diets for 30 days, 19 May – 19 June 1975. Each point represents the mean of three animals.

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Figure 7.2.

*Aplysia dactylomela.*

The growth, food consumption and food production of specimens feeding on *Laurencia* spp. Each point represents the mean of ten animals. May – June 1977.

- Cumulative growth (i.e. mean dry weight).
- Food consumed (i.e. mean dry weight of *Laurencia* spp.).
- Faeces produced (i.e. mean dry weight).
Figure 7.3.

*Aplysia californica.*

Laboratory growth curve for length and weight of living specimens showing that post-hatching development can be divided into three major phases.

Graph from Krigstein et al., 1974.

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Figure 7.4.

*Aplysia dactylomela.*

Growth of a single animal in the laboratory for five months (18 January - 14 June 1976) on a diet of *Laurencia* spp.
Figure 7.5.

*Aplysia dactylomela.*

Linear plot of oxygen consumption versus dry weight (n = 7).

Oxygen consumption values measured at $17^\circ C$. 
$Y = 0.148X + 0.034$
CHAPTER 8
GENERAL DISCUSSION

This discussion is divided principally into three sections. Firstly, conclusions for each of the four species studied are given in the order *Haminoea zelandiae*, *Bursatella leachii*, *Aplysia parvula*, *Aplysia dactylomela* and a general view of the role of each within its community is depicted. The data collected for each species are sufficient to allow aspects of the life cycle of each to be used to demonstrate one particular ecological hypothesis in quantitative terms. In the next section conclusions are presented for the population of *Aplysia dactylomela* on Echinoderm Reef. Finally, *A. dactylomela* is discussed in a broader context with recourse to overseas accounts of its ecology.

If one advocates a universal ecological nomenclature, then *Haminoea zelandiae* must be a typical representative of the "haminoeid niche". Its adult size is slightly larger than average, but its habit of ploughing at the surface of muddy deposits on sheltered shores and cropping filamentous algae is typical of members of its genus throughout the world (Berrill, 1931; Usuki, 1966; Thompson, 1976). From my studies it is apparent that *H. zelandiae* is an annual animal, but because of its long breeding season animals of many size classes are likely to be present at any one time. Reproduction reaches a peak when water temperatures are at a minimum. Usuki (1966) also recorded a long breeding season for *H. japonica*, however breeding is displaced to the opposite season of year to *H. zelandiae*. *H. japonica* spawns maximally in mid-summer (at seawater temperatures of 20–28°C), and temperatures below 13°C suppress spawning entirely (Usuki, 1966).

*Haminoea zelandiae* accepts a variety of seasonal filamentous algae for its food, and overgrazing could be expected on these because of their ephemeral nature. But overgrazing does not occur because of the abundance and diversity of the algal species present. With respect to nudibranchs, Thompson (1964)
noted overgrazing was not characteristic of those species that feed on non-transient foods such as barnacles, sponges, tunicates and bryozoans. "These nudibranchs tend to be annual or biannual species, reach large size, and have restricted periods of egg production. Minimal damage to the food species results, and the larger size of the predator confers added mobility which tends to disperse feeding activity over a broader area" (Clark, 1975).

Therefore, amongst herbivores opisthobranchs, one would expect Haminoea to overgraze rather than Aplysia dactylomela for example. But the fact that H. zelandiae does not overgraze suggests that such herbivores are not comparable to carnivores and that the possibility of overgrazing of ephemeral algae could be circumvented by herbivores being able to eat a great many algal species - i.e. they have a broader dietary range than most nudibranchs.

Greater densities of H. zelandiae occur between MSL and ELWN, these levels coinciding with the inner third of the low-tidal reef flat at Motukaraka Island. Haminoea zelandiae does not extend subtidally. Population densities are more or less constant throughout the year but verification is difficult owing to the extremely cryptic behaviour of juveniles, a behaviour which has been noted before for nudibranchs (Potts, 1970). Maximum ecological effects of this species are exerted from mid-winter to mid-summer when such algal entities as Colpomenia sinuosa and "green algal stubble" are present on the shore. Patterns of population density for H. zelandiae and for associated algae can be dramatically different at different levels on the same shore. Since migration of H. zelandiae across the shore is of no appreciable extent, then at times processes on the one shore are so completely different that different parts of the same reef platform could quite justifiably be analysed as if they were different shores. Walsby (1977) has already observed this phenomenon in his studies on the archaeogastropod Turbo smaragdus.

**Bursatella leachii** is an enigmatic animal. Analysis of its behaviour has not been simplified by the realization that the study area at Motukaraka Island represents a marginal habitat for this sea hare. Indeed it is probable that **B. leachii** is more at home subtidally rather than intertidally. I did not have
access to a population of this species for long enough to determine such properties as length of life or breeding season. What could be ascertained is that pelagic larvae settle on the cyanophyte *Lyngbya majuscula* in April when this alga has reached maximum cover, the larvae growing rapidly but never annihilating the *Lyngbya*. However, for some unexplained reason a deliberate, directed offshore migration occurs in late April and May, and the entire population vacates the intertidal reef platform in favour of the subtidal despite the continued, though waning, presence of *Lyngbya majuscula*. The principle demonstrated here is that migration does occur, it is not in response to exhaustion of food, nor is it directly related to reproduction - since the migrating individuals are sexually immature. It seems that migration occurs because of social interactions of some kind. The second principle exemplified by this species concerns the erratic nature of its recruitment - populations being present in 1975 and 1977 but not in 1976 or 1978. In years when settlement does occur populations are very dense. It is already well known that recruitment to populations of invertebrates with pelagic larval stages is often erratic (Barker, 1977). Because of these variable and unpredictable patterns of recruitment-dependent occurrence, the implications for exploitation of such populations are immense.

*Aplysia parvula* exists, in Goat Island Bay, as two spatially discrete, non-interbreeding populations, their separation being brought about by association with different algae. In the intertidal *A. parvula* is associated with *Laurencia* spp. (especially *Laurencia* sp. 2), and subtidally with *Plocamium costatum*. The entire Goat Island Bay population may be self-recruiting. Although the different intertidal and subtidal populations could be derived from a common source they have different patterns of colouration (reflecting different diets), of growth and survivorship. The intertidal habitat is marginal, whereas the subtidal is close to being optimal. *A. parvula* has an annual life cycle in agreement with Usuki's (1970) findings for a Japanese population.
For *Aplysia dactylomela*, it is now possible to give a good prediction of the localities and times of occurrence of the population on Echinoderm Reef. It is probable that the recruits on Echinoderm Reef are not the progeny of any of the few sexually-mature adults that occur there. And indeed detailed studies of life histories for other anaspideans have shown no self-recruitment to studied populations (e.g. Carefoot, 1967b), the same holds true for nudibranchs (Potts, 1970; Clark, 1975).

It is apparent that *A. dactylomela* is very dependent on species of the red algal genus *Laurencia* - for recruitment, for nutrition and growth, and for defense.

The central approach maintained through this thesis has been to consider *A. dactylomela* in the context of its food and the dependence of each upon the other. I have considered what effect food has on the demography of *A. dactylomela* and also attempted to separate the effects of density-governing factors as temperature, food and grazing. This approach follows the philosophy of Stephenson & Stephenson (1972) and Clark (1975) which has been stated concisely by Harris (1973): "To understand the ecology of the predator, it is important to know the ecology of the prey". This statement is equally true for herbivorous opisthobranchs and algae as it is for the carnivorous opisthobranch/coelenterate relationships studied by Harris.

It would be desirable to present energy budgets for both the herbivore and food as the culmination to such a study as mine, but the *A. dactylomela* population under surveillance was not in a steady state. I have already given the reasons (Ch. 7.4.5) why I have not done so.

My alternative is to present quantitative data to show the ingestion rate (i.e. the food required) of the *A. dactylomela* population for a particular time and to consider this against the standing crop of *Laurencia* spp. for the same time. Although these are both instantaneous measurements, they are relative to each other and do reflect degree of nutritional dependence of the herbivore.

For *Aplysia dactylomela* the units selected for these comparisons were ingestion (gm dry weight *Laurencia* spp.).ha$^{-1}$ .month$^{-1}$, and these values were
derived by amalgamating known densities of animals.m$^{-2}$.month$^{-1}$ (Ch. 6.1.7) with a figure for ingestion rate per month. Figures for density were divided by 2.76 to give estimates relating to an area of one hectare (i.e. 10,000 m$^2$).

It is known that a medium-sized A. dactylomela (55 gm wet weight) needs to ingest 249.3 kJ in 37 days (Table 7.4), and therefore for one month the amount ingested becomes 202.1 kJ.month$^{-1}$. For the Laurencia spp., values for percent cover.0.1 m$^{-2}$.month$^{-1}$ (Table 5.5) were converted to kJ.ha$^{-1}$.month$^{-1}$. This conversion needs explanation. Firstly the values for cover.0.1 m$^{-2}$.month$^{-1}$ were converted directly to dry weight equivalents. This conversion was done through a regression relationship relating percentage cover to density for known samples. However, when the points for known samples were plotted (Fig. 8.1) it was seen that the points plotted form a dog's leg. What this means biologically is that up to approximately 30% cover, weight and cover values for Laurencia spp. are directly related but beyond that cover only increases gradually for rather large increases in weight - in other words outward spread and upward growth occur together in small patches of Laurencia spp., but beyond 30% upward growth predominates (so weight continues to rise); outward spread still occurs but to a relatively less extent. I have overcome this problem by incorporating a figure for mean maximum height on each sample taken (see Ch. 5.7.2). Because the relationship between percent cover and dry weight could not be adequately explained in terms of a single, simple linear regression model two separate regressions were employed. In this case the first line had to be of the form $Y = mX$, where $m = \frac{X_i Y_i}{X_i^2}$ so that it would go through the origin (i.e. $b = 0$). This was necessary because a lack of Laurencia (i.e. no weight value) can have no cover either. Weight values < 3 gm were used to calculate this regression for which the equation was $Y = 14.397X$ (where $Y = %$ cover and $X = gm$ dry weight). The second line was a simple regression equation and weight values > 2 gm were used in its calculation, the relationship being $Y = 2.98X + 24.38$ (where $X$ and $Y$ are as above). When plotted, the lines intersected at a cover value of approx. 30%. Use of these conversions gave values of gm dry weight.
Figure 8.1.

Combined Laurencia species.

Relationship between dry weight and total cover (for areas of $0.1 \, m^2$) at Echinoderm Reef. Cover values were derived by the mm squared method (ref. Chapter 4.1.4).
0.1 m$^{-2}$.month$^{-1}$, they were then multiplied by 10 to give gm.m$^{-2}$.month$^{-1}$ values. Now from calorimetry it is known that 1 gm dry weight Laurencia = 17, 690 J, so the figures were then multiplied by 17.69 to convert to kJ.m$^{-2}$.month$^{-1}$. The final step was to multiply by 10,000 to convert m$^{2}$ to ha, and to give a final value in units of kJ.ha$^{-1}$.month$^{-1}$. Figures for standard errors for both the Aplysia and the Laurencia were treated with the same conversion procedures as the actual means themselves. Table 8.1 gives the final comparative values.

Table 8.1. Comparative estimates for requirements for ingestion by the Aplysia dactylomela population on Echinoderm Reef and comparison with estimates for the standing crop of Laurencia spp. in the same area. Standard errors accompany means.

<table>
<thead>
<tr>
<th>Month</th>
<th>Population Energy Requirement (kJ.ha$^{-1}$.month$^{-1}$)</th>
<th>Standing crop (kJ.ha$^{-1}$.month$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>0.4 x10$^{5}$ $\pm$ 0.021 x 10$^{5}$</td>
<td>116.4 x 10$^{5}$ $\pm$ 8.85 x 10$^{5}$</td>
</tr>
<tr>
<td>February</td>
<td>0.882 $\pm$ 0.578</td>
<td>89.51 $\pm$ 1.59</td>
</tr>
<tr>
<td>March</td>
<td>4.11 $\pm$ 3.478</td>
<td>142.23 $\pm$ 5.66</td>
</tr>
<tr>
<td>April</td>
<td>4.10 $\pm$ 1.508</td>
<td>142.76 $\pm$ 3.71</td>
</tr>
<tr>
<td>May</td>
<td>2.62 $\pm$ 1.23</td>
<td>138.34 $\pm$ 5.84</td>
</tr>
<tr>
<td>June</td>
<td>4.42 $\pm$ 1.413</td>
<td>59.79 $\pm$ 12.74</td>
</tr>
<tr>
<td>July</td>
<td>3.11 $\pm$ 1.551</td>
<td>18.57 $\pm$ 2.48</td>
</tr>
<tr>
<td>August</td>
<td>1.73 $\pm$ 1.029</td>
<td>16.98 $\pm$ 4.07</td>
</tr>
<tr>
<td>September</td>
<td>0.27 $\pm$ 0.143</td>
<td>27.6 $\pm$ 5.84</td>
</tr>
<tr>
<td>October</td>
<td>0.027 $\pm$ 0.022</td>
<td>41.22 $\pm$ 9.02</td>
</tr>
<tr>
<td>November</td>
<td>0</td>
<td>78.01 $\pm$ 9.2</td>
</tr>
<tr>
<td>December</td>
<td>0</td>
<td>130.9 $\pm$ 1.23</td>
</tr>
</tbody>
</table>

This table shows that for all months, the standing crop of Laurencia spp. was in excess of that capable of being ingested by A. dactylomela. From September to February, when numbers of A. dactylomela are low, ingestion rates were much lower than what algae was available. However from March to May (when A. dactylomela densities were high), and from June to August (when
Laurencia spp cover values are falling), the differences between the two figures lessens greatly. In July the standing crop was only approx. six times that required for minimum ingestion. According to these figures the Aplysia dactylomela population should never be limited by a shortage of Laurencia spp. food. But A. dactylomela is not the only user of the standing crop of Laurencia spp., other grazers such as Aplysia parvula and A. juliana, Etoniella spp. and polychaetes all eat Laurencia and because of the patchy nature of the distribution of Laurencia spp. relative food shortages could occur for A. dactylomela on Echinoderm Reef during June to August. However, it must be emphasised again that these values are instantaneous estimates only, they tell nothing about production.

From the foregoing quantitative treatment, it would appear as though there is seldom an absolute shortage of food for the Aplysia dactylomela population on Echinoderm Reef, particularly if other acceptable food algae are considered. However, from my own observations it is clear that relative shortages do occur, and whilst foraging in search of new supplies, chances of mortality for A. dactylomela are greatly increased.

In a similar fashion Potts (1970) considered the effect of food (the barnacle Balanus balanoides) on a population of the carnivorous dorid Onchidoris fusca. He estimated the population of barnacles in an area of 32 m² to be 16.0 x 10⁵. After seven months a population of Onchidoris (423) are capable of eating only 0.24 x 10⁵ barnacles, and even with the presence of a second, and more effective predator (Thais lapillus) only 2.16 x 10⁵ barnacles would be lost. Potts concluded that even when the barnacles were at their lowest densities, adequate supplies would remain to feed both Onchidoris and Thais.

To return to herbivores, Baker (1970) maintained it was unlikely that seasonal changes in food supply could affect the mortality rate of a pulmonate snail (Cochlicopa lubrica) in a grass sward habitat since there was a plentiful supply of vegetation throughout the year.
Therefore, unless herbivores concentrate narrowly on a short-lived diet, there should always be enough food for all herbivorous and scavenging species of animal (Andrewartha, 1961). Some studies on carnivorous opisthobranchs have shown sufficient food to be continuously available (e.g. Potts, 1970; Nybakken & Eastman, 1977). One of the first signs of food shortage is overgraze where excess feeding damages the food supply itself. Clark (1975) quantified overgrazing in terms of a predation index (= ratio of predator biomass to food species biomass), finding that when the index reached a critical level (1%) the food item will suffer damage through overfeeding by the predator. This index is adequate for species that live in a restricted, easily defined environment (e.g. wharf piles, mooring buoys etc.) where there is a fixed amount of food available, but in most field situations opisthobranchs tend to crop all the food available before moving on and as a consequence the symptoms of overgrazing could appear well above the 1% level. Here shortage of food could only be considered in terms of relative shortage.

If the Echinoderm Reef population of Aplysia dactylomela is not limited by food, then other possible factors that could determine its size or success are/competition and predation. There is evidence for direct competition from the other grazers of Laurencia that have been mentioned already in the discussion. Aplysia dactylomela, however is more efficient. Because of its catholic diet A. dactylomela must also compete with other generalist invertebrate grazers such as gastropods, chitons and echinoids for supplies of algae, particularly the shorter filamentous varieties. However, I feel that A. dactylomela is under considerable pressure from indirect competition for food - through direct competition for refuge space with the echinoid Evechinus chloroticus. At times of rough weather A. dactylomela seek shelter in depressions and beneath ledges and stones. Here individuals can retreat for three or four days, sometimes they become buried beneath wave-transported sand deposits. Evechinus chloroticus also inhabits such microhabitats on Echinoderm Reef and it is certain that because of the small size of such spaces and the spiny nature of E. chloroticus that A. dactylomela would be ousted by the sea urchin. Such
spaces are sufficiently few in number to be a limiting resource. Ayling (1978) gave a histogram of the size-frequencies of urchins on Echinoderm Reef and there was almost equal representation of all size classes from 20 - 40 mm test diameter (62% of the population had test diameters in this range). These sizes were smaller than for subtidal populations in similar areas (e.g. at "Beach Canyon" on the south-eastern tip of Goat Island where 72% of the population had diameters between 55 - 75 mm). Density (and size also) of urchins on Echinoderm Reef has been suppressed by humans gathering them for food. However, since this area has been protected as part of the Leigh Marine Reserve this source of loss has ceased and both density and mean size are now increasing. Because *E. chloroticus* is a superior competitor for space it is probable that the carrying capacity of Echinoderm Reef for *A. dactylomela* will become progressively decreased.

As the *Evechinus chloroticus* population grows, so will its effect as a direct competitor for algae with grazing gastropods and *Aplysia dactylomela*. Urchin browsing could affect, however, the variety of algae existing on Echinoderm Reef. Paine & Vadas (1969) found that removal of urchins (*Strongylocentrotus* spp.) lead to significant changes in algal species composition within periods of less than a year. There was an initial increase in the number of algal species represented but subsequently all the intertidal areas became dominated by a single algal species (*Hedophyllum sessile*).

The data on recruitment, growth and mortality for *A. dactylomela* can be synthesized into a model of population density on the shore at Goat Island Bay (Fig. 8.2). The model is only for post-metamorphic individuals. It starts with settlement of *A. dactylomela* from the plankton since it is at this stage that juveniles become visible and begin to exert grazing pressure on intertidal algae. The first settlers appear on the shore between January and February each year, and since the larvae have already spent approx. one month in the plankton (Switzer-Dunlap & Hadfield, 1977) this implies oviposition starts between December and January. Taking curve A to be the typical case, density rapidly increases with continued settlement. After a maximum, the density drops
Figure 8.2.

*Aplysia dactylomela.*

Graphical model of population density on the shore at Goat Island Bay, Leigh, New Zealand.
only gradually until July or August, this decrease being due to storms and size-selective predation. Density falls steeply through winter and tends towards the zero asymptote as a result of severe storm depletion and relative food scarcity. However, recruitment can continue until June and curves B and C represent density curves for the later settlers. Curve B depicts a settlement that results in a higher density than that initially attained; curve C shows the alternate possibility. Both of these later curves fall very sharply towards zero and this decay rate is more rapid than for the first recruits.

The major source of mortality for all size classes of *Aplysia dactylomela* on Echinoderm Reef is storms, particularly those that occur during winter when their effects reinforce other causes such as lowered temperatures and decreased availability of food that are already affecting the sea hares. Potts (1970) postulated that storm conditions caused high mortality of the dorid *Onchidoris fusca* on upper rock faces and Paine (1965) found that in exposed situations densities of populations of *Aglaja inermis* were inversely correlated with the presence of inclement conditions. Nybakken (1978) suggested that low abundances of nudibranchs and dorids during times of stormy weather could be due to individuals seeking shelter and protection.

As already stated in Chapter 6, it appears that Echinoderm Reef presents a marginal, or sub-optimal, site for habitation by *A. dactylomela* (Ch. 6.1.11). Evidence for this belief comes from my studies on growth rates in the field (Ch. 6.1.4) and laboratory (Ch. 7.3), density (Ch. 6.1.6), the Gonad Index (Ch. 6.1.9), mortality (Ch. 6.1.10) and finally the food (Ch. 5.7). The results of life in this rigorous environment for *A. dactylomela* are a drop in numbers, a density-dependent grazing effect and very low egg production.

Paine (1965) recognized the following characteristics to be possessed by populations of opisthobranchs in poor areas: relative numerical variability; lack of reproductive success; small individual size. In comparison, for a favourable environment there is: numerical stability of local populations; large individual size attained and there is persistence of egg masses and high survival of the developing young. All these characteristics for
unfavourable environments are shown by the Echinoderm Reef population of *A. dactylomela*. It is true for *A. dactylomela* that events independent of population density contribute more to mortality in such a sub-optimal environment (Nicholson, 1958; Watt, 1962).

Therefore in summing up my aims as stated in the introduction - i.e. "to examine the effects the populations of herbivores have on their algal food resources, and if there is any degree of dependence so as to suggest incipient accommodation by the grazers to supplies of food". It appears that when the environment is optimal a herbivore does have an interplay with (i.e. an inter-relation with, or even accommodation to) its food, but as the environment becomes progressively harsh, factors other than food act well before density effects can limit the herbivore's population.

I now consider *A. dactylomela* in a broader world-wide context, examining its population properties at different geographic localities to see how the genetic potential of the species is expressed according to prevailing environmental regimes. It is apparent that *A. dactylomela*, like other *Aplysia* species, is genetically capable of being an exploitist species possessing the following attributes: high fecundity (MacGintie, 1934; Bandel, 1976); ability to delay metamorphosis (Krigstein et al., 1974; Switzer-Dunlap & Hadfield, 1977); short life cycles (Krigstein et al., 1974, found the life cycle of *A. californica* could be completed in the laboratory within 19 weeks; however most species are annuals in the field); rapid growth (Carefoot, 1970). However, the environment dictates how fast and to what degree these attributes will be displayed.

One of the key factors to understanding the biology of opisthobranch molluscs must be temperature (Harris, 1973) and it would seem that temperature does exert overall control on the life history of *A. dactylomela*. For example in Hawaii, Switzer-Dunlap & Hadfield (1977) found that: "Well-fed adults of all species (i.e. *Aplysia dactylomela*, *A. juliana*, *Dolabrifera dolabrifera*, *Stylocheilus longicauda*) spawned throughout the year." Similarly an eight-month survey of egg-laying by *A. dactylomela* at Puerto Rico found no seasonality (Lederhendler, 1977b). Growth rates of *A. dactylomela* in tropical waters are
very rapid (e.g. Hawaii - Switzer-Dunlap & Hadfield, 1977; Puerto Rico - Lederhender, 1977b). These observations on populations of A. dactylomela in the tropics indicate that it is definitely a tropically-centred species.
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16-17.

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APPENDIX I. TAXONOMY OF THE NEW ZEALAND ANASPIDEA

Introduction.

There has never been a systematic review of the sea hares of New Zealand. The only catalogues of species from this country are those by Pilsbry (1896) and Suter (1913) and these works do not compare New Zealand taxa with overseas ones mainly because of inadequacy of original descriptions. Bebbington (1977) has reviewed the aplysidiid species from Eastern Australia. Pilsbry (1896) admitted that the New Zealand and Australian species were so inadequately known that it was impossible even to construct a key for their distinction. Names for three species described from New Zealand are based essentially on shells alone: Aplysia hamiltoni Kirk; Aplysia brunnea Hutton; Aplysia venosa Hutton.

Undoubtedly the works that established a firm basis for descriptions of Anaspidea are those of Eales. Initially the L.M.B.C. Memoir on Aplysia (1921) and much later her 'Revision of the World Species of Aplysia' (1960). Eales emphasized the need for a description to integrate data on the living animal - its colouration, shell, organs of the mantle cavity and reproductive system. These works, particularly the second, not only established the requirements and criteria needed to define any anaspidean adequately, but also gave an impression of the vast synonymy that exists within the genus. Since that time, many descriptions of new taxa belonging to the order (e.g. Phyllaplysia padinae Williams & Goslinger, 1973; Phyllaplysia maragda Clark, 1977) incorporate information on all the above characters and leave no doubt as to the species described.

This revision is based on examination of as much type material as can still be located, a re-examination of specimens studied by Eales before her monograph and subsequently returned to New Zealand, the collections of Anaspidea of museums, universities and private workers.

In the descriptions that follow, the synonymies list in full the New Zealand and Eastern Australian references only since these are relevant
to the species dealt with here and full synonymies would not only involve enormous lists but also unnecessarily duplicate those already given. In the locality records that follow, I have listed only those species I have examined myself.

List of Abbreviations.

A.I.M. Auckland Institute and Museum
C.M. Canterbury Museum, Christchurch
N.M. National Museum of New Zealand, Wellington
Pilgrim Coll. Pilgrim Collection, University of Canterbury, Christchurch
P.B.M.L. Portobello Marine Biological Laboratory, Otago

Higher Classification of the Anaspidea

Pilsbry (1896) in Tryon's 'Manual of Conchology' recognized only one family, the Aplysiidae, with three subfamilies - Aplysiinae, Dolabriferinae and Dolabellinae. Thiele (1931) followed the same scheme. Beeman (1966) divided the Aplysiidae into Aplysiinae, Dolabriferinae, Notarchinae and Dolabellinae. Marcus (1972) laid emphasis on the nervous system and recognized two families - Aplysiidae (containing Aplysiinae and Dolabellinae) and Notarchidae (containing Notarchinae and Dolabriferinae).

Apart from Akera, the other Anaspidea form a compact assemblage sharing such an overall similarity that they are surely monophyletic and can be accommodated within one family. I suggest Marcus' scheme should be amended to reflect this common origin in which the four subfamilies are maintained, two being "longicommissurate" and two being "brevicommissurate", but that these categories are not accorded any status between the family and subfamily levels. The classification proposed is thus:

Order Anaspidea (= Aplysiacea, = Aplysiomorpha)

Suborder Akeracea

Family Akeridae
Suborder Aplysiacea

Family Aplysiidae

Subfamily Aplysiinae  Aplysia Linnaeus, 1767
Syphonota A. Adams, 1854

Subfamily Dolabellinae  Dolabella Lamarck, 1801

Subfamily Notarchinae  Notarchus Cuvier, 1817
Barnardaclesia Eales & Engel, 1935
Bursatella Blainville, 1817
Stylocheilus Gould, 1852 (= Aclesia Rang, 1828)

Subfamily Dolabridferinae  Dolabridfera Gray, 1847
Petalifera Gray, 1847
Phyllaplysia P. Fischer, 1872

The Notarchinae and Dolabridferinae could be combined but I separate them using the following distinguishing features.

Notarchinae - Body high, plump, produced posteriorly, foot relatively narrow, mantle walls able to produce respiratory movements to ventilate mantle cavity, shell usually absent, body covered with branched villous processes, egg-string a loose, tangled mass as in Aplysiinae. Notarchus is distinct because the parapodia are separated from the visceral mass and gill, however the characters separating Bursatella and Stylocheilus are less definite.

Dolabridferinae - Body flattened, rounded posteriorly, foot broad, no contraction of mantle wall, shell usually present, spatuliform, body covered with tubercles or occasionally villi, egg-string a regular, flattened zig-zag structure. The differentiation of Petalifera and Phyllaplysia is uncertain and needs further clarification.
New Zealand Anaspidea.

There is a total of eight species of Anaspidea in New Zealand, five of these belonging to the genus *Aplysia*. All eight occur in northern New Zealand, but only three *Aplysia* species occur at Wellington and further south. One new record is added to the fauna - *Aplysia* (Varria) *extraordinaria* (Allan). No species is endemic.

The eight New Zealand species of the order Anaspidea are as follows:

*Aplysia* (Pruvotaplysia) *parvula* Mörch, 1863
*Aplysia* (Varria) *dactylomela* Rang, 1828
*Aplysia* (Varria) *keraudreni* Rang, 1828
*Aplysia* (Varria) *extraordinaria* (Allan, 1932)
*Aplysia* (Aplysia) *juliana* (Quoy & Gaimard, 1832)
*Bursatella* *leachii* Blainville, 1817
*Stylochellus* *longicauda* (Quoy & Gaimard, 1825)
*Dolabrifera* *dolabrifera* (Cuvier, 1817)

The account that follows gives for each species: synonymy; description from living material; notes on salient anatomical characteristics; New Zealand locality records. All the descriptions of external features are compiled from personal observations on living specimens. I have not repeated geographic distribution records for *Aplysia dactylomela*, *Aplysia parvula* or *Bursatella leachii* since they have already been given in Chapter 3. However these details are given here in descriptions of the five other species.


Three subgenera appear recognisable:

1. *Aplysia* s.str. Parapodia rather small, joined high up posteriorly, purple fluid not secreted, opaline glands simple multiporous, penis short, lies in a sheath armed with spiny warts, sheath with a single retractor muscle, nidamental glands of the "banded-ovoid" type.

Type-species by original designation Aplysia dactylomela Rang, 1828.

Parapodia joined low down posteriorly, purple fluid secreted, opaline glands simple or compound uniporous, penis filiform or broad and spatulate, penial sheath with two retractor muscles, nidamental glands of the "banded-ovoid" type. Varria is the largest subgenus. Although Eales (1960) recognized Neaplysia Cooper, 1863 as a distinct subgenus, this was only on the basis of different shell construction and it is probable that Neaplysia and Varria are synonyms because no other characters can be used to differentiate them.


A subgenus of only two Recent species which display a number of primitive features: shell relatively large and strongly concave; foot narrow with a distinct visceral hump that is more or less central; parapodia joined very high up; nidamental glands of the "flat-pocket" type; mantle glands secrete purple fluid; opaline glands simple and multiporous; mantle foramen large.
APLYSIA (PRUVOTAPLYSIA) PARVULA MORCH, 1863

Figs. 3.2A, B; 9.1d; 9.4D, E.

Synonymy.

1863. Aplysia parvula Guilding MS in Möörch, J. Conchyl. 11 : 22, No. 1;


Vict. 27 : 268, No. 9; 1968. Morton & Miller, N.Z. Seashore : 166,

pl. 11, fig. 5; 1968. Morton & Chapman, Rocky Shore Ecology of the


12 : 76; 1973. Thompson & Bebbington, Malacologia 14 : 148, pl. 4a, b;


1869. Aplysia concava Sowerby, Conch. Icon. 17, pl. 6, figs. 24a, b.

1869. Aplysia norfolkensis Sowerby, Conch. Icon. 17, pl. 10, figs. 42a, b;


Hedley, Proc. linn. Soc. N.S.W. 30 : 536, pl. 33, figs. 33, 34; 1918.

Hedley, J. Proc. R. Soc. N.S.W., Suppl. to Vol. 51 : M 107, No. 1148;


1880. Aplysia tryonii Meinertzhagen, Trans. N.Z. Inst. 12 (1879) : 270

[Waimarama, Hawke's Bay].

1883. Aplysia tryoni Meinertzhagen; Hutton, Trans. N.Z. Inst. 15 : 118, pl. 13,


1896. Tethys norfolkensis Sowerby; Pilsbry, Man. Conch. 16 : 99-100, pl. 59,

figs. 42-43; 1932. Allan, Aust. Mus. Mag. 4 : 423; 1941. Allan,

Vict. Nat. 57 : 181, fig. 5; 1950. Allan, Aust. Shells : 212, fig. 50,

No. 3.
1896. *Tethys concava* Sowerby; Pilsbry, *Man. Conch.* 16: 100, pl. 43, fig. 27.


**Remarks.**

The name *parvula* Mörch, 1863 has been validated by the International Commission on Zoological Nomenclature (ICZN, opinion 560, 1959), and *spuria* Krauss, 1848 rejected. The names *concava* Sowerby, 1869 and *norfolkensis* Sowerby, 1869 were based on shells only, the type material not originating in New Zealand. However the name *tryonii* Meinertzhagen, 1880 is a New Zealand-based synonym that has caused much confusion. So much so, that despite numerous unsuccessful requests to New Zealand biologists for specimens referable to *tryonii*, Eales (1960: 273) rejected the name.

Meinertzhagen's (1880) initial description included no figures or description of the shell apart from its dimensions. Hutton (1883) subsequently figured the radula of a specimen from Napier and Suter (1915) gave a figure of the living animal. However, the holotype had been lost by the time Suter wrote his 'Manual' (1913). That Meinertzhagen had more specimens at hand than just the holotype when he prepared his description is apparent from a reference in his text to "All my specimens...", and in fact a series of syntypes is present in the collection of the Canterbury Museum (Cat. No. M.5960). One was chosen by Professor R.S. Allan (14 June 1954) as lectotype of *Aplysia tryonii* (Cat. No. M.5959). There is no doubt that all seven specimens are *A. parvula*. Similarly, Suter's figure is of this species, so rather than rejecting *tryonii* Meinertzhagen, it should be relegated to synonymy of *parvula* Mörch.
Description.

Extended adult length up to 12 cm. Body elongate, obviously divided into long anterior and posterior foot sections and a plump, central visceral hump, tail relatively larger than in other subgenera of Aplysia and more clearly separated from the visceral hump. Foot long and narrow, hind-portion capable of great suction. Parapodia relatively small and thin, joined very high up posteriorly. They do not meet centrally across visceral hump so that mantle, foramen and shell are visible between them, and on right hand side, the anal spout. Parapodia capable of occasional inward contraction, this movement being accompanied by a downward thrust of anterior part of head and foot - probably merely for ventilating the mantle cavity.

Rhinophores long and quite slender, expanded towards their tips, open at outer sides for approx. half their length.

Shell relatively large, elliptic, concave, covered with a pale, horny periostracum that extends beyond the margins as a clear border; interior of shell whitish, nacreous, smooth with two muscle scars, the larger left one being a long narrow crescent with an expanded terminus, that on the right triangular, high on slope of shell, angle of slope of shell 50°.

Deep purple fluid discharged when animal strongly irritated, purple glands well-developed. Opaline gland simply multiporous, Eales (1960) noted that some ducts coalesce anteriorly.

Whole radula elongate and broad, expanded at growing end and rounded towards oldest end by tooth loss in this region, outer lateral teeth being lost first. Radula formula low, a typical formula of 30 x 16.1.16 holds for adults from New Zealand populations. Rachidian elongate, quite compressed with basal plate produced laterally and humped dorsally on either side of mesocone, there being a small elevation between these two main humps, for an adult animal rachidian measures 300 μm between the extensions of the basal plate, and the tooth 90 μm in width from the hollow to the tip of the mesocone. Rachidian with mesocone and three denticles on each side, central
cusp broad and narrowing to a sharp tip, denticulate along both edges with 8-10 graded denticles (i.e. finest ones closest to the tip), some of the finest denticles being compound; first lateral denticle sharp with one or two weak side serrations 185 \( \mu \text{m} \) in vertical height, outer denticles smaller and smooth. Lateral teeth decrease regularly in size outwards, inner eight rows asymmetric with a large denticulate mesocone pointed towards the midline and two or three sharp, smooth denticles on outer side, inner rows have a broad triangular basal plate which is large compared with the central cusp, however in successive rows the basal plate becomes more elongate and the main cusp larger. Outer laterals decrease regularly in size, extreme outermost five rows reduced to elongate peg-like basal plates, outermost lateral only 48 \( \mu \text{m} \) in vertical height.

Jaws triangular, composed of densely packed rods. All the ganglia of the circum-oesophageal ring distinct, pleuro-visceral cords short, visceral ganglion separate.

Ovotestis yolk-yellow, interlobed with the brown digestive gland, ovotestis covers dorsal part of digestive gland, hermaphrodite duct swollen into a white ampulla that passes beneath the intestine. In the fresh state, all glands of the nidamental complex creamish-white in colour. The regularly folded mucous gland circles about the flattened and disc-shaped albumen gland. These glands of the "flat-pocket" type (Beeman, 1970) as in _Aplysia punctata_. Prostate gland present as a swelling near the base of the gametelytic gland duct, yellow in colour. Penial sac with two retractor muscles, internally the sheath has soft low tubercles in a case surrounding the sperm groove. Penis terminates in a broad, flattened tip, having a central dilated mid portion crossed by parallel folds and grooves.

**Descriptive Notes.**

When dislodged, the two edges of the foot roll together leaving only the extreme anterior border of the foot not inrolled. It is this anterior-most part that attaches when readhesion is initiated.
Colouration and pigment detail depend to a great extent on diet. Two basic colour forms exist:

1. **Brown Form.** This form has a light chocolate-brown ground colouration over which is sprinkled either sparsely or thickly white spots. Each spot is composed of numerous aggregated, tiny white dots. The parapodial border, and free edges of the anal spout, mantle foramen, and tips of oral tentacles and rhinophores always have a black line and this line is occasionally interrupted with white areas. This colour phase is typical of intertidal populations of *Aplysia parvula* that have been feeding on *Laurencia* spp.

2. **Red Form.** The basic body colouration of this form is a deep maroon-red, the whole body is conspicuously peppered with white spots that are aggregated into circular spots. Definite white stripes are present along the genital groove on the right hand side and on an equivalent area on the left hand side of the body, these stripes being widest immediately before the start of the parapodia. Another white stripe runs from the hind end of the parapodia to the tip of the tail on the dorsal side. There is a black edging to the extremities just as in the brown form. In some specimens there is a bright cherry-red zone on the parapodia immediately beneath the black margin. This colour phase is typical of subtidal populations of *Aplysia parvula* that have been feeding on *Plocamium costatum*.

For both colour phases, a black marginal zone is sometimes present around the foot border, but at other times and in other populations it is absent. This may be a polymorphic characteristic.

In the copulating position, the anterior part of the foot of the hind ("male") specimen is attached firmly to the shell of the front ("female") specimen. Such direct foot-to-shell adhesion is not possible in *Aplysia* or other subgenera because the mantle virtually covers the shell completely except for a tiny, central, foramen.
Locality Records.


6, Te Kaha, near Cape Runaway, Bay of Plenty, J.D. Willan, 1 March 1966. Taranaki: 3, Oaonui Beach, Cape Egmont, R. Allan, March 1965 (N.M.) Wellington: 1, low-tidal pool, Lyall Bay, R.K. Dell, 1 Jan. 1950 (N.M.); 1, on Ulva lactuca, 2-3m, "The Gantry", Island Bay, C. Battershill, 12 May 1977. Nelson: 7 shells, from live-taken specimens, under low-tidal stones, Fossil Point, North West Nelson, P.M. Climo, Oct. 1961 (N.M., M.48372). Otago: 1, dredged off Quarantine Id, near Otago Hbr., P.M.B.L., M.C. Miller, 20 Aug. 1962; 1, 2-4m, beam trawl, channel north of Quarantine Id, Otago Hbr., E.J. Batham, 8 April 1956 (Pilgrim Coll.); 1, beam trawl, channel north of Quarantine Id, Otago Hbr., E.J. Batham, 8 April 1956 (P.M.B.L.); 1, intertidal
near P.M.B.L., Otago Hbr., R.L.C. Pilgrim, Jan. 1955 (Pilgrim Coll.);
25, low-tide level, southern end of Little Papanui Beach, E.J. Batham,
12 Feb. 1962 (P.M.B.L.); 5, on seaweed-covered rocks at southern end of
Little Papanui Beach, M.C. Miller, 12 Feb. 1962; 4 shells, Brighton (N.M.,
M.412)

Discussion.

Together with the European *A. punctata*, *A. parvula* shows a number of
features (small size, position of visceral hump and long tail, small para-
podia, large mantle foramen, opaline gland, construction of nidamental
glands, nervous system) that show the subgenus *Pruvotaplysia* to contain
the most primitive members within the genus *Aplysia*. Beeman (1970)
has shown the "flat-pocket" type of nidamental gland arrangement to be
widespread through the Anaspidea (*Phylloplysia*, *Petalifera*, *Notarchus*,
*Dolabella*) and this is found in *Akeria* too. My studies confirm Beeman's
predictions that this arrangement would be expected to occur in *A. parvula*. 
APLYSIA (VARRIA) DACTYLOMELA RANG, 1828

Frontispiece, Figs. 3.1A,B; 4.1a; 9.4F, G.

Synonymy.


1867. Aplysia figrina Rang; Angas, Proc. zool. Soc. Lond. 1867 : 228, No. 266; 1869. Sowerby, Conch. Icon. 17, pl. 2, fig. 5a, 5b (non A. tigrina Rang, 1828).


1869. Aplysia keraudreni Rang; Sowerby, Conch. Icon. 17, pl. 1, figs. 2a, 2b (non A. keraudreni Rang, 1828).


Remarks.

The complete synonymy for Aplysia dactylomela (as given by Engel (1929) and Eales (1960)) is much more extensive than that given above.

Description.

Adult size usually up to 30 cm, but occasionally up to 45 cm (with a corresponding weight of 1.4 kg). Body plump and bulky, tail relatively short. Sole of foot clearly demarcated from sides all round, greenish-brown with smudges of black. Locomotion by a series of muscular waves passing posteriorly down foot (generally only one at a time), never leech-like.

Basic colouration brownish-green, pinkish-brown or chocolate with a superficial pattern of black pigment organized into circles, more numerous and larger on lower parts of parapodia towards foot with an irregular black reticular pattern more obvious near edges of parapodia, a conspicuous black smudge being present on upper side of tail. Edges of parapodia, tips of rhinophores and oral tentacles pink. Interior of parapodia with large circular light green patches, each with one or two central white smudges, these circles being set in deep black pigment, anterior portions of interior of parapodia with a series of longitudinal black lines.

Shell completely internal, covered by mottled green and black mantle. Shell large, broad, rounded anteriorly, with a deeply excavated anal sinus. Purple fluid readily emitted. Opaline gland compound.

Rachidian with a large, broad-based basal plate that has a nearly straight base, mesocone broad, serrated along its whole length with two strong denticles on either side at base of mesocone (18 μm in height). Lateral teeth bend towards midline, basal plates large; inner laterals with a single, large, broad-based mesocone, denticulate along both sides, with
two elongate denticles on one side at base of blade. Middle laterals with a narrower mesocone that is longer and sharper.

Jaws rectangular, composed of numerous tightly-packed, short, curved rods. Jaw rods either broad at their inner ends or straight and truncated. Cerebral ganglia fused, but may show their double origin (Eales, 1960), visceral ganglia also fused.

Ovotestis large, solid, golden-yellow and lying prominently in visceral cavity behind digestive gland, it is discrete and not interlobed with digestive gland. Hermaphrodite duct leaves ovotestis as an already-enlarged, sinusoidal, laterally compressed ampulla, ampulla narrows abruptly to a thin, straight duct that enters nidamental gland complex. Nidamental glands of "banded-cvoid" type (Beeman, 1970) with albumen gland lime-green, membrane gland light pink, mucous gland orange to brick red in colour, these glands wind around albumen gland. Receptaculum seminis large, club-shaped and attached to common genital aperture by a slender curved tube. Gametolytic gland (or bursa copulatrix) present just before common genital aperture, enlarged, stalked and thin-walled and having a distinct orange prostatic region at its base. Penial sac with two retractor muscles, sac very long with a series of internal ridges enlarged towards the base. Penis relatively short, with a large base provided with a spongy gland, penis oval, pointed, white, sperm groove winds spirally round it.

Descriptive Notes.

A full description of the organs of the reproductive system of a mature Aplysia dactylomela has been given because this system has been used as a basis for the gonad index given earlier (Ch. 6.1.9). The remaining species of Anaspidea will be compared with this particular system and only the points of difference noted.

When removed from contact with the substrate and allowed to float freely in the water, Aplysia dactylomela stretches out maximally, the foot becomes long and narrow and may even be arched, the parapodia are held together
and upright (Fig.3.1A). This shape offers the greatest surface area for adhesion by the foot, and simultaneously, to maximum resistance to the water. Any portion of the foot that contacts a firm substrate will adhere immediately. Not one of several thousand animals examined of this species (and of a size range from 3 mm to 450 mm) was ever seen using the parapodia for swimming.

In the resting position (Fig.3.1B) the parapodia fold over the body, either the left or the right parapodium may be uppermost. The edges of the parapodia are often crenulated but four respiratory apertures remain clearly open: an anterior inhalant one formed by the anterior edges of both parapodia; one on each side behind this, each formed by a localized infolding of a separate lobe; behind this both parapodia fold tightly around the upraised anal spout and there is a posterior aperture far back on the tail at the point of fusion of the parapodia. The parapodia are fused far back posteriorly leaving only a low ridge between the hind end of the parapodia and tail, this ridge being higher than in _A. extraordinaria_ or _A. keraudreni._

Little variation is apparent in the actual arrangement of the superficial black pigmentation patterns on the body, however the basic colour can vary through shades of green, brown or pink depending on the food the individual has been eating.

The radula formula varies greatly according to the size of the individual, but generally there is a greater number of rows, and teeth per row, than for an _A. parvula_ of equivalent size.

**Locality Records.**

NORTHLAND: 1, Whatuwhiwhi Beach, Doubtless Bay, F. Begley, 1963 (N.M.); 1, 2-4 m, Rawhiti Bay, Bay of Islands, B.S. 239, 23 Nov. 1971 (N.M.); 3, 3-5 m, Long Bay, Russell, C. Battershill, 1973; many, on intertidal platform, "Echinoderm Reef Flat", Goat Island Bay, Leigh, RCW, 1974-1978; 1, Goat Island Bay, Leigh, M.C. Miller, 2 March 1962; 1, 17 m, "The Point", ...

Discussion.

Considering the distinctive appearance of this large Aplysia and its great abundance, intertidally in certain seasons, in the north of New Zealand, it is surprising that Aplysia dactylomela has never received a regional name in this country. I do not know the material on which Eales (1960) recorded this species from New Zealand as there is no reference to specimens of this species from here having been sent to Eales from any Museum during the course of preparatory studies for her monograph. Early workers who encountered A. dactylomela probably examined it cursorarily and reached an incorrect identification as either Aplysia brunnea Hutton or A. venosa Hutton. For example Ayling's (1975) reference to "Aplysia brunnea" unquestionably refers to A. dactylomela since he also provides a photograph of the species in question. A further reason for lack of recognition of this species by early workers is that it does not occur outside Northland, therefore material of this species would not have been available to workers in the south (e.g. Hutton, Kirk, Meinertzhagen) who could potentially have named it, or at least recognized its presence in New Zealand. On the other hand, A. dactylomela may be a relatively recent immigrant from Australia, that may not have been present at all in New Zealand one hundred years ago.

Probably the best illustration of Aplysia dactylomela is a hand-painted drawing. This painting, by Dr J. Stewart, was published by Hedley (1923,
APLYSIA (VARRIA) KERAUDRENI RANG, 1828  Figs. 9.1a, b.

Synonymy.


Remarks.

Hutton (1875) gave the briefest of descriptions when he defined Aplysia venosa, but two clues in his description suggest venosa is conspecific with keraudreni. Initially the type locality is "Wellington", and the only large (Hutton states "about six inches in length") Aplysia species known from there are A. (Aplysia) juliana and A. (Varria) keraudreni. Hutton described the animal of venosa as "yellowish-brownish, veined with dark brown". Frequently the superficial black reticulum of keraudreni is conspicuous enough to warrant the description of "veined", however the colour of juliana is always uniform amber brown to jet black. Hutton himself designated this latter species as Aplysia brunnea (see latter under Aplysia juliana).
Description.

Adult size up to 30 cm. Body plump, but neck region rather slender, large mantle region and visceral hump. Rhinophores particularly long. Oral tentacles connected to sides of mouth by flaring tissue connections. Hind end of tail more expanded than A. dactylomela, sole of foot oval, elongate but not particularly long and narrow, no light areas or dark smudges on foot, foot margins distinct from sides of body all round. Parapodia separated very far back.

Shell relatively large, chitinous, with a clear marginal extension, angle between right hand side of shell and curve for anal sinus rather acute, shell often has prominent concentric growth striae.

A. keraudreni readily discharges a purple "ink". Opaline gland simple.

Radula with a large number of rows, formulae for two specimens:
53 x 32.1.32 (length of preserved specimen 90 mm); 45 x 20.1.20 (length of preserved specimen 56 mm). Many of oldest rows of teeth incomplete. Rachidian rather high with an extended mesocone, 4 to 7 alternating denticles down sides of mesocone and becoming progressively smaller towards apex, denticles simple and not bifid or serrate. Lateral teeth similar, inner laterals extended and triangular, asymmetric; ectocone large, smooth, triangular and pointed; mesocone large, elongate, with 4-6 denticles laterally. Laterals increase in size away from midline to approx. two-thirds of way across, cusp becomes larger and narrower and upper denticles enlarge so as to be nearly equal in size to distal dentine. One to four simple, peg-like vestigial outer lateral teeth.

Jaws rather large, rectangular, consisting of many packed, slender rodlets that are either curved or straight.

Ovotestis of mature individuals bright pink and interlobed with posterior portions of digestive gland. Nidamental glands of the "banded-ovoid" type and situated between pericardium and ovotestis, membrane gland tightly compacted and creamish-white; mucous gland large, pale green; albumen gland
pale orange. Vagina pale orange with white oviduct running parallel.
Prostate gland a rather low yellow swelling, duct to gametolytic gland
rather short. Penial sac elongate, two retractor muscles present; interior
of penial sheath with a series of folds running parallel to sperm groove,
one opposite the sperm groove being particularly enlarged. Penis very
long, flagelliform, smooth, pure white in colour.

Descriptive Notes.

When irritated, *A. keraudreni* produces copious quantities of purple
fluid. This is mixed with a smaller amount of milky fluid from the opaline
gland. In general this species discharges its purple fluid as the result
of a weaker stimulation than *A. dactylomela*; even picking up *A. keraudreni*
in the field provides sufficient irritation to cause it to "ink".

Active locomotion is by pedal movements only. Either by waves of
contraction passing along the permanently attached foot or by leach-like
motion. In this latter method the anterior and middle portions of the
foot are pushed forward and the hind end is then lifted off the substrate
and brought forward, thus the hind end of the foot is actually lifted off
the ground. This species never swims.

The species displays two colour forms, a normal dark form and a "mottled"
form. In the normal form, the basic colouration is brownish to greenish,
but generally of a very light colour and almost translucent, much more so
than *A. dactylomela*. Overlaying this are blotches of pale chestnut-brown
that form streaks especially over the head and up the oral tentacles and
rhinophores. Interspersed through these brown patches are white spots,
especially on the sides of the parapodia and tail. These white areas consist
of two or several grouped spots. Over the head and upper parts of parapodia
and tail is an irregular reticulum of interrupted black lines. Interior of
parapodia very hyaline, pale, with pale brown streaks and white spots. Mantle
overlaying shell hyaline, and showing brownish chitinous shell beneath,
rather weak brownish rays radiate from the central papilla. In the "mottled"
colour form the brownish areas are broken into very irregular spots
or bars of colour and these are interrupted by pale areas. The black
reticulum is present in both colour forms regardless of whether the
underlying colour is brown or pale. Fig.9.1A shows a copulating pair of
A. keraudreni consisting of one individual of each colour form.

Locality Records.

NORTHLAND: 1, in a low-tidal pool, Paxton Point, Great Exhibition Bay;
1, dredged 4-5m, channel between Moturua and Motukiakia Id, Bay of Islands,
25 Nov. 1971 (N.M.); 1, Goat Island Bay, Leigh, M.C. Miller, 4 March 1968;
2, "Echinoderm Reef Flat", Goat Island Bay, Leigh, RCW, 6 June 1976, 22 May
1977; 1, 6m, Ti Point Channel, entrance to Whangateau Harbour, Leigh, RCW,
16 May 1974; 1, 8 m, southern side of Takatu Peninsula (near tip), Leigh,
RCW & K. Warne, 1 Dec. 1976. GISBORNE: 2, Lottin Point, Cape Runaway,
R.K. Dell, 10 March 1962 N.M. (M.14894). WELLINGTON: 3, feeding on Ulva
lactuca, 3-4 m, "The Gantry", Island Bay, RCW, 26 May 1977; 1, in a drag
net, Pauatahanui Inlet, Porirua Harbour, P.C. Bull, 30 Jan. 1965 (N.M.,
M.18006); 1, Boat Harbour, Wellington, G. Whitfield, 6 April 1926 (N.M.,
OTAGO: 1, beam-trawl 2-3 m, near Protobello Marine Station, Otago Harbour,
E.J. Batham, April 1956 (Pilgrim Coll.); 2, Portobello, Otago Harbour,
E.J. Batham, no date (Pilgrim Coll.); 1, 2 m, channel north of Quarantine Id,
Otago Harbour, E.J. Batham, 10 May 1956 (P.M.B.L.); 1, beam trawl, 2-3 m,
harbour bottom near Portobello Marine Station, Otago Harbour, E.J. Batham,
April 1956 (P.M.B.L.). SOUTHLAND: 3, beam trawl, 16-18 m, Port Adventure,

Geographic Distribution.

The type-locality is the Society Islands. However no mention of A.
keraudreni was made by Marcus & Marcus (1965) in their survey of
opisthobranchia from Micronesia. Eales (1960) had a much-contrasted and
juvenile specimen from Sydney, Australia that she referred to A. keraudreni, but Bebington (1977) gave no further records of this species from Australia. Similarly Eales (1960) tentatively placed Mazzarelli & Zuccardi's (1889) record of a single aplysiid from Hawaii (identified by them as Aplysia lessoni Rang) in the synonymy of A. keraudreni. But Kay (1964) collected none during her studies on the Aplysiidae of the Hawaiian Islands (1962-1963).

Discussion.

Eales (1960) recorded the parapodia as "natatory", but this is an error, probably the result of her inability to examine live specimens. The most important specific characters displayed by A. keraudreni are the low fusion of parapodia posteriorly, quite broad foot, inability to swim and slender, filiform penis.
Synonymy.


Remarks.

Although Allan (1932a; 1932b) gave no anatomical details, her descriptions are fully adequate to identify this species. Subsequently Eales (1957; 1960) re-examined the holotype and supplemented the original description with an anatomical account. The species is very distinctive. Parish (1974) gives excellent illustrations of swimming specimens. Although specimens have been known from New Zealand since 1962 they have not been distinguished from Aplysia keruadreni, so A. extraordinaria is formally recorded here for the first time.

To confirm the New Zealand records of Aplysia extraordinaria, I have examined the holotype (Australian Museum, Sydney. Reg. No. C57496). Here details of live material are supplemented with my observations on the holotype.

Description.

Body large, up to 45 cm in length, elongate and not plump, neck slender and head expanded anteriorly to a pair of very large, elaborately frilled oral
tentacles. Rhinophores elongate, pointed. Foot very narrow, broader anteriorly and narrowing posteriorly; when crawling rapidly leech-like pedal locomotion is displayed as in A. keraudreni, tail short, foot sole unpigmented. Parapodia exceptionally large, separated posteriorly, edges smooth.

Body colour rich amber-brown, numerous large white spots and dashes being present over dorsal surface especially towards lower surfaces near foot edges. Broad, irregular, longitudinal, white bands with small white spots between them outline edges of parapodial lobes, these extend downwards. Whole surface covered by a fine black reticulum, accomapnying the reticulum are numbers of small black spots, two larger black spots being situated together near oral tentacles. Insides of parapodia white-banded and similar to outsides, but lacking a black reticulum. Mantle mottled with white markings too. Shell broadly ovate, and sinus shallow, shell deep yellow in colour with strong concentric striae externally.

Purple ink secreted. Opaline gland small, simple multiporous.

Radula with formula approx. 70 x 32.1.32. Rachidian with a short, narrow basal plate, tooth with a short mesocone and fine lateral denticulations. Laterals with a narrow basal plate, short mesocone and numerous denticles on both sides, the basal denticle being larger than the others and having serrate edges. All laterals similar but denticulations become highly elaborate and irregular though cusps remain of moderate length. Three outermost lateral teeth vestigial.

Jaws curved, consisting of rather short rods that are truncated apically.

Cerebral ganglia fused, visceral ganglia joined and spread along visceral cords.
Examination of Holotype.

In her figure of *Aplysia extraordinaria*, Eales (1960: Fig. 22, p. 313) has ringed a small "papilla on the mantle", but in the holotype the mantle has been opened at this point to allow removal of the shell and no papilla is visible.

In this same figure, Eales has drawn the hind end of the parapodia as being continuous posteriorly, whereas in the actual specimen there is a definite (albeit very small) posterior point of separation of the parapodia.

All traces of the black reticulum have now vanished; only the white spots remain.

**Locality Records.**

**NORTHLAND:** 1, 15 m, "Nursary Cove", between Aorangi and Tawhiti Rahi Is, Poor Knights Islands, A.M. Ayling, June 1975; 1, among *Carpophyllum maschalocarpum*, 8 m, eastern side of High Island, Whangarei Heads, RCW, 21 June 1975; 1, collected intertidally, McGregor's Bay, Whangarei Heads, R. Harager, 15 May 1961.

**Geographic Distribution.**

The above specimens represent the first records of this species from New Zealand. In Australia it is known from New South Wales and Queensland (Syndey Harbour - Allan, 1932a, 1932b; Gunnamatta Bay, Port Hacking - Bebbington, 1977; Southern Queensland - Burn 1966; Queensland - Kenny, 1970).

Locality records beyond Australasia require confirmation. Eales (1960) examined a specimen, attributable to this species from Hawaii (collected by M. Ballieu in 1874, Paris National Museum), but the species has not been recollected there since then. It is possible the distribution of *A. extraordinaria* is confined to Australasia or that the species is known from elsewhere but remains concealed under another name.
Discussion.

This species attains the largest size of all the Aplysia species in New Zealand. However it is rarely encountered and may not have breeding populations established permanently. The situation is different in New South Wales, Allan (1932a) recording that specimens were very numerous in Athol Bay, Port Jackson early in April 1931.

With its large size, very large parapodia, locomotion by swimming and long narrow foot, Aplysia extraordinaria is a very distinctive species. It is the only member of the genus in New Zealand that is capable of swimming. In a search for an earlier name, I have checked through the literature for authentic reports of swimming in other Aplysia species.

1. Aplysia tanzanensis Bebbington, 1934 - may well be synonymous with A. extraordinaria. It is known from a single juvenile specimen. It swam actively in the laboratory.

2. Aplysia fasciata Poiret, 1789 - a European species with a distribution range from the southern coasts of Britain (rarely) to the Mediterranean Sea to Angola, also the Red Sea. Bebbington & Hughes (1973) have elegantly described and illustrated the swimming cycle of this species. Its colouration is quite unlike that of A. extraordinaria.

3. Aplysia brasili ana Rang, 1828 - from Cape Cod to both sides of Florida and Texas. Strength & Blankenship (1977) reported it to be an "excellent swimmer", Hamilton & Ambrose (1975) and Andrews (1971) also recorded its swimming ability. This species appears to have a heavier body than A. extraordinaria and colouration also seems to differ.

From the description of Aplysia maculata Rang, given by Bebbington (1974), it appears that this species is conspecific with A. extraordinaria, and one would expect it to be capable of swimming.
APLYSIA (APLYSIA) JULIANA (QUOY & GAIMARD, 1832)

Figs. 9.4 A-C.

Synonymy.

1832. *Aplysia juliana* Quoy & Gaimard, Voy. l' Astrolabe Zool. 2 : 309,


Trans. zool. Soc. Lond. 34 : 114-115, fig. 14b.

1869. *Aplysia hyalina* Sowerby, Conch. Icon. 17, pl. 4, fig. 13; 1877.


1896. *Tethys brunnea* Hutton; Pilsbry, Man. Conch. 16 : 97-98, pl. 59; fig. 44;


1918. *Tethys hyalina* Sowerby; Hedley, J. Proc. R. Soc. NSW, Suppl. to Vol. 51 :

M.107, No. 1147; 1932. Allan, Aust. Mus. Mag. 4 : 420; 1950. Allan,


fig. 42 [Tristan da Cunha; Cook Strait, New Zealand]; 1977. Bebbington,


1964. Tethys tryoni Meinertzhagen; Williams, Moll. Bay of Plenty : 21 illust. [non Aplysia tryonii Meinertzhagen, 1880].


Remarks.

The early descriptions of Aplysia brunnea and Aplysia hamiltoni are very cursory and only really provide information on the shape of the shell. Suter (1913) recognized Aplysia hamiltoni as synonymous with brunnea Hutton, shells of the holotype and a paratype of hamiltoni being in the National Museum, Wellington (Reg. Nos. M.42 and M.43 respectively) and are shown in Fig. 9.4A. Eales (1960) placed both brunnea Hutton and hamiltoni Kirk, along with the Australian hyalina Sowerby, into the synonymy of Aplysia nigra d'Orbigny.

In New Zealand there are no grounds to recognize brunnea, hamiltoni, dura Eales, nigra d'Orbigny of Eales, or nigra delli Eales as taxa that are in any way separable from juliana Quoy & Gaimard.

In her monograph, Eales (1960) regards juliana Quoy & Gaimard, nigra d'Orbigny and dura Eales n.sp. as distinct and recognizable entities and lists all from N.Z. Bebbington (1977 : fig, 14) likewise recognizes all three and gives figures of them all together from the dorsal aspect, however, all of his specimens were preserved and the varying size of the mantle in relation to the body length is merely an artifact of preservation. The reasons that Eales recognizes all three species as separate and all occurring in New Zealand are unclear. In private correspondence to Dr E.J. Batham and Prof. R.L.S. Pilgrim (1956, 1957) Eales recognized only one Aplysia s.str. - Aplysia juliana in New
Zealand material sent for her study. Although the holotype and a paratype of Aplysia dura Eales, 1960 are from Tristan da Cunha Island, South Atlantic Ocean, Eales also recorded one specimen under this name from "Cook Strait, New Zealand"; this specimen was returned to Wellington. In fact the National Museum's wet collection now contains three specimens labelled as Aplysia dura Eales (Reg. Nos. M.11107; M.18005; M. 14995). The identifications of the former two were verified by Eales. Full data for the three is as follows:


All three specimens are no more than massively contracted Aplysia juliana. This contraction is probably due to being tossed about in surf and cast ashore following storms; it should be noted that information accompanying two of the individuals mentions they were collected after storms. It is quite probable the specimens were dead by the time they were washed ashore or found by the collectors. The skin of all three is exceedingly tough and leathery, and pigmentation is partially lost from some regions of the body. M.11107 has its penis partially everted which is a typical symptom, in opisthobranchs, of death before preservation. M.14995 also has the penis partially everted, the shell is shattered although the mantle cavity has not been opened, the gill has a portion missing at its centre - all these features tell of a moribund specimen washed ashore after a heavy storm and partially eaten by beach scavengers. I have seen specimens of Aplysia dactylomela taken in precisely this same tough, contracted facies after washing ashore on the main beach, Goat Island Bay, following a severe winter storm.
Aplysia nigra d'Orbigny, 1837 is undoubtedly close to A. juliana, however the posterior end of the foot is "court et subacumine" (d'Orbigny, 1837), not enlarged and rounded to form a temporary sucker as in A. juliana. In A. nigra the parapodia are united about the middle of their length, the animal is almost completely black although there is a slight pinkish hue inside the parapodia; there is no mention of paler areas or white speckling. Therefore I feel true A. nigra does not occur in New Zealand, the name should probably be restricted to South American material.

Even though specimens of A. juliana may be feeding on the same diet a population will display a large colour range. These different colour variants have probably been unnecessarily recognized as different species. At Island Bay, Wellington I have observed A. juliana with colours from amber-brown to velvet black; all members of this population were feeding on Ulva sp. and many individuals of all the various colour forms were copulating together in pairs or chains.

Description.

Adult size up to 30 cm, but sexually mature individuals only 12 cm long have been encountered by me. Body plump, tail quite long posteriorly, rounded. Foot broad and elongate, anterior and posterior parts have a margin separating them distinctly from upper parts of body, but middle portion not demarcated and merges smoothly into parapodia. Hind end of foot referred to as "posterior caudal sucker" but there is no morphological distinction. Sole of foot uniformly brown-coloured with abundant darker wrinkles. Locomotion regularly leech-like.

Parapodia moderately large, wrapping over body, thickened posteriorly where they are fused high up (almost to level of anal spout), but thinner laterally, margins simple; parapodia start as low ridges not far behind eyes. Anal spout does not project up through parapodia as in A. dactylomela. Mantle foramen discrete, small, with a small, low papilla where mantle overlies shell.
Ground colour varies from light, warm, amber-brown to jet black, sometimes with a lighter speckled pattern or none at all; in patterned specimens a narrow white streak passes from oral tentacles through eye to rhinophores, occasional pale areas or light spots on outer sides of parapodia. Internally parapodia can have pale streaks or light areas, particularly towards anterior regions. Some other colour forms can have clusters of bluish-white spots on head, outer sides of parapodia and mantle foramen.

Unable to secrete purple "ink", despite forceful and repeated stimulation. Opaline gland small, simple multiporous. Cerebral ganglia fused, pleuro-pedal mass fused, visceral ganglion relatively small.

Shell relatively large, moderately convex, uniformly amber-brown, outside with narrow reddish rays, apex rather broad; the only sculpture is of weak, concentric, rather regularly-spaced growth lines; a clear, flexible, periostracal extension being present all round shell. Interior smooth, nacreous, with two muscle scars.

Whole radula rather long and narrow. Formulae for three specimens: 47 x 20.1.20 (live length 85 mm); 55 x 31.1.31 (live length 110 mm); 55 x 27.1.27 (live length 100 mm). Rachidian with highly arched flanges to basal plate, mesocone rather broad and short, denticulate on either side of blade with 3-5 denticles, but generally denticles are indefinite and irregular. Innermost laterals asymmetric, with a large, triangular mesocone that bears 1-3 small serrations alternately on either side, ectocone rounded and rather blunt, bearing minute serrations all round. Towards midline of each half of radula, laterals bear longer and larger mesocones - inner edges smooth, outer edges irregularly denticulate. Outermost laterals progressively smaller with exaggerated curves to their basal plates; eventually only vestigial rod-like teeth left on outer sides of rows. Jaws long and narrow, consisting of numerous, short, curved rods.
Ovotestis yellowish, interlobed with digestive gland. Where hermaphrodite duct emerges from ovotestis it is long and sinous, white, fairly narrow; subsequently it swells into a pinkish ampulla. Nidamental glands lie flat on the dorsal surface of the digestive gland, immediately beneath the floor of the mantle cavity, of the "banded-ovoid" type, mucous and membrane glands pale golden-yellow. Receptaculum seminis finger-like, recurved, golden-yellow. Oviduct pinkish. Gametolytic gland with a rather long connection back to the common genital duct, no distinct prostatic swelling where the stalk of the bursa joins the common genital atrium.

Penial sheath elongate with a considerable amount of dark pigment visible internally on the dorsal side, two penial retractor muscles with additional smaller muscle slips laterally on the anterior part of the sac, retractor muscles both very long (8-9 mm) and greatly subdivided at their points of insertion. Interior of sac brownish, base pustulose with 12-15 longitudinal rows of knobbed tubercles, not at all chitinous, apices of these tubercles whitish, medial section of penial sac quite smooth, brownish with weak longitudinal folds, terminal portion (i.e. that part closest to the exterior) with numerous undulating wavy folds. Penis itself long and curved, occupying the full length of penial sac, base covered with small, white tubercles, penis broad, laterally compressed reaching a sharp tip.

Descriptive Notes.

Undoubtedly _A. juliana_ is the most variable, in terms of size and colour range, of any of the species of Anaspidea in New Zealand.

In still water the parapodia remain wide open and are periodically brought together to create respiration currents over the gill, generally the left parapodium overlies the right.
The anterior part of the mantle covering the shell is thickened, glandular and rather flaccid. During copulation this area dilates and serves as an attachment pad for the anterior part of the foot of the co-copulant. This part of the mantle overlying the shell is rather loosely attached to the shell, in great contrast to the posterior region that is thin and closely adherant to the shell. This ability to present a glandular region to the foot of the copulating partner represents a development from the situation in *Pruvotaplysia* species where the foot is placed directly on the shell of the partner.

**Locality Records.**


OTAGO: 1, beam trawl, 2-3 m, near Portobello Marine Station, Otago Harbour, E.J. Batham, 29 April 1956 (Pilgrim Coll.); 1, ELWS level, off shipping channel, Quarantine Id, Otago Harbour, E.J. Batham, 3 April 1956 (P.M.B.L.).

SOUTHLAND: 1, Stewart Island, W. Traill, Sept. 1916 (Pilgrim Coll.).
Geographic Distribution.

As I doubt that records of Aplysia nigra d'Orbigny or Aplysia dura Eales from overseas are conspecific with material of A. juliana from New Zealand, I have restricted records of distribution to those for the latter species only. A. juliana has an immense world-wide distribution, comparable to that of A. dactylomela. Eales (1960) records it from Florida to Brazil, including the West Indies; Morocco; Ghana; Canary Islands; Seychelles Islands; Mauritius; Madagascar; Kenya to Cape of Good Hope; India; Pakistan; Japan; China; Formosa to East Indies; Polynesia; Australia; Tasmania; New Zealand; California; Galapagos Islands; Peru. Records of A. juliana subsequent to those of Eales are from: Hawaii (Kay, 1964; Frings & Frings, 1964; Watson, 1973); Queensland (Burn, 1966); Victoria (Burn, 1969); Japan (Usuki, 1969; 1970); Barbados (Carefoot, 1970); Mexico (Marcus & Marcus, 1967); Gulf of California (Abbott, 1974); Venezuela (Marcus, 1972); Mediterranean Sea (Barash & Danin, 1971); Ghana (Edmunds, 1977).

Discussion.

Although A. juliana displays great variation in size and colour range it is readily identifiable by its large size, high fusion of parapodia, large foot with the lateral areas confluent with the bases of the parapodia, inability to "ink" and penial structure. In New Zealand, this species appears less common in the north, other species such as A. dactylomela and A. parvula exceeding it in abundance. Northern individuals also appear smaller and others possess more white and turquoise pigmentation. Greatest size and abundance appears to be reached in Wellington and further south.

Aplysia juliana appears to favour species of the chlorophycean Ulva rather than red algae, although these are accepted. Since growths of Ulva are frequently characteristic of estuarine or brackish areas or regions of freshwater springs (Carefoot, 1970) and A. juliana occurs in these
Genus Bursatella Blainville, 1817. Dict. Sci. Nat. Suppl. 5 : 138. Type-
species by monotypy, Bursatella leachii Blainville, 1817. Aclesia Rang,
1828 is a synonym (Eales & Engel, 1935).

BURSATELLA LEACHII BLAINVILLE, 1817

Synonymy. Figs. 9.2a; 9.3.

1817. Bursatella leachii Blainville, Man. de Malacol. : 473, pl. 43, fig. 6;
1828. Rang, IN Férussac, Hist. nat. générale et particulière des Moll. :
51, pl. 4, figs. 1-6; 1968. Morton & Miller, N.Z. Seashore : 166,
322, 545, 570, 571, fig. 202, No. 4.

fig. 4, No. 3 [Auckland Harbour]; 1879. Cheeseman, Trans. N.Z. Inst.
11 : 379, pl. 16, fig. 4.

1896. Notarchus glaucus Cheeseman, Pilsbry, Man. Conch. 16 : 146, pl. 43,
fig. 34; 1900. Hedley, Proc. linn. Soc. NSW, 25(1) : 97-98, pl. 4;
1904. Hutton, Index Faunae Novae Zelandiae : 69; 1900. Hedley,
Soc. NSW, Suppl. to Vol. 51 : M.107, No. 1151; 1913. Suter, Man. N.Z.
Moll. : 547; 1915. Suter, Atlas, pl. 36, fig. 10.


Mus. 11 : 91, No. 1911.

1937. Bursatella glauca Cheeseman; Powell, Shellfish N.Z. (1st ed.) : 84,
No. 1230; 1946. Powell, Shellfish N.Z. (2nd ed.) : 89, No. 1401;
the Leigh Area, North Auckland : 17; 1976. Powell, Shells N.Z. (5th
ed.) : 111.
1950. *Bursatella leacheii* rex Allan; Allan, Aust. Shells : 215, fig. 50, No. 5.


**Remarks.**

Cheeseman (1878) described *Aclesia glauca* almost entirely on external characters without making any comparisons with similar foreign material. Iredale (1929) cursorily created a new genus for Cheeseman's species. Allan (1932) differentiated Australian specimens as being larger and exhibiting some slight colour differences, she proposed the specific name *rex* for them. In an excellent review of the genus *Bursatella*, Eales & Engel (1935) classified Cheeseman's species as a variety of *Bursatella leachii leachii*. Despite their thorough treatment and statement (1935 : 302): "After an examination of many specimens and a survey of the literature we have come to the definite conclusion that all the forms of *Bursatella* hitherto described must be united as a single species", they divided *B. leachii* into six geographical subspecies without providing any distinguishing characters at all. Their subspecies, their geographical regions and what characters I can abstract from their paper are as follows:-


4. *Bursatella leachii pleii* (Rang). West Indies. Not so woolly as *africana*, has no green ocelli, greenish ground colouration.

characters given.


The names **africana** Engel and **pleii** Rang have been perpetuated in usage since 1935, however **savigniana** Audouin, **rosea** Engel and **lacinulata** Gould have been ignored by subsequent workers.

7. Bebbington (1969) added a seventh subspecies **Bursatella leachii guineensis**, from Ghana and Nigeria. It is said to differ in having fewer villi than **africana**, being charcoal-grey in colour and having blue ocelli.

As I have already stated in chapter 3, there seems little reason to retain any of these subspecific taxa that are distinguished on a geographic basis alone. This is particularly so here, since no additional characters have been produced since 1935 to support this continued separation. On the other hand, the case for union of these subspecies appears strong—all are based on a very few (mostly preserved specimens), the differences in characters are very minor, and we now have good evidence that trans-oceanic drift of larvae occurs for many marine gastropods (e.g. Scheltema, 1971a; 1971b) so that the possibilities of genetic separation simply because of geographic separation become increasingly remote.

I advocate a reappraisal of **B. leachii** on a population basis. There is no doubt that individuals of this species display allometric growth with ontogeny; for example tiny juveniles have fewer villi, the majority are simple and ocelli are absent, the tail is proportionately longer in juveniles as well. Fig. 9.3 illustrates these changes by dividing growth into five separate phases. When such intraspecific variation within populations is recognized, it will be most likely that **B. leachii** will be able to be treated as yet another circumtropical anaspidean.
Description.

Body plump, evenly rounded in section, widest in middle and tapering posteriorly to a long, narrow tail. Maximum size of New Zealand specimens 12 cm. Foot broad, smooth-soled and expanded anteriorly where there is a very prominent, bilobed, mucus-secreting groove; anterior foot margin crescentic. Two membranous, triangular flaps present on either side of mouth, these flaps down-pointing, lacking villi and not fused with oral tentacles. A tiny black eye visible at base of, and slightly anterior to, each rhinophore. Whole body covered with dendritic villi; villi can be partially retracted; largest villi on head and upper back, there being one conspicuous villus between oral tentacles and rhinophores in midline of head, and this process is of equal length to rhinophores; small, simple villi line foot border.

Overall body colouration dull translucent green with areas of fine, brownish-black, superficial pigment on surface, and this pigmentation often grouped into irregular dark patches particularly near sides of foot. Black areas have circular blue spots surrounded by a narrow black ring and then a broader buff-orange concentric zone. Villi having unpigmented areas from where smaller side-villi arise. Body wall more transparent in juveniles allowing dark visceral mass to be identified.

Readily able to secrete purple "ink". Shell lacking.

Jaws large, crescentic, consisting of numerous polygonal rodlets.

Radula with formula of approx. 35 x 35.0.35. Rachidian broad-based, lower surface deeply arcuate with tapering extensions at each side, mesocone large, pointed, with one or two serrations on either side of blade, two lateral denticles present on either side of mesocone. Inner lateral teeth short, narrow and arched, mesocone with one large denticle on inner side and two on outer face; second lateral with a much-enlarged, flattened denticle on outer side. Third and subsequent laterals have this outer denticle becoming proportionately shorter as length of mesocone increases to make
it very long and narrow; further across each row, angle of base changes
to be perpendicular to blade, mesocone now very long, pointed, and with
one weak denticle. Extreme outer laterals (25-35) bear long, lance-like
smooth cusps arising from relatively short blades.

Ovotestis discrete, mustard-coloured; ampulla dilated upon leaving
ovotestis, white. Nidamental glands of "flat-pocket" type, all three
being saccular and not tubular; membrane gland pale orange; mucous gland
white, oviduct can be seen passing through it; albumen gland apricot-orange
lying on central surface of nidamental complex and surrounded laterally
and dorsally by mucous gland. Receptaculum seminis yolk-yellow, rather small,
finger-like, somewhat sinuous and expanded distally. Gametolytic gland
with a relatively short and broad duct.

Penial sac narrow, spindle-shaped, with a single retractor muscle
attached to hind end; exterior creamish with a few black spots towards
base and longitudinal black lines distally corresponding with deep ridges
internally; internally base of sac lined with chitinous tubercles, a
conspicuous, white penial sheath also being present at base. Penis short
and broad, white, lower two-thirds closely studded with tubercles.

Descriptive Notes.

When the villi first appear in tiny juvenile specimens of Bursatella
leachii they are simple, but they become increasingly branched with growth
to give adult specimens a more woolly appearance than juveniles. This is
especially so in the "neck" region behind the rhinophores, so that in
juveniles, the external genital groove is plainly visible, but in adults
it is obscured by villi. Three types of villus can be recognized in the
adults:

1. Tall, erect simple villi.
2. Low, pointed or conical, simple villi.
3. Tall, erect villi bearing secondary villi that are given off in definite
vertical rows, these secondary villi can be irregular in outline but they
never bear a tertiary series of villi. Occasionally during respiratory expulsions of water from the mantle cavity, several of the larger villi on the outsides of the parapodia are retracted simultaneously.

Three very large, sexually mature adults 12 cm long were collected at Takatu on 17 January 1978, and they showed a variation in colour pattern. The body colour was dull green with the usual extensive areas of black pigment, and the villi were pale chestnut-brown in colour, almost yellowish. In the black patches, ocellar areas were visible as chestnut blotches, one specimen having no turquoise colour to the ocelli at all, the others had peripheral blotches of blue, or some ocelli had a continuous turquoise ring about a chestnut centre.

In the resting state there are 7-10 full respiratory cycles per minute, each consisting of separate inhalant and exhalant phases, there being 9-12 cycles per minute in the active state. These measurements were made at 20°C with 10 cm long adults. Small specimens (up to approx. 50 mm in length) are able to float on the water surface layer in a calm container.

Thompson & Bebbington (1973) have given a scanning electronmicrograph of the radula of Bursatella leachii Thomas (1975) has made a histological investigation of the organs of the reproductive system.

Locality Records.
NORTHLAND: 1, Bay of Islands, R. Wear (N.M., MG-2); 4, 8 m, off High Id, Whangarei Heads, RCW, 21 June 1975; many, a muddy sand, 3-5 m, sheltered bay on southern side of North Cove, North Eastern side of Bon-Accord Harbour, Kauw Island, RCW, 11 May 1977; 3, crawling at water's edge, flooded quarry at rear of Home Bay, Tawharanui Reserve, Takatu Peninsula, near Matakania, Leigh, RCW, 17 Jan. 1978; many, crawling on low-tidal sand flats between Mahurangi Id and Waiwera Beach, L.F.B. Green, 24 March 1974, RCW, 22 July 1974; 6, Waiheke Id, Auckland, G. Chamberlain (N.M.); many, feeding on Lyngbya majuscula, low-tidal reef flat, Motukaraka Id, off Beachlands Beach, Waitemata Harbour, RCW, 1975-1977.
Discussion.

*B. leachii* is distinctive because of its form and colouration. It is apparently only found in Northland and Auckland. It is probably the most common of any species of Anaspidea in New Zealand.

Type-species **Stylocheilus lineolatus** Gould, 1852 (= *Aclesia longicauda* Quoy & Gaimard, 1832).

**STYLOCHEILUS LONGICAUDA** (QUOY & GAIMARD, 1825) Fig. 9.2b.

**Synonymy.**

1852. *Aplysia longicauda* Quoy & Gaimard, Voy "l'Uranie" 2 : 421, pl. 66, fig. 8; 1828. Rang, IN Férussac, Hist. nat. générale et particulière des Moll. : 73, pl. 22, figs. 8-10.


**Remarks.**

My reasons for retaining *longicauda* in this genus, or indeed, even retaining *Stylocheilus* as distinct from *Bursatella* Blainville are conservative prior to a more penetrating examination of their relationship. At this time I have not been able to evaluate the two genera or their contained species, but the characters separating them, as mentioned by Engel & Hummelinck (1936), appear very tenuous indeed.

**Description.**

Body narrow and elongate, mantle cavity enclosed by fused parapodia, body tapering posteriorly with a long tail, body covered with simple or compound villi. A pair of distinct labial palps present on either side of mouth, these being linked with oral tentacles.
Ground colouration of body pale-brown, overlaid with longitudinal
dashes of darker brown, in places brown lines merge to form black blotches;
scattered amongst lines are circular, pale blue spots, these being thinly
marginated in black and with an outer orange-brown zone; external genital
groove outlined in black. Shell lacking. Able to secrete purple "ink"
when irritated.

Radular formulae for three specimens: 38 x 32.1.32 (60 mm preserved length);
21 x 21.1.21 (37 mm preserved length); 32 x 29.1.29 (45 mm preserved length).
Rachidian with a large basal region, concave along base itself and produced
baso-laterally into two long arm-like extensions; cutting edge of rachidian
with an elongate and narrow mesocone, two denticles being present on either
side of blade, laterally are three additional denticles decreasing in size.
Lateral teeth asymmetric, with a large mesocone and three denticles on outer
edge; innermost lateral has first denticle equal in size to cusp, its base
being long and narrow; moving outwards teeth elongate, mesocone becoming
narrower and curved. Outermost laterals long, curved, without denticles,
base small, triangular.

Jaws rather small, triangular, with curved anterior apices, consisting of
rather short, packed and curved rods.

Ovotestis discrete, pale lime-green; ampulla expanded immediately upon
leaving ovotestis, pinkish-brown. Nidamental complex of the "flat-pocket"
type - mucous gland milky-white, with translucent white oviduct visible;
albumen gland compacted besides ampulla and ovotestis, creamish-brown,
ridged externally; receptaculum-seminis long, narrow, finger-like, cream.
Vaginal region of common genital duct brownish-orange. Gametolytic gland
large, exceedingly thin-walled, duct not particularly long. Prostate gland
present as a low swelling at base of bursal duct.

Penial sac large, elongate, with a single, long penial retractor muscle.
Internally penial sac has large, inwardly-directed, conical tubercles over
basal half, tubercles can be traced into a small side caecum where they are
apparently formed, small spines cover walls on upper part of penial sheath. Penis banana-like, circular, with seminal groove on ventral surface, penis covered with small spines, tip mucronate.

Descriptive Notes.

Thompson & Bebbington (1973) gave a scanning electronmicrograph of the radula of \textit{Stylocheilus longicauda}.

Locality Records.


Geographic Distribution.

\textit{Stylocheilus longicauda} is circumtropical. Marcus (1972) has summarized localities in the western Atlantic, Bebbington (1974) for the Indian Ocean and Bebbington (1977) for the Pacific Ocean.

Marcus (1972) gives its bathymetric range as 0-35 m, Kay (1964) gives it as 0-27 m.

Discussion.

It is principally the more elongate body, darker colouration and different arrangement of villi, that serve to separate \textit{S. longicauda} from \textit{B. leachii} in the field. Sometimes mixed populations of both species are encountered. In New Zealand \textit{S. longicauda} is not common and immense aggregations of thousands of individuals, as noted in Hawaii by Kay (1964), have never been witnessed. \textit{S. longicauda} is apparently confined to northern New Zealand.

Possibly the world-wide distribution of this species has been aided by
its liking for species of filamentous algae that occur as part of fouling communities on stationary or temporarily-drifting habitats. For example, I collected two specimens feeding on green filamentous algae that were growing on buoy lines in the main channel of The Lagoon, Lizard Island, North Queensland, Australia, 23 Aug. 1975.

Type-species by monotypy Aplysia (Dolabella) dolabrifera Rang, 1828.

DOLABRIFERA DOLABRIFERA (CUvier, 1817)

Figs. 9.2C; 9.5A, B.

Synonomy.


1828. Aplysia (Dolabella) dolabrifera Cuvier; Rang, IN PéruSSac, Hist. nat. générale et particulière des Moll. : 51, pl. 4, figs. 1-6.


1896. Dolabrifera jacksoniensis Pilsbry, Man. Conch. 16: 120-121, pl. 44, figs. 38-41 [Port Jackson, NSW].


Remarks.

Credit must be given to Bebbington (1977) for realizing the extent of the distribution of Dolabrifera dolabrifera (Cuvier), and that the taxa brazieri Sowerby and jacksoniensis Pilsbry are regional names with no valid specific
status. *Dolabrifera brazieri* is based on shell characters only,
*D. jacksoniensis* on shell characters and details of externals from an
alcoholic specimen. Eales (1944) showed the species to be circumtropical.
Engel & Hummelinck (1936), Kay (1964) and Ferreira & Bertsch (1975) have
produced synonymies combining many of the early names. Bebbington (1974)
listed Indian Ocean records.

Description.

Maximum size 10 cm. Body pyriform, much compressed dorso-ventrally.
Head elongate, rounded anteriorly with a pair of widely expanded oral
tentacles; a large oral flap lies on either side of mouth. Neck region
between oral tentacles and rhinophores slender with prominent eyes two-
thirds of way back. Oral tentacles with flaring, undulating margin and
a wide slit on postero-dorsal side. Rhinophores smooth, with a deep slit
down posterior face. Parapodia small, mantle cavity occupying posterior
third of body, right parapodium overlapping left one and leaving only
slit-like anterior and posterior respiratory apertures, anal spout smooth,
filling whole of posterior respiratory aperture. Common genital groove
arising in front of anterior respiratory aperture.

Sole of foot very large bearing a distinct border all round, border
rolls upwards when animal is removed from its substrate, border anteriorly
and bifid with lateral shoulders, head being able to be retracted between
these expansions. Fig. 9.5A shows a ventral view of the head region.

Upper surface of body smooth and soft, covered with conical tubercles
terminating at sharp apices, there being large solitary tubercles and smaller
compound ones; tubercles can be raised or flattened by animal itself, and
larger tubercles can have a fine, white filament (or filaments) projecting
from their apices.

Body colouration disruptive, resembling the weed, sand and Lithothamnion-
paint that occur in habitats where *D. dolabrifera* is found; on dorsal surface
the crenulated marginal extension is greenish, rest of back having a pinkish
ground colour; head, oral tentacles and rhinophores light brown; overlaying background coloutration is a pattern of black reticulations, large brown or pinkish tubercles, small areas of white pustules and chestnut-brown blotches, black reticulum dividing body into areas within which tubercles are located; white patch present immediately in front of the anterior respiratory aperture; parapodial margins brown with white spots, this patterning being most obvious on the inner face of the hind end of the posterior respiratory aperture.

Shell spatuliform, more solid than in Aplysia, apex sunken, but there is a white, calcareous peg in front of apex. Right hand margin straight, anal sinus on left hand margin shallow and weak, shell angle 35-40°. Interior whitish, weakly nacreous, with two muscle scars - that at the site of the anal sinus being larger. Exterior of shell covered with a pale, straw-coloured periostracum that does not extend beyond the shell at the margins.

This species never discharges purple "ink" when disturbed or irritated.

Jaws small, narrow, rather thin, consisting of numerous, long or curved, striated spikes with pointed tips.

Radula rather short but extremely broad. Radular formulae 52 x 194.1.194 (preserved length 77 mm); 50 x 158.1.158 (preserved length 45 mm). Teeth very small and numerous. Rachidian with a smooth-sided mesocone and 2-3 denticles, base broad and arching. Inner laterals elongate, hooked; mesocone with a rounded, shovel-shaped apex and smooth edges, two or three pointed denticles on outer face. Across the rows laterals become larger and longer, mesoconal blade broader and denticles more widely-spaced. Outer laterals smaller again. Extreme outer laterals tall, narrow, sickle-shaped, with mesocone and lateral denticles equally well spaced.

Ovotestis lies at very rear of visceral cavity and slightly to right, cream-orange in colour with a distinctly granular surface texture; hermaphrodite duct swollen into ampulla immediately upon leaving ovotestis. Nidamental complex rather small, of the "flat-pocket" type; flattened receptaculum seminis arising from ventral face of nidamental complex. Post-bursal common genital
duct very long, the separate oviducal and vaginal regions being clearly
discernable externally. Two organs arise close together from enlarged
distal region, firstly a gametolytic gland with a narrow duct and flattened,
spherical terminal swelling; secondly a separate, white, tubular prostate
gland, the surface of this gland being pustulose. Fig. 9.5B shows the repro-
ductive system.

Penis lies in a very elongate and narrow sac, with a single long
penial retractor muscle and smaller muscle slips laterally, especially
about aperture, retractor muscle being bifurcated towards its end; ridges
overlying seminal groove prominent internally, lower sixth of penial sac
studded with rows of raised tubercles capped with small chitinous spines,
and also a row of these spines at base of penis; penis itself small.

Spawn mass laid on undersides of stones, flattened and zig-zagged
in shape, never a three-dimensional tangle as in species of Aplysia,
Stylocheilus or Bursatella.

Descriptive Notes.

In contrast to the teeth of Aplysia, none of those of Dolabrifera
dolabrifera carries subsidiary denticulations or serrations. Thompson &
Bebbington (1973) give a scanning electromicrograph of the radula of
D. dolabrifera.

One of the more important points about the external reproductive
system is that the common genital aperture does not open to the dorsal
surface in the mantle cavity in any of the New Zealand specimens observed,
it comes straight to the dorsal surface in front of the anterior respiratory
aperture. The genital aperture is located 5-6 mm in front of the respiratory
aperture in adult animals. Although the prostate gland is large and has
a characteristic shape, its presence does not appear to have been described
previously for the reproductive system of Dolabrifera dolabrifera.
Locality Records.

NORTHLAND: 1, beneath a stone, in stream between low-tidal pools, "Pat's Beach", Mahinepua Peninsula, near Whangaroa, RCW, 27 Jan. 1971; 1, crawling over rock rubble, 11 m, "Sand Garden", between Aorangi Id and Tawhiti Rahi Id, Poor Knights Id, A.M. Ayling, 11 Feb. 1976; 1, Taiharuru River mouth, Whangarei, I. Guest, 23 July 1976 (N.M.); 1, beneath a low-tidal stone, "Echinoderm Reef Flat", Goat Island Bay, Leigh, RCW, 14 May 1974; 1, beneath a stone, 2m, near tip of Ti Point, Leigh, RCW, 29 April 1972; several, beneath low-tidal stones, Matheson Bay, Leigh, RCW, 5 Oct. 1975 and 6 June 1978.

Geographic Distribution.

As Bebbington (1977) has provided a full list of the records for Dolabrifera dolabrifera throughout the world, one is not given here.

Discussion.

It is surprising this species was unrecorded in New Zealand prior to 1967 because it is moderately common throughout Northland and extends well into the intertidal zone.

The distinctive features are the flattened, dolabriform shape, distinct, crenulate foot border, tuberculose upper surface, spatuliform shell and conspicuous prostate gland. The presence of this gland does not appear to have been recorded previously in the literature.
KEY TO THE GENERA AND SPECIES OF THE ORDER ANASPIDEA
(SEA HARES) IN NEW ZEALAND

Key based on field characters of living specimens and shells. (Note that identification of 8b, 9a-c on shells alone is impossible).

1. Parapodia fused around visceral mass apart from a small dorsal slit. Body pustulose (Fig. 1) or with villi (Fig. 2). Shell spatulate (Fig. 3) or absent.  

---- 3.

Fig. 1. Tubercles  
Fig. 2. Villi

2. Parapodia entirely separate (except posteriorly), produced as upward extensions or lobes from the foot. Body completely smooth, shell aplysiid (Fig. 4)  

---- Genus Aplysia Linneaus. 6.

Fig. 3. Spathulate shell  
Fig. 4. Aplysiid shell

3. Body flattened, no tail, upper surface tuberculate, marbled in greens, whites and browns, shell spatuliform (Fig. 3)  

---- Dolabrifera dolabrifera (Cuvier, 1817)

4. Body rounded, extended posteriorly into a tail, surface covered with branched villi, shell absent  

---- 5.
5a. Small row of villi around foot sole, single prominent villus between rhinophores. Colour greenish with black smudges, turquoise or green spots often ringed with yellow — *Bursatella leachii* (Blainville, 1817)

5b. Villi absent around foot sole, no single prominent villus between rhinophores. Colour brownish or pale green, overlaid with longitudinal brown stripes, purplish or blue spots sometimes with orange centres

— *Stylocheilus longicauda* (Quoy & Gaimard, 1825)

6a. Parapodia joined high up posteriorly, never able to swim. When irritated, can either produce a purple fluid or not

— 7

6b. Parapodia joined low down posteriorly, either able to swim or not. Always secrete purple fluid when irritated

— 8

7a. Adult body size small, usually no longer than 7 cm visceral mass central, long tail posteriorly. Shell easily observed through widely open mantle foramen. Parapodia thin. Shell relatively large, strongly concave. Sole of foot clearly demarcated from body all round. Body colour brownish or reddish, peppered with white spots, black edge to parapodia and tips of rhinophores, oral tentacles, anterior foot border, anal spout black. Able to eject purple fluid when irritated — *Aplysia parvula* Möörch, 1863

7b. Adult body size much larger (up to 25 cm). Tail short, but with a posterior region on the sole that is particularly adhesive, foot broad. Mantle foramen minute. Shell flattened. Sole of foot merging into body laterally, anterior and posterior regions separate however. Body colouration uniform, warm amber-brown to jet black, occasionally with small irregular white or blue spots. Not able to eject purple fluid. Present throughout New Zealand.

— *Aplysia juliana* Quoy & Gaimard, 1832

8a. Foot narrow, parapodia very large, able to be used for sustained swimming. Colour uniform amber-brown with a fine superficial black reticulum, speckled with black, brown or white, pale white or brown areas especially within the parapodia. Neck elongate, oral tentacles much enlarged with anterior border particularly sinuous. Rare. Northern N.Z. only.

— *Aplysia extraordinaria* (Allan, 1932)
8b. Foot relatively broad, parapodia quite large with thin frilled borders, animal not able to swim. Colour either uniform brown or greenish or mottled or striped with brown and pale areas, fine superficial black reticulum present, some brown and pale spots present. Present throughout New Zealand

--- Aplysia keraudreni Rang, 1828

8c. Foot relatively broad, parapodia quite large but never able to be used for swimming. Colour pinkish-brown to greenish-brown to chocolate, always with a superficial pattern of distinct black circles on outside of body, black smudge on tail, interior of parapodia with large green spots surrounded in black; anterior edges of parapodia with longitudinal black stripes on inner faces. Northern N.Z. only.

--- Aplysia dactylomela Rang, 1828
Aplysia species (Subfamily Aplysiinae)

a - A. (Varria) keraudreni Rang. Pair of copulating individuals belonging to brown (anterior animal) and mottled (posterior) colour forms. From 2-3 m, "The Gantry", Island Bay, Wellington.


c - A. (Varria) extraordinaria Allan. Head Region. From 15 m, Nursery Cove, Poor Knights Islands.

Photo: A.M. Ayling, June 1975.

d - A. (Pruvotaplysia) parvula Mörch. Three specimens of the intertidal, brown colour form; the largest animal lacks a black foot border. From inner part of "Echinoderm Reef Flat", Goat Island Bay.

Figure 9.2.

New Zealand members of the subfamilies Notarchinae and Dolabriferinae.


Figure 9.3.

*Bursatella leachii* Blainville.

Growth stages showing changes in appearance with maturity in this species.

Based on slides of living specimens from Motukaraka Island found from April to June 1977.
Figure 9.4.

Shells of New Zealand *Aplysia* species.

A - *Aplysia* (*Aplysia*) *juliana* Quoy & Gaimard. 41.1 x 31.3 mm (= Holotype of *Tethys hamiltoni* Kirk). National Museum, M. 42.

B, C - *Aplysia* (*Aplysia*) *juliana* Quoy & Gaimard. 21.1 x 16 mm.

From a specimen taken on Echinoderm Reef, Goat Island Bay.

Outer and inner views respectively of same shell.

D, E - *Aplysia* (*Pruvotaplysia*) *parvula* Mörch. 17.8 x 13.3 mm.

From a specimen taken on Echinoderm Reef, Goat Island Bay.

Outer and inner views respectively of same shell.

F, G - *Aplysia* (*Varria*) *dactylomela* Rang. 26.1 x 20.2 mm.

From a specimen taken on Echinoderm Reef, Goat Island Bay.

Outer and inner views respectively of same shell.
Figure 9.5.

*Dolabrisera dolabrisera* (Cuvier).

A - Ventral view of anterior region.

f.b. = foot border, f.s. = foot sole, o.f. = oral flap, o.t. = oral tentacle.

B - Reproductive system of a mature individual.

alb. = albumen gland, a.t. = common genital atrium,
gam. = gametolytic gland, me. = membrane gland,
m.u. = mucous gland, ovi. = oviduct, ovo. = ovotestis,
pr. = prostate gland, r.s. = receptaculum seminis.
APPENDIX II. TAXONOMIC CONSIDERATIONS ON HAMINOEA ZELANDIAE

(GRAY IN DIEFFENBACH, 1843)

This appendix clarifies the taxonomy of Haminoea zelandiae (Gray in Dieffenbach). As part of this investigation it was found that the nomenclature for the higher categories of family and genus had been subject to confusion of use and spelling in recent literature, so these taxa are clarified as well.

FAMILY HAMINOEIDAE Pilsbry, 1895


The name Haminoeidae Pilsbry should be used for this cephalaspidean family group. Pilsbry's spelling on first introduction (Hamineinae) had as type-genus Haminea Gray 1847 (November). But this is a synonym of Haminaea Leach 1847 (October), both names being proposed as replacements for Haminea Leach, Ms. 1819. However an earlier generic name is that of Haminoea Turton & Kingston in Carrington, 1830. Fortunately both genera have the same type-species: Bulla hydatis Linnaeus. Therefore the spelling of Pilsbry's family name should be corrected to Haminoeidae Pilsbry, 1895 (I.C.Z.N. 1964, Art. 10e (ii)).

The name Atyidea Thiele (based on Atys Montfort, 1810) has been used for this genus-group by some recent authors (Rudman, 1971; Thompson, 1976; Powell, 1976) but it can be disallowed on two counts. Firstly the type-genus Atys is a classical Greek noun of the sort that would be expected to give the genative atydis - hence Atyidae for the family. Secondly Atyidae Thiele is a junior homonym of Atyidae de Haan 1849, Dana (1852) corrected the family-group name Atyadea de Haan 1849, based on Atya Weigmann, 1856, to Atyidae). Atyidae de Haan is currently employed for a family-group in the Crustacea.
GENUS HAMINOE A Turton & Kingston in Carrington, 1830

Synonymy.


Remarks.

Apparently no type-species has been designated for *Haminaeae* Leach, 1847. I have designated *Bulla hydatis* Linnaeus. Thus *Haminea* Gray and *Haminaeae* Leach become synonyms of *Haminoea* Turton & Kingston in Carrington because all three have the same type-species.

Locating Turton & Kingston's work and establishing a correct date of publication has proved very difficult. A book entitled "The Teignmouth, Dawlish, and Torquay Guide etc." by N.T. Carrington and others was published
at Teignmouth, and also sold at Exeter, London etc. The Natural History section (Part 2) was succeeded by an article entitled "Conchology, arranged on the amended system"; Iredale (1914) gives evidence for 1830 as date of publication of part 2. Apparently the "Conchology" portion of the Guide was issued separately in 1829 under the title of "Enumeration of Marine Shells found on the Devonshire Coast" (Jeffreys, 1867 : 108) but since it was anonymous no credits for authorship can be given.

Habe (1952) introduced Sericohaminoea as a subgenus of Haloa but gave no description. According to Rudman (1966c) the section to which Haminoea belongs is more closely allied to the Anaspidea than Cephalaspidea because of the reproductive systems and herbivorous habits.

**HAMINOEA ZELANDIAE (GRAY IN DIEFFENBACH, 1843)**

**Synonymy.**


[New Zealand]; 1874. E.A. Smith, Zoology Voy. Erebus & Terror 1839-1843, 2 : 5, pl. 1, fig. 10.


1868. *Haminoea obesa* Sowerby, in Reeve, *Conch. Icon.* 16, pl. 2, fig. 13;


Remarks.

Powell (1964; 1965) has added two other members of the Haminoeidae to New Zealand's recent fauna, these being Limulatys reliquus Iredale and Atys naucum (Linnaeus) respectively, and a shell of a third species Atys (Aliculastrum) cylindricus (Helbling) has been found at Tutukaka Beach, Northland (J.R. Penniket, pers. comm. 1977). It is probable however that only Haminoea zelandiae and Limulatys reliquus have established breeding populations in northern New Zealand.

Hutton (1880) and Suter (1913) followed E.A. Smith (1872) to give records of another haminoeid, Haminoea cuticulifera (E.A. Smith, 1872), from New Zealand. But this taxon is a junior synonym of Liloa brevis (Quoy & Gaimard) (Burn, 1969; 1974) and since no subsequent records of L. brevis are known from New Zealand, that part of Smith's original citation referring to New Zealand is assumed to be erroneous, and the name has been deleted from New Zealand molluscan lists.
### APPENDIX III.1

**Water Temperatures (°C) of Two Study Pools on "Echinoderm Reef", Goat Island Bay, Leigh, Hauraki Gulf. 1975 - 1977**

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### APPENDIX III.2

**Water Temperatures (°C) of Four Study Pools at Motukaraka Island, Waitemata Harbour, Auckland. 1975 - 1978**

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APPENDIX III, 3.

Daily seawater temperature recordings (taken approximately 10.00 hr daily) from outside tank room, Leigh Marine Laboratory. Data for May and June 1976 and 1977 during which times experiments on nutrition and food utilization by *Aplysia dactylomela* were being conducted.

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**Correlation coefficients, mean length, untransformed data**

**Correlation coefficients, % cover**

**Correlation coefficients, dry weight**

**Parts of real platform**

**All weights given refer to dry weights. Abbreviations: In = Inner series; Out = Outer series; S = Series of samples taken from outer.**

Appendix IV-I, Data on areas selected for sediment analysis at Commander Reef, Lethbridge, 15 November 1977.
<table>
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<th>I N . 5</th>
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<th>O U T . 2</th>
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**Transformed data**

**Correlation coefficients & cover**

- Mud depth (cm)
- C.A.C.O3: In. strew sand
- % C.A.C.O3: % of mud
- % of very fine sand (0.064 mm)
- % of fine sand (0.125 mm strew)
- % of medium sand (0.25 mm strew)
- % of coarse sand (0.5 mm strew)

**Total weight of organic material**

**Total weight of sediment (g)**

---

**Notes:**

- All weights given refer to dry weights.
- Abbreviations: I. = Inner series; O. = Outer series; O. = Outer series.
- Data on areas selected for sediment analyses at Motukaraka Island, Hauraki Gulf, 24 December 1977.

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**Appendix IV.2:** Data on areas selected for sediment analyses at Motukaraka Island, Hauraki Gulf, 24 December 1977.
Appendix IV.3. Data on grazing Gastropods in each of ten 0.1 m² areas selected for sediment analysis at Echinoderm Reef, Leigh and Motukaraka Island, Waitemata Harbour. Area nos. correspond to those for which data is given in Appendices.

<table>
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<th>ECHINOderm REeF, Goat ISLAND Bay, LEIgH</th>
<th>Area</th>
<th>Nos. and species of grazing molluscs</th>
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<tr>
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<td>1 Nerita ateramentosa</td>
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<td>4 Turbo smaragdus (juv.)</td>
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<tr>
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<td>In.4</td>
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<td>many Eatoniea olivacea</td>
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<td>In.5</td>
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<td>16 Turbo smaragdus (juv.)</td>
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<td>Off.1</td>
<td>7 Turbo smaragdus (2 juv.)</td>
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<tr>
<td></td>
<td></td>
<td>1 Cookia sulcata (juv.)</td>
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<tr>
<td></td>
<td></td>
<td>1 Sypharochiton pelliserpentis (juv.)</td>
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<td></td>
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<td>1 Siphonaria zelandica (juv.)</td>
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<td></td>
<td></td>
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<td>3 Turbo smaragdus</td>
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<td></td>
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<td>8 Turbo smaragdus (2 juv.)</td>
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<table>
<thead>
<tr>
<th>MOTUKARAKA ISLAND, WAITEMATA HARBOuR</th>
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<th>Nos. and species of grazing molluscs</th>
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<td>1 Turbo smaragdus (juv.)</td>
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The statement "to understand the ecology of the predator, it is important to know the ecology of the prey" (Harris, 1973), is equally applicable to herbivores where "the prey" refers to the standing crop of plant material, as it is to carnivores. In this summary I present information on the ecology of the sea hare Aplysia dactylomela Rang and its algal food species of Laurencia, and show the relationships between the annual cycles of abundance of each. All these data refer specifically to the populations at Goat Island Bay. Additional studies are now needed for other sites in Northland and Auckland (the only provinces of New Zealand in which A. dactylomela occurs) to use as comparisons with the situation described here.

For Aplysia dactylomela, I have considered its recruitment, density and abundance, then growth and finally survivorship. Algal cycles are considered next. These data are related to each other and I have considered whether environmental factors (e.g. temperature, storms) or biotic factors (e.g. competition, predation, food availability) are more important in controlling the structure of the A. dactylomela population studied. These factors can be ranked according to their importance for the Goat Island Bay population but I am not able to quantify their separate effects.

Accounts of growth and reproduction of A. dactylomela indicate that it is a tropically-centered species (e.g. Carefoot, 1970; Switzer-Dunlop & Hadfield, 1977; Lederhendler, 1977 b). No previous studies of its population structure have been undertaken in temperate waters although the species is known to exist in cooler regions such as South Africa (Eales, 1960), New South Wales (Hedley, 1923; Burn, 1966 a; Bebbington, 1975; pers. obs.) and northern New Zealand (Morton & Miller, 1968; Powell, 1976; Gordon & Ballantine, 1977). The population studied by me is at Goat Island Bay, Leigh (36°16'S; 174°48'E). Data presented here are derived from monthly surveys conducted during the period 1975-77.
The population of *Aplysia dactylomela* on the intertidal Echinoderm Reef shows fluctuations corresponding with the seasons, and these suggest an annual life cycle. The species has a planktonic veliger larva. During my study the first recruits appeared on the shore in December and January (corresponding with seawater temperatures of approx. 17°C). However, recruitment was characterized by variations in intensity and tended to be sporadic in nature. Further recruitment occurred at least until June. After that month tiny animals (less than 3.5 gm wet weight) previously classified as recruits, were still present up till October, but these could have been juveniles that were recruited earlier but had not grown because of the low autumn and winter temperatures (below approx. 15°C after June). No recruitment occurred subtidally.

Population densities were monitored at two levels on the low-tidal reef flat (in pools of the inner and outer sections). Densities fluctuated according to recruitment. Densities were considerably higher in the inner pools (with a maximum of 2.3 to 2.7 animals m\(^{-2}\) for each year) than the outer ones (never more than 0.2 m\(^{-2}\)). In the inner areas, maximum density was nearly the same for each of the three years of the study, but this was not the case for the outer areas. Numbers of *A. dactylomela* typically reached, a peak in mid-summer (February to May), declined slowly over autumn (June to August), then very rapidly in winter, eventually reaching zero (September to November). Maximum numbers encountered at any one month during the three years of this study were: 1975-206 (in May); 1976-17 (February and March); 1977-72 (in June). This decline and disappearance was most marked for the inner areas. In 1976 no specimen was found in any of the study pools from August through the rest of that year. However, in 1975 and 1977, although the autumn and winter declines were rapid, the occasional specimen was found through until October and November.

Growth in *Aplysia dactylomela* seems tied very closely to temperature. Data supporting this are derived from a 40-day laboratory study of 10 animals during May and June. These animals displayed an increase in mean weight of
5.14 gm wet weight week\(^{-1}\). But when these data are replotted for each separate week, the growth rate was seen to fall as temperatures declined towards the end of this trial. The same is true for an animal maintained in the laboratory from 18 January to 14 June 1976. Studies with tagged animals in the field confirmed this drop in growth rate as seawater temperatures fall. The change of growth rate was not pronounced when temperatures reached approx. 15\(^\circ\)C in autumn. Best growth was achieved on the Laurencia spp. of alga (60% increase in wet weight); Enteromorpha sp. gave a 49% increase, and Herposipharia sp. 2%. Aplysia dactylomela was found to ingest a mean dry weight of 0.35 gm Laurencia day\(^{-1}\). Starved specimens lost only 0.085 gm wet weight day\(^{-1}\), so the maintenance energy requirement was exceedingly low.

Examination of density data indicates survivorship is low. In 1975 only one individual could be found in November, representing 0.49% of the maximum number encountered that year (May). In 1976 all animals were absent from August onwards. In 1977 only 8.3% of the maximum population (July) remained by October (i.e. 6 collected in October against 72 in July). Causes of mortality were not quantified, but they can be ranked according to the losses to each. The causes being physical (e.g. temperature, storms) or biological (e.g. food shortages, predation, competition) or accidental (e.g. human interference). I suggest storms cause the highest mortality.

Owing to its relatively open character, Echinoderm Reef suffers considerably from storms. Climate data, collected by the Leigh Marine Laboratory show that most gales are recorded in August (Gordon & Ballantine, 1977). From May till October winds from the N.W. or S.W. are almost as common or the prevailing westerlies. In summer, the place of these winds from the N.W. and S.W. is taken by those from the N.E. and E. (Gordon & Ballantine, 1977). The hills adjacent to Echinoderm Reef shelter it from winds from the south, and Goat Island shelters it from the east. It follows therefore, that N. or W. winds will have a more severe effect, and these occur predominantly over winter. Indeed, the roughest month (with most records
of a sea surface between 4 and 7 on the Beaufort Scale) is June (Gordon & Ballantine, 1977). During winter there is a clear relationship between the occurrence of rough seas 4-7 (Beaufort Scale) and waves greater than 2 m (Gordon & Ballantine, 1977 Fig. 21).

For the particular three years of my study, 10 (59%) of the 17 severe storms happened during winter (i.e. over the period from June till October). In fact during the year of 1976, severe storms only occurred from July to October, there being 5 during these winter months. To obtain these data I defined severe storms according to three climatic criteria, and only on days when all existed together did I rate the storm as severe. The criteria used were as follows.

1. Wind direction N.W. or W. or S.W.
2. Wind speed exceeding 20 knots - i.e. 4 on the Beaufort Scale.
3. Sea surface wave height greater than 4.0 on the Beaufort Scale - i.e. 80% rise/fall.

There were 6 periods of severe storms in 1975, 4 in 1976 and 3 in 1977.

This rather full information on marine climate reinforces my impression that storms are most severe on Echinoderm Reef in autumn and winter. So storms that occur during these seasons are thought to be primarily responsible for the mortality of most individuals. Large numbers of dead and dying *Aplysia dactylomela* have been observed to be washed ashore following storms. *A. dactylomela* seek refuges during storms and at such times they may become completely covered by sand.

Animals have never been seen to be killed directly by cold temperatures during winter low tides. Additional sources of mortality that I have witnessed are predation by starfish (*Coscinasterias calamaria*) and deliberate destruction of animals by humans. Actual numbers killed by both of these agencies were probably small. In fact, *A. dactylomela* has a size refuge from each of them - an upper refuge in the former case (*A. dactylomela* outgrows predators), and a lower refuge in the second case (small animals are often missed by casual human visitors).
Competition with other Aplysia species and some herbivorous gastropods for Laurencia spp. does exist, but I do not know its magnitude or effects.

There are three species of the red algal genus Laurencia on Echinoderm Reef, two species possess cylindrical axes (Laurencia sp.1 and Laurencia sp.2) and one has flattened axes (Laurencia distichophylla J. Agardh). All three displayed cycles of abundance independent of any grazing effects, these cycles differing seasonally for each species. Laurencia distichophylla was present continuously, its cover declined to a minimum in mid-winter and reached a peak (of approximately 20% cover) in October and November; its cover appeared to halt over summer, and cover fell into a steady decline that led to the winter minimum. Laurencia sp.1 was apparently absent from June till November (though it overwintered as fine, basal stolons amongst Corallina officinalis turf); growth proceeded rapidly in spring so that by March or April it had reached its full extent - attaining 80% cover in warm, shallow pools close to the reef edge. Laurencia sp.2 followed the same pattern as L. distichophylla; however it achieved full cover more rapidly in spring and regressed earlier (between January and February).

Data on cover values for all these Laurencia species have been combined for all study sites across the reef and presented for a full year. Highest values of cover were in March to May (40-50%), and lowest values in winter from July to September (10% cover or less).

Aplysia dactyломела appears to require the presence of only Laurencia sp.1 for it to settle from the plankton and metamorphose. Tiny juveniles (less than 3 mm in length) were not found on either of the other two Laurencia species. The presence of the greatest amount of Laurencia sp.1 on the inner regions of the reef flat explains the highest densities of A. dactyломела there. During the summer months, populations of sea hares and Laurencia cover rose together. The small A. dactyломела had a low food intake at this time. For March and April I calculated the A. dactyломела population energy requirement to be approx. $4 \times 10^5$ kJ . ha$^{-1}$ . month$^{-1}$, whilst the available crop of Laurencia stood at approx. $140 \times 10^5$ kJ . ha$^{-1}$ . month$^{-1}$. 
Growth of *A. dactylomela* proceeded rapidly, and numbers were augmented by additional recruitment through summer and autumn. Growth of all *A. dactylomela* was being sustained then by only *Laurencia distichophylla* and *Laurencia* sp.1. If available, all three species of *Laurencia* were eaten by *A. dactylomela*; the sea hares appeared not to discriminate between them in the field. Calorific determinations show there is no significant difference between the energy contents of any of the three *Laurencia* species (mean calorific value = 17.69 kJ . gm⁻¹).

Late in May, supplies of both *Laurencia* species were diminishing both through natural regression and grazing. My caging studies showed that in the absence of any grazing, *Laurencia* sp.1 still regressed below the *Corallina officinalis* turf level where it could not be reached by *A. dactylomela*. Throughout May and June the *A. dactylomela* population was exerting maximum pressure on its food through the presence of many large, roaming (? hungry) animals. But at that time the amount of *Laurencia* was comparatively low. The *Aplysia* population energy requirement was at a maximum then (approx. 2–4 x 10⁵ kJ . ha⁻¹ . month⁻¹), whilst the amount of *Laurencia* available was still decreasing (approx. 60 x 10⁵ kJ . ha⁻¹ . month⁻¹ in June, and 18 x 10⁵ kJ . ha⁻¹ . month⁻¹ in July).

In winter this value was a minimum for the standing crop of *Laurencia* (approx. 16 x 10⁵ kJ . ha⁻¹ . month⁻¹ in August), and it was at this time that the relationship between *A. dactylomela* and *Laurencia* spp. was most critical. Therefore the status of the sea hare population at this time must be considered even more carefully. In winter *A. dactylomela* appeared to stop growing, and its feeding rate dropped too; these changes were probably temperature-ddictated. Not only do growth components such as increases in length and weight halt, but my observations on gonad development suggest that gonad development was inhibited as well by these low temperatures. It would appear that the state of sexual maturity is related to total body size, and animals below 120 mm in length (with corresponding wet weights of up to 150 gm) were sexually immature. The gonad does not continue to develop, nor gamete
maturation proceed when somatic growth stops. At this time in winter, growth had not been sufficiently rapid for individuals to produce enough body growth to attain sexual maturity. The result was that the majority of individuals in the population were sexually immature, and this was particularly so for the inshore regions.

I conclude by presenting my opinions about the order in the hierarchy of factors that determines the structure of the Echinoderm Reef Aplysia dactylomela population. Support from the literature is incorporated.

Temperature appears to exert overall control on the life cycle by dictating when growth and reproduction can occur. In the same way, A. californica apparently displays an annual breeding cycle by dictating when growth and reproduction can occur. In the same way, A. californica apparently displays an annual breeding cycle in the field (MacGinitie, 1935; MacFarland, 1966) with growth and reproduction being governed by temperature. But in the laboratory, at temperatures above 18°C, the entire generation time of this species can be compressed into 19 weeks (Krigstein et al., 1974). Smith & Carefoot's (1967) experimental studies support my view that temperature controls reproduction as well as somatic growth. In New Zealand's northern warm temperate waters, temperature appears to exert overall control, effecting every animal regardless of its location or habitat, so I consider it the most important factor in determining observed population cycles.

Below this, regional factors operate in influencing the life histories of particular populations. At Goat Island Bay, I suggest winter storms kill most of the population, accounting for the high losses of animals noted during this season. I do accept that other intertidal reef platforms exist in northern New Zealand that are more sheltered by virtue of their geography. Here losses by winter storms would be ameliorated and A. dactylomela could survive throughout the winter to grow to maturity and reproduce in the following spring. It is possible that such refuges also exist subtidally along the coast of New Zealand, but the paucity of records of subtidal A. dactylomela argue to the contrary.
Finally there are other factors that could potentially limit density, but do not do so on Echinoderm Reef because temperature and storms act before these biotic factors could exert control. Local food shortages can, and probably do, occur on Echinoderm Reef. So in mild, calm winters all the available *Laucencia* could be eaten. Similarly competition from the other grazing invertebrates already mentioned would intensify under such circumstances. However *A. dactylomela* could survive on alternative foods (e.g. *Enteromorpha* spp., *Herposiphonia* spp.) that occur on Echinoderm Reef. However, in comparison to *Laucencia* spp., both the above algae are less abundant, much less bulky (especially the fine, filamentous *Herposiphonia* spp.) and result in poorer growth for *Aplysia dactylomela*. Predation is likely to be the least important population - controlling factor since the single known predator, *Coscinasterias calamaria*, has a catholic diet and takes many other prey species; and also the sea hare itself has a refuge in size, being able to grow too large for starfish to capture.
Composite figure showing the relationship between the Echinoderm Reef population of *Aplysia dactylomela* Rang and severe storms, seawater temperature and availability of *Laurencia* spp. food for the years 1975 to 1977.

A: Arrows indicate dates of severe storms, refer to present text for definition of severe storms.

B: Sea-surface temperatures; plot of monthly averages for the Goat Island region.

C: Absolute density data plots for live *Aplysia dactylomela* per square metre for four study pools on Echinoderm Reef. Note that the T-axis has a logarithmic scale.

- Pool A  - Pool B
- Pool W  - Pool X

D: Plot of mean percentage cover for *Laurencia* spp. on Echinoderm Reef Flat. Transformed data for 7 0.1 m² areas from November 1976 to November 1977. Data from this year are repeated for 1975 and 1976 because assessments of cover were not made then.